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Movement of fishes (Grunts: Haemulidae) across the coral reef seascape: A review of scales, patterns and processes

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Abstract.—Reef fish movements over short and long time frames have important consequences for identifying essential fish habitat, quantifying ecological flows across the seascape and designing marine reserves. We use grunts (Haemulidae) as a representative model group for quantifying movement in terms of distances, time scales, temporal patterns, habitat associations and controls. Here, we provide a review based on recent studies and our own experience. The ritualized, twilight feeding migrations of grunts represent an important mechanism for transferring nutrients and organic matter across habitat boundaries, with movements on the order of 100-300 m. Both compass orientation and vision are used for navigation during feeding migrations. Feeding movements of adults are less ritualized in both space and time and typically occur on the same scale of distance as juveniles, although longer excursions have been documented. Ontogenetic migrations occur over years and take the form of discrete habitat shifts, with most individuals moving progressively offshore. Distances and pathways followed by fish will depend on the exact width of the shelf and distribution of suitable habitats. Transplant experiments suggest there are significant barriers to fish migration, and migration corridors, especially reef margins, seem to be important in determining the direction of ontogenetic habitat shifts, but these may be disrupted by environmental perturbations. Theoretical considerations relative to barrier perception and growth-survival trade-offs appear to explain normal movements of grunts and their responses to environmental perturbations, but lack of information on how fish may sense new locations at distance prevents the full use of theory to generate rules of migration covering timing, distance and direction.

Keywords.—Grunts, *Haemulon*, migration, connectivity, coral reef ecosystems

Introduction

The intense pressures on coral reef ecosystems from commercial and recreational fishing, tourist activities and stress from anthropogenic impacts has forced management to become more comprehensive in scope and develop an ecosystem-based approach, with marine reserves being an integral tool (Appeldoorn 2008). A critical issue in ecosystem-based management is the identification of essential fish habitat and an understanding of how such habitats are ecologically connected. The movement of reef associated fishes represents one of the most important mechanisms of ecological connectivity. Many species feed in one location or type of habitat (including the pelagic realm) but reside in a different one. These feeding migrations, in which fishes act as vectors of transport, represent transfers of organic matter and nutrients, with demonstrated importance to system ecology (Meyer et al. 1983, Meyer and Schultz 1985a,b, Clark et al. 2005). On a larger scale, many reef species make ontogenetic migrations across the reef ecosystem, some from mangroves to shelf-edge and slope habitats (Cocheret de la Morinière 2002, Nagelkerken and van der Velde 2003, Appeldoorn et al. 2003, Aguilar-Perera 2004, Cerveny 2006). Ontogenetic

migrations, involving the movement of fish as they grow, not only represent a significant transfer of biomass (Deegan 1993) but also the transfer of important ecological functions (e.g., herbivory) and services (e.g., fisheries) that fishes provide.

Looking toward eventual modeling of connectivity at the seascape level (e.g., Mumby 2006), the purpose of this paper is to review current studies and our own experience on grunt (Haemulidae) movements as a representative model group for quantifying the movement of reef fishes. In the Caribbean, grunts are ubiquitous and abundant (Kimmel 1985, Dennis 1992), representative of medium sized reef fishes, and have substantial importance commercially (Appeldoorn and Lindeman 1985; Dennis, 1988) and ecologically (Meyer et al. 1983, Meyer and Schultz 1985a,b, Clark et al. 2005). Most significant as a model group, they undergo a variety of movements across several spatial and temporal scales. Thus the study of grunt movements may yield insight generally applicable to the many other reef fishes that undertake ontogenetic, home range, and/or feeding movements, though perhaps not to the same extent. This review addresses the current knowledge on these movements in terms of distances, time scales, temporal patterns, habitat associations and controls. The goals are to build toward an overall understanding of ecological connectivity and to identify gaps in that knowledge. Our approach will be to synthesize what is known about the movements of grunts, divided initially into three spatio-temporal scales. The factors affecting these movements will then be summarized. The information reviewed primarily comes from tagging studies, especially acoustic tagging for larger juveniles and adults, but includes inferred movements based on visual census observations. The review reflects primarily our own work in southwestern Puerto Rico, including some ongoing studies, but also incorporates information from other studies. The vast majority of information is restricted to three species: French grunt (*Haemulon flavolineatum*), white grunt (*H. plumierii*), and bluestriped grunt (*H. sciurus*).

