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Patterns of replenishment of coral-reef fishes in the nearshore waters of the San Blas Archipelago, Caribbean Panama

Abstract The magnitude and synchrony of spatial and temporal patterns of larval supply to the San Blas Archipelago were measured using three replicate light traps in each of three habitats (exposed, lagoon and back-reef) over 18 consecutive lunar months from December 1996 to June 1998. Traps were sampled for 19 consecutive nights centred on the new moon in each month. A total of 125 species from 44 families of reef fishes were collected, of which the Pomacentridae, Girellidae, Synodontidae, Lutjanidae, Blenniidae, Apogonidae and Labridae were the most abundant in catches. The spatial pattern of replenishment for these families was systematic, with highest abundance recorded in the lagoon and lowest abundance in the back-reef habitat (total abundance lagoon = 18,440; back-reef = 5,243 individuals). The timing and magnitude of catches for the 12 most abundant species were often significantly correlated both among species and habitats during the sampling period. I concluded that replenishment to San Blas occurs by the continuous influx of multi-specific, meso-scale (hundreds of metres) larval patches, and that larvae within these patches appear to actively select suitable settlement habitats immediately prior to nightly settlement.

Introduction

Adult populations of coral-reef fishes are replenished by highly complex cyclic supply processes involving the interactions of a suite of physical and biological factors acting on the larval stage prior to its arrival in the benthic environment. The nature of this replenishment process is extremely variable both in time and space (Doherty 1991; Caley et al. 1996) and can play an important role in shaping the demographic structure of reef-fish populations (Doherty and Fowler 1994a, b; Booth and Brosnan 1995). To gain an insight into the mechanisms involved in the replenishment process, we first require basic information on the spatio-temporal patterns of replenishment. To date, work documenting these patterns has involved a variety of techniques, including surveys or collections of newly settled fish, back-calculation of settlement patterns from the otoliths of settled fish (Doherty 1991; Wilson and McCormick 1997) or collections of fish larvae just prior to their settlement in reef habitats, using channel nets (Shenker et al. 1993), crest nets (Dufour and Galzin 1993) or light traps (Sponaugle and Cowen 1996a, b; Hendriks et al. 2001).

Together, these studies have demonstrated that the replenishment process is strongly seasonal in many localities. For example, on the Great Barrier Reef (GBR), the majority of replenishment occurs during a relatively short period over the summer months from October to March each year (Milicich and Doherty 1994). In contrast, in some localities in the Caribbean, replenishment can occur year-round (McFarland et al. 1985; Robertson et al. 1988, 1993). These differences in the duration of replenishment events may result from fundamental differences in the dynamics of populations between regions (Shulman and Ogden 1987; Robertson 1988; Thresher 1991).

While the duration of replenishment events may vary among regions, within-season events are often consistent, with sporadic pulses of larvae on a background of low or negligible replenishment (Doherty 1991). For
example, Milicich (1994) used light traps to document the patterns of replenishment to reef habitats at Lizard Island on the GBR during a single 3-month summer sampling period. She found that approximately 80% of the pre-settlement fishes collected in light traps occurred during one episode that lasted for only six nights. Such peaks in abundance are often multi-specific, with replenishment events closely synchronised among different species (Milicich and Doherty 1994; Sponaugle and Cowen 1996).

In addition to temporal variation, there is also considerable spatial variability in the replenishment process that can be of a fixed or random nature. Active avoidance of some reef habitats, such as lagoons, by pre-settlement fishes implies that they are capable of structuring their distributions in nearshore waters prior to settlement and is an example of fixed variability (Doherty et al. 1996). Examples of random variation in replenishment are shown by the monitoring of recruitment to standard units of habitat separated by tens to thousands of metres. Ten-fold or greater differences in the magnitude of replenishment at such spatial scales are commonplace and it has been suggested that this reflects the patchy nature of spatial distributions of pre-settlement fishes in the plankton (Doherty and Williams 1988; Doherty 1991).

