Observations on Recruitment in Haemulid Fishes

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RESUMEN

Observaciones *in situ* de poblaciones naturales de roncos juveniles están revelando un conjunto de etapas del desarrollo juvenil definibles por cambios de comportamiento, utilización del habitat y sistema de alimentación. Cambios de comportamiento son evidentes por un incremento general de la agresión intra e interespecífica, lo que no es corriente en especies que forman cardúmenes, y por el desarrollo y modificación de los patrones migratorios diarios. Los cambios en el habitat y la cronología en las distintas etapas del desarrollo juvenil están relacionadas con edades diarias específicas.

INTRODUCTION

A common request of biologists by fisheries managers is, "give us facts so we can effectively regulate this fishery." Answers to such simple questions as, How fast does the species grow?, When and at what age do they enter nursery grounds?, and, When do they leave to become juveniles, or to join adult stocks? are, however, frustratingly hard to produce. The difficulty in generating the wanted answers stems not from a lack of trying on the part of the fisheries biologist, but mostly because a simple, easy method to age young fishes has not existed. Recently, however, a new method of aging fish to the exact day, which makes use of the daily marks laid down in the otoliths of fishes, has found favor in a few fisheries programs. When coupled with direct observations on life history stages of a species, the otolith aging method can provide answers to the kinds of questions listed earlier and, in addition, provide an accurate assessment of the rate of growth, all crucial to the management of a fishery.

Here I would like to summarize some of the detailed features that we have been finding about life history stages in the Haemulidae. This family, commonly called grunts, represents a dominant element of tropical reef fish communities, and a substantial component of the trap fisheries in western Atlantic and Caribbean waters (Dammann, 1980). Direct observations of the field behaviors of grunts, especially of the French grunt *Haemulon flaveolineatum,* have revealed a sequence of life stages, each easily definable in eco-behavioral terms. In addition, by using the otolithic aging technique, each of these stages has been assigned a specific daily age. Several colleagues are involved in this research. Central to the results summarized here are the efforts of Dr. John Ogden of The West Indies Laboratory, Fairleigh Dickinson University, on St. Croix, U.S.V.I. and of Dr. Edward Brothers at Cornell University. Our combined investigations are providing detailed

insight into the discrete life history stages of grunts and, also, into their recruitment patterns. The methods therefore provide a potentially powerful new tool for analyzing the early life stages of grunts, that may be widely applicable to many other fisheries.

METHODS AND RESULTS

Life History Stages—Behavioral Ecology Observations

Underwater observations on grunt behaviors and ecology have been carried out for the most part in Tague Bay and its near vicinity, at the island of St. Croix in the U.S. Virgin Islands. Although several species of the genus *Haemulon* occur there, dominant species are the French grunt, *H. flavolineatum,* and the white grunt, *H. plumieri* (Ogden and Erhlich, 1977). Within the confines of Tague Bay young French and white grunts are common. The adult stages are abundant outside the Tague Bay barrier reef where the trap fishery is pursued.

The life history of the French grunt *(Haemulon flavolineatum)* separates into seven stages (Table 1). The last five stages are defined from field observations of discrete differences in ecology and behavior; aspects of the first two stages, the egg and larva, are mostly inferred from the literature and our experience. The juvenile stage (V) is most familiar, because juveniles occur in shallow water and each day they migrate from and return to a specific schooling site (Ogden and Ehrlich, 1977) in a very precise manner (McFarland et al., 1979).

Juvenile French and white grunts (stage V) form mixed species resting schools during the daytime on the various patch reefs in Tague Bay (Ogden and Ehrlich, 1977). The schools function mostly as antipredator devices. Movement to the night-time feeding grounds on the grass beds is preceded by a suite of stereotyped behaviors, which poise the school for migration and occur each evening at the same light intensity levels (McFarland et al., 1979). Return migrations to the same patch reef occur at the same light levels as departure, a pattern believed to represent a balance between the threat from predators (which congregate around the patch reefs before and through migration periods) and visual changes in the retina that are regulated by light intensity (McFarland et al., 1979). Juveniles feed on a variety of benthic organisms (mostly crustaceans and molluscs; M. Robblee, unpublished dissertation) as solitary individuals (Ogden and Zieman, 1977; McFarland et al., 1979). During the daytime juveniles do not feed. Small recently recruited juveniles, however, feed on plankton during daytime over the schooling site (Ogden and Ehrlich, 1977; McFarland and Hillis, unpublished manuscript). Behavioral interactions within the resting daytime schools are frequent. Agonisms are rampant and some school members actively defend territories (McFarland and Hillis, unpublished manuscript). The function of this non-egalitarian unschool-like behavior remains obscure.

