SETTLEMENT AND LARVAL METAMORPHOSIS PRODUCE DISTINCT MARKS ON THE OTOLITHS OF THE SLIPPERY DICK, HALICHOERES BIVITTATUS

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ABSTRACT

Early in the sequence of daily increments on wrasse otoliths there is a transition from clear increments to a band of very faint, often indecipherable, wide increments. After about five of these wide increments clear increments resume. Planktonic larvae do not have the transition on the edge of their otoliths, while newly-metamorphosed juveniles have both the transition and the subsequent band on theirs. Experiments showed that metamorphosis takes about five days, during which the larva remains buried in sand. The transition therefore corresponds to settlement of the planktonic larva onto the reef, and the band is formed during the process of metamorphosis. These findings demonstrate that 1) it cannot be assumed that newly-appeared fish on the reef settled that day and 2) experiments are necessary to ascertain the meaning of marks on the otolith.

INTRODUCTION

Reef fish ecologists have only recently begun to focus their attention on the early life history of reef fishes. These fishes are unusual in that virtually every one of the many thousands of species that live on coral reefs has a planktonic larval stage. The interest in the ecology of larvae and the process of recruitment is indeed timely, for it is becoming increasingly apparent that many of the patterns of diversity and abundance of coral reef fishes are being determined by processes occurring in the plankton. Several studies have demonstrated that reef fish populations are limited by the supply of larval recruits, rather than by some resource on the reef (Williams,1980; Doherty,1983; Victor,1983). Furthermore, some of my recent findings (in prep) indicate 1) that species-specific larval behaviors determine when successful recruitment occurs in some Caribbean wrasses and thus promote the coexistence of species on the reef, and 2) that the duration of the planktonic larval stage affects the distribution of wrasse species in the Indo-Pacific and may well account for the differing degree of speciation that has occurred within wrasse genera.

Much of the progress that has been made on this subject is a result of the power of the daily otolith increment aging technique (Brothers,1981; Brothers & McFarland,1981). Because there are both daily increments and a mark corresponding to the settlement of the planktonic larva on wrasse otoliths (Victor,1982), the date of settlement for any individual can be calculated by subtracting the number of daily increments between the settlement mark and the edge of the otolith from the date of capture. The duration of the planktonic larval period can also be estimated by counting the number of increments between the center of the otolith and the settlement mark. The settlement mark appears under the microscope as a transition where the previously prominent dark lines that delineate each increment abruptly disappear. Regular increments only reappear after a band without clear increments is formed (see Fig. 1C). It is, however, often possible to discern several (usually five) faint increments making up this band in some areas of the otolith. The aim of this study is to clarify which events during the process of settlement account for the transition and the subsequent settlement band on the otoliths of the slippery dick, *Halichoeres bivittatus*, one of the most abundant wrasses in the Caribbean.

METHODS

Planktonic larvae of the slippery dick were captured at a nightlight with an aquarium dipnet on Ukubtupo reef in the San Blas Islands of Panama. They were identified both by fin ray counts and by raising in an aquarium. Only larvae that had their full complement of fin rays and were of a size ready to settle were present at the nightlight. Some of those captured were preserved in ethanol immediately, while others were transferred to a ten-gallon aquarium containing sand and sea-water. Collections of juvenile slippery dicks also were made on Ukubtupo reef about the same time.

The otoliths of all individuals captured were obtained by first removing the top of the cranium and then extracting the larger pair, the sagittae, from the base of the skull and the smaller pair, the lapilli, from the sides of the skull with fine forceps. The otoliths were then cleaned and dried and placed in a drop of immersion oil on a glass slide. They were subsequently examined under a compound microscope with transmitted light and a polarizing filter at magnifications of 400X to 1000X.

RESULTS

All twenty of the slippery dick larvae captured at the nightlight and preserved immediately had no settlement transition on their otoliths. In these fish the alternating light and dark lines that make up daily increments continued all the way out to the edge of the otolith (Fig. 1A).

Those larvae that were put into an aquarium had all disappeared into the sand at the bottom of the tank by the next morning. After a number of days these fish emerged from the sand and after some exploring took up residence in a corner or near some rubble. During those days in the sand they had lost the transparency and the melanophore pattern of larvae and developed the stripes, spots, and colors typical of juveniles of this species. The juvenile slippery dicks usually emerged on the fifth day (mean of 5.5, n=17,

