MIGRATION IN CORAL REEF FISHES: ECOLOGICAL SIGNIFICANCE AND ORIENTATION MECHANISMS

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ABSTRACT

Coral reef fishes are in general rather sedentary and territoriality and home range behavior patterns are highly developed. However, many species migrate, often relatively long distances compared to body size and often with spectacular precision. Migrations in reef fishes may be associated with: 1) life history-movements of planktonic larval stages to reefs or movements of juveniles from nursery areas to reefs; 2) seasons -- precisely timed spawning aggregations drawing fishes to particular locations from wide areas of the reef; and 3) diel patterns -- movements to and from feeding or resting areas associated with dawn and dusk. Of these migratory patterns the latter are the best known in coral reef fishes.

Certain coral reef fishes seem ideal as a model system for studies of orientation mechanisms in fishes. Grunts (Haemulidae), for example, have relatively short, highly regular migrations that occur in all seasons. The fish are numerous, small, and able to withstand tagging and handling. Preliminary work on orientation mechanisms of grunt migrations has indicated the potential use of local landmarks, a distance sense and a sun compass. The persistence of migration routes in grunts and the preliminary demonstration of socially facilitated learning of routes by new recruits sets up the possibility of studies of the development of a "map" in grunts combining a variety of cues. The goal of studies in such a model system will be to develop testable hypotheses that may be applied to the orientation mechanisms guiding fish migrations in general.

INTRODUCTION

Coral reef fishes form one of the most diverse community associations of animals in nature. A nearshore fish fauna in excess of 2,000 species is known from the Philippines, the generally acknowledged center of diversity of coral reef fishes. The Caribbean region, at a higher latitude, geographically smaller, and climatically more variable, has more than 500 species. Within-habitat diversity on coral reefs is high and correlates with measurable parameters of reef structure (Gladfelter et al. 1980) but not necessarily with regional diversity (Sale 1980). While the origin and maintenance of this high diversity is controversial (e.g. Sale 1977; Ogden and Ebersole 1981), coral reef fishes have evolved a high degree of specialization in morphology and behavior most often demonstrated in studies of resource partitioning, particularly space and food.

Coral reef fishes are appealing objects of study and have been subjected to increasing attention in the last 20 years, particularly with the development of scuba diving as a field research tool. They are easily observed at any hour of the day or night and may be relatively easily manipulated. There are numerous recent reviews on coral reef fish ecology, including population biology (Ehrlich 1975), community structure (Helfman 1978), reproductive biology (Johannes 1978) and aspects of social behavior and coexistence (Sale 1977, 1980).

The purpose of this paper is to review what is known of migration in coral reef fishes in relationship to the current status of knowledge of orientation mechanisms in fishes in general. It is proposed that coral reef fishes provide an opportunity to develop a model system for testing hypotheses which will have broad application to the study of fish orientation mechanisms.

CORAL REEF FISH MIGRATIONS

Coral reef fishes are in general rather sedentary with territoriality and home range behavior patterns highly developed in many species. The reef may be viewed as a complex mosaic of spaces in which many species of fishes have rather precisely defined daily activity patterns. However, many species migrate, often relatively long distances (particularly in relation to body size) and often with spectacular persistence and precision. Migrations in reef fishes may be associated with: 1) life history -- movements of planktonic larval stages to reefs or movements of juveniles from nursery areas to reefs; 2) seasons -- precisely timed spawning aggregations drawing fishes to particular locations on the coral reefs from wide areas; and 3) diel patterns -- movements to and from feeding or resting areas associated principally with dawn and dusk. Of these migratory patterns the latter are the best known in coral reef fishes. The evolution of these migratory patterns in coral reef fishes is probably associated with two principal evolutionary pressures: 1) the intensity of predation in tropical waters; and 2) the importance of partitioning time, space and food in a complex fauna.

Life History Migrations

The larval and juvenile stages of most coral reef fishes occupy areas completely different from the adults. A great majority of coral reef fishes exhibit a planktonic larval stage which may last from days to more than a year. While the larval life of most coral reef fishes is poorly known, some species have been studied. Damselfishes (Pomacentridae), for example, lay demersal eggs within a nest in the territory. Upon hatching the larval damselfishes enter the plankton for as brief a period as several days before settling in an area removed from that of their parents (Sale 1980). In contrast, the balloonfish (*Diodon holocanthus*) is known to recruit to nearshore areas in huge schools from the open ocean (J.C. Ogden unpublished data). Based on otolith ring counts (E.B. Brothers personal communication) the age of several individual *Diodon* has been determined to be in excess of 450 days at the time of recruitment into coastal waters. Between these extremes, a more usual pattern of larval life in the plankton might be several weeks, and reef fishes can likely adjust the duration of larval life to a certain extent in response to local conditions (Sale 1980).