Movement and Migration of Grunts

Daily movements

Juveniles.—Juvenile grunts are noted for forming diel resting schools on reef structure. For small juveniles, these schools are typically found off main reef structures and often located in back-reef areas. Larger juveniles are more associated with larger reefs (Ogden and Ehrlich 1977, Dennis 1992, Hill 2001). Mangrove prop roots constitute additional important habitat (Nagelkerken and van der Velde 2004), especially for bluestriped grunts (Mumby et al. 2004) or in embayments where reefs are separated from seagrass habitats (Nagelkerken et al. 2008). At evening twilight, juvenile grunts undergo ritualized migrations off the reef/mangrove to feed, returning again at morning twilight (Helfman et al. 1982, Rooker and Dennis 1991, Nagelkerken et al. 2002), although opportune feeding has been observed during the day in French grunts (Verweij et al. 2006). These migrations follow specific paths, and fish move off in single file. Importantly, these migrations involve distinct cross-habitat movements, with the result of a net transport of organic matter and nutrients from seagrass beds to reef/mangrove habitats.

The range of these daily feeding migrations is variable and may be dependent on the distribution of feeding habitats relative to resting schools. Dennis (1992), in La Parguera, Puerto Rico (PR), found little evidence of long distance movement, with French, white and bluestriped grunts in backreef sea grass beds found less than 100 m from their resident reefs at night, and many were within 50 m. Bouwmeester (2005) was able to track French grunts out to 40 m, but estimated that full migration routes went at least 100 m. In Belize, Burke (1995) tracked evening twilight migrations to initial feeding sites using Cyalum tags. French grunts all migrated from reef to sand flats, with movement on the order of 150 m. Bluestriped grunts mostly migrated from reef to sea grass, at a distance of about 70 m, but a few migrated to gorgonian habitat. In contrast, in St. Croix, USVI, Ogden and Ehrlich (1977) and Ogden and Zieman (1977) found French grunts to

migrate 200-300 m and potentially as much as a kilometer, with pathways being linear for 20-40 m before branching and dispersing over seagrass beds.

Adults.—Several studies have quantified the movement of adult grunts using acoustic tagging in a variety of habitats. Beets et al. (2003) and Friedlander and Monaco (2007) documented the movement of bluestriped grunts in Lameshur Bay, St. John, USVI. Most fish underwent cross habitat migrations (reef-seagrass), but not all the time, and movement generally occurred during twilight periods. Range of movement varied from less that 20 m to potentially as much a kilometer, but most movements were on the order of 300-400 m. One fish that migrated 767 m was also very active, and used multiple sites both day and night (Beets et al. 2003).

Tulevech and Recksiek (1994) recorded the movements of white grunts in reef systems off La Parguera, PR and the Florida Keys. As with previous studies, they found movements to occur primarily during twilight periods, but there were some exceptions. In La Parguera, movements were limited to forereef/backreef excursions (the direction varied by location), generally on the order of 100 to 200 m. One fish moved a maximum of 530 m. Similar observations on temporal periodicity in La Parguera were made for white grunt by Williams (unpublished data). One bluestriped grunt tagged by Merten (unpublished data) showed little evidence of periodicity, as the range of movement was less than 100 m. Appeldoorn (unpublished) tracked three grunts at La Parguera. A bluestriped grunt migrated between forereef and backreef areas in a similar pattern observed for a tagged white grunt at the same reef by Tulevech and Recksiek (1994, see their Fig. 4); while residence during the day was usually at a single location along the forereef, occasional forays during the day into backreef gorgonian beds were observed. Little migration was observed for a Spanish grunt (*H. macrostomum*) tracked on a continuous reef face or a white grunt tracked on a small reef. The latter, however, was active during the day in backreef gorgonian habitat.

In Florida, Tulevech and Recksiek (1994) also found white grunts to move primarily during twilight periods, but migrations were more frequent and consisted primarily of movements between shallow lagoonal patch reefs and adjacent seagrass beds. Distances traveled ranged from 130-170 m. One fish migrated between two patch reefs across 560 m of sea grass.

Intermediate movements

Over longer time frames, while retaining their basic diurnal pattern, adult grunts can shift the area over which they roam. For example, Williams (unpublished) tracked a 20-cm FL white grunt at La Parguera for 48 days using fixed acoustic receivers (Figure 1). The fish shows a pattern of being near the receiver at night, implying twilight migrations. After a week, its daytime habitat shifted to a point close enough to the receiver to be recorded there frequently throughout the day. After another week, this pattern again shifted. Throughout the rest of the record it is clear that the fish periodically spends time near or away from the receiver.

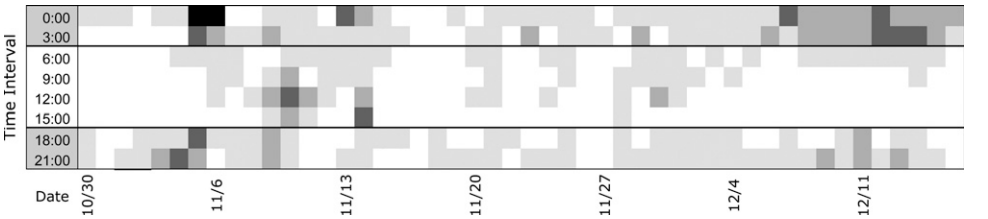

Fig. 1. Daily acoustic detection of a white grunt (*Haemulon plumierii*) per 3-hr period at a single receiver over 48 days. Grey-shaded times at left indicate night. Detections are grouped into 4 categories based on frequency of detection: 0 detections (white); 1-10 detections (light gray); 11-20 detections (medium gray); 21-30 detections (dark gray); and 31+ (black).

