Developmental patterns within a multispecies reef fishery: management applications for essential fish habitats and protected areas

Kenyon C. Lindeman, Roger Pugliese, Gregg T. Waugh, and Jerald S. Ault

SEDAR68-RD26

July 2019

Developmental patterns within a multispecies reef fishery: Management applications for essential fish habitats and protected areas

Article *in* Bulletin of Marine Science -Miami- · January 2000

Jerald S. Ault
University of Miami

BULLETIN OF MARINE SCIENCE, 66(3): 929–956, 2000

DEVELOPMENTAL PATTERNS WITHIN A MULTISPECIES REEF FISHERY: MANAGEMENT APPLICATIONS FOR ESSENTIAL FISH HABITATS AND PROTECTED AREAS

Kenyon C. Lindeman, Roger Pugliese, Gregg T. Waugh and Jerald S. Ault

ABSTRACT

Diverse information sets and regulatory mechanisms are necessary for the management of essential fish habitats (EFH) and protected areas involving multispecies fisheries. We therefore identified key pelagic and demersal developmental patterns among the 73 species of the snapper-grouper complex of the South Atlantic Fishery Management Council. Twenty-two potential spawning aggregation sites for eight snapper species near the Dry Tortugas and Key West were identified by commercial fishermen. Mean larval duration estimates were available for 15 species and ranged from 14 to 75 d. Larval durations for grunts, snappers, and groupers are within the residence times of some gyres. Settlement areas are depth stratified and, settlers often use shallower habitats than adults. Demersal stages of at least 50 species showed some degree of ontogenetic migration across the shelf, but most evidence suggests that strict estuary dependence is a rare life-history strategy among the species in the complex; facultative use of estuaries is more common. Including key nursery habitats in protected areas may not safeguard early life stages affected by coastal construction projects unless the design process is coordinated among agencies responsible for water quality and habitat protection through tools such as EFH. Sites that consistently support spawning aggregations for multiple species require management both as EFH-Habitat Areas of Particular Concern and, potentially, as no-take protected areas. The most important known snapper spawning aggregation site in the lower Florida Keys is Riley's Hump. Despite a site closure in May and June, aggregations of several other snapper species are heavily fished later in the year. A year-round closure to protect both fish stocks and remaining habitat integrity is warranted.

Coastal development and fishing activities may affect multiple life stages of the same species, although these activities are often managed under different regulatory regimes. The need to unify coastal land management with fishery management was reinforced by the essential fish habitat (EFH) provisions in the reauthorization of the Magnuson-Stevens Act (NOAA, 1996). Accordingly, the South Atlantic Fishery Management Council characterized EFH for species in its jurisdiction (federal waters of North Carolina through the east coast of Florida) in a comprehensive amendment that included seven fishery management plans (SAFMC, 1998a,b).

Development of regulatory initiatives for multispecies management units can be confounded by high phylogenetic and ontogenetic variability. This problem is particularly apparent in the Snapper-Grouper Fishery Management Plan, which includes 73 species. The snapper-grouper complex is the most diverse management unit under council jurisdiction, and its species use a broad array of habitats across the entire continental shelf. In addition to the EFH initiative, many researchers and managers now suggest that no-take areas, commonly called marine protected areas or reserves, may be necessary for sustainable fishery management (Plan Development Team, 1990; Allison et al., 1998; Johnson et al., 1999). The council's protected-area work has largely emphasized the snapper-grouper complex.

Both EFH management and protected-area design are aided by the identification of shared patterns of development for key species groups. Many managed species (e.g., lutjanids, serranids) spawn at aggregation sites that serve as concentrated sources of larvae. Interactions among larval developmental patterns (such as planktonic durations), behaviors, and current systems determine dispersal distances. Settlement areas can be inshore of spawning areas, and cross-shelf migrations to deeper habitats often connect settlement areas to spawning sites. Therefore, spatially discrete areas within much broader distributions can serve as foci for the management of both habitats and fisheries.

The present study summarizes available information on key pelagic and demersal developmental patterns to build a foundation for EFH and protected-area decision making for the snapper-grouper complex. We identify potential spawning-aggregation sites and larval-duration patterns and estimate inshore and offshore boundaries of demersal life-stage occurrence among species. The use of such information in the management process can be influenced by political factors unrelated to research, and knowledge of administrative procedures can better focus research applications. Therefore, we also summarize the council's administrative approaches toward EFH and protected-area management for the snapper-grouper complex.

METHODS

SPAWNING AGGREGATIONS AND LARVAL DURATIONS.—Published information on spawning sites was limited for species of the snapper-grouper complex, and detailed habitat information was almost absent, but some spatial information on spawning was available in Thresher (1984), Grimes (1987), García-Cagide et al. (1994), and Domeier et al. (1996). Because information was so limited within council waters, experienced commercial fishermen were also interviewed. Only sites with unusually high catches of fishes with running-ripe or enlarged gonads during known spawning months were identified as potential spawning-aggregation sites. These fishermen averaged over 20 yrs of commercial hand-line, spear, or rod experience and included members of the Florida Keys National Marine Sanctuary Advisory Council, the Tortugas 2000 Working Group, and the South Atlantic council. Two areas in the council's southern jurisdiction were emphasized: the lower Florida Keys (D. DeMaria and P. Gladding) and east-central Florida (B. Hartig). Snappers were emphasized, as less information was available than for groupers (Koenig et al., 1996; Domeier and Colin, 1997).

Planktonic larval durations (PLDs) can be estimated from microstructural transitions in otoliths (Keener et al., 1988; Victor, 1991) or from the age of fishes after first demersal appearance (McFarland et al., 1985; Robertson, 1988). Available PLD estimates were tabulated from the literature. When estimates were available for more than 1 yr (e.g., Sponaugle and Cowen, 1997), we used the mean for all years. Several attributes of presettlement stages were also examined. We focused only on postflexion larvae (late stages in which notochord flexion is complete). Larval identification status was based on input from experts in ichthyoplankton taxonomy.

DEMERSAL DISTRIBUTION PATTERNS.—Because cross-shelf distributions have been summarized for few species within the snapper-grouper complex, we characterized three fundamental attributes: (1) inner and outer distributional boundaries of newly settled stages, (2) distributions of juveniles and adults, and (3) presence or absence of ontogenetic cross-shelf migrations. The term 'newly settled' refers here to the life stage that first associates with or remains near demersal structures. Because fine-scale information is lacking for many species, comparative cross-shelf distribution patterns were based on depth ranges (<10 m, 10–30 m, and >30 m). The presence of ontogenetic cross-shelf migrations was based on occurrences of successively older life stages from at least two of these depth zones. Three broad structural habitat categories were used: submerged aquatic vegetation (SAV), hard bottom (including oyster-shell habitats and hard/soft corals), and unconsolidated sediments.

Information on habitat use was obtained from a diverse literature (e.g., Hildebrand and Schroeder, 1928; Longley and Hildebrand, 1941; Nakamura et al., 1980). More recent information was obtained from council source documents (SAFMC, 1983a, 1998b) and from Munro (1983), Polovina and Ralston (1987), Sale (1991), Claro (1994), and Arreguín-Sánchez et al. (1996). Most original studies on snapper-grouper species from within or near the council's jurisdiction were also reviewed, including studies on individual species or species groups (e.g., Matheson et al., 1986; Manooch, 1987; Grimes et al., 1988; Sedberry et al., 1994) or on specific habitat types (e.g., seagrasses: Sogard et al., 1987; mangroves: Thayer et al., 1987; Ley et al., 1999; coral reefs: Bohnsack et al., 1987; Chiappone and Sluka, 1996; gorgonians: Ault and Bohnsack, unpubl. data; hard bottom: Sedberry and Van Dolah, 1984; Lindeman and Snyder, 1999; mid-shelf and deep reefs: Chester et al., 1984; Parker and Mays, 1998).

ADMINISTRATION OF EFH AND PROTECTED AREAS.—Essential fish habitats (EFH) were defined (NOAA, 1996) as "those waters and substrate necessary to fish for spawning, breeding, feeding, or growth to maturity." All fishery-management councils had to amend management plans to identify EFH and human-caused threats by October 1998. To identify information sources and gaps, the South Atlantic council held workshops on wetlands, oyster/shell habitat, seagrasses, pelagic habitats, coral and hard bottom, artificial reefs, mapping, and research needs. A draft habitat plan was then generated by 13 writing teams. After public and agency comments were received, final editing was conducted by the council's Habitat Committee, Habitat and Environmental Protection Advisory Panel (AP), and Coral AP. Ultimately, two documents were produced: a comprehensive amendment that identified EFH for seven management plans (SAFMC 1998a) and a habitat source document (SAFMC, 1998b).

The EFH guidelines recognized subunits termed Habitat Areas of Particular Concern (HAPCs) that can be identified by at least four criteria: (1) importance of ecological functions, (2) sensitivity to degradation, (3) probability and extent of effects from development, and (4) rarity. The council had previously used the term HAPC in 1983 to manage habitats and snapper-grouper species at the Oculina Bank area of east-central Florida under the Coral Fishery Management Plan (SAFMC, 1983b). In the EFH amendment (SAFMC, 1998a), the council also designated new habitat areas of particular concern, but these were termed Essential Fish Habitat—Habitat Areas of Particular Concern (EFH-HAPCs) to differentiate them from the Oculina Bank HAPC.

The term protected area can include many management goals and regulatory tactics. We use the term for areas that are completely closed to all fishing effort (also termed no-take areas or marine reserves). The administrative context of our approach is based on a variety of council initiatives. These include gear and species closures at the Oculina Bank (SAFMC, 1983b,c), analyses of protected-area functions (Plan Development Team, 1990), public scoping meetings, and an action plan to guide design and implementation processes. Council approaches are also derived from protected-area design experiences with the Florida Keys National Marine Sanctuary (Bohnsack, 1997) and the Tortugas 2000 Initiative to site reserves in the lower Florida Keys. Because of the recency of this initiative and the role that habitat issues played, we focus here on several examples from the Dry Tortugas area.

RESULTS

THE SNAPPER-GROUPER FISHERY MANAGEMENT UNIT

Ten families are managed under the Snapper-Grouper Fishery Management Plan (Table 1). Association with coral or hard-bottom structure during part of the life cycle and contributions to an interrelated reef ecosystem were the primary criteria for inclusion of species (SAFMC, 1983c). The management unit is phylogenetically diverse and includes representatives of two perciform suborders (Percoidei and Labroidei) and the order Tetraodontiformes. Groupers, snappers, and grunts, all percoids, comprise 46 species (63% of the total). Currently, the late planktonic stages of over 40 species cannot be

Table 1. Preliminary summary of developmental patterns within the SAFMC snapper-grouper fishery management unit. Gon, gonochoristic; Protog, protogynous hermaphrodite. ?, suggested by available evidence but not confirmed. Sarg, *Sargassum*; SAV, submerged aquatic vegetation; HB, hard bottom or coral; SD, sediments. +, juvenile or adult stages recorded. Cross-shelf (CS) migration, ontogenetic demersal migration from shallow to deep habitats. P, piscivore; I, invertivore. *, overfished (SGA, 1999). **, incomplete demersal transition.

