

Population Regulation of Coral Reef Fishes

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Introduction

Populations of reef fish are widely believed to be limited by availability of larval recruits, not by density dependent processes operating during and after settlement of young stages in the reef environment. Our research explores and challenges this thinking. We are utilizing field observations and experiments to determine what factors affect spatial distribution, abundance, and population dynamics of four reef-dwelling damselfish in the Family Pomacentridae: three-spot humbug (*Dascyllus trimaculatus*), yellow-tail humbug (*D. flavicaudus*), banded humbug (*D. aruanus*), and orange-fin anemonefish (*Amphiprion chrysopterus*). In related research, we explore the relationships between structural reef habitat (types and sizes of corals and other reef substrates) and the abundance and diversity of local assemblages of lagoon fish.

Knowledge of factors that regulate populations of marine fish is essential to a general understanding of the ecology of coral reef ecosystems. This knowledge is invaluable for management and conservation of fish populations, and can aid in these practices. Species of Pomacentrids are very typical and abundant coral reef fish; we anticipate that our findings will have general applicability, including to species of fish that are consumed by humans. Our research on the relationships between fishes and the corals they inhabit will reveal techniques that could aid in restoration of degraded reef areas. This work is also providing important data about the factors that affect distribution and abundance of lagoon fish, as well as the temporal and spatial scales over which these assemblages vary. Such information is important for planning of fishing practices and in other types of natural resource management (for example, establishment of marine protected areas).

Results of Work Conducted during 2002

Experimental Tests of Early Post-settlement Mortality. A critical gap in our knowledge is the pattern of very early mortality of organisms when they settle to a reef. Because some period inevitably exists between settlement of an individual and when it is first observed ("recruitment"), it has not been possible to evaluate if mortality during this period is compensatory (and therefore contributes to population regulation). During 2002, we conducted a major experiment to assess spatial and temporal variation in mortality of newly settled damselfish. At a set of eight sites situated on the north shore of Moorea, we outplanted cohorts of very young *D. flavicaudus* and measured mortality for 48 hours. Each 48 hour trial involved outplanting of different numbers of young fish on each coral, to simulate natural settlement pulses that vary in strength over time. This was replicated ten times. Fractional mortality varied among the sites, depending both on densities of outplanted fish and among-site spatial variation in overall intensity of predation.

Patterns of Settlement and Recruitment in Damselfish Populations. Young *D. trimaculatus* display a settlement pulse every 14 days (with two such pulses occurring each month). During 2002, we continued our study of daily settlement of this species on anemones on reefs located near the Gump Research Station. This information allows us to explore the temporal patterns of settlement and early mortality. We have found that pulses of settlement differ tremendously in their magnitude, and the early mortality is density dependent (Schmitt and Holbrook 1996, 1999a, 1999c). As we add to our data set we will be able to make comparisons of intensity of settlement among different years and at various times within the year. We also videotaped behavior of young *D. trimaculatus* on anemones in the presence or absence of a second competing species of fish, the anemonefish *Amphiprion chrysopterus*. Study of these videotapes enables us to understand the specific behavioral mechanisms underlying the competitive interaction between the two species.

Whole Reef Colonization Experiments. Based on results of spatial surveys, in 1993 we initiated a field experiment to test the extent to which local abundance of three-spot humbugs was shaped by availability of settlement/juvenile habitat (anemones). Anemones without fish were transplanted to 9 reef patches that previously lacked both anemones and humbugs; 4 control reefs without anemones and 3 reefs with naturally occurring anemones also were established. We varied the number (area) of anemones added among experimental reefs. The number of three-spot humbugs on anemones and on 20x2 m band transects were counted daily for the initial 2 weeks, then after 3, 6, and 12 months. All "anemone-addition" reefs were colonized by three-spot humbugs. Densities increased between successive sampling periods at all manipulation sites, but did not change appreciably on control reefs. Population establishment was that expected by larval colonization: beginning with new recruits, successive life stages appeared sequentially. After 1 year, the density of sub-adults and adults (which no longer associate with anemones) varied among experimental sites as a function of the density of added anemones ($r^2 = 0.85$; $P < 0.001$). During 2002, we continued to study and sample the whole reef colonization experiment. Although the number of anemones on the addition sites is

declining gradually, they are continuing to attract settlers and to produce free-living older stages (sub-adults and adults). Additionally, we continued to sample two more colonization experiments in the lagoons on the north side of Moorea. These are utilizing coral as a colonization substrate, and are testing the relationship between amount of available living substrate and settlement and recruitment of two additional pomacentrids, *Dascyllus aruanus* and *Dascyllus flavicaudus*. We have a large paper published in *Ecology* (Schmitt and Holbrook 2000) that reports some of the results of these experiments, and we anticipate additional publications in the future as we project that these experiments will run for 10-15 years.

