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HABITAT CONNECTIVITY IN COASTAL ENVIRONMENTS: PATTERNS AND MOVEMENTS OF CARIBBEAN CORAL REEF FISHES WITH EMPHASIS ON BLUESTRIPED GRUNT, *HAEMULON SCIURUS*

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ABSTRACT Habitat connectivity within tropical marine seascapes may be greatly dependent on the movement of large organisms, particularly fishes. Using visual and trap sampling within two small bays in Virgin Islands National Park/Biosphere Reserve, St. John, U.S. Virgin Islands, we documented that large coral reef fishes, particularly large adult grunts, which shelter by day on coral reefs and make nocturnal feeding migrations into seagrass beds, accounted for the greatest biomass and abundance of fishes sampled in seagrass habitat. Using passive tags and sonic telemetry, we documented the nocturnal migration patterns of large adult grunts (bluestriped grunts, *Haemulon sciurus*), which are similar to the well-documented migration patterns of juvenile grunts. Large grunts showed high site fidelity to nocturnal foraging sites in seagrass beds. Sonic-tagged grunts demonstrated little movement in their diurnal shelter sites in the boulder-coral zone, with most individuals making nocturnal migrations into the adjacent seagrass bed. These results provide evidence for strong linkage among adjacent habitats at a small spatial scale and emphasize the importance of inclusion of a diversity of habitats in Marine Protected Areas.

INTRODUCTION

The connectivity among various tropical marine habitats, specifically in terms of organism movements, nutrient exchange, and energy flow, has been described extensively (Ogden and Zieman 1977, Hemminga et al. 1994, Marguiller et al. 1997, Duarte 2000, Beck et al. 2001, Ley and McIvor 2002), but few investigations have clearly documented the linkages. Two dominant tropical marine ecosystems, coral reefs and seagrass beds, have received much focus, with overwhelming emphasis on interactions within habitats rather than among habitats. The importance of ecosystem interactions is still mostly speculative due to scarce quantitative information.

Habitat connectivity in tropical marine environments has been demonstrated, primarily by documentation of fish movements among habitats and ontogenetic patterns among cross-shelf habitats (Holland et al. 1993, Holland et al. 1996, Appeldoorn et al. 1997, 2003, Meyer et al. 2000). Results from these investigations provide valuable insights, but the generality of these results must be considered. The variability of environmental conditions (e.g., disturbance regimes, nutrient inputs, reef type and development) is very great even within a geographic region. Community structure and ecosystem interactions may vary greatly from location to location.

Linkages among tropical marine ecosystems potentially yield strong positive effects on components of the communities (reviewed by Ogden 1997). Direct ex-

change of nutrients and production by migrating organisms, particularly fishes, is one obvious mechanism. One of the most important empirical demonstrations of strong linkages is for coral reef fishes that forage in seagrass beds. Juvenile grunts, which make nocturnal forays into adjacent seagrass beds, release nutrients onto coral reef resting sites resulting in enhanced coral growth (Meyer et al. 1983, Meyer and Schultz 1985). Although juvenile grunts represent a small proportion of fish biomass on reefs, and probably import a small amount of nutrients to reefs, this type of linkage provided by reef fishes requires additional investigation for a more thorough understanding of inputs and interaction strengths.

Numerous fish species potentially contribute to ecosystem linkages between coral reefs and seagrasses. Although several investigations have documented the nocturnal migration behavior of juvenile grunts, much less is known about the foraging behavior and movements of many large fishes, including large adult grunts. Most reef fishes are small and very site specific, and large herbivorous fishes forage diurnally over large reef sections, which provide shelter (Helfman 1993). Large mobile invertebrate feeders, which can account for a large proportion of reef fish biomass, forage diurnally and nocturnally over large areas, and have been observed in habitats adjacent to reefs, e.g., seagrass beds (Wolff et al. 1999). Although general patterns of fish distribution, movements and migrations are documented, more intensive investigations are needed to determine ecosystem linkages, their strengths, and their influence on ecosys-

tem function and community structure. This information will also allow for an improved understanding of the function, design and benefits of Marine Protected Areas (Plan Development Team 1990, Roberts and Polunin 1991, Polunin and Roberts 1993, Murray et al. 1999)

The investigation of habitat connectivity requires examination at various temporal and spatial scales. We chose to investigate potential mechanisms for linkages between coral reef and seagrass habitats within two insular bays. We hypothesize that large adult reef fishes contribute greatly to habitat connectivity between reefs and seagrass beds by means of nutrient exchange. Therefore, a large abundance and biomass of reef fishes must forage in seagrass beds in order to maintain the connectivity. The purpose of our study was 1) to compare the abundance of large reef fishes between reefs and adjacent seagrass beds by visual sampling, 2) to document the abundance and biomass of large reef fishes in seagrass beds using trap sampling, and 3) to document the general movements and activity patterns of large, abundant, adult reef fishes, which forage in adjacent seagrass habitats using passive tags and sonic telemetry. Two coral reef species, bluestriped grunt (*Haemulon sciurus*) and red hind (*Epinephelus guttatus*), were selected for investigation of movement patterns because of their observed presence in seagrass habitat and their large size and abundance on adjacent reefs. Juvenile grunt movements are well documented, but large adult grunt behavior is poorly understood.

METHODS

Study sites

Greater and Little Lameshur Bays, located on the south side of St. John, US Virgin Islands, are protected bays within Virgin Islands National Park (Figure 1). Although park regulations provide a level of protection, fishing is not prohibited and fishers are frequently observed. Both bays have seagrass beds bounded by beaches on the northern shoreline with boulder and coral reef zones on the eastern and western shores.

The seagrass bed, which is contiguous around Yawzi Point between these bays, is composed of *Thalassia testudinum* and *Syringodium filiforme* and varying densities of rhizophytic algae. Seagrasses range in depths from 2–20 m with *T. testudinum* dominant in shallow areas and replaced by *S. filiforme* dominance in the deeper areas. Although portions of the seagrass bed were damaged by recent hurricanes (Marilyn -1995, Bertha-1996, Lenny-1999), other areas were undamaged and recovery has continued gradually (Muehlstein, unpubl.

data, Rogers and Beets 2001). Adjacent fringing reefs, ranging in depth from 3–20 m, are dominated by *Montastraea annularis*, but have been greatly altered by storm damage and disease (Rogers et al. 1991, Rogers and Miller 2001). The boulder and reef zones are structurally complex and inhabited by diverse assemblages of fishes. Several small caves are located along the shoreline and are occupied by large numbers of snappers and grunts.

