

# ***A Review of Movement in Gulf of Mexico Red Snapper: Implications for Population Structure***

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*Abstract.*—A review of studies examining stage-specific distribution and movement of various life stages of red snapper, *Lutjanus campechanus*, in U.S. waters of the Gulf of Mexico (GOM) was conducted to draw inference about population structure. Hydrodynamic modeling of neither egg nor larval transport has been conducted for GOM red snapper; thus, the potential for planktonic dispersal among regions is currently unknown. However, recent studies of other reef fishes have demonstrated that larval fishes may not act as passive particles. Postsettlement movement, or the lack thereof, may be just as important for describing population connectivity and structure as planktonic transport. Red snapper juveniles display thigmotaxis and have been shown to undergo an ontogenetic shift in which the dimension and complexity of their habitat increases with fish size. Tagging data demonstrate that while a substantial percentage of tagged fish were recaptured near their release sites, movement on the scale of hundreds of km also has been reported. Direct estimates of movement and population mixing from ultrasonic tagging, conventional tagging, and otolith chemistry studies indicate movement of some individuals may be sufficient to promote genetic exchange among regions, but overall movement is likely insufficient to affect population demographic differences observed among regions. Therefore, GOM red snapper meet criteria for consideration as a metapopulation: subpopulations are distinct, dispersal mechanisms exist among subpopulations, and asynchrony in population demographics is apparent among subpopulations.

## **Introduction**

Red snapper, *Lutjanus campechanus*, have been intensively managed in U.S. waters of the Gulf of Mexico (GOM) since the late 1980s when they were first estimated to be overfished and undergoing overfishing (Goodyear 1988; reviewed in Hood et al. 2007, this volume). Despite increasingly stringent harvest regulations placed on the di-

rected fishery since the early 1990s, the stock has failed to recover, or even show significant signs of moving toward recovery (Hood et al. 2007, this volume; Porch 2007, this volume). Goodyear (1995) estimated shrimp trawl bycatch was the most significant source of mortality for GOM red snapper, the implications of which were the directed fishery would have to be either severely curtailed or closed in order to recover the stock if bycatch could not

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be minimized. Although more restrictive size and daily catch limits were put in place, other management options also have been explored in hopes of lessening the impact of regulations on the directed fisheries. Bycatch reduction devices (BRDs) were required in 1998 for shrimp trawlers operating west of Cape San Blas, Florida, and in the entire U.S. GOM in 2004 (Hood et al. 2007, this volume). Stock enhancement also has been suggested as a means to recover red snapper without restricting the directed fishery (Papanikos et al. 2003; Ogle and Lotz 2006). Last, marine protected areas (MPAs) have been recommended as another alternative to increase red snapper biomass, although MPAs may provide additional conservation benefits that extend well beyond the fishery (Holland and Brazee 1993; Trexler and Travis 2000; Baskett et al. 2005).

Nearly all of the significant conservation questions concerning GOM red snapper have at their core the issues of population structure and the stage-specific distribution and movement of individuals. Clearly, red snapper are not unique in that respect as the importance of understanding population structure and connectivity has been stressed since early in the 20<sup>th</sup> century (Hjort 1914; Secor 2002, 2006). In reef fishes, eggs and larvae traditionally have been viewed as the most likely life history stages during which population mixing may occur given the potential for long-distance dispersal of planktonic early life stages and the often sedentary nature of adults (Jones et al. 1999; Swearer et al. 2002). Following that logic, several authors invoked planktonic transport of red snapper early life stages to explain the lack of genetic divergence reported among northern GOM regions (Goodyear 1995; Gold et al. 1997, 2001; Saillant and Gold 2006). Recent studies of other reef fishes, however, have indicated larvae may not act as passive particles in the sea and that self-recruitment mechanisms are prevalent (Cowen and Castro 1994; Jones et al. 1999, 2005; Swearer et al. 2002; Cowen et al. 2006; Almany et al. 2007). As a corollary, postsettlement movement may be more important than previously realized in facilitating population mixing in reef fishes, especially in large reef fishes, such as snappers and groupers, that may at times move great distances (Patterson et al. 2001; Lindberg et al. 2006).

The objective of this paper was to review the literature on GOM red snapper movement in order to draw inference about the implications observed movement has for red snapper population structure. Little is known about oceanographic transport of red snapper eggs and larvae, but what has been described about the occurrence of these life stages and their distributions is discussed briefly. The bulk of the paper reviews studies of postsettlement habitat, site fidelity, and movement of red snapper. Much research effort has been expended in recent years describing ontogenetic shifts in red snapper habitat-specific distribution, as well as the potential for postsettlement movement to affect population connectivity, or the lack of movement, to shape localized population demographics. Overall, this review is aimed at facilitating a better understanding of GOM red snapper population structure and connectivity.

