



Dufour et al. 1996) measure the supply of larvae over the reef crest while channel nets (Shenker et al. 1993, Thorrold et al. 1994a, b, c) measure the supply of larvae through channels across the reef. Both methods are based on passive nets that intercept larval fishes as they enter the reef with the currents. Passive nets only sample larvae incoming with the current. Any larval movement toward a reef in a direction opposite to the currents would not be detected by either method.

Mortality of newly settled recruits is very high (Doherty & Sale 1985, Victor 1986, Shulman & Ogden 1987). Predation is considered to be an important factor in reducing survivorship and ultimately influencing reef fish populations (review by Hixon 1991). Dufour & Galzin (1992) indicated the great differences between abundance of presettlement colonizing larvae at the reef crest and settled individuals in the reef, indicating high mortality of larvae during the colonization of the reef, which was attributed to predation by resident small piscivorous fish.

This study presents the direct observation of a colonizing event by *Ctenochaetus strigosus* (Acanthuridae) larvae and describes the behavior of these pelagic larvae while encountering a reef. The observed larval behaviors in relation with the water flow have important implications for the interpretation of data on colonization obtained with passive collection methods.

## METHODS

Johnston Atoll is in the Central Pacific (16°45' N, 169°30' W), 760 km south from French Frigate Shoal, one of the northwestern Hawaiian islands which is the closest shallow reef system. The atoll has a maximum width of 20 km and a reef crest only along its N-NW edge (Fig. 1). Tide amplitude ranges about 1 m.

A colonization event by *Ctenochaetus strigosus* larvae (Observation 1) was observed and videotaped by 2 of the authors (G.S. and D.M.) while SCUBA diving at a channel that transects the reef crest (Fig. 1). The channel is on average 4.5 m deep and 28 m wide, and has a substrate composed of broken coral rubble and patches of live coral (*Acropora* spp. and other species). Two current meters (S4 InterOcean, San Diego) were in place at the time of this observation. The first one was located in the channel and mounted on a tripod at a height of 1.5 m above the substrate. The second unit was moored offshore 200 m from the reef crest, directly in front of the channel at a depth of 13 m (10 m off the bottom). Two temperature loggers (XL-100 Braencker Research, Toronto) were deployed with the current meters. Direct observations of incoming larvae were made at this site from 19:00 until 20:00 h (sunset at 19:41 h) on May 12, 1994, a day after new moon. Set-

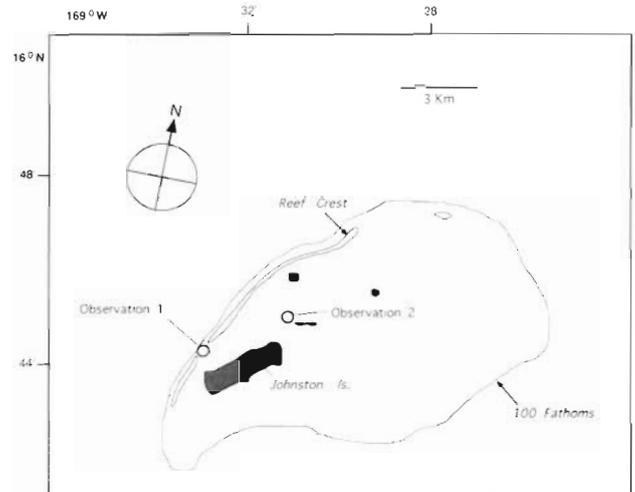


Fig. 1 Map of Johnston Atoll indicating the location of the reef channel where observations were made in 1994 (Observation 1) and the location of the 1995 observation inside the lagoon (Observation 2)

tled individuals were collected from the reef the next day (10:00 h) for identification purposes using quinaldine and hand nets.

A second event of colonizing acanthurid larvae (Observation 2) was observed and videotaped by 1 of the authors (P.S.L.) on May 1, 1995, from 14:00 until 16:00 h approximately. Observation 2 took place inside the lagoon (Fig. 1), close to a deep (10 m) channel and over a bottom of industrial debris and coral heads. The depths at this location ranged from 5 to 8 m.

## RESULTS

### Currents

Currents in both the reef channel and offshore from the reef crest were tidally influenced. The water flow in the channel at the time of the larval observations was oriented in an outward direction, with an average speed of  $27 \text{ cm s}^{-1}$  at 1.5 m off the bottom (Fig. 2). Using the logarithmic law for velocity distributions in turbulent flows (Schlichting 1979), we estimated the water velocity at different heights off the bottom. Considering a substrate composed of coral gravel of 2 to 5 cm in diameter, the current speed 2 to 5 cm above the bottom should vary between 10 and  $15 \text{ cm s}^{-1}$ .