We have some data of interest on stages III (postlarva) and IV (prejuvenile) (Helfman, Meyer and McFarland, unpublished manuscript). Both phases are typified by diurnal plankton feeding. The postlarvae feed in the water column from 10-20 cm over grass beds or sand and, as a school, slowly move about in

TABLE I. CORRELATION OF LIFE HISTORY STAGES IN FRENCH GRUNTS WITH VARIOUS BEHAVIORS, HABITAT, AGE AND SIZE

LIFE STAGE	I	II	III	IV	V	VI	VII
NAME	EGG	LARVA	POSTLARVA	PREJUVENILE	JUVENILE	SUB-ADULT	ADULT
HABIT	PELAGIC		LITTORAL JUST ABOVE SUBSTRATE				
BEHAVIOR	SOLITARY (?)		FORM SCHOOLS DURING DAY				
HABITAT (day)	OCEAN		GRASS OR SAND	DIADEMA	STATIONARY ON PATCH REEF	ROAM ON PATCH REEF	DEEPER REEFS
MIGRATION	NONE[a]		TO GRASS OR SAND BEDS AT NIGHT				
FEEDING	YOLK	DIURNAL PLANKTIVORE			NOCTURNAL BENTHIC OMNIVORE		
COLORATION	TRANSPARENT	JUVENILE STRIPES			ADULT BODY COLORS		
MAXIMUM SIZE (SL mm)	1	4	12	21	ca. 120	(b)	
MAXIMUM AGE (days)	ca. 1-2	13	ca. 30	ca. 50	ca. 700[c]	?	?

a -- Vertical movements in water column by larva likely

b -- Not yet determined in our study

c -- Estimated from age-growth curve extrapolation

the vicinity of patch reefs. When threatened, the school tightens and if objects are nearby they will swim between them. As dusk falls the post larvae do not show migratory behaviors, but merely spread out over the substrate, remaining about 1-2 cm above the bottom (McFarland and Hillis, unpublished manuscript). In contrast, the prejuveniles which form schools about the base of the patch reefs during the day migrate at dusk and dawn (Helfman, Meyer and McFarland, unpublished data). Prejuveniles associate with the sea urchin *Diadema* or the finger coral *Porites porites*. When threatened they swim between the spines, finding refuge in a virtually impenetrable fortress. Behaviorally, the prejuvenile migrations are similar to the juvenile migrations, but differ in timing. They occur earlier and at considerably "brighter" light levels than the juvenile migrations. Like postlarvae, the prejuveniles do not feed at night.

Our information on stages VI and VII is anecdotal, for as yet we have not directed attention to the subadult and adult grunts. We can say that subadults school on the patch reefs during the day, but roam about the entire reef a good deal, and migrate at dusk and dawn. At an undetermined size they move to deeper reef sites offshore, or take up solitary daytime positions along the barrier reef. We have no direct data on when individuals mature (Billings and Munro, 1974) or when and where they breed. We also are in the dark concerning stages I and II, Saksena and Richards' (1975) paper on laboratory-reared white grunts representing the only substantive report on the egg and larval stages.

This short summary of the life history stages of the French grunt reveals that each stage is clearly definable using only ecologial and behavioral criteria (Table 1). I stress that stages III (the postlarva) through VII (the adult) can be

recognized easily in the field and, importantly, can be collected as discrete life stages.

A crucial question can be posed—How old are the French grunts as they pass from each life stage to the next? We have an initial answer for the St. Croix French grunts.

Age and Growth—Use of the Otolithic Aging Method

The use of otoliths to age fishes relies on counts of daily growth increments (Pannella, 1971; Brothers et al., 1976). In French and white grunts growth increments in the otoliths, and especially in the lapillus, are distinct and readily countable in all fish for the first 100 days (Brothers and McFarland, 1980). Counting daily marks beyond 100 days is possible in some fish, but with less precision. By aging individual French grunts of different sizes to the day a very detailed age-growth curve can be constructed (Fig. 1). The method is very sensitive and, for example, can reveal different rates of growth at different seasons of the year (see summer versus winter fish, Fig. 1).

An additional feature is the presence of four transitional regions in the otoliths that represent increases or decreases in the "width" of the daily increments. Presumably, the described changes in the ecology and/or behaviors of young grunts might invoke metabolic shifts that would produce these transition marks. Suspecting that the transition marks might coincide with switches from one life history stage to another, we collected groups of grunts in several life stages (stages III, IV and V) and recorded the presence or absence of each transition mark in all fish (Brothers and McFarland, 1980). In recording the average daily age and the corresponding body size at which each transition mark is laid down, it became clear that the first three marks fall between the size ranges associated with each life stage (Fig. 1). Thus, transition mark 1(T_1) seems to relate to the transition from larva to post larva, that is, it may signal the change from a planktonic to a benthic mode of life. Transition mark 2 (T_2) identifies the transition for postlarva to prejuvenile, mark 3 (T_3) the switch from prejuvenile to juvenile and mark 4 (T_4), we suspect, indicates the transition in feeding from planktonic to benthic foods.