## Methods

A literature search was conducted for GOM red snapper within Cambridge Scientific Abstracts' Natural Sciences Database ([www.csa.com](http://www.csa.com)). Separate searches were conducted for "*Lutjanus campechanus*" or "red snapper" appearing anywhere within citations published between 1980 and 2006. Unique citations of peer-reviewed publications were placed into one of ten categories: age and growth, bycatch, culture, diet/bioenergetics, fisheries management, genetics, habitat, movement, MPAs, reproduction and early life history, and miscellaneous. Papers were evaluated in the context of red snapper movement, population connectivity, and population structure. Additional papers reviewed include technical documents presented at the 2004 Southeast Data Assessment and Review (SE-DAR) workshops for GOM red snapper (SE-DAR7), technical reports featuring red snapper movement that were cited in other studies, and peer-reviewed publications published prior to 1980 and cited in subsequent papers.

## Results and Discussion

The literature search within Cambridge Scientific Abstracts' Natural Sciences Database

yielded 149 GOM red snapper papers that appeared in the literature between 1980 and 2006. More papers were published in the genetics ( $n = 23$ ) category than any other. Nine of those manuscripts detailed studies examining molecular markers in red snapper fillets in order to distinguish them from mislabeled species in the marketplace (e.g., Marko et al. 2004), but the subject of the majority of the genetics papers ( $n = 13$ ) was estimating genetic population structure in GOM red snapper (e.g., Pruett et al. 2005; Saillant and Gold 2006). Papers examining red snapper fisheries management ( $n = 15$ ) ranged from examining the effect of regulatory discards in the directed fisheries to estimating the value of the recreational fishery to an assessment of implementing an individual transferable quota system in the commercial fishery. Several papers ( $n = 19$ ) described red snapper habitat affinity and ontogenic shifts in habitat utilization, with papers split among juvenile habitat studies ( $n = 9$ ), natural hardbottom habitat of adults ( $n = 1$ , but 2 others in the MPA category), and artificial reefs ( $n = 9$ ). Diet and bioenergetics studies ( $n = 7$ ) also tended to emphasize ontogenic shifts and habitat-specific differences in diet. Age and growth papers were prevalent ( $n = 16$ ), but only in one were differences in red snapper size at age tested among GOM regions (Fischer et al. 2004). Movement studies ( $n = 13$ ) examined life stage specific site fidelity and movement, as well as the residency of adult red snapper at artificial reef sites. Twenty-one percent ( $n = 32$ ) of the studies examined alternative management strategies for rebuilding red snapper, including stock enhancement (culture;  $n = 15$ ), bycatch reduction ( $n = 11$ ), and the efficacy of MPAs for rebuilding red snapper spawning stock biomass ( $n = 6$ ). Relatively few studies were directed at reproductive biology ( $n = 4$ ) or early life stages ( $n = 4$ ), the latter result highlighting the paucity of information available on red snapper eggs and larvae in the wild.

### Dispersal of Early Life Stages

Authors of early studies of GOM red snapper reproductive biology concluded that fish began reaching sexual maturity at small size (<300 mm total length TL) and had protracted

spawning seasons extending throughout summer months (Bradley and Bryan 1975; Futch and Bruger 1976; Moseley 1966). Collins et al. (1996) were the first to estimate batch fecundity in red snapper and to establish that the spawning season extended from April through October in both the eastern and western GOM. The protracted spawning season for red snapper, combined with a larval stage duration of approximately 20 d (Szedlmayer and Conti 1999; Drass et al. 2000; Rooker et al. 2004), provides the potential for significant planktonic dispersal, and several authors have hypothesized that oceanographic transport of eggs and larvae is at least partially responsible for the lack of significant differences reported in selectively neutral genetic markers among GOM regions (Goodyear 1995; Gold et al. 1997; Saillant and Gold 2006). Despite the lack of significant genetic differences, Jackson et al. (this volume) reported maturity schedules and size-specific fecundity were significantly different between red snapper populations east and west of the mouth of the Mississippi River. They suggested early maturity at smaller size in the eastern GOM may be a genotypic response to high fishing mortality having selectively removed later maturing genotypes, a response that would not be apparent in selectively neutral genetic markers such as mitochondrial DNA (mtDNA) or nuclear DNA microsatellites (Pruett et al. 2005; Saillant and Gold 2006). Regardless of the causative factor of differences in reproductive biology parameters between the eastern and western GOM, the fact that regional population demographic differences exist implies some degree of isolation between the eastern and western GOM. Regional differences in size at age reported by Fischer et al. (2004) further support that population structure exists in GOM red snapper, which has not been revealed by traditional fisheries genetics applications (Pruett et al. 2005; Gold and Saillant 2007, this volume).