The "nursery" phenomenon is common in coral reef fishes. For example, stands of mangroves and seagrass beds selectively attract larvae of certain coral reef fishes, such as snappers (Lutjanidae) and grunts (Haemulidae). These fishes move to coral reefs later in life, usually in a pre-adult stage. The recruitment pattern in grunts has been followed by Brothers and McFarland (1981), McFarland (1979) and W.N. McFarland, E.B. Brothers, J.C. Ogden and M.J. Shulman (unpublished data) in the Virgin Islands. After a larval life of about 14 days (determined from counts of otolith daily rings) post-larval grunts settle in seagrass beds and gradually associate in schools. These schools slowly move to the base of the coral reef over a period of several months arriving at the reef in a juvenile stage at which time they join the pre-adult schools commonly found there in persistent sites.

Seasonal Migrations

Seasonal patterns of migration are widespread in fishes. In temperate zone these movements are usually associated with changes in climate, water temperature, food supply or similar seasonal variation in resources. In the tropics seasonal migrations are most commonly associated with reproductive cycles. Smith (1972) noted spawning aggregations of Nassau grouper (*Epinephelus striatus*) in the Bahamas. This yearly phenomenon, well known to local fishermen, is commonly observed in groupers throughout the Caribbean. One particular reef area draws fish from an entire region and spawning activity proceeds over a period of several weeks. Smith (1972) suggested that the fish migrate to the spawning sites by following depth contours on the coral reefs and that these traditional spawning sites are maintained as younger fish have a tendency to follow older more experienced fish. Some areas of the reef are particularly advantageous for spawning. These probably coincide with favorable patterns of current and tide which assist in the dispersal of the newly released eggs. Johannes (1978) reviewed seasonal spawning movements of fishes in the Pacific and found a striking coincidence of these movements with seasonal variations in oceanic current patterns. This coincidence of behavior with long term oceanographic phenomena may assure the entrainment of larvae within the coastal zone rather than their random dispersal into the deep ocean. P.S. Lobel (unpublished data) has continued this work in a detailed examination of spawning patterns of coral reef fishes and seasonal current patterns in the Hawaiian Islands.

Diel Migrations

It is well established that communities of coral reef fishes undergo major diel changes, especially around dawn and dusk. Diurnal and nocturnal feeders exchange roles, migrating between refuge areas and feeding areas. Studies have detailed the temporal changes in community structure during these transition periods, emphasizing the sequence of appearance of various species and the predator-prey interactions (Hobson 1972, 1973; Starck and Davis 1966; Domm and Domm 1973). The time of appearance of particular species is highly predictable, based on light levels (Hobson and Chess 1973; Gladfelter 1979; McFarland et al. 1979). Not only species but size classes and maturity states within species have readily distinguishable migration patterns (Fishelson et al. 1971; Ogden and Ehrlich 1977).

Other less spectacular migrations are associated with daily spawning patterns. The wrasse *Thalassoma bifasciatum*, for example, spawns every day (Warner et al. 1975). Terminal-phase males break off feeding activities and move directly over considerable distances to a favored spawning site where spawning activities are initiated at particular times each day (Warner and Hoffman 1980). Such spawning sites have been known to persist for long periods of time. Colin and Clavijo (1978) showed that a daily spawning site originally described by Randall and Randall (1963) for *Sparisoma rubripinne* persisted for over 17 years.

Thus large numbers of nocturnal, diurnal and crepuscular species of coral reef fishes migrate daily. These migrations are spatially and temporally predictable and are an important part of the reef ecosystem. In contrast to the attention given to the timing and ecological role of the migrations, the guidance mechanisms underlying them have been scarcely considered. The daily migrations of parrotfish (Scaridae) between diurnal feeding areas and nocturnal resting areas (Ogden and Buckman 1973; Dubin and Baker 1982; Clavijo, unpublished data) are apparently guided in part by a time-compensating sun compass (Winn et al. 1964). With the exception of this study virtually nothing is known about the mechanisms guiding reef fish migrations. Waterman and Forward (1970) demonstrated a polarized light response in tropical halfbeaks (Hemirhamphidae), but it is not clear how these fish use polarization patterns.