A similar pattern was reported for bluestriped grunt in Lameshur Bay by Friedlander and Monaco (2007), where initially the day and night habitats were both near the receiver, but after a week the daytime habitat shifted away from the receiver. Two months later, the nocturnal migration shifted markedly, passing by several receivers as it swam across the bay. Later still, it returned to its original daytime area for brief periods, while retaining its cross-bay migration at night. Similarly, Beets et al. (2003) recorded one bluestriped grunt to change primary feeding areas from the outer bay to the inner bay over a 30 day period.

Ontogenetic movements

Grunts undertake ontogenetic migrations, typically from shallow inshore areas to deeper offshore habitats, as evident by systematic increases in mean size of length-frequency distributions (Figure 2). These migrations consist of discrete shifts in location that are accompanied by changes in habitat use (Helfman et al. 1982, Dennis 1992, Appeldoorn et al. 1997, Lindeman 1997, Lindeman et al. 1998, Cocheret de la Morinière et al. 2002, Appeldoorn et al. 2003, Nagelkaken and van der Velde 2003, Cerveny 2006, Aguilar-Perera and Appeldoorn 2007) diet (Dennis 1992, Cocheret de la Morinière et al. 2003a,b) and behavior (Table 1). The timing between shifts seems to increase with size, and that a large jump occurs about the size of sexual maturation.

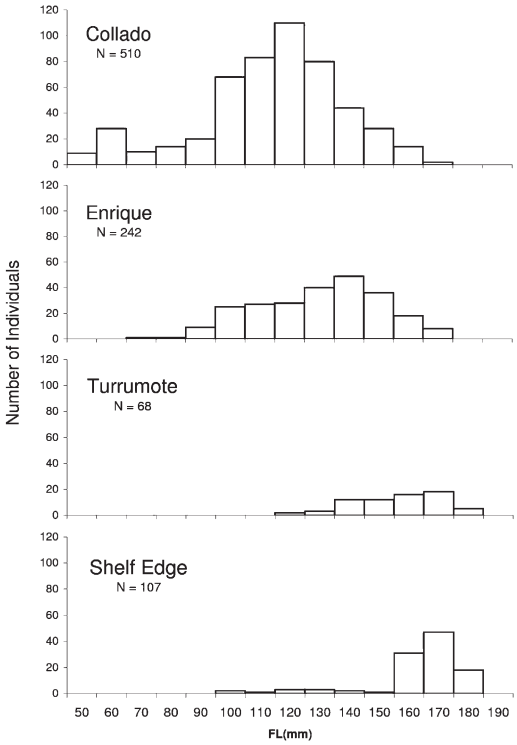

Fig. 2. Length-frequency distributions of French grunt (*Haemulon flavolineatum*) from inshore (top) to the shelf edge (bottom). Redrawn from Dennis (1992).

Bouwmeester (2005) using coded wire tags in French grunt was able to follow the movement of small juveniles as they migrated out of small back-reef coral patches to fore-reef areas (Figure 3, Right) and found that the distance moved by individual fish is only a function of size and not of time at liberty. Mateo (1999) investigated the relationship between ontogenetic stage (as defined by behavior), location, size and gonad maturation state. Ontogenetic stage only clearly correlated with size, and was not correlated with maturation state. That size is a dominant factor related to the timing of ontogenetic shifts suggests that the overall process will be driven by growth rate.

Distances covered during ontogenetic migrations seem to be variable and determined by the width of the shelf and the distribution of habitats. For example, in Florida, Tulevech and Recksick (1994) found subadult and adult white grunts to migrate out to patch reef and seagrass habitats in the back reef lagoon behind the outer reef line and to be uncommon on the forereef. In contrast, in Curaçao, characterized by a narrow inlet separating inshore nursery areas from the offshore reef, Cocheret de la Morinière et al. (2002) found that French grunts initially settled in the mouth of the bay before moving to sea grass and mangrove areas further into the bay at larger size, with adults moving out on to the reef. In La Parguera, Appeldoorn et al. (1997) and Cerveny (2006) found a general offshore ontogenetic trend for both French and white grunts, but for both species there were significant deviations. As in Curaçao, some initial

Table 1. Life-history stages of the white grunt, *Haemulon plumieri* and French grunt, *H. flavolineatum*.