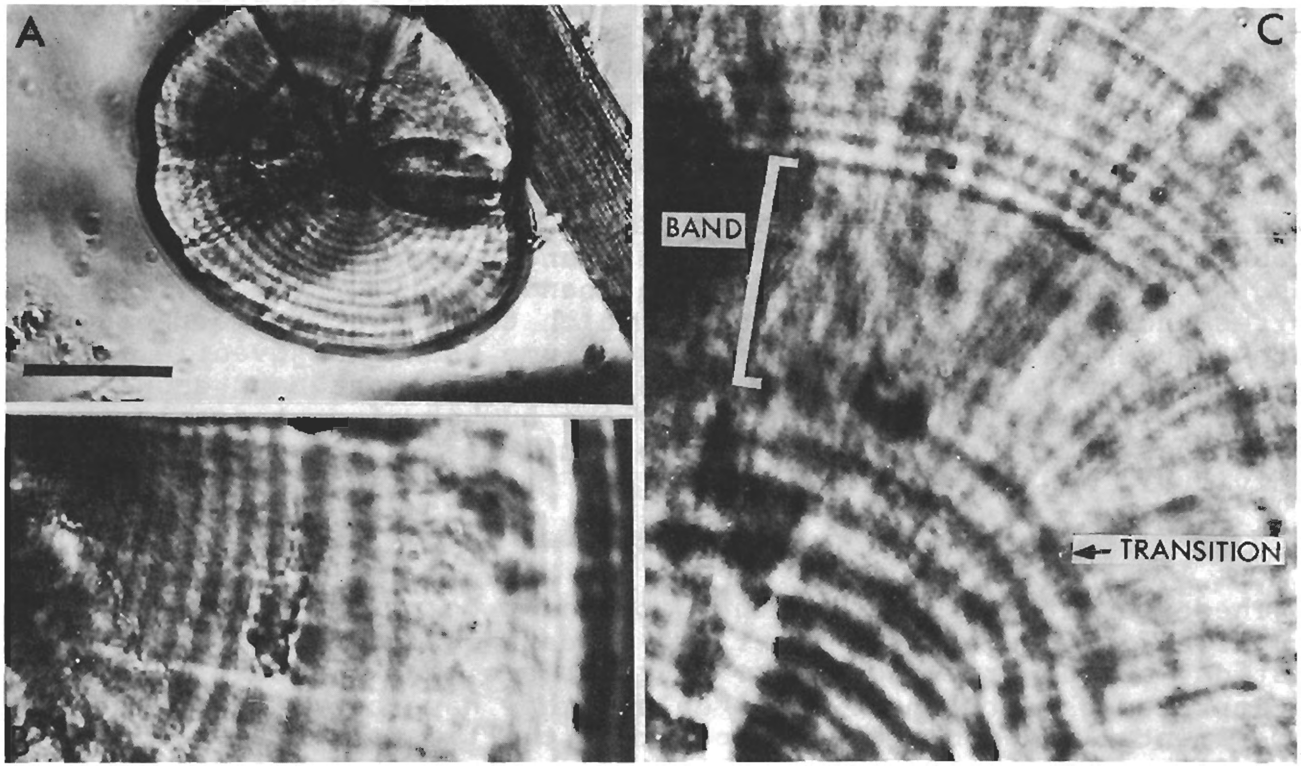

Fig. 1: Otoliths of slippery dicks. A: 9.9 mm SL, bar=100 microns. B: 10.1 mm SL, bar=20 microns. C: 21.0 mm SL, bar=30 microns.