Relatively little was known until recently about the distribution of red snapper eggs and larvae in the GOM, and the extent to which interregional mixing may occur in the plankton remains unresolved (Hanisko et al. 2007, this volume; Lyczkowski-Shultz and Hanisko 2007, this volume). Collins et al. (1980) described morphometric and meristic characteristics of

larvae and Potthoff et al. (1988) described their osteological development. Drass et al. (2000) were the first to describe characters that distinguished larval red snapper as small as 3.5 mm (mid-flexion) from potentially co-occurring congeners and confamilials. Based on those characters, Lyczkowski-Shultz and Hanisko (this volume) reported a total of 1,692 red snapper larvae were identified in >14,000 bongo and neuston net samples collected on National Marine Fisheries Service (NMFS) research surveys between 1982 and 2003. Those data were used to compute fishery-independent indices of spawning stock biomass (Hanisko et al. 2007, this volume), but as yet no modeling exercise has been conducted to estimate the effect of oceanographic processes on the distribution and potential dispersal of larvae (e.g., Hanisko and Lyczkowski-Shultz 2003; Fitzhugh et al. 2005; Cowen et al. 2006).

Several authors hypothesized that oceanographic transport of eggs and larvae may be sufficient to facilitate population mixing despite the lack of hydrodynamic modeling of egg or larval transport in the northern GOM. Gold et al. (1997) reported mtDNA haplotype frequencies were not significantly different among northern GOM regions; thus, the authors failed to reject the null hypothesis that GOM red snapper constitute a single panmictic stock. They suggested genetic mixing among regions, or populations, may occur during planktonic egg and larval stages due to the preponderance of evidence, at that time, that red snapper adults were sedentary. However, the authors also suggested, based on intrapopulational mtDNA diversity differences, that GOM red snapper might include recently derived, but as yet not genetically distinct, population subunits. Pruett et al. (2005) conducted nested clade analysis of mtDNA haplotypes and concluded the genetic history of GOM red snapper was complex, as mtDNA frequencies suggested periods of both range expansion and ones of restricted flow resulting from isolation by distance. They hypothesized that apparently restricted gene flow among contemporary red snapper populations may yield metapopulation structure, but that hypothesis likely is not testable with selectively neutral genetic markers. Nevertheless, Pruett et al. (2005) suggested

asynchrony observed in red snapper population demographics among northern GOM regions (Fischer et al. 2004; Jackson et al. 2007, this volume) was evidence that metapopulation structure may exist within GOM red snapper, despite the lack of divergence in selectively neutral genetic markers. Last, the authors concluded that precise estimates of exchange (i.e., movement) among regions was required to further examine the existence of metapopulation structure.

Discussions of interregional or interpopulational connectivity in GOM red snapper, as presented above, typically have centered on hypothesized, but as yet untested, oceanographic transport of eggs and larvae. Recent studies of other reef fishes, however, have indicated that larvae may not behave as passive particles in the sea and that self-recruitment mechanisms, including ones promoting endemism, are prevalent (Cowen and Castro 1994; Jones et al. 1999, 2005; Swearer et al. 2002; Cowen et al. 2006; Almany et al. 2007). Cowen et al. (2000) reported hydrographic model simulations of larval fish transport within the Caribbean Basin tended to overestimate dispersal when simple advection was assumed, thus demonstrating the importance of local retention in maintaining population structure. Other authors have demonstrated retention mechanisms in meroplanktonic invertebrates that metamorphose into sessile adults (e.g., Ayre and Hughes 2000; Johnson and Black 2006; Gilg and Hilbish 2003), as well as in reef fishes that display limited postsettlement home ranges (e.g., Doherty et al. 1995; James et al. 2002; Almany et al. 2007). However, the potential for interpopulational mixing clearly is greater, postsettlement, for reef-associated fishes that do not demonstrate high long-term site fidelity (Ingram and Patterson 2001; Patterson et al. 2001; Meyer et al. 2007) or that display ontogenetic habitat shifts that occur over significant distances (Bryant et al. 1989; Lindberg et al. 2006).