Families and species: SAFMC Snapper-Grouper Fishery Management Unit	*Spawning patterns*		*Presettlement stages*		*Newly settled stages*		*Juvenile & Adult CS distributions*				
	Sexuality	Spawning aggregations	Structural association	Species ID possible	Typical depth (m)	Structural association	<10m	10–30m	>30m	Cross-shelf migration	Adult trophic level
Lutjanidae—snappers											
Apsilus dentatus	Gon		None	Yes	>30	HB, SD?			+		I/P?
Etelis oculatus	Gon		None	Yes	>30	HB?, SD?			+		P/I
Lutjanus analis	Gon	Yes	None	Yes?	<10	SAV, HB?	+	+	+	X	P/I
Lutjanus apodus	Gon	Yes?	None	No?	<10	SAV, HB?	+	+	+	X	P/I
Lutjanus buccanella	Gon		None	No?	10–30	HB	+	+	+	X	P/I
Lutjanus campechanus	Gon	Yes	None	Yes?	<10	SD, HB?	+	+	+	X	P/I
Lutjanus cyanopterus	Gon	Yes	None	No	<10	SAV, SD	+	+	+	X	P/I
Lutjanus griseus	Gon	Yes?	None	Yes?	<10	SAV, SD	+	+	+	X	P/I
Lutjanus mahogoni	Gon		None	Yes?	<10	HB, SD	+	+	+	X	P/I
Lutjanus jocu	Gon	Yes	None	No	<10	SAV, SD	+	+	+	X	P/I
Lutjanus synagris	Gon	Yes?	None	Yes	<10	HB, SAV, SD	+	+	+	X	P/I
Lutjanus vivanus	Gon		None	No	>10	HB?, SD?		+	+	X	P/I
Ocyurus chrysurus	Gon	Yes?	None	Yes	0–20	HB, SAV, SD	+	+	+	X	I/P
Rhomboplites aurorubens	Gon		None	Yes	>20	HB, SD		+	+	?	I
Serranidae—groupers											
Centropristis ocyurus	Protog		None	No	>10?	HB?, SD?	?	+	+	?	I/P
Centropristis philadelphica	Protog		None	No	<10	SD?	+	+?		?	I
Centropristis striata	Protog		None	Yes	<20	HB, SD?	+	+	+	X	I/P
Epinephelus adscensionis	Protog?	Yes	None	Yes?	5–20	HB, SD?	+?	+	+	X?	I/P
Epinephelus cruentatus	Protog		None	Yes	5–20	HB, SD?	+	+	+	X?	P/I
Epinephelus drummondhayi	Protog?		None	Yes?	>10	HB, SD?		+	+	X?	P/I
Epinephelus flavolimbatus	Protog?		None	Yes?	>20	HB, SD?		+?	+	X?	P/I
Epinephelus fulvus	Protog		None	Yes	5–20	HB, SD?	+	+	+	X?	P/I
Epinephelus guttatus	Protog	Yes	None	Yes?	5–20	HB, SD?	+	+	+	X?	I/P

Table 1. Continued.

Families and species: SAFMC Snapper-Grouper Fishery Management Unit	Spawning patterns		Presettlement stages		Newly settled stages		Juvenile & Adult CS distributions				Adult trophic level
	Sexuality	Spawning aggregations	Structural association	Species ID possible	Typical depth (m)	Structural association	<10m	10–30m	>30m	Cross-shelf migration	
Serranidae—groupers											
Epinephelus itajara	Gon?	Yes	None	Yes	<10?	SAV?, HB?	+	+	+	X?	I/P
Epinephelus morio	Protog	No	None	Yes?	<10	SAV, HB	+	+	+	X	P/I
Epinephelus mystacinus	Protog?		None	Yes?	>10	HB, SD?		+	+	X	P/I
Epinephelus nigritus	Protog?		None	Yes?	>20	HB, SD?		+	+	X	P/I
Epinephelus niveatus	Protog	Yes?	None	Yes?	>10	HB, SD?		+	+	X	P/I
Epinephelus striatus	Gon	Yes	None	Yes	<10	SAV, HB	+	+	+	X	P/I
Mycteroperca bonaci	Protog	Yes?	None	No	<10	SAV, HB?	+	+	+	X	P/I
Mycteroperca interstitialis	Protog		None	No	>15	HB, SD?		+?	+		P/I
Mycteroperca microlepis	Protog	Yes	None	Yes?	<10	SAV, HB?	+	+	+	X	P/I
Mycteroperca phenax	Protog	Yes	None	Yes?	10–20	HB, SD?		+	+	X	P/I
Mycteroperca tigris	Protog	Yes	None	Yes?	5–20?	HB, SD?	+?	+	+	X	P/I
Mycteroperca venenosa	Protog	Yes	None	Yes?	5–20?	HB, SD?	+	+	+	X	P/I
Haemulidae—grunts											
Anisotremus surinamensis	Gon		SD?	Yes	1–10	HB, SD	+	+	+	X	I
Anisotremus virginicus	Gon		SD?	Yes	1–20	HB, SD	+	+	+	X	I
Haemulon album	Gon			Yes?	1–10		+	+	+	X	I
Haemulon aurolineatum	Gon		SD?	Yes	1–30	HB, SD	+	+	+	X	I
Haemulon chrysargyreum	Gon		SD?	Yes	1–10	HB, SAV?	+	+	+?	X	I
Haemulon flavolineatum	Gon		SD?	Yes	1–10	HB, SAV, SD	+	+	+	X	I
Haemulon macrostomum	Gon			Yes?	1–10	HB, SD	+	+	+	X	I
Haemulon melanurum	Gon		SD?	Yes?	5–20	HB, SD	+?	+	+	X	I
Haemulon parra	Gon		SD?	Yes	1–10	HB, SAV, SD	+	+	+	X	I
Haemulon plumieri	Gon		SD?	Yes?	1–20	HB, SAV, SD	+	+	+	X	I
Haemulon sciurus	Gon		SD?	Yes?	1–10	SAV, SD	+	+	+	X	I

Table 1. Continued.

Families and species: SAFMC Snapper-Grouper Fishery Management Unit	Spawning patterns		Presettlement stages		Newly settled stages		Juvenile & Adult CS distributions				
	Sexuality	Spawning aggregations	Structural association	Species ID possible	Typical depth (m)	Structural association	<10m	10–30m	>30m	Cross-shelf migration	Adult trophic level
Ephippidae—spadefishes											
Chaetodipterus faber	Gon		None?	Yes	<10	SAV	+	+	+	X?	I
Sparidae—porgies											
Archosargus probatocephalus	Gon		None?	Yes	<10	SAV, HB, SD	+	+		?	I
Calamus arctifrons			None?	No	<10	SAV, SD?	+	?		?	I
Calamus bajonado	Protog		None?	No			+	+	+	X?	I
Calamus calamus			None?	No			+	+	+	X?	I
Calamus leucosteus	Protog		None?	No			+?	+	+	X?	I
Calamus nodosus	Protog		None?	No			+?	+	+	X?	I
Pagrus pagrus	Protog		Sarg	Yes	>10	HB, SD?		+	+	X	I/P
Stenotomus caprinus	Gon		None?	No?	>10?	HB?, SD?	+	+	+	X?	I
Stenotomus chrysops	Gon		None?	Yes	>10?		+	+	+	X?	I
Malacanthidae—tilefishes											
Caulolatilus microps	Gon		None	No	>10	SD		+?	+		I
Lopholatilus chamaeleonticeps	Gon		None	Yes	>20	SD		?	+		I/P
Malacanthus plumieri			None	Yes	>5	HB?, SD?	+	+	+?		I
Carangidae—jacks											
Caranx bartholomaei	Gon		Sarg	Yes?	**	**	+	+	+		P/I
Caranx crysos	Gon		Sarg	Yes?	**	**	+	+	+		P
Caranx hippos	Gon		Sarg	No?	**	**	+	+	+		P
Caranx ruber	Gon		Sarg		**	**	+	+	+		P
Seriola dumerili	Gon	Yes?	Sarg		**	**		+	+		P/I
Seriola fasciata	Gon		Sarg		**	**		+	+		P
Seriola rivoliana	Gon		Sarg		**	**		+	+		P
Seriola zonata	Gon		Sarg	Yes	**	**		+	+		I/P

Table 1. Continued.

Families and species: SAFMC Snapper-Grouper Fishery Management Unit	Spawning patterns		Presettlement stages		Newly settled stages		Juvenile & Adult CS distributions				
	Sexuality	Spawning aggregations	Structural association	Species ID possible	Typical depth (m)	Structural association	<10m	10–30m	>30m	Cross-shelf migration	Adult trophic level
Percichthyidae—wreckfish											
Polyprion americanus	Gon	Yes?	None	Yes	>40				+		I/P
Labridae—wrasses											
Halichoeres radiatus	Protog		None	Yes	<10	HB, SD?	+	+	+	X?	I
Lachnolaimus maximus	Protog	Yes?	None	Yes	<10	SAV	+	+	+	X	I
Balistidae—triggerfishes											
Balistes capriscus	Gon		Sarg	Yes	<20	HB, SAV	+	+	+?	X?	I
Balistes vetula	Gon?		Sarg	Yes	<20	HB, SD?	+	+	+	X?	I
Canthidermis sufflamen	Gon?		Sarg	Yes	<20	HB, SD?		+	+	X?	I

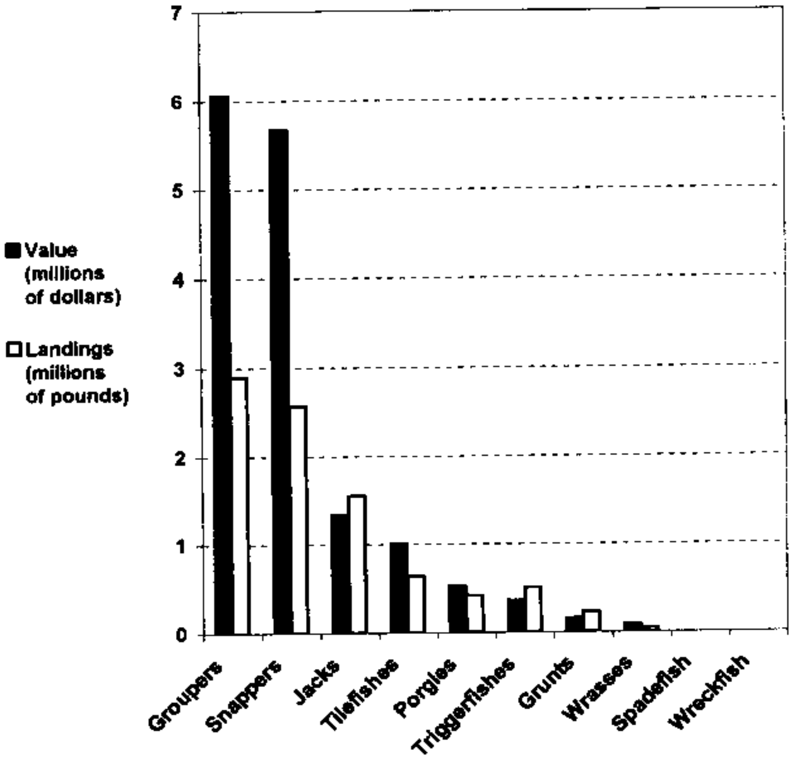

Figure 1. Commercial landings and values for families managed under the Snapper-Grouper Fishery Management Plan. Means were plotted from 1995 through 1997 commercial logbook data.

definitely identified at the species level (Table 1). This problem constrains empirical analyses of larval dispersion and recruitment processes.

The most valuable commercial families from 1995 through 1997 were groupers, snappers, jacks, tilefishes, and porgies (Fig. 1). The most valuable species were yellowtail snapper (*Ocyurus chrysurus*), vermilion snapper (*Rhomboplites aurorubens*), gag (*Mycteroperca microlepis*), greater amberjack (*Seriola dumerili*), and golden tilefish (*Lopholatilus chamaeleonticeps*), which had mean annual values ranging from $3.0 to $0.9 million. Recreational catches may exceed commercial catches in some species (e.g., gray snapper, *Lutjanus griseus*). An absence of detailed recreational catch statistics confounds direct comparisons. A porgy not currently in the management unit, spottail pinfish (*Diplodus holbrooki*), now forms a substantial fraction of some Carolina fisheries, perhaps because of reduced abundances of red porgy (*Pagrus pagrus*) (Manooch and Potts, 1996).