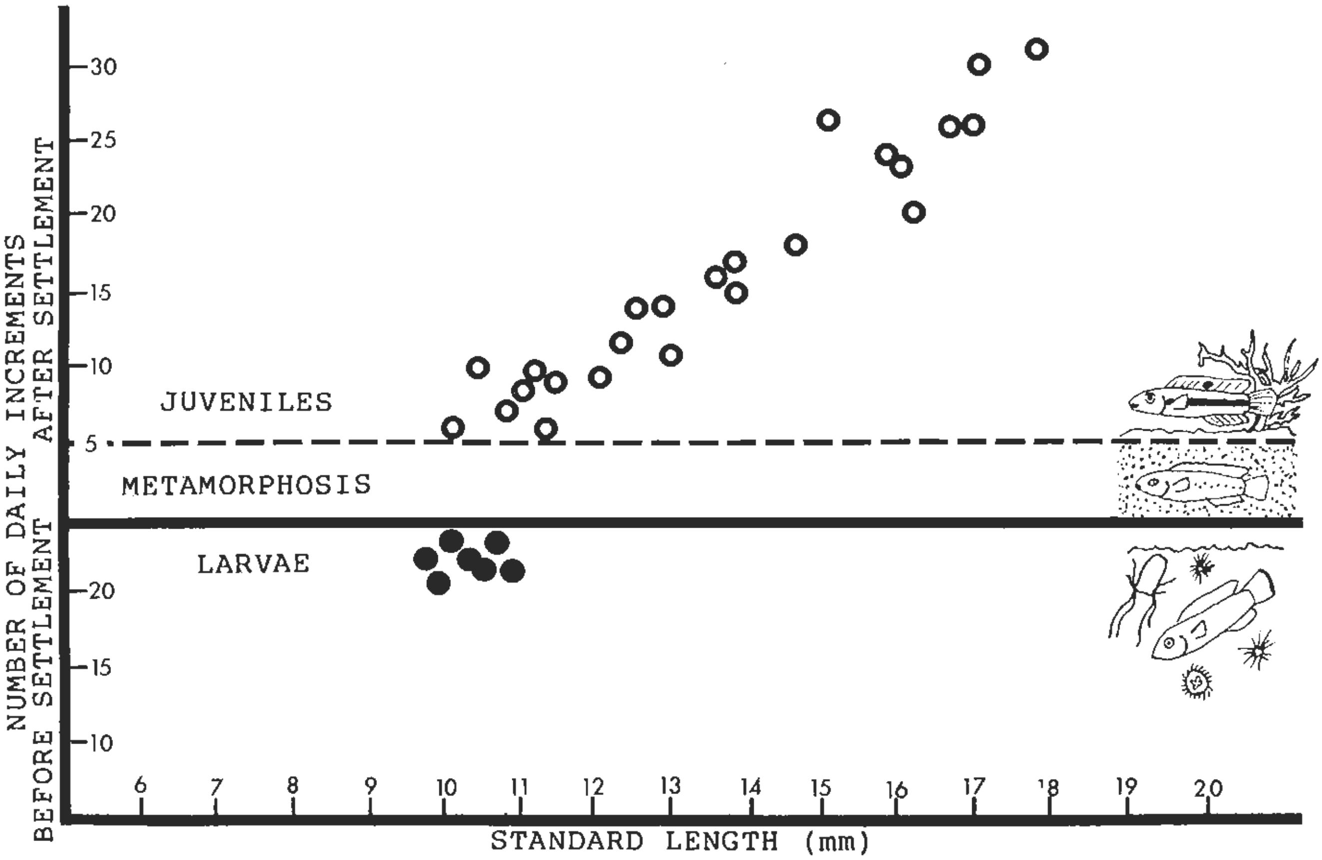

Fig. 2: Number of daily increments on the otoliths of slippery dicks.

SD=.87, range=4 to 7). Individuals killed immediately after emergence had a completed settlement band after the settlement transition (Fig. 1B). Juveniles captured on the reef had the settlement band as well as some number of clear increments after the band (Fig. 1C and 2). The smallest fish captured had only one increment in addition to the five faint increments making up the band.

Clearly, the abrupt settlement transition occurs when the planktonic larva settles onto the reef and buries itself in the sand to metamorphose. The settlement band of five faint increments corresponds to the five days during which the larva metamorphoses into a juvenile. Regular increments resume when the juvenile emerges. The faint increments within the settlement band should, therefore, be included when counting the number of post-settlement increments in order to determine the settlement date for an individual.

DISCUSSION

These results demonstrate that it cannot be assumed that juvenile fish caught at their first appearance on the reef settled that day or the previous night. Furthermore, marks should not be interpreted as settlement marks unless they have been experimentally demonstrated to occur at the time of settlement rather than during the process of metamorphosis, which could take place at some other time. Many fishes metamorphose (i.e., take on the body form and color of juveniles) before settlement; as in the barracudas (Sphyraenidae), butterflyfishes (Chaetodontidae), angelfishes (Pomacanthidae), some damselfishes (Pomacentridae), scorpionfishes (Scorpaenidae), filefishes (Monacanthidae), triggerfishes (Balistidae), and pufferfishes (Tetraodontidae). Others metamorphose after settlement, as in the wrasses (Labridae), parrotfishes (Scaridae), and some of the drums (Sciaenidae)(Victor, unpublished data). Sciaenids of the genus *Pareques* in the Caribbean not only settle when very small and transparent, but even before their full complement of fin rays have developed (Powles & Burgess, 1978).

The settlement transition is particularly clear on the otoliths of wrasses, probably because the transition from life in the plankton to entombment in the sand is so profound. More subtle changes in life style have been demonstrated to produce quite subtle changes in the character of increments in grunts (Brothers & McFarland, 1981). The increments that can often be discerned within the settlement band in wrasses are unusual in being fainter and often wider than increments anywhere else on the otolith. If the width of otolith increments were a measure of the daily growth rate, it would mean that during metamorphosis the larva is growing quickly, even though it is, presumably, not eating. Since light, temperature, and food cycles appear to control the formation of daily increments in fishes (Mugiya, *et al.*, 1981; Neilson & Geen, 1982), and wrasse larvae remain buried in the sand while increments are produced, it is quite possible that some entrained circadian rhythm continues during metamorphosis. Juvenile wrasses that are maintained unfed in a dark insulated container for several days put down a very different kind of mark on their otoliths (Victor,1982). It is much narrower than the settlement band and does not show any internal pattern of light and dark lines.

Further confirmation of a five day period of metamorphosis during which wrasse larvae remain hidden comes from my data on the pattern of settlement of bluehead wrasses, Thalassoma bifasciatum, onto patch reefs in the San Blas Islands. Settlement was monitored by daily censuses of an area of coral outcrops in a seagrass bed for two years. At the same time, nightly collections of fish larvae were made at a nightlight. A preliminary analysis of the data indicates that a lag of about five days occurs between peaks of larval fish abundance and diversity and subsequent peaks of juvenile wrasse appearances.

Despite the fact that the process of settlement is such a critical period in the life of an individual and can greatly influence the abundance and distribution of adult populations, it remains both one of the least understood and least examined phases in the life history of reef fishes. The settlement strategies of reef fishes are probably as varied and complex as any other feature of this notably diverse assemblage, and clearly deserve closer and more rigorous attention.

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Note: Photos by B. Victor