Visual sampling

We visually sampled fishes along transects to compare abundance of fishes in three selected families [groupers (Serranidae), snappers (Lutjanidae), and grunts (Haemulidae)] in the seagrass bed and the adjacent reef/boulder habitat in Greater Lameshur Bay in 1998 and 1999. These three families were selected because of their large size, abundance, and observed presence in seagrass habitat. Using a belt transect method, all fishes were counted and total length estimated, within one meter on either side of a 50 m tape that a diver deployed during a census. Transect starting points and directions were selected haphazardly. In the seagrass habitat, all other fish species observed within the transect were noted. All samples were conducted during the day (10:00–18:00). For analysis, large fishes (defined as greater than 15 cm) were selected from the database.

Standardized trap sampling

Fish traps (1.0 x 1.0 x 0.4 m; mesh size: 38.1 mm [1.5 in]) were used to estimate the species richness, relative abundance, size, and general movement patterns of large reef fishes throughout the large seagrass bed in Greater Lameshur Bay. Six stations were established throughout the seagrass bed, between 200–300 m apart and 100 m from the adjacent boulder/reef zone (Figure 1). Traps were hauled every three days, and all fishes were identified, recorded and released. All bluestriped grunts (*Haemulon sciurus*) were measured, tagged with sequentially numbered spaghetti tags (Floy tags) and released at the capture site. Recaptured fish were inspected for condition and released beside the trap of last capture. Weights were not recorded in order to expedite release; therefore, estimated weights were calculated using established length-weight relationships and data from previous research (Bohnsack and Harper 1988, Beets 1996).

Telemetry studies

Several families of reef fishes in the mobile invertebrate feeder guild contribute greatly to reef fish biomass

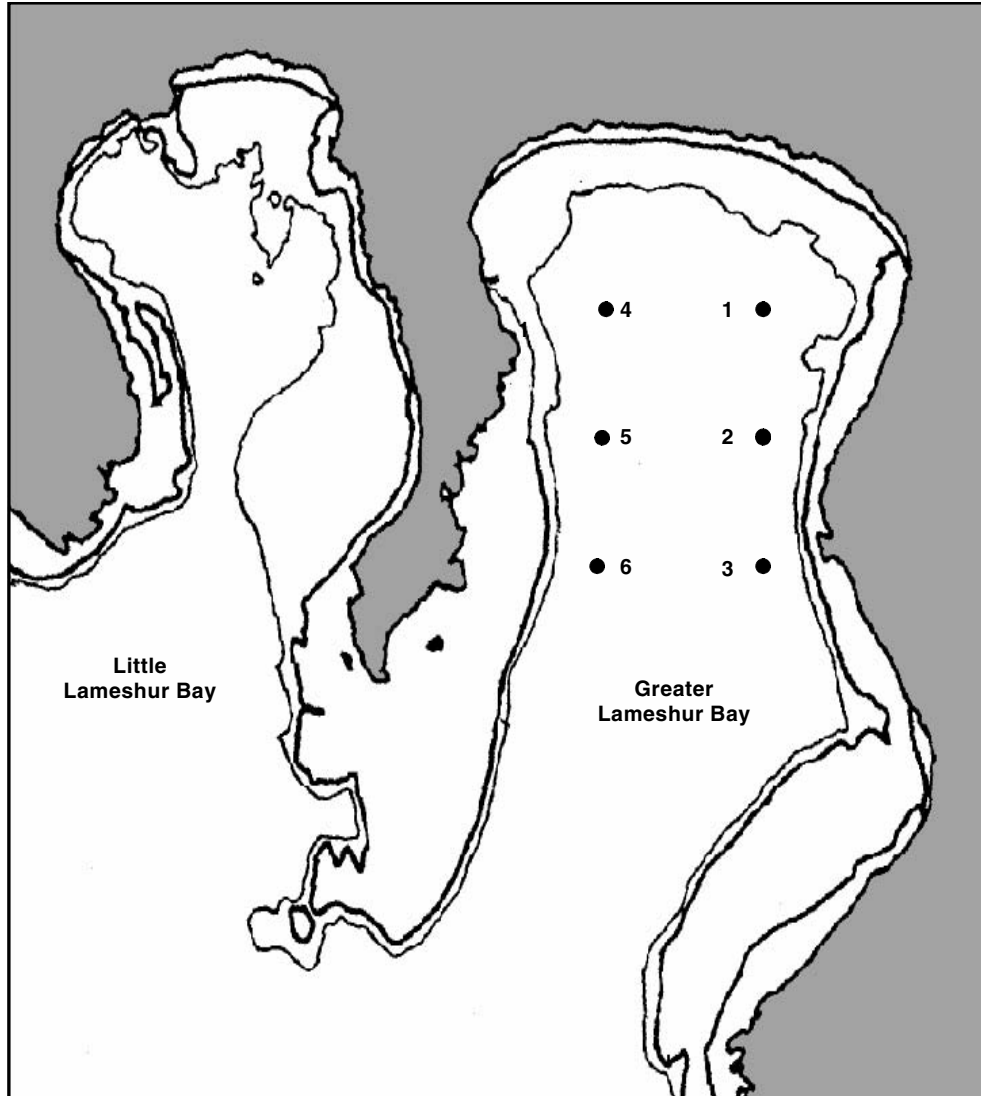


Figure 1. Habitat map of Greater and Little Lameshur Bays located on the southern coast of St. John, U.S. Virgin Islands. For all figures, innermost lines define the boundaries of the seagrass beds adjacent to fringing reef habitat along the shoreline; upland in gray. Locations of trap stations are designated by solid circles with respective station numbers.

in the Virgin Islands (Beets 1997, 1999) and are known to engage in nocturnal foraging from reefs into adjacent seagrass beds (Helfman 1993). The primary species selected for telemetry study, bluestriped grunt (*H. sciurus*), is more abundant on inshore reefs than offshore reefs. Grunts dominate biomass of fishes on reefs in the study area (15.5% of total reef fish biomass in visual monitoring samples, National Park Service, unpubl. data). Large individuals form large shoals in large crevices and shelters but are also found as solitary individuals in isolated shelters. This species also primarily consumes invertebrates, particularly crabs and shrimps (Randall 1967).

The second species selected for telemetry study was a hermaphroditic grouper, the red hind (*Epinephelus*

guttatus), which is common on inshore reefs and is captured across the insular shelf to outer shelf edge reefs. Individuals on inshore reefs tend to be smaller females, with larger males found offshore especially on shelf edge reefs (Shapiro et al. 1993). Typical of epinepheline groupers, red hind primarily consume invertebrates, particularly crabs and shrimps (Randall 1967). The range of movement of red hind into adjacent habitats has not previously been investigated.