The Magnuson-Stevens Act provides that, if a species is overfished, all habitats it uses should be considered essential (NOAA, 1996). Sixteen species of the snapper-grouper complex are overfished according to recent council assessments (SGA, 1999): 10 groupers, two snappers, two porgies, one grunt, and one tilefish (Table 1). Recent assessments for the Florida Keys identified 13 grouper, seven snapper, and two grunt species as overfished (Ault et al., 1998).

Table 2. Potential snapper spawning aggregation sites near the Dry Tortugas (83°30′–82°30′ N) and Key West (82°30′–81°30′ N). Based on sites with abundant catches of fishes with running-ripe or enlarged gonads during spawning months.

Species	Location	Approximate depth (m)	Structural habitat	Peak months
Gray snapper	Dry Tortugas area			
L. griseus	(1) Riley's Hump	26	Coral/hard bottom	Jul–Aug
	(2) NW Dry Tortugas Natl. Park	15–18	Hard bottom/coral	Jul–Aug
	(3) Tail End Buoy	21–34	Coral slope	Jul–Aug
	Key West area			
	(1) SSW West. Dry Rocks (WDR)	15–37	Coral/hard bottom	Jul
	(2) W of WDR (on reef slope)[a]	18–34	Coral/hard bottom	Jul
	(3) WNW of WDR (inside reef)	9–14	Coral/hard bottom	Jul
	(4) Eyeglass Bar (SE of Sand Key)	20–26	Coral/hard bottom	Jul
	(5) Maryland Shoals	20–24	Coral/hard bottom	Jul
Cubera snapper	Dry Tortugas area			
L. cyanopterus	(1) Riley's Hump	26–35	Coral/hard bottom	Jun–Aug
	(2) Wreck[a]	67–85	High-relief wreck	May
	Key West area			
	(1) Wreck[a]	67–85	High-relief wreck	June
Mutton snapper	Dry Tortugas area			
L. analis	(1) Riley's Hump[a]	26–34	Coral/hard bottom	May–Jun
	(2) Quicksands	4–6	Sand/hard bottom	May–Jun
	(3) Tail End Buoy	26	Coral slope	May–Jun
	Key West area			
	(1) Western Dry Rocks	12–37	Coral/hard bottom	May–Jun
Yellowtail	Dry Tortugas area			
O. chrysurus	(1) SW Riley's Hump	26–30	Coral/hard bottom	May–Jun
Lane snapper	Dry Tortugas area			
L. synagris	(1) N of Rebecca Shoal	17	Hard bottom/grass	Jun
Red snapper	Key West area			
L. campechanus	(1) SE of Cosgrove Shoal[b]	55	Mud/hard bottom	
	(2) SW of Cosgrove Shoal[b]	79–98	Hard bottom	
Dog snapper	Dry Tortugas area			
L. jocu	(1) Riley's Hump	26	Coral/hard bottom	Summer
Schoolmaster	Dry Tortugas area			
L. apodus	(1) Tortugas Bank	18	Coral/hard bottom	Jun
	(2) Vestal Shoals	6–9	Coral ledge	Jun

[a] Identified as a potential snapper spawning site by Domeier et al. (1996).
[b] Aggregations absent since 1970s.

Developmental Patterns: Spawning through Settlement

Spawning Aggregation Sites.—Seven families of the snapper-grouper complex are gonochoristic, and two are protogynous (Table 1). Both patterns are present within the porgy family. To identify specific spawning sites, we focused on aggregations, the most apparent source of spatial spawning information. Limited published information existed only for two grouper and four snapper species (Wicklund, 1969; Gilmore and Jones, 1992; Domeier et al., 1996), but considerable commercial fishery evidence of snapper spawning aggregations existed in the southwest Florida Keys, particularly in the Dry Tortugas

Table 3. Planktonic larval duration estimates for species managed under the Snapper-Grouper Fishery Management Plan. Larval durations are based on otolith increment transitions (settlement marks) in groupers, snappers, and wrasses. In grunts and triggerfishes, discrete settlement transitions were not found, and larval-duration estimates were based on otolith-derived ages from newly settled specimens. In all taxa, estimates reflect postfertilization larval durations; a correction factor of 3 d was added if necessary to reflect the approximate number of days between fertilization and first otolith increment deposition.

Species in Snapper-Grouper Fishery Management Unit	Planktonic larval duration (days)		Region	Reference
	Mean	Range		
Serranidae—groupers				
Epinephelus striatus	42	37–45	Bahamas	Colin et al. (1997)
Mycteroperca bonaci	41	31–45	South Carolina	Keener et al. (1988)
Mycteroperca microlepis	43	33–66	South Carolina	Keener et al. (1988)
Lutjanidae—snappers				
Lutjanus analis	31	27–37	SE Florida/NW Cuba	Lindeman (1997a)
Lutjanus apodus	32	27–39	SE Florida/NW Cuba	Lindeman (1997a)
Lutjanus griseus	25	22–29	W Florida	Allman (1999)
Lutjanus griseus	39	33–48	SE Florida	Lara et al. (unpubl. data)
Lutjanus griseus	33	25–40	SE Florida/NW Cuba	Lindeman (1997a)
Lutjanus griseus	30	24–37	North Carolina	Tzeng (2000)
Lutjanus synagris	34	28–40	SE Florida/NW Cuba	Lindeman (1997a)
Lutjanus synagris	18	15–23	W Florida	David (unpubl. data)
Ocyurus chrysurus	31	25–35	SE Florida	Lindeman (1997a)
Ocyurus chrysurus	38	32–47	SE Florida	Lara et al. (unpubl. data)
Haemulidae—grunts				
Anisotremus surinamensis		17–22	Florida	Lindeman et al. (unpubl. data)
Anisotremus virginicus		15–20	Florida	Lindeman et al. (unpubl. data)
Haemulon flavolineatum	15	13–20	St. Croix	McFarland et al. (1985)
Haemulon flavolineatum		14–17	Panama	Victor (1991)
Haemulon flavolineatum		13–17	Florida	Lindeman et al. (unpubl. data)
Hameulon parra		14–18	Florida	Lindeman et al. (unpubl. data)
Labridae—wrasses				
Halichoeres radiatus	24	20–28	Barbados	Sponaugle and Cowen (1997)
Halichoeres radiatus	25	22–31	Panama	Victor (1986)
Lachnolaimus maximus	26	21–30	Panama?	Victor (1986)
Balistidae—triggerfishes				
Balistes vetula	75	63–83	Panama	Robertson (1988)

(83°30′–82°30′N) and Key West areas (82°30′–81°30′N). We therefore focused on these areas because of an ongoing initiative to establish protected areas near the Dry Tortugas.

Thirteen sites for seven species were tentatively identified in the Dry Tortugas area (Table 2). Riley's Hump was a potential spawning-aggregation site for five snapper species, more than any other area (Table 2). Peak mutton snapper spawning probably occurs in the early summer (May and June), followed by cubera and gray snapper in July and August. The Tortugas Bank area is heavily fished, and gray snapper are caught with enlarged gonads, yet spawning aggregations comparable to those at Riley's Hump are not known (P. Gladding, pers. comm.). Gray snapper was the only snapper commercial fishermen believe may aggregate for spawning within Dry Tortugas National Park. East of the park, spawning mutton snapper may aggregate at Tail End Buoy and the Quicksands, and aggregations of gray snapper and lane snapper were reported from Tail End Buoy and Rebecca Shoal, respectively (Table 2). Interannual variations in aggregation presence can occur, particularly in sites subjected to heavy fishing (D. DeMaria and P. Gladding, pers. comm.).

In the Key West area, nine probable spawning sites for four snapper species have been commercially or recreationally fished (Table 2). Five of these were for gray snapper. Three were in the Western Dry Rocks area of the outer reef tract, only several kilometers apart (D. DeMaria, pers. comm.). An additional gray snapper spawning site, at Eyeglass Bar, is 5 km from the outer boundaries of the Western Sambos protected area. Spawning cubera snapper are fished on a deep wreck (45–80 m), and mutton snapper are taken at one of the Western Dry Rocks sites that spawning gray snapper use (D. DeMaria, pers. comm.). Two of the sites identified in the Key West area were once used by the red snapper (Table 2), but these aggregations were apparently fished out in the 1970s.

Commercial fishermen identified a potential spawning aggregation of large yellowtail snapper at Riley's Hump (Table 2). Domeier et al. (1996) suggested that this species does not form spawning aggregations. These interpretations arise from several factors. Yellowtail are observed by fishermen to spread out along the reef tract and to show less site fidelity. They also have a protracted spawning season (García-Cagide et al., 1994), and heavy chumming by fishermen may induce artificial aggregations. We tentatively conclude that yellowtail spawning aggregations can occur in the lower Keys but probably involve fewer individuals and less site fidelity than many other snapper species.

Planktonic Larval Durations and Settlement.—PLD estimates were available for 15 snapper-grouper species (Table 3). The high estimate was for *Balistes vetula* (75 d), followed by those for three grouper species (means 41–43 d; Table 3). Means for five snapper species ranged from 31 to 39 d in samples from southeast Florida. Means for gray and lane snappers from northwest and southwest Florida samples were lower: 25 d (Allman, 1999) and 18 d (David, unpubl. data). In two wrasse species, means ranged from 24 to 26 d. Grunts had the shortest PLDs; estimates ranged from 13 to 20 d in *Haemulon* and *Anisotremus* species (Table 3).

Geographic variation of mean PLDs was low (less than 1–2 d) in *Halichoeres radiatus* from Barbados and Panama and *Haemulon flavolineatum* from St. Croix, Panama, and southeast Florida (Table 3). Gray and lane snappers from northwest and southwest Florida may not differ significantly in larval duration (Allman, 1999; David, unpubl. data). Differences on the order of 1–3 wks occurred between gray and lane snapper specimens from west and southeast Florida (Table 3). Estimates for four snapper species from both southeast Florida and northeast Cuba did not differ significantly (Lindeman, 1997a), but sample sizes were low, and this conclusion is tentative.

Planktonic durations can be influenced by associations with structural features of the water column or the bottom during transitional periods before the completion of settlement. Jack and triggerfish species have been commonly recorded from floating *Sargassum* (Settle, 1993; Table 1). Sixty-one species in the fishery management unit have not been recorded in appreciable numbers from *Sargassum* (Table 1). Species within two genera of grunts may ephemerally associate with the bottom before irreversible settlement (Lindeman, 1997a).

DEVELOPMENTAL PATTERNS: POSTSETTLEMENT

Distributions of Newly Settled Stages.—On the basis of the available literature and writing-team reviews (SAFMC, 1998b), distributional patterns of newly settled stages were summarized in terms of depth ranges and structural types. The most common depth range for newly settled stages was 0–10 m (over 35 species; Table 1). At least 80% of snapper and grunt species use this depth zone for settlement. Despite the well-documented inshore occurrence of gag, jewfish (*E. itajara*), and black grouper (*M. bonaci*), many grouper species do not appear to settle in areas shallower than 5 m (Table 1). Various grouper species are cryptic for days or weeks after settlement, however, and depths and structural habitats used are poorly known.

At progressively smaller spatial scales, numerous habitat types can be defined by both structural and water-quality attributes. Detailed information is often lacking, but evidence suggests that 33 species primarily use hard bottom, corals, or oyster bars (and possibly associated sediments) at settlement (Table 1). Use of both SAV and hard bottom has been recorded for 15 species. Evidence of only SAV use was found for 17 species. SAV here includes grasses and algae but not mangrove roots, which may be unfavorable settlement sites because of high abundances of predators. These differing patterns of structural habitat use at settlement were present within some of the most diverse families in the management unit (e.g., snappers and grunts). For example, *Lutjanus griseus* and *Haemulon sciurus* predominantly settle in SAV (Table 1). *Lutjanus mahogoni* and *H. macrostomum* settle predominantly or entirely on hard bottom or corals (or associated sediments). *Lutjanus synagris* and *H. parra* can settle on either SAV or hard bottom habitats. Usage of both habitats by newly settled stages is best documented in the latter two species. Opportunistic habitat use at settlement is common in at least eight species of grunts and snappers (Lindeman et al., 1998).