Stage	Size (mm) White[1]	Size (mm) French	Location & Behavior
Newly Settled	8-20 TL	10-15 TL[2] 6-11 SL[3]	Settlement in seagrass or isolated coral heads. Plankton feed.
Stage 0 Juvenile	15-50 TL 14-45 FL	15-30 TL[2] 11-21 SL[3]	Before recruit on to reef proper. Plankton feed. Migrate at night but do not feed.
Stage 1 Juvenile	45-95 TL 40-85 FL	30-55 TL[3] 21-32 SL[3]	Daytime resting school on the reef. Twilight migrations to feed in seagrass at night.
Stage 2 Juvenile	80-150 TL 70-130 FL	55-120 TL[2,3]	Daytime resting school on the reef. School found more seaward closer to the reef-seagrass interface. French school slightly higher on the reef. Twilight migrations to feed in seagrass at night.
Subadult	140-180 TL 120-160 FL	120-150 TL[4]	Whites form roaming monotypic schools; no ritualized twilight migrations. French still in resting schools with twilight migrations.
Adult	> 180 TL > 160 FL	>150 TL[5]	Whites are roaming, solitary. French are solitary or in groups, associated with shelter.

[1]Appeldoorn et al. 1997, Hill 2001
[2]Helfman et al. 1982
[3]Brothers & McFarland 1981
[4]Difference between Adults and Stage 2 juveniles
[5]Ogden & Ehrlich 1977

settlement occurred at shallow backreef areas of the outer emergent reefs, with subsequent movement further inshore. Additionally, some individuals were able to occupy inshore reefs as adults (Figure 4). While the arrangement of habitats may affect distribution during ontogeny, there is little indication that offshore movements are limited by absolute distance as evidenced by the much greater shelf width at La Parguera compared to Curaçao. Indeed, on the Providencia, Col. insular platform Appeldoorn et al. (2003) found grunts to disperse in all directions away from nearshore nursery areas (e.g., windward forereef, leeward shelf edge and laterally out over 10 km on the platform). However, both Appeldoorn et al. (2003) and Mumby (2006) reported that adult habitats near nursery areas supported higher grunt densities, again indicating the importance of habitat distribution.

Barriers and navigation

It is clear from the above studies that the various species of grunts have specific, although perhaps still broad, habitat requirements, and that these will ultimately determine the extent of distribution. However, it is equally clear that there are barriers to dispersal, at least over shorter time periods and that these, along with navigation cues, may affect the directions that migrations occur. For example, Tulevech and Recksiek (1994) acoustically tracked displaced individual white grunts to investigate homing ability. In Florida, where one fish was tracked across 560 m of seagrass from one low-relief patch reef to another; another fish displaced from one patch reef to a point halfway to the other was able to immediately return to the first patch reef. In Puerto Rico, emergent reefs are separated by deep water (> 18m) and a soft-mud bottom. No migrations of adults between reefs were noted and one fish displaced 1 km remained resident at the new reef and developed movement patterns of resident fish. This suggests that for adult white grunts, the medium relief reef-sea grass boundary does not act as a barrier to dispersal while the high relief reef-deep mud bottom boundary does. Appeldoorn and Aguilar-Perera (unpublished) conducted further transplants (Figure 5). Using anchor tags, white grunts were displaced to various points