MECHANISMS OF ORIENTATION AND NAVIGATION IN FISHES

In contrast to coral reef fishes the mechanisms of migration in other fishes and birds have been studied in some detail. These studies have generally fallen into two categories: observations of the movements of released individuals and analysis of the spontaneous or conditioned directional movements of animals in experimental areas.

A consideration of the vast bird literature (see reviews by Emlen 1975; Schmidt-Koenig 1979; Wallraff 1984 -- this volume) reveals two factors which may have been critical to success in this discipline. First, experimental research has included many species but has focused on relatively few. The indigo bunting (*Passerina cyanea*), European robin (*Erithacus rubicula*), and especially the homing pigeon (*Columba livia*) have been favored. In-depth understanding of orientation in a few species can then be extrapolated to species with similar migratory patterns. Second, the wide range of techniques used in laboratory and field research prevents undue emphasis on the results of any single technique or experiment and allows more complete understanding of the total process of orientation. This total process must include such aspects as the initial selection of direction, maintenance of direction, compensation for natural or artificial displacement, and termination of migration.

Though bird studies are more numerous than those with fishes, a considerable body of literature on fish orientation exists. Most numerous and relevant to this discussion are tracking studies and arena experiments. Hasler et al. (1958) were among the first to study compass orientation of fish in the field, using bobbers attached to the backs of white bass, *Morone chrysops*. Recently, tracking studies have tended to involve ultrasonic telemetry (reviewed by Stasko and Pincock 1977). In some cases multichannel transmitters relay information on swimming speed, depth, and ambient light and temperature (Standora and Nelson 1977) or compass heading (Harden Jones 1981), but usually the transmitters only indicate the position of the fish. Sonic-tracking studies tend to provide information on a small number of fish over a brief period. Transmitter size limits distance and duration of signal, but the studies are often limited by the endurance of the trackers and the distribution of the subjects. A serious drawback in most tracking studies is the lack of detailed, accurate information on the immediate environment of the fish. Studies of fish movements have seldom employed direct observation because the fish are generally too swift and the water too turbid to permit useful visual tracking.

The phenomenon of homing and home-site fidelity has been used in some studies designed to distinguish the cues used by fishes in orientation. Green and Fisher (1977) and Goff and Green (1978) looked at homing in a benthic stichaeid using normal, blind and anosmic fish. Homing appears to involve a complex set of olfactory and visual cues.

Arena tests of fish orientation have provided a fruitful way to overcome some of the problems of field work. Naturally- or artificially-conditioned sun-compass orientation has been indicated in mosquitofish (*Gambusia affinis*) by Goodyear (1973), in the starhead topminnow (*Fundulus notti*) by Goodyear (1970), in largemouth bass (*Micropterus salmoides*) by Loyacano et al. (1977) and bluegill (*Lepomis macrochirus*) by Goodyear and Bennett (1979).

In addition to the sun-compass studies various species have been shown to orient to light polarization patterns. Spontaneous orientataion to polarized light has been shown in hemirhamphids (Waterman and Forward 1970) and goldfish (*Carassius auratus*) (Kleerekoper et al. 1973). Conditioned orientation has been shown in a cichlid, *Pseudotropheus macrophthalmus* (Davitz and McKaye 1978) and in sockeye salmon (*Oncorhynchus nerka*) (Dill 1971).

Most of the above species have limited migratory tendencies, but Atlantic anguillid eels and Pacific salmon (*Oncorhynchus* spp.) have been the subjects of tracking and arena orientation studies. Adult silver European eels (ocean phase) (*Anguilla anguilla*) have been tracked with ultrasonic equipment (Tesch 1978; Westerberg 1979), but no consensus has been reached regarding guidance mechanisms. Compass orientation in the absence of solar cues has been indicated in adult American eels (*Anguilla rostrata*) (Miles 1968) and European eels (Tesch 1974), but attempts to establish electric or magnetic sensitivity in adult and juvenile eels have met with mixed success (see discussion in McCleave and Power 1978).

Perhaps the greatest amount of fish orientation research has been conducted on Pacific salmon. Tracking studies of adults in coastal areas generally revealed some passive individuals and some which were actively swimming homeward, usually along tidal axes (Stasko et al. 1973; Groot et al. 1975; Stasko et al. 1976). Besides tracking individual fish, salmon biologists have set up sonar stations to monitor the movements of yearling sockeye salmon leaving a large lake (Groot 1972). While all of these studies have provided useful information, they have the limitations of remote-sensing work described earlier. To date there appears to be no published report of adult salmon tracking on the high seas. The ocean distribution of salmon has been roughly mapped out by research fishing and mark-recapture work (Neave 1964; Royce et al. 1968), but the details of movement patterns are still unknown.