Distributions of Juveniles and Adults.—Cross-shelf distributional patterns of juvenile and adult stages were compiled from occurrence information from three depth zones (<10 m, 10–30 m, >30 m) that generally correspond to inner shelf, mid-shelf, and outer shelf regions. Adults of almost all species occurred in outer shelf areas (Table 1). Mid-shelf and inner-shelf areas were commonly occupied by immature life stages. This pattern held for all 11 grunt species and nine of 14 snapper species within the management unit (Table 1). Juveniles of many species occupy shallower water than adults commonly inhabit (Longley and Hildebrand, 1941; Starck, 1970; Nakamura et al., 1980; Nelson et al., 1991), and we estimated that at least 50 species show some degree of ontogenetic cross-shelf migrations (Table 1).

Ontogenetic migrations often do not involve movements across the entire shelf. In the northern council jurisdiction, where the shelf is wider, many species may settle in mid-shelf areas and move to deeper waters with growth. In contrast, juvenile gray snapper are relatively common in North Carolina estuaries but are uncommon offshore as adults (C. Manooch, pers. comm.). On the narrow shelf of southeast Florida, nearshore settlement outside of inlets occurs in some species of *Haemulon*, *Scarus*, *Diplodus*, and *Lutjanus* that also settle inside bays and lagoons (Lindeman and Snyder, 1999).

Adults may migrate tens or hundreds of kilometers to reach spawning sites, either across or parallel to the shelf. In the Florida Keys, gray snapper abundances in canals and mangroves can drop substantially as mature stages move to deeper areas to spawn (Starck, 1970). Mutton snapper aggregations at the Quicksands area west of the Marquesas (Table 2) are composed of smaller adults (30–45 cm) than mutton aggregations on reefs

Table 4. Preliminary estimates of facultative and obligate use of estuaries by species within the Snapper-Grouper Fishery Management Unit. Additional information in text and Table 1.

Family (total spp.)	~No. of estuary facultative species	~No. of estuary dependent species
Groupers (21 spp.)	3 (*Epinephelus morio, Mycteroperca bonaci, Centropristis striata*)	1–2 (*M. microlepis, E. itajara*?)
Snappers (14 spp.)	5 (*Lutjanus analis, L. apodus, L. mahogoni, L. synagris, Ocyurus chrysurus*)	1–3 (*L. cyanopterus, L. griseus*?, *L. jocu*?)
Grunts (11 spp.)	7–8 (*Haemulon parra, H. plumieri, H. flavolineatum, H. chrysargyreum, H. aurolineatum, Anisotremus virginicus, H. sciurus, H. album*?)	0
Porgies (9 spp.)	3–5 (*Archosargus probatocephalus, Calamus arctifrons, C. bajonado, C. leucosteus*?, *C. calamus*?)	0
Jacks (8 spp.)	0–2 (*Caranx bartholomaei*?, *C. crysos*?)	0
Tilefishes (3 spp.)	0	0
Triggerfishes (3 spp.)	1 (*Balistes capriscus*)	0
Wrasses (2 spp.)	1 (*Lachnolaimus maximus*)	0
Wreckfishes (1 sp.)	0	0
Spadefish (1 sp.)	1 (*Chaetodipterus faber*)	0
Totals	~21–26 species	~2–5 species

in deeper water (P. Gladding, pers. comm). Gag tagged off South Carolina have been caught off east-central Florida within 6 mo, presumably after a 600-km migration (Van Sant et al., 1994).

Estuary Dependence and Opportunistic Habitat Use

We use 'dependence' to mean an obligate behavioral or physiological association. Tests of estuary dependence require consistent evidence that at least one life stage is restricted only to estuarine waters. For example, in the Dry Tortugas area, gray snapper settle in grass habitats in strictly euhaline waters and use a variety of other high-salinity habitats through maturity (Longley and Hildebrand, 1941; Starck, 1970). The nearest sizeable estuary is in northern Florida Bay, over 150 km away. Gray snapper can possibly migrate this distance, but because all demersal size classes occur in the Dry Tortugas area, estuary dependence as a species-wide paradigm is excluded.

Consistent evidence of an obligate association with low-salinity habitats during at least one life stage exists for at least two to five species in the management unit (Table 4). Many other species also occur in estuarine bays or lagoons, but conspecifics of the same age can also be found outside of coastal bays or in outer portions of bays that are largely euhaline. Evidence for such facultative associations with estuarine habitats, estuary opportunism, was found in 21–26 species (Table 4). Only the grouper and snapper families had estuarine-dependent species, whereas eight families had species that used estuaries opportunistically. The latter pattern appeared most commonly among grunts and snappers but also among some species of groupers, porgies, and jacks.

EFH Identification and Management

Building the EFH source document and comprehensive amendment involved extensive input from writing teams and outside biological reviews (SAFMC, 1998b). However, it

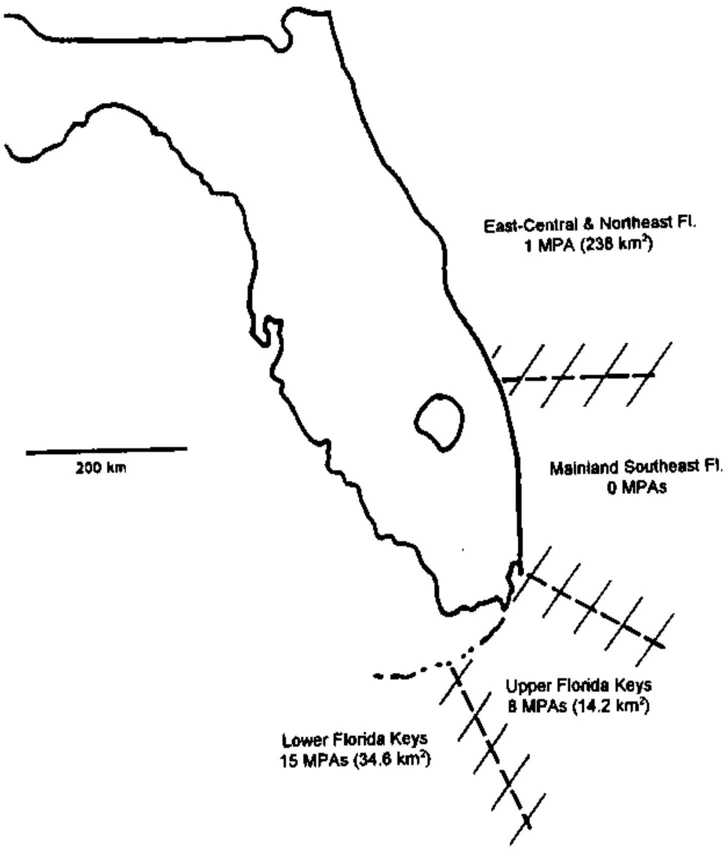

Figure 2. Several geographic subsystems of the east coast of Florida and the number and areas of no-take marine protected areas (MPAs) within each. Various geographic systems can be identified in this area; those used here have been distinguished by differing geomorphology and sediment types (Hoffmeister, 1974; Marszalek et al., 1977), water temperatures (Briggs, 1974; Gilmore, 1995), or current systems (Lee et al., 1994).

also required input from many other interest groups and administrative agencies, further modifying the path between research and administrative rule-making. As a result of (a) the diversity of species in the snapper-grouper fishery management unit, (b) the potential for ontogenetic habitat shifts within these species, (c) the absence of precise habitat information for much of the area, (d) the diverse array of interest groups that shaped the administrative language, and (e) the requirement for a "risk averse" approach (NOAA, 1996), almost every structural habitat type within council jurisdiction was considered EFH (SAFMC, 1998a). EFH-HAPC designations were also used for a variety of spatial categories within council jurisdiction. These include structural habitat types (e.g., seagrasses, mangroves, corals), specific locations (Charleston Bump, Ten Fathom Ledge), and areas used during key biological processes (spawning sites) (SAFMC, 1998a).

The actual contribution of EFH to habitat management will involve the net outcome of hundreds of site-specific consultation processes among many federal and state permitting agencies. Application of EFH provisions will differ according to the source of the potential impact: fishing gear or threats unrelated to fishing gear. During development of the EFH amendment, existing council habitat management processes (summarized in

SAFMC, 1998b) were modified to accommodate the new provisions. In coordination with NMFS, the council will file comments with lead agencies when project impacts are significant. The Habitat Advisory Panel and Committee will have several guidelines for assessing project significance. Of particular concern are (1) projects that may set precedent or involve critical or unique areas and (2) projects that may be elevated for NMFS headquarters action pursuant to the National Environmental Policy Act or the Clean Water Act.

Zoogeographic Subsystems and Siting of Protected Areas

An idealized system of protected areas will support fish populations within primary areas of abundance and also protect potential sources of larval exchange among adjacent regions. Characterizing differing geographic subsystems and the potential for regional connectivity within council waters may be important in protected-area design. The council jurisdiction includes two broad geographic regions: Cape Hatteras to the Cape Canaveral area and Cape Canaveral to the Dry Tortugas. These areas differ substantially in biology, climate, and geology and represent temperate, wide-shelf systems and tropical, narrow-shelf systems, respectively. The primary zoogeographic transition zone occurs between Cape Canaveral and Jupiter Inlet (Briggs, 1974), a distance of approximately 230 km.

Eastern Florida contains several geographic subsystems that may be relevant to protected-area siting (Fig. 2). The lower Florida Keys extends from the Dry Tortugas to the Big Pine Key area, consists of oolitic facies of the Miami limestone, and has limited reef development because of the many channels connecting with the turbid waters of Florida Bay (Hoffmiester, 1974; Marszalek et al., 1977). Approximately 34.6 km^2 of this area is within one large and 14 small protected areas administered by the Florida Keys National Marine Sanctuary (Fig. 2). The upper Florida Keys subsystem, terminating off Biscayne Bay, has less exchange with Florida Bay and more-developed reef systems (Marszalek et al., 1977). Eight small protected areas encompass about 14.2 km^2 of sanctuary waters (Fig. 2). Substantial gyres or countercurrents can be present within both subsystems during spawning seasons of many snapper-grouper species (Lee et al., 1994). These gyres can last longer than the known PLDs of snappers and groupers (Table 3), and within-subsystem retention is possible. The presence of these gyres is variable, however, and propagules in the Florida Current that are not influenced by meanders of the western frontal boundary may also be transported downstream (Lee and Williams, 1999).

The mainland and associated sedimentary barrier islands of southeast mainland Florida differ from the Keys in geologic origin (Hoffmeister, 1974), reef characteristics (Goldberg, 1973), and flow fields (Lee and Mayer, 1977; Lee et al., 1994). There are no reserves within this area (Fig. 2). In east-central and north Florida, the shelf becomes wider, turbidity increases, and the climate is more temperate. The southern portion of this area includes the Experimental Oculina Research Reserve (238 km^2) off Fort Pierce, where catches of all snapper-grouper species have been prohibited by the council since 1994. From southeast mainland Florida through the Carolinas, the western boundary of the Gulf Stream sheds occasional eddies that last 2–14 d and are associated with upwelling and elevated production (Lee and Mayer, 1977; Atkinson et al., 1985). As in the Keys, known current systems may promote either retention within or advection among adjacent shelf systems.