Adult individuals of both species (*H. sciurus*: 17.4–28.0 cm FL [Lm = 17.0 cm FL]; *E. guttatus*: 26.5–33.0 cm FL [Lm = 25.0 cm FL]) were captured using fish traps set adjacent to seagrass and boulder/reef zones and were tagged with sonic tags (Sonotronics IBT-96-1; 23 x 8

mm; 21 day battery) and spaghetti tags, using a modification of the method by Holland et al. (1996). Transmitters were attached externally on the left side of the dorsum below the spinous dorsal fin. Short segments of monofilament nylon line (60 lb. test) were tied to rings attached to both ends of the transmitter. Once the transmitter was positioned on the fish, monofilament lines attached to needles were run through the dorsal musculature between pterygiophores and then tied tightly on the right side of the dorsum. The procedure required 2–3 minutes and was conducted without anesthetic. Fish were retained with conspecifics until behavior appeared normal, then released near capture site (usually within 15 min). We retained fish in captivity with sonic tags, spaghetti tags, and no tags, and observed no differences in behavior. Tagged fish were directly observed following release by snorkeling. Tagged fish (sonic- and spaghetti-tagged) released near conspecifics joined the shoal and behaved normally. Tagged fish were observed numerous times throughout the study, with no adverse tag effect apparent.

Tagged individuals were followed continuously for 24 hours, using a Sonotronics receiver (USR-5W) with directional hydrophone. When sonic-tagged fishes were initially released, position fixes were obtained every hour for 24 hours. Position fixes were taken by a combination of GPS data, recorded landmarks, and bouys (with attached cyalume sticks at night). Subsequent fixes were taken on all tagged fishes at least 4 times per day to determine diel site fidelity. Twelve bluestriped grunt were tracked (10 were relocated after the initial 24-hour tracking period, June–July 1999), and six red hind were tracked (5 were relocated after the initial 24-hour tracking period, June–July 1998). Most tags were active for the duration of the sampling period, although variability in tag longevity was observed. One tag transmitted for at least 31 days, whereas, another tag was active for only 12 days. The latter specimen was sited during snorkeling observations on several occasions at its diurnal resting site, with the attached inactive tag.

Throughout the study period, some tagged individuals were lost shortly after the initial capture and tagging process. These losses were potentially due to tag loss or failure, to predation or to movement out of the bay. We attempted to locate lost signals in adjacent bays without success.

RESULTS

Visual sampling

Large fishes (> 15 cm) were much more abundant on reef/boulder habitat than in seagrass (Table 1). Grunts

were dominant in transect samples in reef/boulder habitat, with bluestriped grunt being the most commonly observed species. Only 23 fishes > 15 cm in the target families were observed in seagrass transects ($n = 46$). The only other fishes > 15 cm observed in seagrass transects were two barracuda (*Sphyraena barracuda*) and three lizardfishes (*Synodus* spp.). Large numbers of small and juvenile fishes were observed in seagrass habitat, especially in algal mats of *Dictyota* spp. (Muehlstein, unpubl. data).

Standardized trap sampling

Trap sampling provided valuable data on reef fish species composition in seagrass habitat. Over a period of 11 sampling dates, between June 23–July 21, 1999, a total of 21 species in 10 families (557 fishes) were captured in 66 trap hauls from the six sampling stations in the seagrass bed. The mean trap catch varied greatly both temporally and spatially (Table 2). Grunts and porgies dominated catches, with large variation in mean catch per station (Table 2c). Station 4, located in shallow water with dense seagrass (primarily *T. testudinum*; mean density = 227 short shoots m^{-2}) in the northeastern corner of the bay, consistently yielded greater numbers of grunts (Haemulidae), primarily bluestriped grunt (*H. sciurus*), and surgeonfishes (Acanthuridae). Porgies (Sparidae) were most abundant at station 1, located in the northeastern portion of the bay in an area of red algal overgrowth of *Bryothamnion triquetrum* along the edge of the seagrass bed. Snappers (Lutjanidae) were most commonly captured at station 2, located nearest to boulder/reef habitat. The most abundant snapper in samples was lane snapper (*Lutjanus synagris*; $n = 46$; 79.3% of all snappers captured), which is common in seagrass habitat, but forms large resting shoals on and around reefs during diurnal periods.

Grunts had highest abundance and calculated biomass per trap haul (Table 2a). Porgies had the second highest abundance, with a calculated biomass similar to grunts (Table 2a). Reef fishes known to forage nocturnally in seagrass habitats (squirrelfishes, snappers, grunts, goatfishes, and surgeonfishes) represented greater than 50% of the abundance and estimated biomass of trap samples.

Bluestriped grunts were the most abundant species captured ($n = 192$; 33.7% of all fish captured; 95.2% of all grunts), ranging from 13.5 to 25.5 cm SL (mean = 20.6 \pm 2.38 cm SL [23.4 \pm 2.60 cm FL]). Of 123 bluestriped grunts tagged and released at the six seagrass stations, 36 (29.3% of all grunts tagged) were captured at station 4 (Table 3). A total of 29 fish were recaptured, with 14 of

TABLE 1

Summary of data from visual transect samples taken in reef/boulder and seagrass habitats in Greater Lameshur Bay, St. John, US Virgin Islands, 1998–1999. Data are means (± 1 s.d.) of large fishes (> 15 cm) per transect for the three target families sampled.

SPECIES	REEF/BOULDER <i>n</i> = 46	SEAGRASS <i>n</i> = 42
Serranidae		
<i>Epinephelus guttatus</i> Red hind	0.31 \pm 0.54	0
<i>E. striatus</i> Nassau grouper	0.29 \pm 0.90	0.07 \pm 0.26
Lutjanidae		
<i>Lutjanus apodus</i> Schoolmaster	0.54 \pm 3.43	0
<i>L. griseus</i> Gray snapper	0.41 \pm 2.34	0
<i>L. mahogoni</i> Mahogany snapper	0.10 \pm 0.62	0
<i>L. synagris</i> Lane snapper	0.37 \pm 2.19	0.10 \pm 0.30
<i>Ocyurus chrysurus</i> Yellowtail snapper	0.15 \pm 0.36	0.05 \pm 0.22
Haemulidae		
<i>Haemulon flavolineatum</i> French grunt	0.41 \pm 1.52	0
<i>H. plumieri</i> White grunt	0.32 \pm 0.98	0.37 \pm 2.34
<i>H. sciurus</i> Bluestriped grunt	3.00 \pm 9.01	0

these originally from station 4. At station 4, 12 of 36 fish (33.3%) initially captured and tagged in this trap were recaptured. Five fish were recaptured in their original trap more than twice, and four were from station 4. Two fish originally captured at station 4 were recaptured five times, and one was recaptured four times.