The currents in the offshore station ran parallel to the reef and, at the observation time, were flowing towards the NE at an average speed of  $14 \text{ cm s}^{-1}$  (Fig. 2). A sharp rise in temperature ( $0.25^\circ\text{C}$ ) at the offshore station coincided in time with the colonization event.



served over the coral rubble maintaining their position against the current about 10 to 20 cm above the substrate. They struck individual larvae swimming past them along their side or underneath them. Finally, 1 individual *Aulostomus chinensis* (Aulostomidae) was observed striking once at a swimming acanthurid larvae. No predatory events by any of the above piscivores have ever been observed at this site during the dusk period on other dates.

No wrasses (Labridae) were observed to attack larvae at dusk, but during the following morning (10:00 h), while collecting settled larvae, we observed various successful attacks by *Epibulus insidiator* on undisturbed individual larvae which were poking from underneath corals. *Thalassoma duperrey*, *T. lutescens* and *Coris gaimard* actively followed divers and preyed upon larvae that were evacuated from their refuges by divers while collecting. These were the only successful predation events observed in the morning hours, none of the predatory species observed during the dusk period were active during the morning.

No attacks on swimming larvae by piscivorous fish were observed during the second colonization event inside the lagoon.

## DISCUSSION

Our observation of *Ctenochaetus strigosus* larvae swimming through a reef channel against the water flow to the inner reef environment suggests that the colonization of coral reefs by presettlement pelagic larvae can be an active process, controlled by behavioral responses of the larvae. Larval movement is not constrained to transport by currents, specially for large larvae with strong swimming abilities such as Acanthuridae, which have been measured swimming at speeds of  $13.5 \text{ cm s}^{-1}$  and for distances equivalent to 90 km in an experimental apparatus (Stobutzki & Bellwood 1997). We observed directly surgeonfish larvae advancing against an estimated current of 10 to  $15 \text{ cm s}^{-1}$ .

Our observation of tightly aggregated groups of surgeonfish larvae swimming upstream along the substrate using topographical features to avoid high flows and predators is analogous to the behaviors displayed by temperate larval gobiids on oyster beds (Breitburg 1991, Breitburg et al. 1995). Presettlement demersal shoaling behaviors have been observed in the field for various families of temperate (Marliave 1986, Breitburg 1991) and tropical (Kaufman et al. 1992) reef fishes, which have also been observed to school while in the neuston (McCormick & Milicich 1993). Future observational efforts to detect demersal shoaling behaviors in tropical reefs should focus on the dusk

period, since it is used by many species as a colonization time (Dufour 1991, Dufour & Galzin 1993) and light levels are sufficient for visual observations.

The use of channel nets (Shenker et al. 1993, Thorold et al. 1994a, b, c) and crest nets (Dufour 1991, 1994, Dufour & Galzin 1992, 1993, Doherty & McIlwain 1996, Dufour et al. 1996) has recently facilitated the direct sampling of colonizing larvae as they enter the reef system. Channel nets sample only larvae that are transported by the currents or are actively swimming in the same direction as the water flow. The colonization event through the reef channel described in this paper (Observation 1) would have been undetected by channel nets since the larvae were swimming against the current while advancing through the channel. Crest nets sample the whole water column and depend on the currents and turbulence created by breaking waves over the reef crest to capture larvae. Colonizing larvae swimming against an outflowing current along the reef crest substrate might detect and avoid a crest net encountered in their way, resulting in an under-sampling of incoming larvae. It is unknown how widespread this kind of swimming behavior is in reef fish larvae, but it points towards a potential source of error when estimating larval supply with sampling methods based on current transport. The degree of underestimation of larval flux will vary with sampling gear used, the flow characteristics of different reef systems, and with differences in swimming behavior and abilities of different taxa.

Predation has been considered the principal cause for the high mortality rates of juvenile fishes (Victor 1986, Shulman & Ogden 1987, Hixon 1991). Dufour & Galzin (1992) discovered large differences in abundance between the flux of larvae over the reef crest and the number of resident fish detected afterwards in the lagoon. The differences were attributed to predation of colonizing larvae by resident piscivorous fishes. Our observations of 5 species of small piscivores successfully consuming colonizing surgeonfish larvae along the reef channel supports the potential importance of predation during the transitional period of reef colonization.

In comparison, during Observation 2 no signs of predation were detected. It is unknown if the absence of predation events observed during this second event was due to the abnormal time of colonization, a lower abundance of predators at the observation site or to previous satiation of predators due to the large number of incoming larvae. But this lack of daytime predation brings up the question of whether the usual time of larval colonization during low light levels (dusk and nights) is to avoid predation or due to other causes.

In conclusion, our observation of presettlement surgeonfish larvae swimming along the reef in shoals