DISCUSSION

SPAWNING LOCATIONS

Spawning aggregations are useful focal points for EFH and protected-area management, as they are concentrated production sites and can be predictable in space and time. Detailed documentation of spawning aggregation sites for snapper-grouper species is lacking, however, for the southeast United States. Constraints on studying spawning events (e.g., gathering behavioral data in deep water at dusk or at night) also limit knowledge of habitat attributes that favor spawning. Increased scientific use of fishermen can aid timely identification of sites, because their sampling efficiency in locating aggregations is high (Johannes, 1981; Poizat and Baran, 1997). Such exercises may also increase confidence in the regulatory process (Dyer, 1994; DeMaria, 1996). Failure to build support among fishermen can terminate protected-area initiatives as in the proposed National Marine Sanctuary at La Parguera, Puerto Rico (Valdes-Pizzini, 1990; Fiske, 1992). With new information, the council will build maps of spawning areas for use in both protected-area and EFH management (SAFMC, 1998b).

In the present study, fishermen identified 22 areas in the lower Keys that may serve as spawning-aggregation sites for eight snapper species. Evidence for spawning aggregations for four of these species and 18 of these sites was previously unavailable. In total, spawning aggregations of three grouper and eight snapper species at 25 sites have now been potentially identified within or adjacent to council jurisdiction (Wicklund, 1969; Gilmore and Jones, 1992; Domeier et al., 1996; Eklund et al., this issue; present study). Various behaviors can characterize such groupings, and available information suggests most species form transient aggregations, but simple migratory spawning may also occur (e.g., gray snapper, Domeier and Colin, 1997).

The most important site currently known is Riley's Hump, where aggregations of five snapper species were tentatively identified. Other families may also spawn at these sites, including black grouper and permit (*Trachinotus falcatus*) (D. DeMaria, pers. comm.). Other major sequential spawning sites are unidentified in or adjacent to council waters. The attributes that make Riley's Hump attractive to spawning fishes may involve cross-shelf positioning and, on a finer scale, structural habitat types. It is one of the most upstream projections of the 80–110-ft contour of the Florida Reef Tract and is at the convergence of currents from the Yucatán Channel, Gulf of Mexico, and Florida Straits. Comparative studies of Riley's Hump and similar sites nearby that lack aggregations (Ault and Bohnsack, unpubl. data) are necessary before primary causal mechanisms of the Riley's Hump aggregations can be identified. It is often assumed that shelf-edge environments of moderate to high structural relief are ideal release sites because they reduce predation on batches of eggs. Many sites that appear to meet these criteria, however, are not used for spawning (e.g., Colin and Clavijo, 1988; Shapiro et al., 1988).

There may be substantial geographic differences in spawning aggregation patterns. In contrast to the Florida Keys, available evidence suggests that more temperate shelf areas of east-central Florida and the Carolinas may have fewer snapper-grouper spawning aggregations and less site fidelity (Govoni and Hare, in press; B. Hartig and F. Rohde, pers. comm.). For example, potential spawning aggregations of gray snapper south of the Jupiter Inlet have been fished for over 10 yrs, but consistent use from year to year of any individual site has not been observed (B. Hartig, pers. comm.). Grimes (1987) assembled evidence that insular snapper populations spawn over longer periods than continental populations. Other intraspecific patterns of spawning may also vary geographically (Coleman et al., 1999). Lane snapper aggregations occur at shelf-edge areas of Cuba (Claro, 1981) but are recorded only from shallow areas inside the shelf edge in the lower Keys (Table 2). Within snapper species, spawning seasons in Cuba, Jamaica, and Puerto Rico can differ substantially (García-Cagide et al., 1994; Munro, 1983; J. Garcia-Saez, pers. comm.). These and other examples suggest that broad management assumptions about spawning may be counterproductive and that expanded research efforts are necessary.

Larval Durations and Settlement

Grouper larvae may be less subject to retention than snappers, as they may be in the water column one-third longer, but larval behaviors and seasonal current variations that foster retention may influence transport more than larval durations alone. Besides differences in spawning seasons and PLDs, larvae of these two families show similar morphologies, abundance patterns, and possibly diel behaviors (Houde and Dowd, 1976; Leis, 1987). At settlement, the use of nighttime flood tides also appears similar (Keener et al., 1988; Halvorsen, 1994; Colin et al., 1997), as do the microstructure of otolith transition areas, settlement size, and the rates of metamorphosis (Keener et al., 1988; Lindeman et al., in prep.).

Other families differ in many of these characteristics. Grunts settle at half the size and half to one-third the age of many species. Late-stage grunt larvae are epibenthic, feeding on plankton for weeks after settlement and undergoing a slow metamorphosis characterized by several discrete morphological and ecological transitions over several months after settlement (Lindeman, 1997a). On the basis of PLDs and behavioral evidence, the grunts may be more subject to larval retention than any other family in the snapper-grouper fishery management unit.

The species with the longest PLD, *Balistes vetula*, is well documented from *Sargassum* collections. Little evidence suggests that snappers, groupers, or grunts associate with *Sargassum* offshore, although older larvae may associate with floating vegetation when advected through channels before or at settlement. Collections from *Sargassum* entering channels on flood tides during documented periods of grouper and snapper ingress (see, e.g., Keener et al., 1988; Halvorsen, 1994) could be used to test this possibility.

Two types of evidence used to predict larval connectivity, PLDs and surface drifter paths, may also be misleading. Information is needed on larval behaviors that may counteract the effects of currents or long PLDs, such as vertical maneuvering ability. Some information can be indirectly obtained from plankton surveys and laboratory rearing and may be most feasibly obtained from late-stage larvae. Exceptional swimming speeds have been observed in older larvae (Leis et al., 1996; Stobutzki and Bellwood, 1997). Late-stage larvae have well-developed sensory capabilities and mobility and may maneuver toward temperature or auditory cues (Doherty et al., 1996; Stobutzki and Bellwood, 1998). Substantial maneuvering abilities may also be necessary to traverse frontal boundaries before settlement (Miller, 1988; Govoni, 1993; Limouzy-Paris et al., 1997). The period between initial competency to settle and continuous association with the bottom may be characterized by several life-history strategies (Leis, 1987; Richards and Lindeman, 1987), including varying degrees of habitat sampling by individuals or groups of potential settlers (Leis, 1991; Kaufman et al., 1992; Cowen and Sponaugle, 1997; McCormick and Makey, 1997). Characterizing structural and water-quality attributes influencing behavior of settlement-competent stages is fundamental to identifying primary nurseries and EFH-HAPCs.

Cross-Shelf Habitat Use

The time between spawning and settlement does not exceed 3–4 mo for snapper-grouper species, whereas the demersal period lasts 4–40 yrs (Claro, 1994). Fine-scale information on demersal life-stage distributions across the shelf is limited for almost all species. Our estimates of cross-shelf distribution patterns and dependence on estuaries are hypotheses suggested by available evidence. Interpretations of distributions will be modified by new information. Even with detailed information, long-term fishing effects on population structure and habitats may have modified cross-shelf distributions in manners that confound the postdisturbance identification of natural patterns (C. Koenig, pers. comm.).

A reexamination of fundamental assumptions about estuary dependence in the snapper-grouper fishery-management unit may be necessary. Few criteria have been explicitly considered in designating species estuary-dependent. The dependence of fishes on temperate salt marshes is often assumed, although the mechanisms can be difficult to confirm (Boesch and Turner, 1984). This assumption has grown to include a variety of habitats in the tropics (Robertson and Duke, 1987). The term 'dependence' implies obligate use. This criterion suggests testable hypotheses. For example, if a species can use estuarine habitats, but all life stages are also recorded from nonestuarine areas, dependence is logically excluded. In addition to a lack of assessment criteria, alternatives to estuary dependence are often unexamined. Exceptions include Lenanton and Potter (1987), Blaber et al. (1989), and Able and Fahay (1998), who concluded on the basis of juvenile occurrence outside of estuaries as well as inside, that many species used estuaries facultatively rather than obligately.

An ongoing habitat-management issue concerns the Dry Tortugas, where two protected areas are proposed, the majority of snapper-grouper species occur, and no true estuaries are present. Most shallow-water habitats near the proposed areas are within Dry Tortugas National Park. The park has substantial *Thalassia* beds and some beachrock outcroppings (Ginsburg, 1953). Yellowtail snapper have been abundantly seined in grassbeds (Longley and Hildebrand, 1941), and newly settled gray snapper (>100 specimens from one rotenone collection) have been collected at depths less than 1 m in dead *Thalassia* blades next to beachrock (Starck, 1970). No submerged mangrove habitats occur in the park, however, and juvenile stages have been most commonly recorded from shallow, hard-bottom areas and grassbeds (Longley and Hildebrand, 1941). The Marquesas Keys, about 60 km to the east, have the nearest submerged mangrove habitats as well as the largest and most complete suite of grassbed, mangrove, and shallow-reef habitats for juvenile stages of any area in the vicinity of the proposed protected areas.

Administration of Essential Fish Habitats

EFH Identification and Management.—All regional fishery-management councils with reef-fish plans generated broad EFH designations. The amendment to the Gulf of Mexico Reef Fishery Management Plan (39 species in five families) identified EFH based on where life stages of 13 representative species and the coral complex commonly occur. The Reef Fishery Management Plan of the Caribbean Fishery Management Council includes 139 species in 39 families. EFH was based on the occurrence of 17 selected species and the coral complex. Both councils concluded that life stages of some managed species occurred in all marine and estuarine waters of their areas, and EFH included all waters and substrates from the shoreline to the seaward limit of the Exclusive Economic Zone (CFMC, 1998; GMFMC, 1998).

The EFH definitions for the multispecies reef-fishery plans of the South Atlantic, Gulf of Mexico, and Caribbean councils reflected the input of every federal and state agency concerned with fish or habitat management in their regions, as well as dozens of university, private-sector, nonprofit, and fishery-industry reviewers. The broad designations are the result of incomplete information, a short administrative time line, a mandate for risk-averse management, and a rule-making process that encourages diverse interest groups and agencies to influence the final administrative language.

The initial EFH designations serve as reference points for agencies commenting on activities that may threaten important habitats. The council seeks more precise EFH designations and will amend fishery-management plans as new methods and information allowing more detailed characterizations become available (e.g., Christensen et al., 1997; Rubec et al., 1999; Ault et al., 1999). For example, the council is working with many agencies to develop GIS data layers that identify fine-scale habitat distributions, abundances of differing life history stages of managed species, and distributions of both EFH and EFH-HAPCs. Ultimately, such information will correlate species production rates with habitat requirements.

Through plans and amendments first implemented in 1983, the council has restricted fishing impacts on habitats (summarized in SAFMC, 1998a,b) to the extent that few activities identified in reviews of gear impacts (e.g., Auster and Langton, 1999) are unregulated in its jurisdiction. As a result of these past actions and the new EFH amendment, the council has prevented, mitigated, or minimized many habitat impacts by most fisheries under its jurisdiction. Research on fishing-gear impacts on EFH is still badly needed, however, and may reveal further regulatory needs.

Protecting EFH from nonfishing impacts is more complicated for several reasons. First, dozens of possible stressors result from nonfishing sources (SAFMC, 1998b). Second, the diversity of interest groups and their influences are much greater than those of fishing interests alone. Third, a greater diversity of agencies must continuously process high numbers of permit requests. The councils and NMFS can comment on projects that affect EFH in any waters but have no direct regulatory authority over construction activities, a continuous source of nearshore impacts. Existing review processes can be improved in several ways, however. For example, the Army Corps of Engineers generates Findings of No Significant Impact (FONSIs) to release projects from formal environmental assessments or impact statements. FONSIs could be less frequent if impacts to EFH-HAPCs are considered. Establishing solid precedents during initial interagency consultations will critically influence the utility of EFH in managing nonfishing impacts.