Competition between Damselishes. We have established two similar experiments to examine competitive interactions between pairs of species that co-occur on particular reef substrates. These experiments examine competition between *D. flavicaudus* and *D. aruanus*, on shared coral heads, and between *D. trimaculatus* and *A. chrysopterus* on shared anemones. Outplanted substrates have been inoculated with starting densities of one or both competitors, and population trajectories will be followed for about 4 to 6 years. During 2002 we continued sampling these experiments every three months.

Patterns of Settlement of *Dascyllus* on Moorea. In 1996 we established 12 sites within the lagoons around the island of Moorea to monitor settlement and population development of the three species of *Dascyllus*. These sites consist of small groups of corals and anemones. We studied settlement of the fish onto these substrates on a daily basis during a major settlement pulse in August 1996, and periodically at other times. Additional study in 1997 revealed that patterns of settlement of the fish vary greatly among the sites, but for a site the intensity of settlement was temporally consistent (reported in Schmitt and Holbrook 1999c). Early mortality was high and strongly density dependent. These studies have enabled us to explore the relative importance of processes that affect abundance of coral-dwelling fish, reported thus far in papers in the journals *Ecology* (Schmitt and Holbrook 1999b) and *Ecology Letters* (Schmitt *et al.* 1999, Osenberg *et al.* 2002). In 2002, we continued to sample these sites to record patterns of population development on them, and to study interactions between the two *Dascyllus* species that co-occur on the same coral heads. Another paper on patterns of settlement and competition between species was published in the journal *Oecologia* (Schmitt and Holbrook 1999a). We are now utilizing the temporal data on settlement of the *Dascyllus* species around Moorea in analyses of the effect of current on patterns of settlement of different species. We have found that settlement of each of the three species of *Dascyllus* responds differently to current velocity. Two papers resulted from these studies and were published during 2002 (in *Oecologia* and in *Marine and Freshwater Research*).

Spatial and Temporal Patterns of Fish Assemblages on Patch Reefs. Attributes of fish assemblages on coral patch reefs reflect both deterministic and stochastic processes. Our inability to predict assemblage characteristics accurately may stem from a lack of knowledge of underlying mechanisms or the inherent stochasticity in these systems. During 2001 and again in 2002, we surveyed fish associated with 60 colonies of the common patch-forming coral, *Porites rus*, in the lagoon on the north

side of Moorea to examine the degree to which attributes of the coral predicted aspects of the fish assemblage. Physical characteristics of the colonies such as size, morphology, and degree of isolation from other patch reefs varied greatly, as did species richness, total abundance and composition of the fish assemblage. Multiple regression analyses revealed that variation in potential living space (live surface area; number of holes; amount of interior empty space) accounted for over half of the variation in species richness and total abundance of fish on a coral. In contrast, species composition appeared to be influenced more by the physical setting within the lagoon (water depth; distance to deep-water; degree of isolation). Relationships derived from the initial analyses predicted 65 to 78 percent of the variation in species richness among a different set of corals. In addition, our analyses revealed that the more a particular taxonomic group of fish utilized specific microhabitats on *P. rus* (such as interior cavities or branches), the greater the decline in their abundance on other types of *Porites* patch reefs that lack the microhabitats. Together the results indicate that physical attributes of the corals can help account for a large measure of spatial variation in assemblage structure and provide a starting point for studies of the underlying mechanisms. This work has resulted in one paper published in 2002 in *Marine and Freshwater Research*, and a second paper is in press at the same journal. We will continue to resample the set of *Porites* patch reefs to assess temporal variation in assemblages they contain, and expect additional publications exploring the temporal (seasonal and interannual) patterns.

Larval light lures. During 2002, we employed a set of 9 light traps to test responses of larval reef fish to different qualities of light, particularly sources with and without light in the ultraviolet part of the spectrum. This preliminary experiment is part of a longer-term effort in which light will be tested as a means to attract young stages of fish to settle to depleted areas on the reef, and we hope that someday light lures could be used as part of reef restoration strategies. We plan to continue testing light trap technology in 2003.