The tagging and tracking work in open water with adult salmon has not been complemented with arena orientation studies (except the work of Churmasov and Stepanov 1977, and Stepanov et al. 1979). However, the open-water orientation of juvenile salmon has been studied in some detail. The migration of sockeye salmon smolts to the outlet of Babine Lake, British Columbia, has been shown to be a directed movement by genetically distinct populations within the lake, cued by the sun's position, light-polarization patterns, and magnetic fields (Groot 1965; Simpson 1979; Quinn and Brannon 1982).

Young sockeye salmon not only show compass orientation when leaving their lake but also when entering it. Brannon (1972) showed that fry in experimental six-armed arenas would orient in the appropriate direction for their lake movements. These findings have been confirmed, and it is now clear that fry orient using a combination of celestial cues and the magnetic field in directions representing inherited adaptations to the geography of particular lake-river systems (Quinn 1980; Brannon et al. 1981).

Although the arena experiments have revealed a great deal about the sensory basis of juvenile salmon orientation, their interpretation has been hindered by the lack of detailed information on the pattern of salmon movements in the lakes and estuaries. While some progress has been made in this regard (in Lake Washington, for example, Woodey 1972), most of the sockeye salmon lakes are remote and largely unstudied. A second drawback in studying salmon is the unavailability of fish during much of the year. In a typical fry or smolt run most of the fish enter or leave their lake over a 2-3 week period. This greatly restricts the number of experiments which can be carried out, because it is difficult to catch the fish when they are in the lake itself, and in any case they would not be in the proper state of migratory motivation.

Briefly the current understanding of compass orientation by fishes is as follows. Several non-migratory species show a shoreline-related (Y-axis), predator-conditioned, sun-compass orientation. Two species of hemirhamphids, a cichlid, goldfish and sockeye salmon have been shown to orient using light-polarization patterns. However, the function of this response is not clear. A stingray, *Urolophus halleri*, has been conditioned to use magnetic fields for orientation (Kalmijn 1978), but this ability has not been related to migrations in this species. Compass orientation has been shown in eels, but the importance of electric, magnetic and other cues is not clear at this time. Compass orientation in juvenile Pacific salmon (especially sockeye) is now well established, and some progress has been made towards understanding the sensory inputs and genetic basis of the behavior. However, the short field season and lack of information on the behavior of eels and salmon at sea are drawbacks to understanding the role of compass orientation in ocean migrations. Thus the species whose migrations have been most intensively studied have, in many ways, been difficult ones, selected more for the spectacular nature of their migrations and their economic importance than for their convenience or appropriateness as models of fish migration.

CORAL REEF FISHES AS A MODEL SYSTEM FOR THE STUDY OF MECHANISMS OF ORIENTATION

Fish migration research has been unduly confined to tagging studies of large fish and controlled studies of small ones. The former reveal too little about guidance mechanisms, and the latter (too often conducted on non-migrants) can only establish the potential use of a particular cue, not its actual role in guiding the fish through the complex environment.

In order to understand the role of compass orientation and active navigation in the migrations of fish a battery of field and arena tests must be conducted on the same species. An ideal subject would be of modest size, display spatially and temporally regular migrations, be available for study during much of the year, have a well-known distribution pattern, and live in an area permitting displacement studies and direct observations. The feeding migration patterns of juvenile French grunts and white grunts (*Haemulon flavolineatum* and *H. plumieri*) appear to meet these criteria. These fishes are small (<15 cm total length), display relatively short but very regular migrations to and from feeding areas, are available almost all year, and can be readily studied in the field as well as in the laboratory. They can be easily collected on patch reefs, whose promixity to each other facilitates displacement experiments. The clear water makes it possible to observe the behavior of fish released after displacement or other experimental manipulations.

Diel Migrations of Grunts

Ogden and Ehrlich (1977) documented the existence of persistent diel migration routes in French and white grunts leading from patch reefs into surrounding seagrass beds in the Caribbean. The behavior on these routes was very regular and correlated with light level (McFarland et al. 1979). The routes followed were linear for 50 to 100 m, and then migrating groups fragmented in a dendritic pattern until single individuals remained at a particular location, feeding through the night on benthic invertebrates. In the morning individuals and then small groups apparently aggregated, returning with precision along the initial route at dawn (Ogden and Zieman 1977; Ogden and Ehrlich 1977). Mark-release-recapture experiments showed that grunts did not reaggregate randomly on reefs following nightly feeding forays but appeared to recognize a home reef and further a home schooling-site on a particular reef. Translocation experiments showed homing over distances ranging from 0.1-2.8 km from the home reef (Ogden and Ehrlich 1977).

