

Behavioral observations of an upcurrent reef colonization event by larval surgeonfish *Ctenochaetus strigosus* (Acanthuridae)

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ABSTRACT: Two reef colonization events by larval acanthurids were observed at Johnston Atoll, Central Pacific. In one event, pelagic larvae of *Ctenochaetus strigosus* were observed swimming in groups along the bottom of a reef channel and actively settling to caves and crevices. These larvae were swimming against a current that averaged 27 cm s^{-1} at a height of 1.5 m above the substrate. This observation confirms the importance of larval swimming abilities during colonization of some reef fishes and indicates a potential undersampling of larvae by passive plankton nets. Predation occurred on these incoming larvae by 8 piscivorous species, while no predation was observed during the second colonization event.

KEY WORDS: Coral reef · Colonization · Recruitment · Reef fish larvae · Swimming behavior · *Ctenochaetus strigosus*

INTRODUCTION

Most coral reef fishes have a life history which includes a pelagic larval stage. The movement of competent larvae from the pelagic environment to the reef environment is referred to as 'colonization' (Dufour & Galzin 1993). Once fish are situated over the reef, 'settlement' of the larvae onto the reef can take place or not. Settlement patterns influence the population dynamics of coral reef fishes (Victor 1983, Doherty & Williams 1988, Jones 1990, Robertson 1992). Recent studies of temperate fishes indicate the importance of presettlement larval behavior in the proximity of the reef in determining the actual settlement of larvae onto the benthic environment (Breitburg 1991, Breitburg et al. 1995). The defined patterns of larval supply (Dufour 1991, Dufour & Galzin 1993) combined with measurements of larval swimming abilities (Stobutzki & Bell-

wood 1994) support the notion that larval behavior during the transitional period of colonization is important in determining the settlement patterns of tropical reef fishes (Kaufman et al. 1992).

Many studies regarding the supply of larvae to the reefs have relied on censuses of recently recruited juvenile fishes on the reef, as well as on the measurement of daily otolith increments to estimate time of settlement. These are indirect methods that can be confounded by mortality of settlers (Doherty & Sale 1985, Hixon 1991, Connell 1996) and specific habitat selection (Sweatman 1985, Booth 1992). Planktonic larvae have been sampled with a variety of towed nets, but net avoidance by large larvae has always hindered the results concerning late-stage presettlement fishes (Choat et al. 1993). Light aggregating devices (night-lights and light-traps) have also been used to sample late-stage larval fishes in the proximity of reefs (Victor 1983, Doherty 1987), but these methods are selective for certain taxa (Thorrold 1992, Choat et al. 1993). Recently developed techniques now allow one to sample presettlement larvae during the actual transition period of reef colonization. Crest nets (Dufour 1991,

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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-

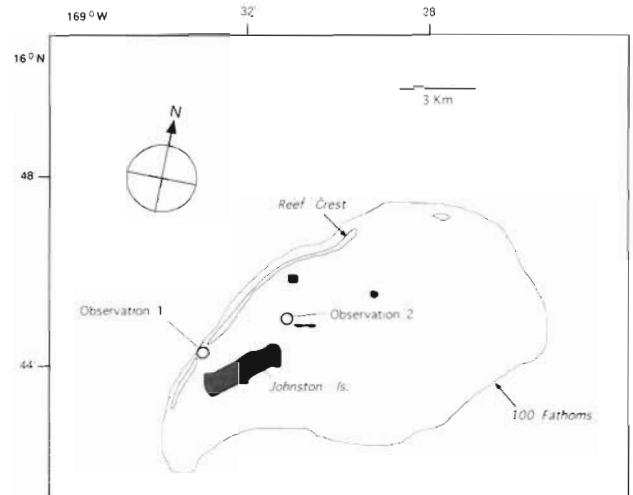


Fig. 1 Map of Johnston Atoll indicating the location of the reef channel where observations were made in 1994 (Observation 1) and the location of the 1995 observation inside the lagoon (Observation 2)

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 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 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 cm s^{-1} (Fig. 2). A sharp rise in temperature (0.25°C) at the offshore station coincided in time with the colonization event.