Telemetry studies

Of eleven bluestriped grunts tagged, ten were relocated following the initial 24-hour tracking period. Individual movement patterns varied greatly, with two individuals remaining on the reef and moving less than 20 m and eight individuals moving hundreds of meters among several habitats (Table 4; Figures 2–4). These eight individuals made nocturnal migrations into the adjacent seagrass habitat, presumably for foraging (Table 4). The grunts, which migrated into adjacent seagrass habitat, moved 87–767 m from diurnal resting sites.

Most fish exhibited very high site fidelity to diurnal resting sites on the reef, with little movement during diurnal periods. Six fish were relocated at the same diurnal resting site for ten days or more. Three fish moved from solitary diurnal sites to sites with large shoals. Two fish moved between two solitary resting sites. High site fidelity was also observed to nocturnal seagrass sites. Four of five fish that were relocated in seagrass on more than one night were observed in the same site within the seagrass bed. Although most fish appeared to have consistent nocturnal migrations (Figure 4), one adult individual made nocturnal forays to other sites, suggesting greater variability for adults (Figure 5).

Five red hind were relocated following the initial 24-hour period (Table 4). All fish had very great site fidelity. Fish were more active during diurnal periods than nocturnal periods. Only one fish moved more than 100 m. All fish were tracked over reef habitat with no movement into

TABLE 2

Results of standardized trap sampling conducted at six stations within the seagrass bed in Greater Lameshur Bay, St. John, US Virgin Islands. Abundance data (mean number of fish per trap haul \pm s.d.) are presented for each family in samples.

A. Mean number of fish per trap haul, percent abundance, and percent estimated biomass by family; dates and stations pooled.

	Haemulidae	Sparidae	Acanthuridae	Lutjanidae	Carangidae	Ostraciidae	Mullidae	Tetraodontidae	Echeneidae	Holocentridae
Mean abundance	2.85 \pm 3.87	2.39 \pm 2.95	1.21 \pm 4.67	0.88 \pm 1.39	0.42 \pm 1.38	0.42 \pm 0.76	0.21 \pm 0.97	0.02 \pm 0.12	0.02 \pm 0.12	0.02 \pm 0.12
Percent abundance	33.8	28.4	14.4	10.4	5.0	5.0	2.5	0.2	0.2	0.2
Percent biomass	35.0	34.7	5.2	7.8	9.2	3.8	2.8	1.1	0.2	0.1

B. Mean number of fish per trap haul by family for each date; stations pooled.

Date (M/D/Y)	Haemulidae	Sparidae	Acanthuridae	Lutjanidae	Carangidae	Ostraciidae	Mullidae	Tetraodontidae	Echeneidae	Holocentridae
6/23/1999	0.50 \pm 0.84	0.83 \pm 1.33	0.00 \pm 0.00	0.33 \pm 0.82	0.00 \pm 0.00	0.17 \pm 0.41	0.00 \pm 0.00	0.00 \pm 0.00	0.00 \pm 0.00	0.00 \pm 0.00
6/26/1999	6.17 \pm 2.50	2.50 \pm 3.89	0.33 \pm 0.82	1.83 \pm 1.83	1.17 \pm 2.86	0.17 \pm 0.41	1.00 \pm 2.00	0.17 \pm 0.41	0.00 \pm 0.00	0.00 \pm 0.00
6/29/1999	4.50 \pm 3.50	3.50 \pm 3.56	4.33 \pm 10.61	0.67 \pm 1.21	0.00 \pm 0.00	0.17 \pm 0.41	1.00 \pm 0.00	0.00 \pm 0.00	0.00 \pm 0.00	0.17 \pm 0.41
7/02/1999	4.17 \pm 3.33	3.33 \pm 2.94	0.00 \pm 0.00	1.00 \pm 1.26	0.00 \pm 0.00	0.83 \pm 1.17	0.00 \pm 0.00	0.00 \pm 0.00	0.00 \pm 0.00	0.00 \pm 0.00
7/04/1999	3.00 \pm 1.50	1.50 \pm 1.76	2.17 \pm 5.31	1.33 \pm 1.97	1.50 \pm 2.81	0.00 \pm 0.00	0.00 \pm 0.52	0.00 \pm 0.00	0.17 \pm 0.41	0.00 \pm 0.00
7/07/1999	4.83 \pm 3.00	3.00 \pm 4.20	1.67 \pm 4.08	1.33 \pm 1.03	0.00 \pm 0.00	1.67 \pm 1.51	0.33 \pm 0.00	0.00 \pm 0.00	0.00 \pm 0.00	0.00 \pm 0.00
7/09/1999	3.67 \pm 2.83	2.83 \pm 3.66	3.83 \pm 9.39	0.50 \pm 0.84	0.00 \pm 0.00	0.17 \pm 0.41	0.00 \pm 0.00	0.00 \pm 0.00	0.00 \pm 0.00	0.00 \pm 0.00
7/12/1999	1.17 \pm 2.33	2.33 \pm 3.01	1.00 \pm 2.45	1.67 \pm 2.66	0.50 \pm 0.84	0.33 \pm 0.52	0.00 \pm 0.00	0.00 \pm 0.00	0.00 \pm 0.00	0.00 \pm 0.00
7/15/1999	1.33 \pm 1.83	1.83 \pm 2.32	0.00 \pm 0.00	0.17 \pm 0.41	0.00 \pm 0.00	0.33 \pm 0.52	0.00 \pm 0.00	0.00 \pm 0.00	0.00 \pm 0.00	0.00 \pm 0.00
7/18/1999	2.00 \pm 3.17	3.17 \pm 3.43	0.00 \pm 0.00	0.67 \pm 0.82	1.17 \pm 1.83	0.33 \pm 0.52	0.00 \pm 0.00	0.00 \pm 0.00	0.00 \pm 0.00	0.00 \pm 0.00
7/21/1999	0.00 \pm 1.50	1.50 \pm 2.35	0.00 \pm 0.00	0.17 \pm 0.41	0.33 \pm 0.82	0.50 \pm 0.55	0.00 \pm 0.00	0.00 \pm 0.00	0.00 \pm 0.00	0.00 \pm 0.00