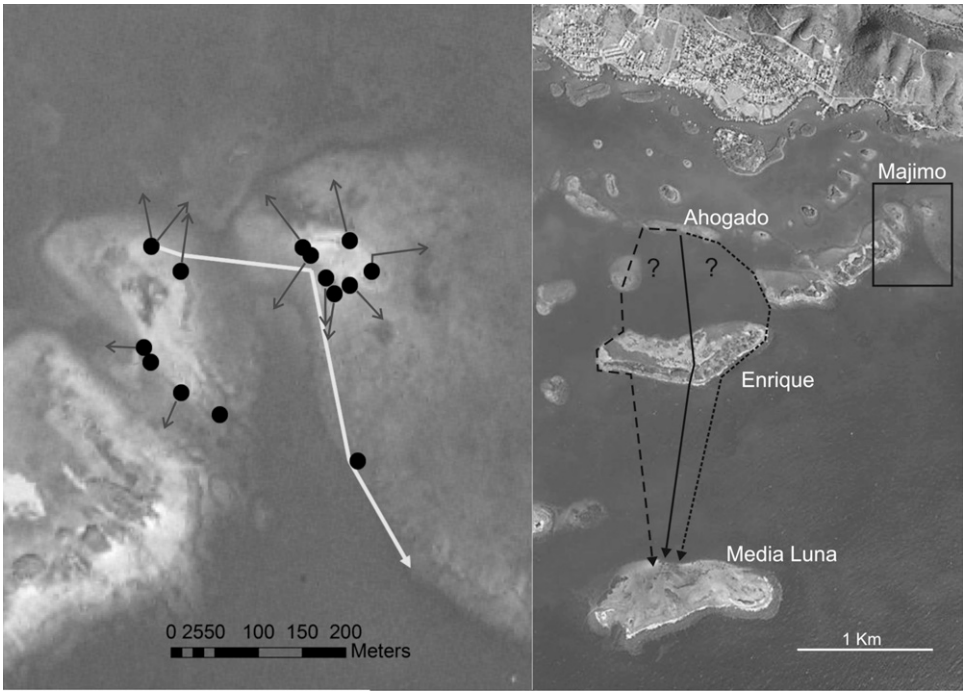

FIG. 3. **Left:** Ontogenetic migration of juvenile French grunts (*Haemulon flavolineatum*) from Majimo, an inshore reef in La Parguera, Puerto Rico. Black dots indicate locations of resting schools. Black arrows are the initial tracks of off-reef twilight feeding migrations. White line indicates the primary migratory path as determined by mark recapture studies (N = 31 recaptures; initial size range: 7.9-13.7 cm FL; days at liberty: 34-239). Area shown is indicated in the black box to the right. **Right:** Potential pathways for ontogenetic migration of a batch-tagged white grunt (~8-cm FL) tagged at Ahogado and recorded at the back reef of Media Luna 3 years later. Black box at Majimo indicates the area shown to the left.

on a large emergent reef, and in all cases fish quickly returned to their original locations; however when acoustically tagged fish were displaced off their resident reef platform there were mixed results depending on the context. When the new location consisted of favorable habitat and was separated by a deep boundary, the results (1 white, 1 bluestriped grunt) were similar to those of Tulevech and Recksiek (1994) and the fish remained in the new habitat. One Spanish grunt was displaced to a shallow mangrove stand harboring only small juvenile grunts and separated from the original site by a shallow narrow channel and backreef sea grass. This fish was found at its original site the morning after release.

Orientation and navigation have been studied only for juvenile, primarily French grunts. Ogden and Quinn (1989) reported on transplant experiments related to twilight migration pathways. Fish captured at night and moved to a new location before release would attempt to follow the same direction they would have traveled at their resident reef, indicating some degree of compass orientation. Vision was also shown to be important for navigation and social-learning of migratory routes (Helfman and Schultz, 1984). We have occasionally seen returning juveniles along one path to suddenly turn and follow fish retuning to a different location on an intersecting path (e.g., Bouwmeester 2005), and hypothesize this as a mechanism whereby small juveniles make ontogenetic shifts among widely space resting schools using similar feeding areas. Since migration time is related to size and retinal development (McFarland and Wahl 1996), older juveniles would change the timing of their migration and increase the probability of encountering larger individuals from different resting schools.