The effects of many human-caused stressors on habitat function are difficult to measure at the population level. Cumulative effects can develop even when the effects of individual projects are subtle and administratively acceptable. Yet analyses of cumulative effects are often absent from individual coastal construction permits, despite the profound effects that multiple habitat modifications can have (Odum, 1982; Vestal and Rieser, 1995). Habitat permitting requires repetitive reviews of limited databases and can emphasize why impacts seem acceptable, rather than what is not known about project effects on habitat functions or potentially lethal and sublethal effects over time on key populations. Therefore, optimistic assumptions from past permit decisions can, in time, be codified as administrative dogma (Lindeman, 1997b). Given the potential for long-term negative effects on EFH, expanded assessment of cumulative effects during permitting is necessary.

MARINE PROTECTED AREAS

Two fundamental spatial scales in protected area planning correspond to the demersal and pelagic stages of reef-associated species: the cross-shelf area enclosed within no-take reserves (within-reserve scale) and the potential for connectivity, or lack thereof, among multiple protected areas (among-reserve scale). Design decisions may be aided by explicit consideration of both scales.

The Within-Reserve Scale.—Protected areas boundaries should encompass a wide diversity of habitats (Salm and Clark, 1989; Roberts et al., 1995). Because many species settle in shallow areas, inshore of areas inhabited by adults, the identification of ontogenetic cross-shelf migration paths can suggest reserve boundaries. The distance, timing, and habitats used in these migrations can vary within families. For example, several important grouper species settle inshore and use both vegetated and reef habitats as they migrate offshore (e.g., gag, black grouper). Many other grouper species associate primarily with reef habitats and often settle in deeper areas (Table 1). Cross-shelf migration patterns of adults may vary within species as well (Appeldoorn et al., 1997). No-take areas of the Florida Keys National Marine Sanctuary do not extend beyond 18 m depth and do not encompass nearby spawning aggregations (e.g., Carysfort, Eklund et al., this issue; Sand Key, Table 2).

One protected-area design may not be optimal for all species within multispecies management units, but species groups of particular economic and ecological importance can be identified to help focus design decisions. These groups should be identified early in the process to foster consensus among decision makers and to filter out less significant biological information. Such groups can be stratified according to many characteristics including economic value, shared nursery areas, cross-shelf migratory paths, and spawning patterns. In addition, ecosystem management concepts based on trophic (Pauley et al., 1998) or other interspecific relationships may be better organized by identification of shared patterns among key species groups within multispecies management units.

Design alternatives under council consideration include the placement of artificial reefs on relatively barren portions of the shelf on which limited or no catch would be permitted. Favorable attributes include experimental value and popularity among fishermen. If such structures are not used as off-site mitigation for impacts from shoreline construction projects and do not substitute for reserves that include natural reefs, they could serve as useful management tools that effectively allow the fine-scale positioning of both new habitats and protected areas.

Without both research monitoring and consistent law enforcement, effects of protected areas on fish diversity and biomass cannot be assessed, and a primary value of these areas, their potential as control sites, is lost. Protected-area implementation should require a clearly defined monitoring program and, as important, mechanisms to fund it. Inconsistent law enforcement can also make the science moot (e.g., when concentrated poaching events take place during spawning aggregations). Enforcement input is therefore a critical component of the council's design process. For example, the Law Enforcement Advisory Panel has recommended that boundary lines intersect at right angles and align with primary longitude and latitude lines whenever possible.

The Among-Reserve Scale.—Interreserve connectivity may be a key component of protected-area function (Roberts, 1997; Sladek Nowlis and Roberts, 1999). As connectivity may be driven by pelagic developmental pathways (in cases where larval transport is more likely than retention), it is logical to establish pairs or triads of protected areas in networks that overlie shared flow fields among adjacent geographic systems. In council waters, a preliminary network arguably exists between the lower and upper Keys, which have 15 and 8 reserves, respectively. The mainland southeast coast of Florida, however, an area of high reef-fish diversity (Lindeman and Snyder, 1999) that probably receives some larvae spawned in the Keys, has no protected areas (Fig. 2). In addition to pelagic stages, demersal adults can migrate large distances (e.g., gag from South Carolina to northwest Florida, G. Sedberry, pers. comm.).

Networks of protected areas may maximize stock sustainability in the presence of varying external and local recruitment. This approach is prudent, as the geographic paths, and variability, between specific source and sink areas are rarely known. Also, large-scale zoogeographic distributions and underlying mechanisms are incompletely detailed. In addition to new genetic information, delineating metapopulations and probability distributions of their 'boundaries' across multiple spatial scales may require the use of otolith microchemistry (Thorrold et al., 1998) and, possibly, new approaches to zoogeographic analysis (e.g., Humphries and Parenti, 1999).

One approach to evaluating interregion connectivity may not be optimal for all species. Spawning behaviors and sites vary widely among species as do PLDs and larval behaviors, but species groups can also be identified to help focus decision making. Important group attributes include: (1) presence of spawning aggregations, (2) site characteristics of primary spawning areas, (3) PLDs, and (4) potential larval behaviors. Available information on local and downstream flow-field characteristics can be summarized for alternative sites, and indices of relative advection or retention can potentially be developed for some species groups in well-studied areas.

In application, connectivity among downstream protected areas has not always been an explicit design component within or adjacent to council waters. The Tortugas 2000 Working Group identified six criteria (biodiversity/habitat protection, fishery sustainability, law enforcement, sufficient size, socioeconomic impacts, and reference area use) to aid the plotting of boundaries. None of these criteria explicitly focused on connectivity with other reserves. The order of these criteria reflected the importance assigned to each in a group ranking exercise involving many diverse parties within the working group. This design exercise paralleled procedures employed in decision-support systems. Such tools have aided group-based decision making within many disciplines and are underused in fisheries management (Ault and Fox, 1989) and coastal land management (Lindeman, 1997b).

EFH AND PROTECTED AREAS AS COMBINED MANAGEMENT INITIATIVES

This integration of EFH and protected-area initiatives is practical and necessary, as it combines valuable tools that link coastal land management and fishery management. These initiatives have common goals (e.g., ensuring sustainable use of exploited, interdependent coastal resources) but involve differing administrative rules and regulated interests. Coordinated use of EFH and protected areas by decision makers clearly complements the goals of integrated coastal management.

Protected-area regulations involve discrete restrictions on effort and are typically based on law enforcement. In contrast, habitat regulations typically involve permit restrictions on construction projects and site-specific review processes among multiple agencies. If restrictions in a protected area only apply to size classes susceptible to fishing gear, early life stages using inshore nursery areas and migratory habitats across the shelf can be left unprotected. EFH-HAPC designations for habitats used by settlers and juveniles, combined with no-take regulation of adult catches, can ensure that no life stages are unmanaged.

The most immediate protected-area issue involves the Dry Tortugas area, where the Tortugas 2000 Working Group has proposed two no-take areas—Tortugas North (428 km^2) and Tortugas South (207 km^2). If implemented, this proposal will increase the total area of no-take zones in the Florida Keys by more than an order of magnitude. Importantly, the locations of these areas were based on a proposal by representatives of the commercial fishing industry, those most directly affected, and were approved by representatives of a diverse array of interest groups and agencies.

The Tortugas South area was chosen specifically because it includes Riley's Hump, the most-upstream spawning-aggregation site of the Florida Reef Tract. The Gulf of Mexico Council has jurisdiction over Riley's Hump and previously established a two-month seasonal closure (May–June) to protect mutton snapper aggregations. Evidence now suggests that aggregations of gray snapper, cubera snapper, and other species are still heavily fished during their peak spawning months, immediately after the closure ends. As many species use Riley's Hump for a sequential series of heavily fished spawning events, the area qualifies as an EFH-HAPC for both habitat- and fishery-management purposes. A year-round closure of Riley's Hump or an extension of the existing closure is warranted to sustain primary snapper stocks of the lower Keys and possibly areas to the north.

ACKNOWLEDGMENTS

We thank the habitat plan writing teams and their leaders, and the members of the Habitat and Environmental Protection Advisory Panel, Habitat Committee, and Coral Advisory Panel. The insights of Captains D. DeMaria, P. Gladding, and B. Hartig are sincerely appreciated. Comments on the full manuscript by several anonymous reviewers, J. Bohnsack, J. Govoni, C. Grimes, A. Mager, and A. Thistle were essential. Information in Table 1 was provided or reviewed by M. Collins, D. Drass, A. Eklund, D. Harper, D. Jones, C. Koenig, W. Laroche, J. McGovern, C. Manooch, O. Pashuk, A. Powell, B. Richards, F. Rohde, J. Schultz, G. Sedberry, L. Settle, and D. Snyder. Some information in Table 1 was contradictory or incomplete; in such cases, the decisions are the authors' responsibility. B. Haskell contributed information for Figure 2. Council staff, particularly B. Mahood, D. Buscher, and K. O'Malley, were of great assistance. Additional assistance was provided by R. Appeldoorn, K. DeMaria, M. Eng, G. Meester, G. García-Moliner, R. Hill, J. Kimmel, R. Leard, T. Lee, M. Monaco, and J. Rester. This research received support from the South Atlantic Fishery Management Council; Coastal Research and Education, Inc.; NMFS Habitat Conservation Division, NOAA Coastal Ocean Program Grant No. NA37RJ0200; United States Man and the Biosphere Marine and Coastal Ecosystems Directorate Grant No. 471014223B; and South Florida Ecosystem Restoration Protection Modeling Grant No. NA67RJ0149.

LITERATURE CITED

Able, K. W. and M. P. Fahay. 1998. The first year in the life of estuarine fishes in the Middle Atlantic Bight. Rutgers Univ. Press, New Brunswick, New Jersey. 342 p.

Allison, G. W., J. Lubchenco and M. H. Carr. 1998. Marine reserves are necessary but not sufficient for marine conservation. Ecol. Appl. 8: S79–S92.

Allman, R. J. 1999. The temporal and spatial dynamics of spawning, settlement and growth of gray snapper (*Lutjanus griseus*) determined using otolith microstructure. M.S. Thesis, Florida State Univ., Tallahassee, Florida. 70 p.

Appeldoorn, R. S., C. W. Recksiek, R. L. Hill, F. E. Pagan and G. D. Dennis. 1997. Marine protected areas and reef fish movements: the role of habitat in controlling ontogenetic migration. Proc. 6th Int'l. Coral Reef Symp. 2: 1917–1922.

Arreguín-Sánchez, F., J. L. Munro, M. C. Balgos and D. Pauly, eds. 1996. Biology, fisheries and culture of tropical groupers and snappers. ICLARM Conf. Proc. 48. Int'l. Center for Living Aquatic Resources Management, Makati, Philippines. 449 p.

Atkinson, L. P., D. W. Menzel and K. A. Bush, eds. 1985. Oceanography of the southeastern U.S. continental shelf. Am. Geophys. Union, Washington, D.C. 156 p.

Ault, J. S. and W. W. Fox, Jr. 1989. FINMAN: simulated decision analysis with multiple objectives. Am. Fish. Soc. Symp. 6: 166–179.

__________, J. A. Bohnsack and G. Meester. 1998. A retrospective (1979–1995) multispecies assessment of coral reef fish stocks in the Florida Keys. Fish. Bull., U.S. 96: 395–414.

__________, J. Luo, S. G. Smith, J. E. Serafy, J. D. Wang, R. Humston and G. Diaz. 1999. A spatial dynamic multistock production model. Can. J. Fish. Aquat. Sci. 56: 1–22.

Auster, P. J. and R. W. Langton. 1999. The effects of fishing on habitat. Am. Fish. Soc. Symp. 22: 150–187.