C. Mean number of fish per trap haul by family for each station; dates pooled.

Station	Haemulidae	Sparidae	Acanthuridae	Lutjanidae	Carangidae	Ostraciidae	Mullidae	Tetraodontidae	Echeneidae	Holocentridae
1	3.00 \pm 4.17	4.82 \pm 3.40	0.00 \pm 0.00	0.82 \pm 0.98	0.45 \pm 1.04	0.09 \pm 0.30	0.09 \pm 0.30	0.00 \pm 0.00	0.00 \pm 0.00	0.00 \pm 0.00
2	1.45 \pm 1.97	1.55 \pm 1.21	0.00 \pm 0.00	1.45 \pm 2.02	0.00 \pm 0.00	0.82 \pm 1.17	0.00 \pm 0.00	0.09 \pm 0.30	0.00 \pm 0.00	0.00 \pm 0.00
3	3.91 \pm 4.35	0.09 \pm 0.30	0.00 \pm 0.00	1.00 \pm 2.10	0.64 \pm 2.11	0.64 \pm 1.21	0.00 \pm 0.00	0.00 \pm 0.00	0.09 \pm 0.30	0.00 \pm 0.00
4	5.91 \pm 4.28	2.00 \pm 2.24	7.27 \pm 9.65	0.45 \pm 0.93	1.09 \pm 2.30	0.00 \pm 0.00	0.73 \pm 1.79	0.00 \pm 0.00	0.00 \pm 0.00	0.00 \pm 0.00
5	0.91 \pm 1.38	3.82 \pm 3.82	0.00 \pm 0.00	0.55 \pm 0.69	0.00 \pm 0.00	0.73 \pm 0.47	0.45 \pm 1.51	0.00 \pm 0.00	0.00 \pm 0.00	0.09 \pm 0.30
6	1.91 \pm 4.28	2.09 \pm 2.88	0.00 \pm 0.00	1.00 \pm 1.00	0.36 \pm 0.81	0.27 \pm 0.47	0.00 \pm 0.00	0.00 \pm 0.00	0.00 \pm 0.00	0.00 \pm 0.00

TABLE 3

Results of passive tag sampling of bluestriped grunt, *Haemulon sciurus*, in Greater Lameshur Bay, St. John, US Virgin Islands. Data are number of fish tagged and recaptured in traps at the six established stations (Figure 1).

Station	Total Fish Tagged	Total Recaptures	Number of Fish Recaptured in Original Trap	Number of Fish Recaptured in Original Trap > 1 Time	Number of Fish Recaptured in Original Trap > 2 Times
1	20	5	4	1	1
2	10	2	1	0	0
3	32	5	1	0	0
4	36	14	12	5	4
5	8	2	2	0	0
6	17	1	1	0	0
Totals	123	29	21	6	5

TABLE 4

Summary of observations of telemetry investigations of reef fishes captured and released in boulder/reef zones adjacent to the seagrass beds in Greater and Little Lameshur Bays, 1998–1999.

A. Bluestriped grunts (*Haemulon sciurus*), 1999

Tag number	Size (cm FL)	Period tracked	Number of days tracked	Maximum distance moved from release site	Number of nocturnal movements into grass/number of 24-hour samples
605	21.0	Jun 10–19	9	< 20 m	0/6
507	17.5	Jun 12	< 1	< 20 m	0/0
508	22.5	Jun 13–25	12	87 m	0/7
534	28.0	Jun 16–18	2	419 m	2/3
535	22.0	Jun 16–Jul 7	21	312 m	2/6
3551	17.4	Jun 18–Jul 4	16	373 m	1/4
3552	26.4	Jun 18–Jun 29	11	465 m	2/4
3555	23.5	Jun 22–Jul 23	31	767 m	2/4
3725	23.5	Jun 22–Jul 7	15	327 m	3/3
3083	23.8	Jul 18–23	5	194 m	1/2
2842	25.0	Jul 18–19	1	87 m	1/1

B. Red hind (*Epinephelus guttatus*), 1998

701	26.5	Jun 5–Jul 28	43	~ 100 m	0/10
711	27.5	Jun 22–24	2	*	*
717	28.0	Jun 23–25	3	< 100 m	0/2
611	30.0	Jul 1–28	27	~ 200 m	0/2
3501	28.5	Jul 1–19	5	< 100 m	0/3
724	33.0	Jun 26	<	< 100 m	0/0

C. Coney (*E. fulvus*), 1998

709	27.5	Jun 1–22	6	~ 100 m	0/3
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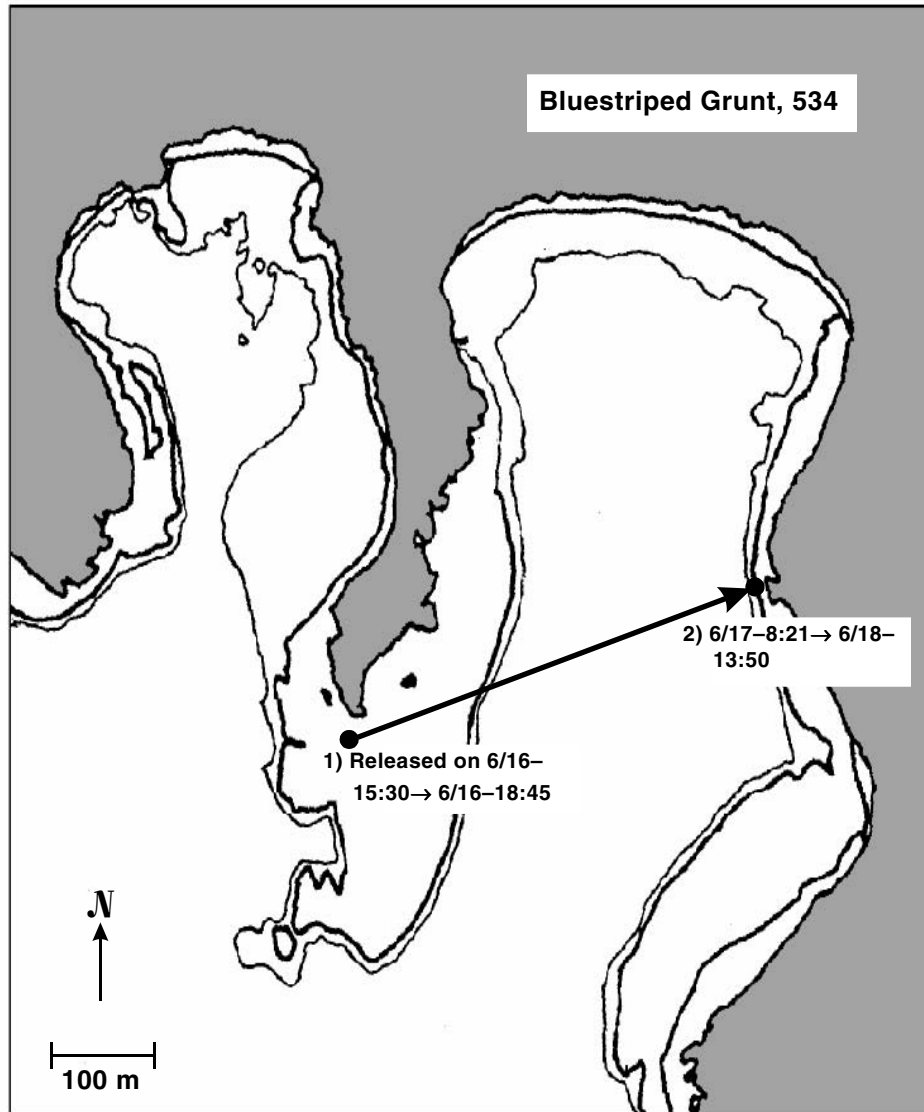