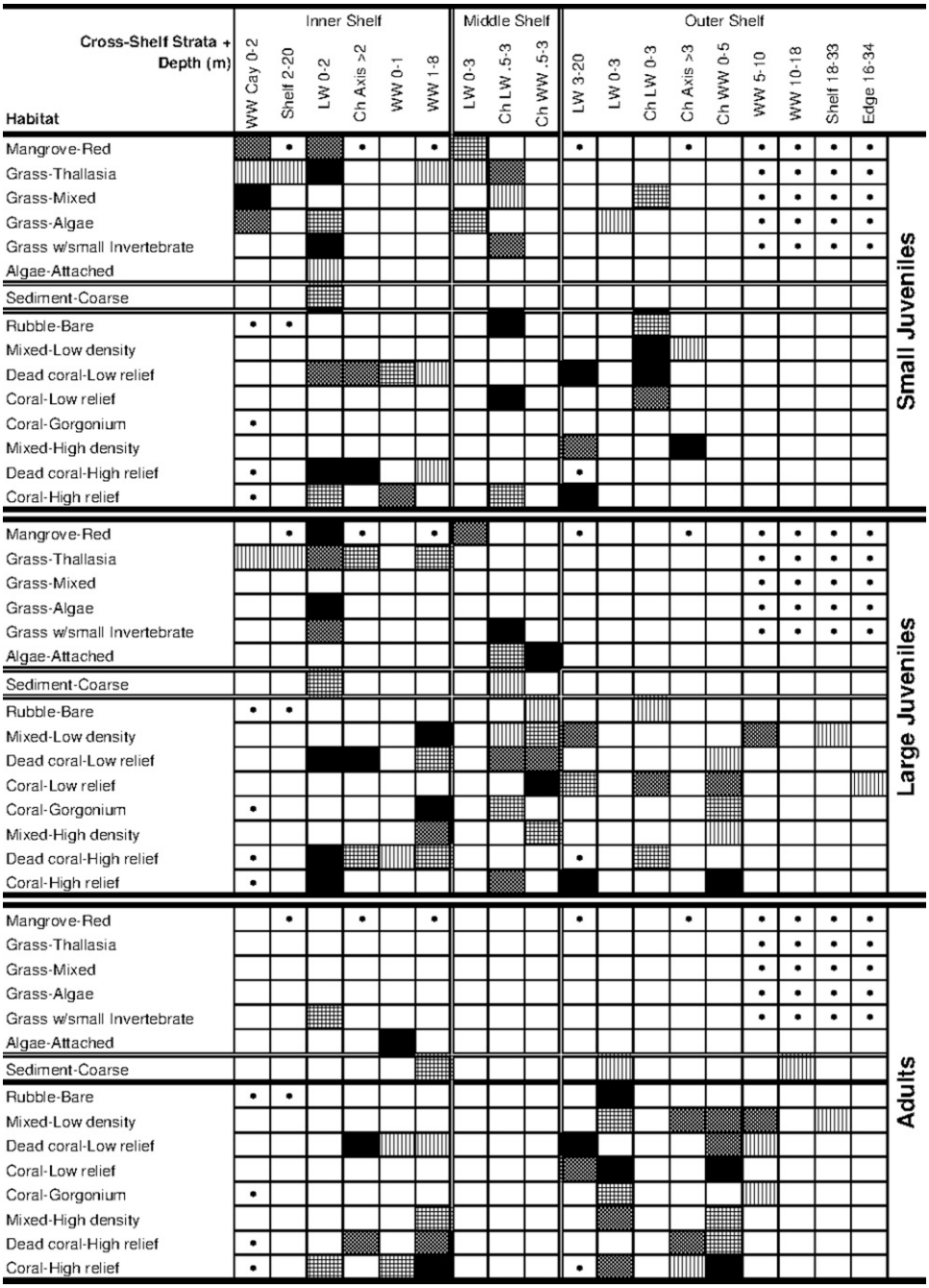

FIG. 4. Distribution and relative abundance in La Parguera Puerto Rico of French grunt (*Haemulon flavolineatum*) for three life stages by habitat type and cross-shelf strata. Habitat types and strata not sampled or where fish were not observed are not shown. Boxes with dots indicate habitat-stratum combinations that do not occur. Relative abundance is by quartile, with larger black patterns indicating higher abundance. For cross-shelf strata: WW = Windward, LW = Leeward, Ch = Channel. Thin double vertical lines separate the three shelf zones divided by emergent reef lines. Thin double horizontal lines separate habitat types into higher categories of submerged aquatic vegetation, unconsolidated sediment and consolidated sediment. Modified from Cervany (2006).

Larger scale displacement experiments in St. Croix by Ogden and Ehrlich (1977) showed a few juveniles to be able to navigate back to their resident reef after a displacement of 2.8 km; importantly, they thought that the fish could have used the backreef margin for navigation on the long run back to familiar territory before turning toward their resident patch reef. In La Parguera, Bouwmeester (2005) documented the collective movement of tagged juvenile French grunts (6.4 – 13.1 cm FL) through a series of ontogenetic shifts covering 450 m from a back reef area to and along the fore reef (Figure 3, Left). The route essentially follows the reef margin, again suggesting that the fish were using the reef margin for orientation.

While these studies are useful for understanding potential orientation and navigation mechanisms over the short term, they do not address orientation and navigation at larger spatial scales, such as when ontogenetic shifts are made across the outer shelf. We have documented the movement of only one fish in this regard. In La Parguera, a small juvenile white grunt (< 8 cm FL) batch tagged on an inshore reef was subsequently found three years later in the back lagoon of an outer emergent reef that was directly offshore of the point of tagging. However, the migration pathway could not have been direct due to the presence of large mid-shelf emergent reef between the two (Figure 3, Right). Huijbers et al. (2008) showed newly settled French grunt to be able to discriminate water collected from reef versus mangrove/seagrass habitats, indicating that olfaction is highly developed at an early stage; this may also serve to identify suitable upstream habitats.