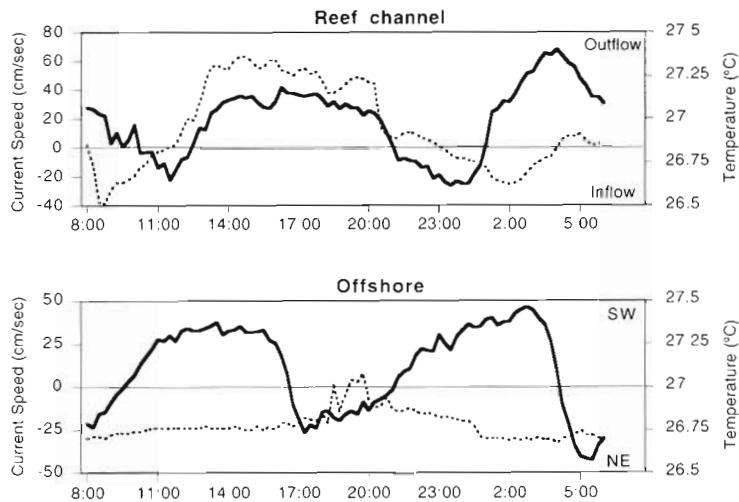


Fig. 2. Water flow and temperature measurements on May 12, 1994. Solid lines represent water flow velocity, dotted lines represent water temperature. Grey areas indicate the time when observations of larvae were made (Observation 1). On the reef channel (1.5 m off the bottom) positive flow velocity values indicate outflowing direction (exiting the lagoon) and negative values represent inflowing direction (into the lagoon). At the offshore site (10 m off the bottom) positive flow velocity values indicate alongshore southwest direction and negative values indicate alongshore northeast direction

Larval behavior

During Observation 1, large numbers (hundreds) of *Ctenochaetus strigosus* larvae were observed to be actively swimming along the substrate. The colonizing fish were typical pelagic unmetamorphosed larvae, with transparent bodies and little pigmentation. The average standard length of 10 randomly collected specimens was 2.8 cm (SD = 0.1).

Two distinct larval behaviors were observed at the channel: (1) Fish would hide along the substrate, occupying small holes, and underneath rocks. These 'settled' fish aggressively defended their positions from new incoming larvae. (2) The majority of larvae were observed to be actively swimming in tight schools that varied in size from 5 to approximately 25 individuals. Almost no fish were observed swimming alone. Their swimming was very directional, always moving from the outside of the reef towards the lagoon. All fish were swimming a few centimeters off the bottom along the channel, no larvae were observed swimming in mid-water or at the surface. Larvae appeared to use the topographic obstacles to help in their advance against the current, resting momentarily behind boulders before continuing their advance. Many sought refuge in the irregularities of the substrate, mostly underneath flat broken pieces of *Acropora*. If these corals were already occupied, resident larvae would attack the new incoming fish. On most occasions the rejected

fish would resume swimming along the bottom towards the lagoon. We observed several groups of larvae traveling 30 to 40 m up-current without taking refuge in the reef.

This was the only direct observation of a larval colonization event at this site after 191 h of behavioral observations by 1 of the authors (G.S.), 30 of which were done at dusk. All observations were done during the peak reproductive season of *Ctenochaetus strigosus* at Johnston Atoll (Sancho pers. obs.) and Hawaii (Lobel 1989).

Observation 2 took place in daytime (14:00 to 16:00 h) during a flood tide. Tight groups of surgeonfish larvae, varying in number from 30–40 individuals up to a few thousand, were observed advancing at heights of 0.5 to 2 m above the substrate following the contour. These large schools were composed mostly of dark pigmented presettlement surgeonfish larvae of various sizes, with a few partially transparent individuals mixed in the schools. Currents were not measured directly, but the highly directional swimming of the larvae appeared to be oriented in the same direction as the weak existing current, flowing in from a deep shipping channel on the south side of the Atoll.

Predation

Predatory fish of various families were very active at the reef channel during Observation 1, attacking groups of larvae as they progressed along the bottom. Five species were observed to successfully attack and ingest larvae during the colonization event. Individuals of *Caranx melampygus* (Carangidae) of small and medium size (20 to 40 cm approximately) patrolled the bottom of the channel at very high speeds and rushed violently against moving groups of larvae, grabbing coral rubble in the process which was quickly ejected. Large *Parupeneus cyclostomus* (Mullidae) were observed swimming very agitatedly around broken flat pieces of coral, using their barbels to search underneath them and moving adjacent gravel in search of hiding larvae. One male (33 cm standard length) was collected by spear and its stomach contained 5 undigested acanthurid larvae. Individual *Cirrhitus pinnulatus* (Cirrhitidae) were observed stalking and attacking passing groups of larvae while perched on the edge of large coral heads. One individual (21 cm standard length) was collected by spear and its stomach contained 2 undigested *Ctenochaetus strigosus* larvae. Four *Fistularia commersonii* (Fistulariidae) were ob-

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 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 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

against a current demonstrates the capabilities of tropical reef fishes to gain access to the reef against the water flow. This behavior should be considered in the design of future studies of reef colonization events, specially when sampling strong swimming larvae with passive nets in locations with variable currents. It should also be taken into account when estimating absolute rates of larval flux (Doherty & McIlwain 1996, Dufour et al. 1996) over reefs where offshore currents exist. Larval colonization may be higher than estimates based on passive net sampling techniques. More work describing and quantifying the behavior of the colonizing larvae is needed to address these questions.

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