While these studies provide an insight into the processes determining replenishment, the patterns they describe may be confounded by a number of factors, particularly where supply is determined from collections of individuals that have already become established in adult reef habitats. In these situations, mortality and migration may act to alter or obscure recruitment patterns (Robertson and Kaufmann 1998). For these reasons, sampling techniques that target larval fish immediately prior to or during the replenishment process, such as light traps, crest or channel nets, are preferred. Of these, light traps have the advantage that they can operate in numerous localities simultaneously allowing synoptic pictures of distributions to be constructed (Doherty 1987).

The implicit assumption in studies measuring larval supply is that the number of larvae arriving in nearshore waters (replenishment) accurately represents the number of fish settling into juvenile habitats (recruitment). This has previously been examined in the Caribbean for two coral-reef fishes, *Stegastes parfitus* and *Acanthurus bahianus* (see Sponaugle and Cowen 1996a). These workers used light traps and biweekly visual census, coupled with settlement patterns back-calculated from otoliths, to show that patterns of replenishment and recruitment were closely linked. A similar study by Milicich et al. (1992) also identified a close link between catches in light traps and recruitment of three pomacentrid species on the GBR.

To date, most studies examining both spatial and temporal variations in replenishment have been conducted on the GBR (Milicich 1994; Doherty and Carlton 1997) and at one locality (Barbados) in the Caribbean (Sponaugle and Cowen 1996a, b). No study has attempted to use this technique in the extensive coral-reef habitats of the western Caribbean. This region is of particular interest, since studies of newly settled fish have suggested that the replenishment process can occur throughout the year, unlike the GBR and Barbados (Robertson et al. 1988). In this study, I used light traps to examine spatial and temporal patterns in the replenishment of populations of reef fishes. By describing the distribution patterns of larvae simultaneously at various spatial and temporal scales, trends in replenishment may provide the basis for interpreting the processes acting on larvae as they approach reef habitats. Specifically, the present study aimed to describe the temporal (nightly) patterns in the magnitude of replenishment by sampling over 18 consecutive lunar months. Additionally, I aimed to describe spatial patterns of replenishment by sampling concurrently in three reef habitats.

### Materials and methods

#### Study site

San Blas Point is a fringing reef extending up to 5 km offshore (9° 34′ N, 78° 58′ W). The region undergoes distinct wet (May–December) and dry (January–April) seasons (Cubit et al. 1989). The former is characterised by light and variable winds, mild currents and intense periods of rainfall, while the latter is characterised by very low rainfall and consistent 25–30 km h⁻¹ northerly winds that produce strong currents and turbid waters (D’Croz and Robertson 1997). Surface temperature ranges from 26°C to 32°C during the year and salinity, between 33‰ and 35‰ (Marine Environmental Science Program, MESP 1999). The maximum tidal range in San Blas is 0.6 m (Panama Canal Commission 1998). The Main Caribbean Current (MCC) flows westward off the coast of Panama and generates two large eddies that circulate along the coast (Lessios et al. 1984; Fig. 1a). Although upwelling events do not occur on the Caribbean coast, intense periods of rainfall create substantial river discharge that are enriched with nutrients that flood nearshore reefs (D’Croz and Robertson 1997; Robertson et al. 1998). For greater oceanographic detail, including local current patterns, see Robertson et al. (1999).

#### Field sampling

The study was conducted in the nearshore coral-reef environment in the San Blas Archipelago over 18 consecutive lunar months from 31 December 1996 to 4 June 1998 (Fig. 1). Originally, a sampling period of 2 years was planned in order to compare seasonal patterns in replenishment between years; however, owing to the unexpected closure of the Smithsonian’s research facilities in San Blas, the sampling period was reduced to only 18 months.

The light-trap design used throughout the study is described elsewhere (see Stobutzki and Bellwood 1997). Briefly, the trap consisted of a single Plexiglass chamber with a tube running through its centre. The chamber was open to the exterior by four horizontal slits (7 cm high by 25 cm wide), through which photopositive organisms entered the trap. The slits were tapered to a height of 1.5 cm inside the trap to inhibit escape. An 8 W DL (Day-Light) fluorescent tube was used as a light source. The light was encased within a central tube of clear Plexiglass, while the power pack was housed in a high-tensile (70 m WR) plastic case above the light. The Plexiglass chamber was protected by an aluminium frame, to which a surface buoy was tied. When the trap was removed from the water after fishing, catches accumulated in a detachable plastic collection box at the trap base. Mesh sides per-