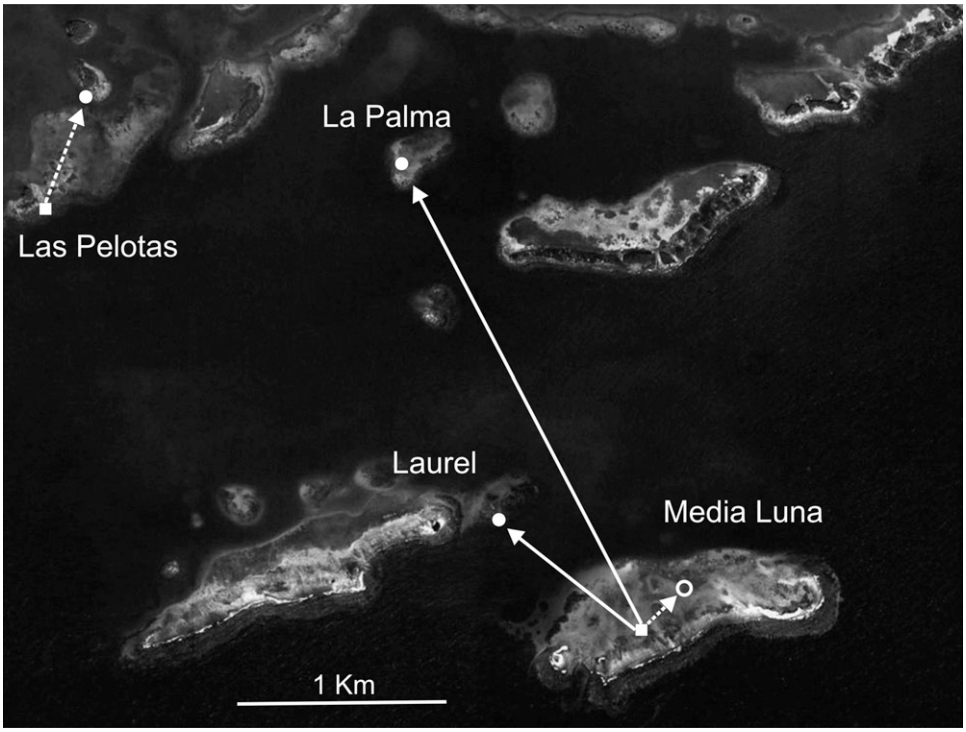

Fig. 5. Transplant experiments of grunts in La Parguera, Puerto Rico. Squares indicate capture site; circles indicate release sites. Open circle indicates use of anchor tags, solid circles indicate use of acoustic tags. Solid arrows indicate no return to original capture location; dashed arrows indicate fish returned to original capture location.

Responses to environment perturbations

General responses to barriers and orientation mechanisms may breakdown in response to strong environmental variations that force fish to vacate resident areas. For example, McFarland and Hillis (1982) found only one of ten tagged juveniles remaining, and the whole resting school reduced, following five days of rain and high turbidity (visibility < 1m). They hypothesized that the high turbidity interfered with navigation, allowing fish to stray, or made juveniles more susceptible to predators. However, in the Bahamas after a storm, McLean and Herrnkind (1971) observed two schools of white grunt migrating over sand 2 km from the nearest reef during the day swimming away from a large body of turbid water resulting from land runoff. This suggests the grunts were actively avoiding the turbid water, and that the reductions observed by McFarland and Hillis (1982) were due to the same process. Cold temperatures may similarly represent conditions that force grunts to abandon resident reefs. Off North Carolina, Parker (1990) failed to observed white grunts during one winter sample when temperature drop below 11°C and presumed they left to avoid the unusual cold water. Even small scale perturbations can be significant. For example, in La Parguera, Hill (unpublished) periodically surveyed a small school (30-40 juveniles) of white grunt mixed with other species that had taken residence within the prop roots and dead tree branch on the windward side of an inshore mangrove islet. Depth was less that 0.5 m. During an extended period of low water that exposed not only the prop roots but also the adjacent seagrass/rubble bottom, the fish were observed to school in the open water out in front of their previous prop root location. Shortly thereafter, however, no fish were observed near the mangrove islet indicating either complete predation in the absence of shelter, or more probably, the loss of shelter caused the school shift to another location.

Discussion

It is probably accurate to state that more is known about the recruitment, movements, feeding habits, growth and habitat preferences of the principle species of grunts than any other comparable group of mid to large sized coral reef fish. These constitute most of the important dynamics needed for modeling movement and ecological impacts across the seascape, with assessments of predation risk (e.g., Shulman 1985, Danilowicz and Sale 1999) being the least studied component. Nevertheless, gaps remain in our understanding of movements, particularly with respect to movements relative to reproduction and to a theoretical context that would simplify rule-making for modeling purposes.

Wiens (1992) developed a theoretical framework for studying the movement of organisms relative to crossing habitat boundaries. The probability that an organism will cross a habitat boundary is a function of that boundary's permeability and the habitat preference of the organism. Permeability is a function of the thickness of the boundary (e.g., can the individual detect suitable habitat across the boundary, such as a patch reef across an algal plain), and the boundary contrast (the perceived difference between adjoining habitats, e.g., reef-silt [high contrast] versus reef-hard bottom [low contrast]). The concept of permeability and low or high contrast habitat boundaries would explain the empirical observations on transplanted individuals. Those fish encountering low contrast boundaries, such as low-relief patch reef and seagrass were able to immediately return to their resident reef, while those encountering a high contrast boundary (reef to soft bottom) did not return. Yet, these observations are confounded by habitat preference. In all but one of the transplant experiments in La Parguera, fish were transplanted and released at sites deemed suitable for residence. Thus, failure to cross the habitat boundary could have been just as much due to preference for the new location as to the strength of the boundary. In the one exception, where a Spanish grunt was transplanted to an inshore mangrove stand, the boundary to returning to its resident reef was of low contrast.