Blaber, S. J. M., D. T. Brewer and J. P. Salini. 1989. Species composition and biomass of fishes in different habitats of a tropical northern Australian estuary: their occurrence in the adjoining sea and estuarine dependence. Estuar. Coast. Shelf Sci. 29: 509–531.

Boesch, D. F. and R. E. Turner. 1984. Dependence of fishery species on salt marshes: the role of food and refuge. Estuaries 7: 460–468.

Bohnsack, J. A. 1997. Consensus development and the use of marine reserves in the Florida Keys, U.S.A. Proc. 8th Int'l. Coral Reef Symp. 2: 1927–1930.

____________, D. E. Harper, D. B. McClellan, D. L. Sutherland, and M. W. White. 1987. Resource survey of fishes within Looe Key National Marine Sanctuary. NOAA Tech. Memo. NOS MEMD 5. 108 p.

Briggs, J. C. 1974. Marine zoogeography. McGraw-Hill, New York. 475 p.

CFMC (Caribbean Fishery Management Council). 1998. Essential fish habitat generic amendment to the fishery management plans of the U.S. Caribbean, volume 1. San Juan, Puerto Rico.

Chester, A. J., G. R. Huntsman, P. A. Tester and C. S. Manooch III. 1984. South Atlantic Bight reef fish communities as represented in hook-and-line catches. Bull. Mar. Sci. 34: 267–279.

Chiappone, M. and R. Sluka. 1996. Fishes and fisheries. Site characterization of the Florida Keys National Marine Sanctuary and environs, vol. 6. The Preserver, Zenda, Wisconsin. 149 p.

Christensen, J. D., T. A. Battista, M. E. Monaco and C. J. Klein. 1997. Habitat suitability index modeling and GIS technology to support habitat management: Pensacola Bay, Florida, Case study. Rpt. to NOAA Strategic Environmental Assessment Division, Washington, D.C. 90 p.

Claro, R. 1981. Ecologia y ciclo de vida del pargo criollo, *Lutjanus analis* (Cuvier), en la plataforma Cubana. Informe cientifico-técnico, no. 186. Editora de la Academia de Ciencias de Cuba, Havana. 83 p.

____________, ed. 1994. Ecología de los peces marinos de Cuba. Centro de Investigaciones de Quintana Roo, Chetumal, Quintana Roo, Mexico, and Instituto de Oceanología, Habana, Cuba. 525 p.

Coleman, F. C., C. C. Koenig, A. Eklund and C. B. Grimes. 1999. Management and conservation of temperate reef fishes in the grouper-snapper complex of the southeastern United States. Am. Fish. Soc. Symp. 23: 233–242.

Colin, P. L. and I. E. Clavijo. 1988. Spawning activity of fishes producing pelagic eggs on a shelf edge coral reef, southwestern Puerto Rico. Bull. Mar. Sci. 43: 249–279.

__________, W. A. Laroche and E. B. Brothers. 1997. Ingress and settlement in the Nassau grouper, *Epinephelus striatus* (Pisces: Serranidae), with relationship to spawning occurrence. Bull. Mar. Sci. 60: 656–667.

Cowen, R. K. and S. Sponaugle. 1997. Relationships between early life history traits and recruitment among coral reef fishes. Pages 423–448 *in* R. C. Chambers and E. A. Trippel, eds. Early life history and recruitment in fish populations. Chapman & Hall, London.

DeMaria, K. 1996. Changes in the Florida Keys marine ecosystem based upon interviews with experienced residents. Rpt. to The Nature Conservancy and Center for Marine Conservation.

Doherty P., M. Kingsford, D. Booth and J. Carleton. 1996. Habitat selection before settlement by *Pomacentrus coelestis*. Mar. Freshw. Res. 47: 391–399.

Domeier, M. L., C. C. Koenig and F. C. Coleman. 1996. Reproductive biology of the gray snapper (*Lutjanus griseus*), with notes on spawning for other Western Atlantic snappers (Lutjanidae). Pages 189–201 *in* F. Arreguín-Sánchez, J. L. Munro, M. C. Balgos and D. Pauly, eds. Biology, fisheries and culture of tropical groupers and snappers. ICLARM Conf. Proc.. International Center for Living Aquatic Resources Management, Makati, Philippines.

____________ and P. L. Colin. 1997. Tropical reef fish spawning aggregations: defined and reviewed. Bull. Mar. Sci. 60: 698–726.

Dyer, C. L. 1994. Proaction versus reaction: integrating applied anthropology into fisheries management. Human Organization 53: 83–88.

Fiske, S. J. 1992. Sociocultural aspects of establishing marine protected areas. Ocean Coastal Manage. J. 18: 25–46.

García-Cagide, A., R. Claro, and B. V. Koshelev. 1994. Reproducción. Pages 187–262 *in* R. Claro, ed. Ecología de los peces marinos de Cuba. Centro de Investigaciones de Quintana Roo, Chetumal, Quintana Roo, Mexico, and Instituto de Oceanología, Habana, Cuba.

Gilmore, R. G., Jr. 1995. Environmental and biogeographic factors influencing ichthyofaunal diversity: Indian River Lagoon. Bull. Mar. Sci. 57: 153–170.

________________ and R. J. Jones. 1992. Color variation and associated behavior in the epinepheline groupers, *Mycteroperca microlepis* (Goode and Bean) and *M. phenax* Jordan and Swain. Bull. Mar. Sci. 51: 83–103.

Ginsburg, R. N. 1953. Beachrock in south Florida. J. Sed. Petrol. 23: 85–92.

Goldberg, W. M. 1973. The ecology of the coral-octocoral communities off the southeast Florida coast: geomorphology, species composition, and zonation. Bull. Mar. Sci. 23: 465–488.

Govoni, J. J. 1993. Flux of larval fishes across frontal boundaries: examples from the Mississippi River plume front and the western Gulf Stream front. Bull. Mar. Sci. 53: 538–566.

__________ and J. A. Hare (in press). The Charleston Gyre as a spawning and larval nursery habitat for fishes. Am. Fish. Soc. Symp.

Grimes, C. B. 1987. Reproductive biology of the Lutjanidae: a review. Pages 239–294 *in* J. J. Polovina and S. Ralston, eds. Tropical snappers and groupers: biology and fisheries management. Westview Press, Boulder, Colorado.

__________, C. F. Idelberger, K. W. Able and S. C. Turner. 1988. The reproductive biology of the tilefish, *Lopholatilus chamaeleonticeps*, Goode and Bean, from the U.S. Mid Atlantic Bight, and the effects of fishing on the breeding system. Fish. Bull., U.S. 86: 745–762.

GMFMC (Gulf of Mexico Fishery Management Council). 1998. Generic amendment for addressing essential fish habitat requirements in the following fishery management plans of the Gulf of Mexico: shrimp, red drum, reef fish, coastal pelagics, stone crab, spiny lobster, and coral reefs. Tampa, Florida.

Halvorsen, K. L. 1994. Recruitment of larval snappers (Pisces: Lutjanidae) in Exuma Sound, Bahamas. M.S. Thesis, Florida Institute of Technology, Melbourne, Florida. 81 p.

Hildebrand, S. F. and W. C. Schroeder. 1928. Fishes of Chesapeake Bay. U.S. Fish and Wildlife Service, Fishery Bulletin no. 43, part 1. U.S. Government Printing Office, Washington, D.C. 366 p.

Hoffmeister, J. E. 1974. Land from the sea: the geologic story of South Florida. Univ. Miami Press, Coral Gables, Florida. 143 p.

Houde, E. D. and C. E. Dowd. 1976. Lutjanid and serranid larvae from the eastern Gulf of Mexico. Univ. Miami, NOAA Contract NMFS P001-6042-11080.

Humphries, C. J. and L. R. Parenti. 1999. Cladistic biogeography: interpreting patterns of plant and animal distributions, 2nd ed. Oxford Univ. Press, New York. 187 p.

Johannes, R. E. 1981. Working with fishermen to improve coastal tropical fisheries and resource management. Bull. Mar. Sci. 31: 673–680.

Johnson, D. R., N. A. Funicelli and J. A. Bohnsack. 1999. Effectiveness of an existing estuarine no-take fish sanctuary within the Kennedy Space Center, Florida. N. Am. J. Fish. Manage. 19: 436–453.

Kaufman, L. S., J. Ebersole, J. Beets and C. C. McIvor. 1992. A key phase in the recruitment dynamics of coral reef fishes: post-settlement transition. Environ. Biol. Fishes 34: 109–118.

Keener, P., G. D. Johnson, B. W. Stender, E. B. Brothers and H. R. Beatty. 1988. Ingress of postlarval gag, *Mycteroperca microlepis* (Pisces: Serranidae), through a South Carolina barrier island inlet. Bull. Mar. Sci. 42: 376–396.

Koenig, C. C., F. C. Coleman, L. A. Collins, Y. Sadovy, and P. L. Colin. 1996. Reproduction in gag (*Mycteroperca microlepis*) (Pisces: Serranidae) in the eastern Gulf of Mexico and the consequences of fishing spawning aggregations. Pages 307–323 *in* F. Arreguín-Sánchez, J. L. Munro, M. C. Balgos and D. Pauly, eds. Biology, fisheries and culture of tropical groupers and snappers. ICLARM Conf. Proc. International Center for Living Aquatic Resources Management, Makati, Philippines.

Lee, T. N. and D. A. Mayer. 1977. Low-frequency current variability and spin-off eddies along the shelf off southeast Florida. J. Mar. Res. 35: 193–220.

__________ and E. Williams. 1999. Mean distributions and seasonal variability of coastal currents and temperature in the Florida Keys with implications for larval recruitment. Bull. Mar. Sci. 64: 35–56.

__________, M. E. Clarke, E. Williams, A. F. Szmant and T. Berger. 1994. Evolution of the Tortugas Gyre and its influence on recruitment in the Florida Keys. Bull. Mar. Sci. 54: 621–646.

Leis, J. M. 1987. Review of the early life history of tropical groupers (Serranidae) and snappers (Lutjanidae). Pages 189–237 *in* J. J. Polovina and S. Ralston, eds. Tropical snappers and groupers: biology and fisheries management. Westview Press, Boulder, Colorado.

__________. 1991. The pelagic stage of reef fishes: the larval biology of coral reef fishes. Pages 183–230 *in* P. F. Sale, ed. The ecology of fishes on coral reefs. Academic Press, San Diego.

__________, H. P. A. Sweatman and S. E. Reader. 1996. What the pelagic stages of coral reef fishes are doing out in blue water: daytime field observations of larval behavioural capabilities. Mar. Freshw. Res. 47: 401–411.

Lenanton, R. C. J. and I. C. Potter. 1987. Contribution of estuaries to commercial fisheries in temperate western Australia and the concept of estuarine dependence. Estuaries 10: 28–35.

Ley, J. A., C. C. McIvor and C. L. Montague. 1999. Fishes in mangrove prop-root habitats of northeastern Florida Bay: distinct assemblages across an estuarine gradient. Estuar. Coast. Shelf Sci. 48: 701–723.

Limouzy-Paris, C. B., H. C. Graber, D. L. Jones, A. W. Ropke and W. J. Richards. 1997. Translocation of larval coral reef fishes via sub-mesoscale spin-off eddies from the Florida Current. Bull. Mar. Sci. 60: 966–983.

Lindeman, K. C. 1997a. Development of grunts and snappers of southeast Florida: cross-shelf distributions and effects of beach management alternatives. Ph.D. Dissertation, Univ. Miami, Coral Gables, Florida. 419 p.

____________. 1997b. Comparative management of beach systems of Florida and the Antilles: applications using ecological assessment and decision support procedures. Pages 134–164 *in* G. Cambers, ed. Managing beach resources in the smaller Caribbean islands. UNESCO Coastal Region and Small Island Papers #1. 269 p.