Figure 2. Movements of bluestriped grunt 534 over 2 tracking days. Fish was captured and released at large shoal resting site off Yawzi Point and crossed Greater Lameshur Bay to a solitary resting site. Arrows represent approximate movement between two locations, as in subsequent figures. Dates and times of duration are sequentially provided for each visit to each location.

seagrass habitat for individuals released at their capture site. In order to further investigate site fidelity, one fish was captured, tagged and translocated from a reef in the eastern portion of Greater Lameshur Bay to Yawzi Point reef between Greater and Little Lameshur Bays. These sites are separated by about 1 km of seagrass. The morning following release (at dawn, about 18 hours after release), the fish moved rapidly in a direct course (effectively a straight trajectory) from the release site to the home site (near point of capture) in less than one hour. A single coney (*E. fulvus*) was tracked for six days but was never observed moving off the reef.

DISCUSSION

Using a combination of methods, our results demonstrated that large reef fishes, specifically adult grunts, are abundant in seagrass beds adjacent to reefs, exhibit patterned movements between reefs and seagrass beds, and have high site fidelity to both diurnal reef and nocturnal seagrass sites. Visual sampling established the pattern of large abundance of large fishes in reef/boulder habitat and small abundance in adjacent seagrass habitat during diurnal periods. Trap sampling documented the species composition, abundance, and temporal and spatial variability in patterns of large reef fishes in seagrass

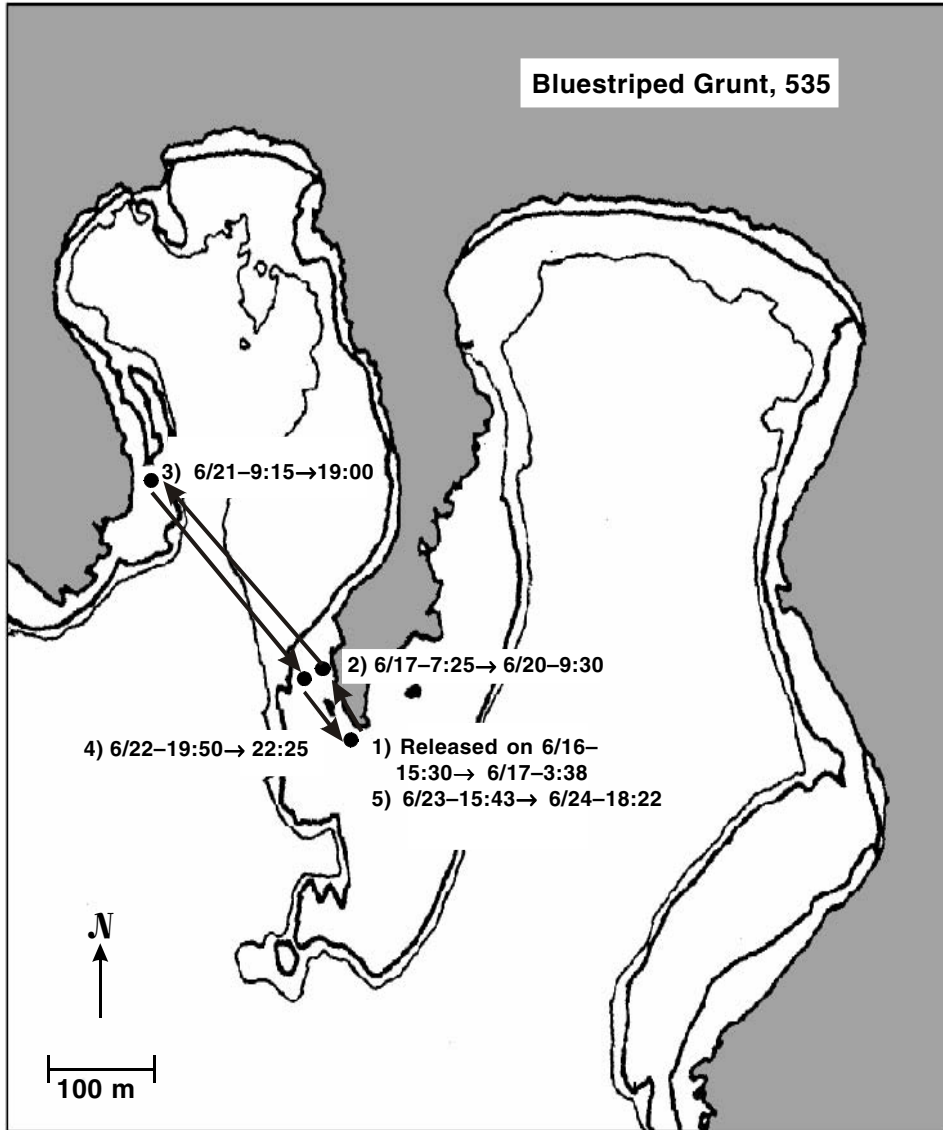


Figure 3. Movements of bluestriped grunt 535 over 21 tracking days. Fish was captured and released at large shoal resting site off Yawzi Point and crossed Little Lamershur Bay to a solitary resting site, then returned to shoal resting site. This fish remained at final site with little movement from 6/24 to 7/7.

habitat. Passive and sonic tagging documented the movement patterns among habitats and site fidelity of one of the most locally abundant species, bluestriped grunt.