According to Weins (1992), habitat preference is not only a function of the perceived

differences in environmental quality of adjoining habitats but also of the behavior of the species. Bardach (1958) reported that fishes resident in specific areas on 100-m diameter patch reefs were incapable of homing back to their reef when displaced to a similar reef 100 m away, while those species that roamed over the entire range of their resident reef (over a period of weeks) showed a strong homing ability when similarly displaced. This view is consistent with the concepts of Weins (1992) in that widely-roaming fish view their world as fine-grained, but it also suggests that these fish have developed better navigation skills as a whole. Since juvenile grunts make daily off-reef feeding migrations, this may explain why at least some of the juvenile French grunts displaced 2.8 km by Ogden and Ehrlich (1977) were able to return. Adult grunts are not only capable of crossing habitat boundaries and ranging 100+m on a daily basis, but over intermediate time frames can shift over multiple resident and feeding areas, so they may have considerable navigation skills.

An important aspect of both behavior and assessment of habitat quality is risk of predation (Chittaro et al. 2005). Indeed, risk of predation is thought to be responsible for juvenile grunts to school during the day, to feed off the reef at night and to conduct this migration as a train of individuals (McFarland et al. 1979). As such, individuals of a school might be less likely to change habitat if it meant leaving one school with no certainty of finding another. The observation of fish of one school altering their return path to join fish of another school on a crossing path (Bouwmeester 2005) offers one mechanism whereby shifts to new areas can be made without sacrificing the protection that schooling may offer.

Werner and Gilliam (1984) presented a theoretical framework for predicting ontogenetic habitat shifts of fishes based on the trade-off between risk of predation and availability of food for growth. As an individual grows, shifts occur when either increasing predation or decreasing food supply (or both) render a site less optimal relative to other sites. Predictions of this model for reef fish have been validated for the Nassau grouper (Dahlgren and Eggleston 2000). The fact that size correlated to both ontogenetic stage (Mateo 1999) and distance traveled during ontogenetic migrations (Bouwmeester 2005) suggests that risk of predation holds equal importance for grunts. This model might not only provide a framework for understanding ontogenetic habitat migration of grunts, it may explain responses to environmental perturbations. Thus, grunts may suddenly leave resident sites when conditions change that either significantly decrease the availability of food or increase the risk of predation (e.g., low visibility in turbid water following storms or loss of mangrove shelter during low tide). The trade-off between predation risk and growth would be a key factor in assessing habitat preference in the sense of Weins (1992), including also changes in physiological state resulting from, for example, cold temperature.

One factor preventing fusion of the Weins (1992) and Werner and Gilliam models as applied to ontogenetic migrations is our understanding of how fish might sense the quality (or even existence) of suitable habitat at a distance (i.e., when boundary thickness is very large). In the original Werner and Gilliam (1984) model, fish were able to make forays into adjacent habitat to assess both food availability and risk of predation relative to current habitat. This does not seem likely when ontogenetic shifts are large and cross a seemingly impermeable boundary, as may be expected when larger scale environmental factors significantly decrease habitat quality. Keys to potentially suitable new habitat at a distance may come from acoustic, olfactory or water motion cues, but can quality be assessed at distance? If not, the use of migration corridors may play an important role is these migrations, whereby migrations are made in small, although possibly continuous steps, for example along reef margins or as a series of jumps across neighboring patch reefs.

Mumby (2006) made two assumptions regarding habitat connectivity during ontogenetic migrations in developing algorithms for MPA design. The first was that migrating fishes can move directly between mangroves and reef habitats, passing over

deep water and seagrass beds. While it is clear that grunts can move over deepwater, it is also clear that at times deepwater may act as a barrier, and that fish may move along corridors offering closer contact with the bottom and this may affect direction of movement. The second assumption was that the maximum distance fish migrate between mangroves and reefs is ≥10 km. The potential to migrate over this distance has been clearly demonstrated in different areas (Appeldoorn et al. 2003, Cervany 2006, Mumby 2006), yet both Appeldoorn et al. (2003) and Mumby (2006) recorded lower densities of grunts at increasing distance from nursery areas. Thus, while the potential for long migrations clearly exists, it is not clear whether there also exits a gradient in individual migratory capabilities or whether that additional adult habitat closer to juvenile areas acts as a filter, with only a reduced proportion of the population needing to seek adult habitat at greater distances (Appeldoorn et al. 2003). Refining such assumptions should lead to more robust models generally applicable over a variety of seascape configurations.

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