Helfman et al. (1982) have shown that the development and persistence of diel migration routes in grunts is dependent upon social facilitation. Particular resting sites on coral reefs have persistent groups of juvenile and subadult grunts. These groups are joined continually by recruiting juveniles which have settled elsewhere and move gradually into the sub-adult schooling sites. Young fish have been shown in a series of observations and experiments to readily follow older, more experienced fish and thus the persistence of the routes appears to be assured.

McFarland et al. (1979) felt that avoidance of predators provides the most obvious adaptive significance for these precisely staged and timed migrations. Predation surrounding coral reefs is intense at dawn and dusk, and predators gather at grunt migration routes before their departure. The migration takes place in a narrow range of light levels, and changes in body coloration and photomechanical movements in the retina affords the grunts a maximum visual advantage over their predators. Once clear of the immediate vicinity of the reefs, the predation rate drops, and by the time individual fish reach their feeding areas, night has interrupted any advantage of continued schooling.

A second and less thoroughly examined consequence of migration patterns is the partitioning of feeding areas by grunts. Given the presumed necessity for solitary feeding in grunts, the dendritic migration route pattern with the extraordinary stereotypy of behavior of the fish assures that individual fish will arrive in an isolated part of the seagrass bed to feed. Furthermore, Ogden and Zieman (1977) and M. Robblee (unpublished data) have shown that the migration routes from a series of patch reefs several hundred meters apart surrounded by seagrass beds tended to be non-overlapping. Thus, a large foraging area may be effectively partitioned by large numbers of several species of feeding fishes.

Preliminary Experiments

J.C. Ogden (unpublished data) conducted a series of preliminary experiments on orientation mechanisms in juvenile grunts (5-10 cm long). Fish were trapped in a seagrass bed near a patch reef on their dawn migration routes at varying distances from their home reefs and were subsequently released and followed visually. Three kinds of releases took place at varying times following capture: 1) at several locations along the route; 2) within approximately 100 m of the route in various compass directions; and 3) in totally unfamiliar territory in a seagrass bed over 5 km from the home reef.

Fish released on the route immediately after capture at dawn continue their migration rapidly and directly back to their home reef regardless of the distance they were from the home reef when captured. If the migrating fish are delayed until approximately noon, they return to their home reef but more slowly and with some meandering. If the sun angle serves as a reference point for compass orientation, then the delay appears to result in a substitution of knowledge of local landmarks as the major cue to homing, although the apparent lack of landmarks in a seagrass bed is striking.

Fish released at a site displaced up to 100 m from the route just after dawn capture move in the compass direction they were taking when captured and then meander, in most cases eventually arriving at the home reef. Fish released near noon tend to meander and generally do not reach their home reef. These observations indicate that fish appear to recognize their routes. On several occasions fish would approach the route from the side and immediately turn in the appropriate direction as they crossed it. The routes are through thick waving seagrass and are not perceptible to a human observer.

Fish trapped at dawn, displaced rapidly to an unfamiliar seagrass bed 5 km to the west, and immediately released, follow the compass course appropriate to their normal route over a distance approximately equal to the distance at which they were trapped from the patch reef and then meander. Fish released later in the day meandered, either returning to the release site or moving slowly away before being lost to sight.

FUTURE WORK

These preliminary experiments demonstrate some of the possibilities of observation and manipulation that may be used in the study of orientation in coral reef fishes. While the scale of these movements is small when compared to the long distance movements of ther coastal and open ocean species, the generality of, for instance, a sun compass in fish may allow studies in such a model ystem to be extended to other species.

The routes of grunts, featureless to our eyes, are clearly perceived by them. Some form of socially facilitated learning is implied in the persistence of routes over long periods of time. New recruits readily follow older school members and learn the parameters of what likely amounts to a "map" -- combining a compass sense with visual and possibly olfactory landmarks. The ontogeny of development of this map could conceivably be studied using observation and manipulation of grunts of different ages. The results of releases far from the home reef suggest that individual fish have a "time-distance" sense. This is implied also in the repeated observation of particular tagged fish on particular sections of seagrass bed following evening migrations. The destination of migrating individuals within the route system is apparently not random. Finally, homing over long distances following displacement occurs in grunts as in many other species. The results of studies on such a model system using a coral reef fish will not only lead to an understanding of the mechanisms orienting reef fish migrations, but also to the generation of testable hypotheses of the orientation mechanisms guiding fish migrations in general.

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