Although most previous investigations demonstrated the nocturnal migrations of juvenile grunts, we documented high fidelity of adult grunts to both diurnal resting sites and nocturnal foraging sites. Previous studies, in which large numbers of reef fishes were tagged, demonstrated the high site fidelity of fishes in reef habitat. Among small patch reefs in Bermuda, Bardach (1958) observed high short-term site fidelity by groupers (mostly *E. striatus* and *E. guttatus*) on reefs and long-term site fidelity by bluestriped grunts (up to 200 days;

$n = 8$). On three small patch reefs in the Florida Keys, Springer and McErlean (1962) had large numbers of recaptures of groupers (*Mycteroperca bonaci* and *E. striatus*) and white grunts (*H. plumieri*), with numerous multiple recaptures. Working in the same bays as the present investigation, Randall (1962) had large numbers of recaptures of groupers, but low recapture rates for most other fishes, including grunts and snappers (except for *L. apodus*). He did recapture 4 of 9 tagged bluestriped grunts. In back-reef habitat in Puerto Rico, Recksiek et al. (1991) noted a large proportion of recaptures for white grunts, with multiple recaptures. At a spawning aggregation site for red hind in Bermuda, Luckhurst

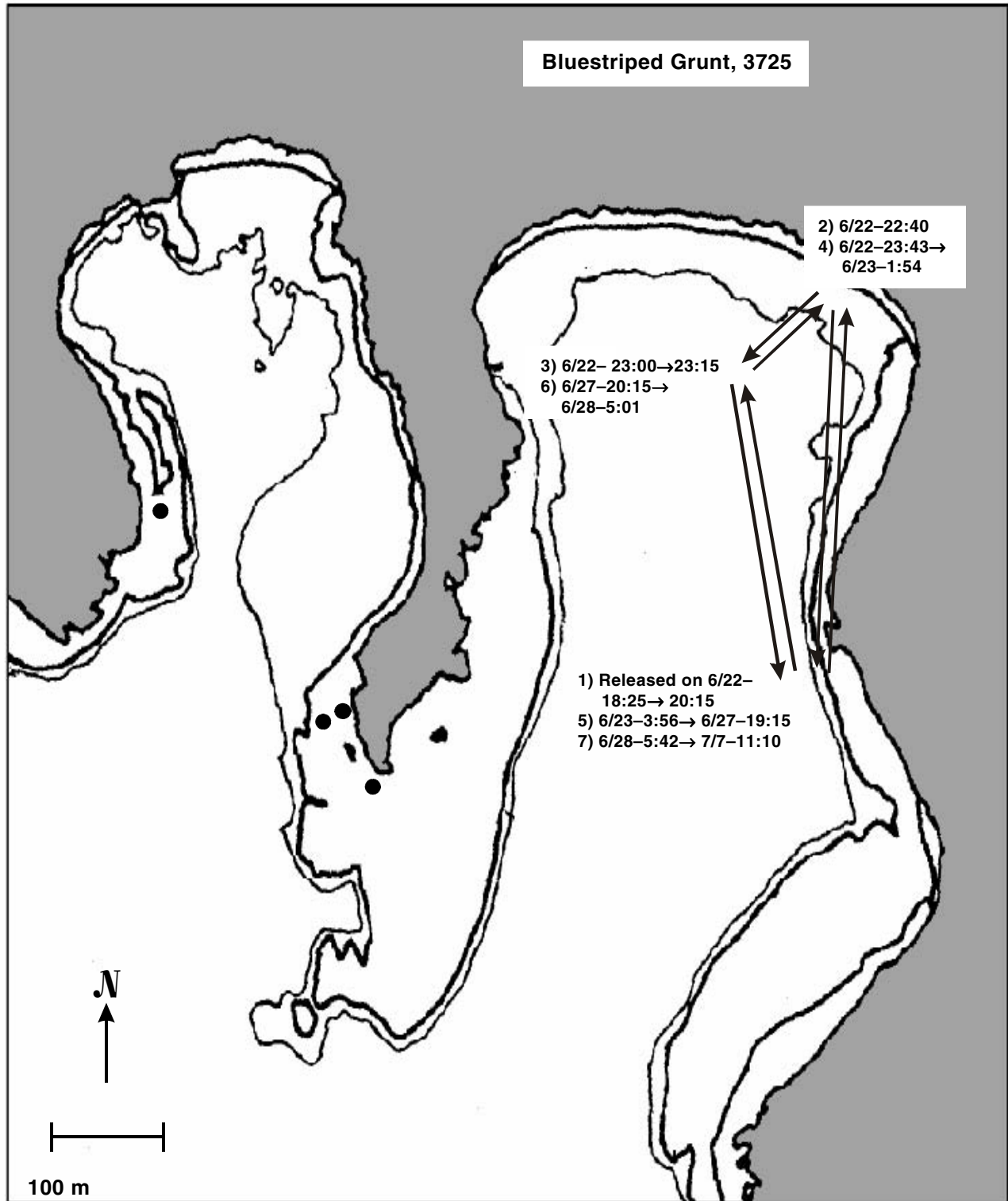


Figure 4. Movements of bluestriped grunt 3725 over 15 tracking days. This fish represented a typical pattern of consistent return to nocturnal foraging site.