____________ and D. B. Snyder. 1999. Nearshore hardbottom fishes of southeast Florida and effects of habitat burial caused by dredging. Fish. Bull., U.S. 97: 508–525.

____________, G. Diaz, J. E. Serafy and J. S. Ault. 1998. A spatial framework for assessing cross-shelf habitat use among newly settled grunts and snappers. Proc. Gulf Carib. Fish. Inst. 50: 385–416.

Longley, W. H. and S. F. Hildebrand. 1941. Systematic catalogue of the fishes of Tortugas, Florida, with observations on color, habits and local distribution. Carnegie Institute of Washington, Washington, D.C. 331 p.

McCormick, M. I. and L. J. Makey. 1997. Post-settlement transition in coral reef fishes: overlooked complexity in niche shifts. Mar. Ecol. Prog. Ser. 153: 247–257.

McFarland, W. N., E. B. Brothers, J. C. Ogden , M. J. Shulman, E. L. Bermingham and N. M. Kotchian-Prentis. 1985. Recruitment patterns in young French grunts, *Haemulon flavolineatum* (family Haemulidae), at St. Croix, Virgin Islands. Fish. Bull., U.S. 83: 151–161.

Manooch, C. S., III. 1987. Age and growth of snappers and groupers. Pages 329–373 *in* J. J. Polovina and S. Ralston, eds. Tropical snappers and groupers: biology and fisheries management. Westview Press, Boulder, Colorado.

____________ and J. C. Potts. 1996. Growth characteristics of the spottail pinfish, *Diplodus holbrooki*, off North Carolina. J. Elisha Mitchell Sci. Soc. 112(1): 7–19.

Marszalek, D. S., G. Babashoff, Jr., M. R. Noel and D. R. Worley. 1977. Reef distribution in south Florida. Proc. 3rd Int'l. Coral Reef Symp. 2: 223–229.

Matheson, R. H., III, G. R. Huntsman and C. S. Manooch III. 1986. Age, growth, mortality, food, and reproduction of the scamp, *Mycteroperca phenax*, collected off North Carolina and South Carolina. Bull. Mar. Sci. 38: 300–312.

Miller, J. M. 1988. Physical processes and the mechanisms of coastal migrations of immature marine fishes. Am. Fish. Soc. Symp. 3: 68–76.

Munro, J. L., ed. 1983. Caribbean coral reef fishery resources. Int'l. Center for Living Aquatic Resources Management, Manila, Philippines. 276 p.

Nakamura, E. L., J. R. Taylor and I. K. Workman. 1980. The occurrence of life stages of some recreational marine fishes in estuaries of the Gulf of Mexico. NOAA Tech. Memo. NMFS-SEFC-45. 53 p.

Nelson, D. M., E. A. Irlandi, L. R. Settle, M. E. Monaco and L. Coston-Clements. 1991. Distribution and abundance of fishes and invertebrates in southeast estuaries. ELMR Rpt. no. 9., NOAA/NOS Strategic Environmental Assessments Division, Silver Spring, Maryland. 167 p.

NOAA (National Oceanic and Atmospheric Administration). 1996. Magnuson-Stevens fishery conservation and management act, as amended through October 11, 1996. NOAA Tech. Memo. NMFS-F/SPO-23. 121 p.

Odum, W. E. 1982. Environmental degradation and the tyranny of small decisions. BioScience 32: 728–729.

Parker, R. O., Jr. and R. W. Mays. 1998. Southeastern United States deepwater reef fish assemblages, habitat characteristics, catches, and life history summaries. NOAA Tech. Rpt.138. 41 p.

Pauly, D., V. Christensen, J. Dalsgaard, R. Froese and F. Torres, Jr. 1998. Fishing down marine food webs. Science 279: 860–863.

Plan Development Team. 1990. The potential of marine fishery reserves for reef fish management in the U.S. southern Atlantic. Snapper-Grouper Plan Development Team Report for the South

Atlantic Fisheries Management Council. NOAA Tech. Memo. NMFS-SEFC-261. National Marine Fisheries Service, Southeast Fisheries Center, Miami, Florida. 45 p.

Poizat, G. M. and E. Baran. 1997. Fishermen's knowledge as background information in tropical fish ecology: a quantitative comparison with fish sampling results. Environ. Biol. Fishes 50: 435–439.

Polovina, J. J. and S. Ralston, eds. 1987. Tropical snappers and groupers: biology and fisheries management. Westview Press, Boulder, Colorado. 659 p.

Richards, W. J. and K. C. Lindeman. 1987. Recruitment dynamics of reef fishes; planktonic processes, settlement and demersal ecologies, and fishery analysis. Bull. Mar. Sci. 41: 392–410.

Roberts, C. M. 1997. Connectivity and management of Caribbean coral reefs. Science 278: 1454–1457.

__________, W. J. Ballantine, C. Buxton, P. K. Dayton, L. Crowder, W. Milon, M. Orbach, D. Pauly, J. Trexler and C. Walters. 1995a. Review of the use of marine fishery reserves in the U.S. southeastern Atlantic. NOAA Tech. Memo. NMFS-SEFSC-376. Miami, Florida. 31 p.

Robertson, A. I. and N. C. Duke. 1987. Mangroves as nursery sites: comparisons of the abundance and species composition of fish and crustaceans in mangroves and other nearshore habitats in tropical Australia. Mar. Biol. 96: 193–205.

Robertson, D. R. 1988. Extreme variation in settlement of the Caribbean triggerfish, *Balistes vetula*, in Panama. Copeia 1988(3): 698–703.

Rubec, P. J., J. C. W. Bexley, H. Norris, M. S. Coyne, M. E. Monaco, S. G. Smith and J. S. Ault. 1999. Suitability modeling to delineate habitats essential for sustainable fisheries. Am. Fish. Soc. Symp. 22: 108–133.

SAFMC (South Atlantic Fishery Management Council). 1983a. Source document for the snapper grouper fishery of the south Atlantic region. Charleston, South Carolina.

________. 1983b. Fishery management plan for coral and coral reefs of the Gulf of Mexico and south Atlantic. Charleston, South Carolina. Prepared in collaboration with Gulf of Mexico FMC, Tampa, Florida.

________. 1983c. Fishery management plan, regulatory impact review and final environmental impact statement for the snapper grouper fishery of the south Atlantic region. Charleston, South Carolina.

________. 1998a. Final comprehensive amendment addressing essential fish habitat in fishery management plans of the south Atlantic region. Including a final environmental impact statement/supplemental environmental impact statement, initial regulatory flexibility analysis, regulatory impact review, and social impact assessment/fishery impact statement. Charleston, South Carolina. 136 p.

________. 1998b. Final habitat plan for the south Atlantic region: essential fish habitat requirements for fishery management plans of the South Atlantic Fishery Management Council. Charleston, South Carolina. 639 p.

SGA (Snapper Grouper Assessment Group). 1999. Results of snapper-grouper assessment panel meeting, February 1999. South Atlantic Fishery Management Council, Charleston, South Carolina.

Sale, P. F., ed. 1991. The ecology of fishes on coral reefs. Academic Press, San Diego. 754 p.

Salm, R. V. and J. R. Clark. 1989. Marine and coastal protected areas: a guide for planners and managers, 2nd ed. Int'l. Union for the Conservation of Nature, Gland, Switzerland. 302 p.

Sedberry, G. R. and R. F. Van Dolah. 1984. Demersal fish assemblages associated with hard-bottom habitat in the South Atlantic Bight of the U.S.A. Environ. Biol. Fishes 11: 241–258.

__________, G. F. Ulrich and A. J. Applegate. 1994. Development and status of the fishery for wreckfish, *Polyprion americanus*, in the western North Atlantic. Proc. Gulf Carib. Fish. Inst. 43: 168–192.

Settle, L. R. 1993. Spatial and temporal variability in the distribution and abundance of larval and juvenile fishes associated with pelagic *Sargassum*. M.S. Thesis, Univ. North Carolina at Wilmington. Wilmington, North Carolina. 64 p.

Shapiro, D. Y., D. A. Hensley and R. A. Appeldoorn. 1988. Pelagic spawning and egg transport in coral-reef fishes: a skeptical overview. Environ. Biol. Fishes 22: 3–14.

Sladek Nowlis, J. and C. M. Roberts. 1999. Fisheries benefits and optimal design of marine reserves. Fish. Bull., U.S. 97: 604–616.

Sogard, S. M., G. V. N. Powell and J. G. Holmquist. 1987. Epibenthic fish communities on Florida Bay banks: relations with physical parameters and seagrass cover. Mar. Ecol. Prog. Ser. 40: 25–39.

Sponaugle, S. and R. K. Cowen. 1997. Early life history traits and recruitment patterns of Caribbean wrasses (Labridae). Ecol. Monogr. 67: 177–202.

Starck, W. A. 1970. Biology of the gray snapper, *Lutjanus griseus* (Linnaeus), in the Florida Keys. Stud. Trop. Oceanogr. (Miami) 10: 1–150.

Stobutzki, I. C. and D. R. Bellwood. 1997. Sustained swimming abilities of the late pelagic stages of coral reef fishes. Mar. Ecol. Prog. Ser. 149: 35–41.

__________ and __________. 1998. Nocturnal orientation to reefs by late pelagic stage coral reef fishes. Coral Reefs 17: 103–110.

Thayer, G. W., D. R. Colby and W. F. Hettler. 1987. Utilization of the red mangrove prop root habitat by fishes in South Florida. Mar. Ecol. Prog. Ser. 35: 25–28.

Thorrold, S. R., C. M. Jones, P. K. Swart and T. E. Targett. 1998. Accurate classification of juvenile weakfish (*Cynoscion regalis*) to estuarine nursery areas based on chemical signatures in otoliths. Mar. Ecol. Prog. Ser. 173: 253–265.

Thresher, R. E. 1984. Reproduction in reef fishes. TFH Publications, Neptune City, New Jersey. 399 p.

Tzeng, M. W. 2000. Patterns of ingress, age, and growth of snappers (principally *Lutjanus griseus*) near Beaufort Inlet, North Carolina. M.S. Thesis, Univ. North Carolina at Wilmington, Wilmington, North Carolina.

Valdes-Pizzini, M. 1990. Fishermen associations in Puerto Rico: praxis and discourse in the politics of fishing. Human Organization 49: 164–172.

Van Sant, S. B., M. R. Collins and G. R. Sedberry. 1994. Preliminary evidence from a tagging study for a gag (*Mycteroperca microlepis*) spawning migration with notes on the use of oxytetracycline for chemical tagging. Proc. Gulf Carib. Fish. Inst. 43: 417–428.

Vestal, B., and A. Rieser. 1995. Part I—Syntheses, with annotated bibliography. Pages 1–135 *in* Methodologies and mechanisms for management of cumulative coastal environmental impacts. Decision Analysis Series no. 6. NOAA Coastal Ocean Office, Silver Spring, Maryland.

Victor, B. C. 1991. Settlement strategies and biogeography of reef fishes. Pages 231–260 *in* P. F. Sale, ed. The ecology of fishes on coral reefs. Academic Press, San Diego.

Wicklund, R. 1969. Observations on spawning of lane snapper. Underwater Nat. 6: 40.

ADDRESS: (K.C.L., J.S.A.) *Division of Marine Biology and Fisheries, Rosenstiel School of Marine and Atmospheric Science, University of Miami, 4600 Rickenbacker Causeway, Miami, Florida 33149;* (R.P., G.T.W.) *South Atlantic Fishery Management Council, One Southpark Circle, Suite 306, Charleston, South Carolina 29407.* CORRESPONDING AUTHOR'S NEW ADDRESS: (K.C.L.) *Environmental Defense, Miami Field Office, 14630 SW 144 Terrace, Miami, Florida 33186.*