Presentations. We presented three talks based on this research at the international workshop "Restoring and Sustaining Diversity of Tropical Pacific Coral Reef Fish Communities" held jointly at the U.C. Berkeley Gump South Pacific Research Station and CRIOBE in Moorea (April 1-7, 2002).

Publications. The following is the list of publications resulting from our work in French Polynesia. Reprints of recently published papers are enclosed with this report. Please do not hesitate to contact us if you would like additional copies of these reprints.

Bernardi, G., Holbrook, S.J., Schmitt, R.J. and Crane, N.L. Long-distance dispersal in an edge population of the coral reef three-spot damselfish *Dascyllus trimaculatus*. Completed manuscript.

Holbrook, S.J., A. J. Brooks and R.J. Schmitt. Variation in structural attributes of patch-forming corals and patterns of abundance of associated fishes. In press, *Marine and Freshwater Research*.

Holbrook, S.J. and R. J. Schmitt. Spatial and temporal variation in mortality of newly settled damselfish: patterns, causes and co-variation with settlement. In press, *Oecologia*.

Osenberg, C.W., St. Mary, C.M., Schmitt, R.J., Holbrook, S.J., Chesson, P. and Byrne, B. 2002. Rethinking ecological inference: density-dependence in reef fishes. *Ecology Letters* 5:715-721.

Holbrook, S.J. and R.J. Schmitt. 2002. Competition for shelter space causes density-dependent predation mortality in damselfishes. *Ecology* 83:2855-2868.

Bernardi, G., S.J. Holbrook, R.J. Schmitt, N.L. Crane and E. DeMartini. 2002. Species boundaries, populations, and color morphs in the coral reef three-spot damselfish (*Dascyllus trimaculatus*) species-complex. *Proceedings of the Royal Society of London B* 269:599-605.

Schmitt, R.J. and S.J. Holbrook. 2002. Spatial variation in concurrent settlement of three damselfishes: Relationships with Near-field current flow. *Oecologia* 131:391-401.

Schmitt, R.J. and S.J. Holbrook. 2002. Correlates of spatial variation in settlement of two tropical damselfishes. *Marine and Freshwater Research* 53:329-337.

Bolker, B., C. St. Mary, C.W. Osenberg, R.J. Schmitt and S.J. Holbrook. 2002. Management at a different scale: Marine ornamentals and local processes. *Bulletin of Marine Science* 70:733-748.

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Bernardi, G., Holbrook, S.J. and R.J. Schmitt. 2001. Gene flow in the coral reef three-spot dascyllus, *Dascyllus trimaculatus*, at three spatial scales. *Marine Biology* 138:457-465.

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- Schmitt, R.J. and S.J. Holbrook. 1999a. Settlement and recruitment of three damselfish species: larval delivery and competition for shelter space. *Oecologia* 118:76-86.
- Schmitt, R.J. and S.J. Holbrook. 1999b. Mortality of juvenile damselfish: implications for assessing processes that determine abundance. *Ecology* 80:35-50.
- Schmitt, R.J. and S.J. Holbrook. 1999c. Temporal patterns of settlement of three species of damselfish of the genus *Dascyllus* (Pomacentridae) in the coral reefs of French Polynesia. Pp. 537-551 in Proc. 5th Indo-Pacific Fish Conf., Noumea, 1997. B Seret and J-Y Sire, eds. Paris: Soc. Fr. Ichtyol.
- Holbrook, S.J. and R.J. Schmitt. 1999. *In Situ* Nocturnal Observations of Reef Fishes Using Infrared Video. Pp. 805-812 in Proc. 5th Indo-Pacific Fish Conf., Noumea, 1997. B Seret and J-Y Sire, eds. Paris: Soc. Fr. Ichtyol.
- Holbrook, S.J. and R.J. Schmitt. 1997. Settlement patterns and process in a coral reef damselfish: *In situ* nocturnal observations using infrared video. *Proceedings of the 8th International Coral Reef Symposium* 2:1143-1148.
- Schmitt, R.J. and S.J. Holbrook. 1996. Local-scale patterns of larval settlement in a planktivorous damselfish - do they predict recruitment? *Marine and Freshwater Research* 47:449-463.