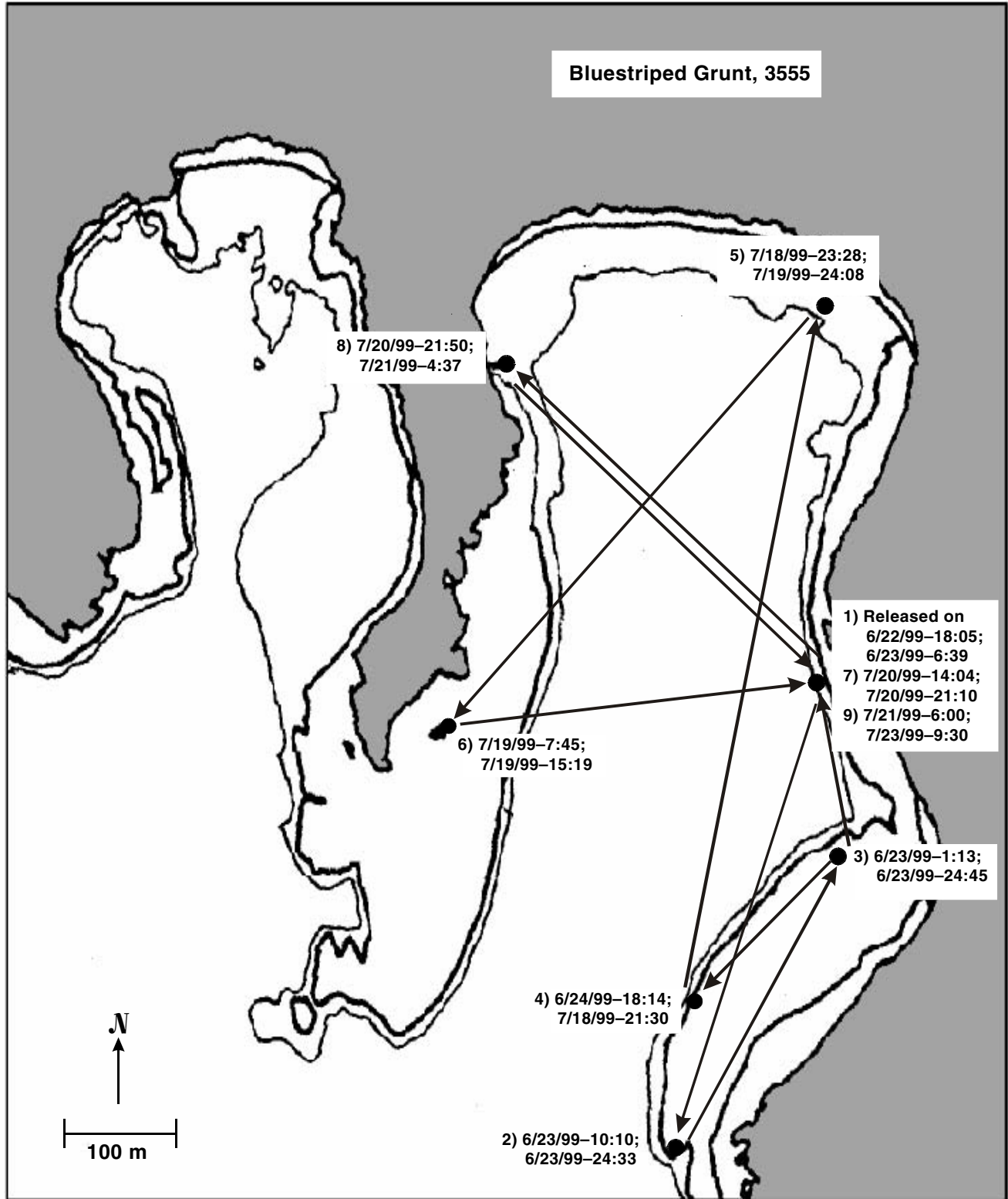


Figure 5. Movements of bluestriped grunt 3555 over 31 tracking days (the longest period a fish was tracked). Although diurnal resting site fidelity was great for this individual, nocturnal forays were more variable than others observed.

(1998) recorded a large proportion of short-term and long-term recaptures in reef habitat. Our trap sampling, passive tagging, and telemetry results demonstrated that bluestriped grunts show high short-term site fidelity in seagrass habitat. Visual sampling was not an effective method for assessing seagrass habitat utilization by reef fishes because of their nocturnal migration behavior. Recksiek et al. (1991) noted a similar result, with trap sampling being more effective than visual sampling for white grunt in backreef habitat.

Numerous investigations have documented movements of reef fishes among adjacent seagrass and gorgonian habitats (reviewed by Helfman 1993, Appeldoorn et al. 1997, Wolff et al. 1999), demonstrating the importance of adjacent habitats to reef fishes. Although most previous work on nocturnal migration of grunts was with small juveniles, two investigations have provided evidence of movements of larger grunts into adjacent habitats, including seagrasses. Using telemetry, Tulevech and Recksiek (1994) tracked white grunt (*H. plumieri*; $n = 14$; 21.0–25.7 cm FL) movements among habitats, including seagrass beds, adjacent to resting sites on reefs. In an innovative study using cyalume tags, Burke (1995) tracked French grunts (*H. flavolineatum*; $n = 10$; 12.0–16.0 cm FL) and small bluestriped grunts ($n = 10$; 14.7–20.5 cm FL) from reefs into adjacent seagrass habitat.

As in the study of movements of smaller bluestriped grunts (Burke 1995), we observed nocturnal movements of adult bluestriped grunts (17.4–28.0 cm FL) into adjacent seagrass habitat using sonic telemetry. These fish move repeatedly to the same location in the seagrass bed over subsequent nights. This behavior was also demonstrated by passive-tagged fish, which were recaptured in traps (several repeatedly) at their capture station in the seagrass bed. While the behavior of large grunts is not as patterned as juveniles, nocturnal migration of large grunts into seagrass habitat is consistent, at least for most individuals.

Although the red hind (*E. guttatus*) is an invertebrate-feeding grouper and invertebrates are abundant in seagrass habitat, red hinds were not observed moving away from reef habitat. These observations were consistent with results of other investigations on groupers (Shapiro et al. 1994, Samoilys 1997, Zeller 1997). The translocated red hind did cross about 1 km of seagrass to return to its point of capture (home reef), but traveled rapidly and directly between the release and home reefs without stopping. Homing behavior in this species has been documented previously (Bardach 1958, Luckhurst 1998).

Our results provide evidence of the direct linkage between coral reef and seagrass ecosystems. Although not observed in visual sampling of seagrass habitat during daylight, large grunts dominated abundance and biomass of reef fishes captured in traps set in seagrass habitat in Greater Lameshur Bay. Documentation of the nocturnal foraging migrations of large adult grunts from reef to adjacent seagrass habitat provided further evidence for the strong connectivity between these two habitats. The transfer of nutrients to the coral reef by the large biomass of invertebrate feeders could provide a large enhancement effect to corals and the entire ecosystem, as was demonstrated for juvenile grunts (Meyer et al. 1983).

Our findings provide supporting evidence that habitat diversity should be considered in the design of Marine Protected Areas. The connectivity of habitats and the strength of the linkages to species within management units must be considered. The indirect effects of human disturbance, especially by fisheries exploitation (Jackson et al. 2001), may be very significant. In the Virgin Islands, the biomass of large predators has been greatly reduced, whereas, herbivore and invertebrate feeder biomass has proportionally increased, as fishing intensity along with other disturbances has increased (Beets 1996, 1997, Beets and Rogers in press, Rogers and Beets 2001). The effects of these changes, particularly on habitat linkages, are important future areas of research.

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