DISCUSSION AND CONCLUSIONS

Several conclusions basic to understanding the early life history and for elucidating recruitment patterns in young French grunts result when the field observations are combined with results derived from the aging technique. Specifically, the average number of days spent in each life stage can be estimated from the maximum age of individuals for each stage (Table 1). The time from fertilization to hatching probably never exceeds 1 to 2 days, and the larvae settle after about 11 days at sea. These data indicate that at St. Croix the entire planktonic phase does not exceed 14 days; the pelagic existence of grunts therefore is quite short compared to many coral-reef fishes (Marshall, 1966; Randall, 1961). On the basis of the short pelagic life, spawning, which has not been directly observed in French and white grunts, likely takes place in the near vicinity of St. Croix. In fact, surface current gyres, as described in this region (Lee et al., 1978; Molinari and Atwood, 1980), may recirculate the

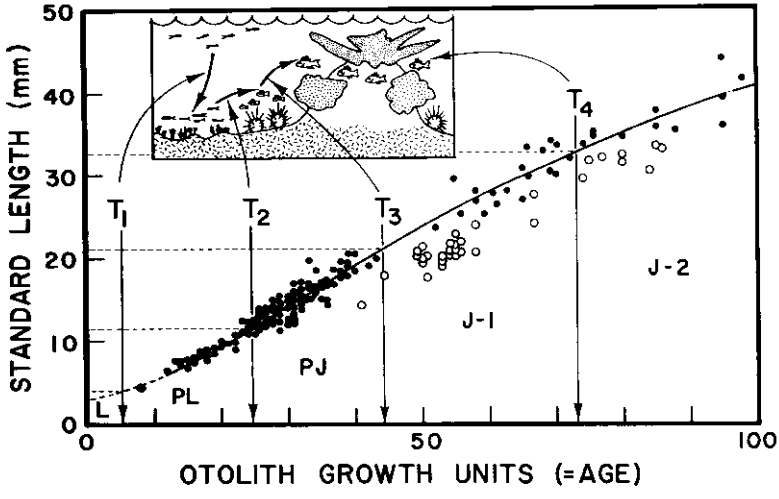

Figure 1. Age growth curve for young French grunts.

Each otolith growth unit represents one day. Zero age represents the beginning of the first countable increment. Absolute age from the time of fertilization to the first otolithic increment is uncertain, but probably does not exceed 4 to 5 days. The curve is a running average for the filled circles, which are counts and sizes for grunts collected during the spring and summer. The curve has been extrapolated to zero age on the basis of growth data for laboratory reared white grunts (Saksena and Richards, 1975). The larger filled circle at 8 growth units is for a single grunt collected from the plankton. Open circles are for grunts collected during mid-winter (January) and indicate that growth is suppressed for fish that were spawned during the fall (October and November). T_1, T_2, T_3 and T_4 represent the mean otolithic age for the transition marks found in the growth increments of the French grunt (see text). The average standard length associated with these four transitions are obtained from their intersection with the growth curve (finer dashed lines). The letter symbols refer to the life history stages of the French grunt as summarized in Table I. L = larva (stage II), PL = postlarva (stage III), PJ = prejuvenile (stage IV), J-1 = juvenile 1 (early stage V), and J-2 = juvenile 2 (late stage V). The inset depicts the general habitat of each of these life history stages, their transformation sequence (arrows), and the average age and size at which transformations tend to occur. The precise relationship of T_1 to transformation from the larval to postlarval phase is somewhat uncertain, but we think it is laid down in the otolith 2 to 3 days before the actual settlement of the larva takes place. T_4 most likely signals the end of diurnal plankton feeding.

larval grunts back to their site of origin (Johannes, 1978; Lobel, 1978), in this instance the island of St. Croix.

Once settled as postlarvae the young fish grow rapidly and after approximately 17 days become prejuveniles. Twenty days later they join the resting juvenile schools on the patch reefs of Tague Bay. For the first 30 days as juveniles, however, they continue to feed on plankton during the day. The period from fertilization to the end of a dependence on plankton as a prime source of food lasts approximately 80 days. At this time growth rate starts to slow (Fig. 1). The juveniles remain on the patch reefs for about 2 years before starting to roam about the reefs, a behavior typical of the subadult stage (Table 1).

These data clearly indicate the postlarval, prejuvenile and juvenile stages each have different habitat requirements, all of which are crucial to survival. Together the young stages cover a period of about 2 years, and every day the

fish require the use of a large fraction of Tague Bay (most patch reefs during the day, and most sand and sea grass beds at night).

The insights gained lead to initial guidelines for management policy. For example, the short pelagic phase, and the likelihood that local recruitment of young grunts into the populations results from the activities of sexually mature adults at that locality, suggest prudence against overly lenient limits for the harvesting of adults. Also, the continuing requirements of the young for protective covering and large forage areas over at least a two-year period, if not longer, require vigilance against excessive industrial and recreational development and pollution if a grunt fishery is to be protected. My point is not that these suggestions for management are novel to a grunt fishery, for they are the essence of common sense. Rather, my point is to stress that the careful application of new techniques in biological investigations of a fishery can supply the fisheries managers with the data base they so desperately require to arrive at decisions.

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