### **Ontogenetic Shifts in Red Snapper Habitat**

Postsettlement movement in GOM red snapper has been investigated with several different approaches to address various questions about red snapper population ecology. Several authors

have examined ontogenetic habitat shifts (e.g., Bradley and Bryan 1975; Szedlmayer and Howe 1997; Szedlmayer and Conti 1999; Rooker et al. 2004), with recent studies aimed at defining essential fish habitat (EFH) of juveniles in order to mitigate shrimp trawl bycatch (e.g., Patterson et al. 2005; Wells 2007). When results of habitat studies are considered in totality, some consistent themes begin to emerge relative to red snapper habitat requirements and how they shift ontogenetically. First, like most reef fishes, juvenile red snapper display a strong thigmotaxis, thus seek structured environments (Workman et al. 1994; Szedlmayer and Howe 1997; Bailey et al. 2001; Franks et al. 2004). Szedlmayer and Howe (1997) reported juvenile red snapper selected oyster shell versus sand habitat in tank trials, while Patterson et al. (2005) reported highest juvenile red snapper densities in trawl samples off Alabama and Mississippi came from high-relief (2–3 m) shell rubble ridge habitats. Seemingly contrary results were presented by Rooker et al. (2004) and Geary et al. (this volume) that demonstrated juvenile red snapper associated with Texas bank systems were found in high densities in relatively unstructured mud habitats, and Patterson et al. (2005) reported moderately high juvenile densities occurred in sand habitats off Alabama and Mississippi. However, sampling trawls deployed by Rooker et al. (2004) and Geary et al. (this volume) contained small-mesh bags that retained recently-settled juveniles for which biogenic structures such as worm tubes may provide sufficient structure in soft sediments (Workman et al. 2002). Furthermore, mud habitats were immediately adjacent to shell rubble habitats and may have served as foraging areas. Patterson et al. (2005) reported red snapper juvenile density in sand habitats was significantly correlated with sponge biomass. Hence, they concluded sponges provided habitat complexity at a scale sufficient for juvenile snapper. Similarly, Workman and Foster (1994) reported juvenile red snapper encountered in sand habitats typically were associated with objects, such as squid egg cases, woody debris, or discarded drink cans, that fish used for either refuge or orientation.

Much evidence suggests that as red snapper age they recruit to habitats characterized by

increasing vertical dimension. Patterson et al. (2005) demonstrated age-0 red snapper were found in low-relief shell rubble and sand (interspersed with sponge) habitats, but age-1 fish were found at deeper (40 versus 20 m depth) sites that had greater vertical relief and complexity. Bailey et al. (2001) conducted tank trials in which they tested the effect of structure (concrete blocks) and the presence of adult conspecifics on the location of juvenile red snapper within tanks. When adults were not present, juveniles oriented to experimental reefs, but when present, adults displayed agonistic behavior in excluding juveniles from the preferred habitat. Wells (2007) reported that age-0 fish off Alabama were abundant in shell rubble habitats, but larger, older (age-2+) fish were concentrated in natural reef habitats. Bradley and Bryan (1975) reported ontogenetic movement of red snapper to structured habitats of increasing dimension occurred as an onshore to offshore migration throughout the juvenile stage. [It should be noted that natural hardbottoms and banks that constitute the most significant natural reef areas in both the western and eastern GOM are found predominantly on the outer shelf, while lower-relief shell rubble ridges and banks are found in relatively shallow (<20 m) nearshore waters (Parker et al. 1983; Schroeder et al. 1988; Laswell et al. 1990; Dufrene et al. 2003; Gledhill and David 2004; Rooker et al. 2004; Kraus et al. 2006)]. Mitchell et al. (2004) reported larger (median TL ranged from 545 to 815 mm among surveys), older red snapper were captured at higher rates in outer shelf habitats during experimental longline surveys in the eastern (off Alabama-Mississippi) and western (off Texas) GOM. Fishery-dependent data confirm that larger, older fish are captured much more frequently in commercial fishery sectors operating farther from shore (Allman and Fitzhugh 2007, this volume).

Analysis of natural ontogenetic shifts in red snapper habitat utilization is complicated due to the proliferation of artificial reefs deployed in the north-central GOM and the vast number of petroleum platforms, which function as artificial reefs, erected in the northwestern GOM (Wilson and Nieland 2004). However, examination of the literature on red snapper recruitment to and resi-

gency at artificial reefs and platforms reveals the same pattern of increasing dimension of utilized habitats with increasing fish size. Szedlmayer and Lee (2004) reported juvenile red snapper as small as 18 mm settled in relatively unstructured open shelf habitats in summer, but by winter age-0 fish had recruited to experimental artificial reefs that provided greater habitat complexity and relief. Nieland and Wilson (2003) randomly sampled red snapper ( $n = 300$ ) killed during the explosive removal of an obsolete oil platform off Louisiana. Otolith-based aging revealed the majority of fish were 2 and 3 year olds (53% and 37%, respectively), while virtually no ( $n = 2$ ) age-1 fish were present in their sample. Similarly, size frequency data from small-scale (<5 m<sup>3</sup>) artificial reefs off Alabama and north-west Florida indicate the majority of red snapper present are 2 and 3 year old fish (Strelcheck et al. 2005; Patterson, unpublished data). The lack of older red snapper at both platforms and artificial reef sites may indicate thigmotaxis or the threat of predation subsides with age and size; thus, larger, older fish display lower site fidelity and greater movement (Patterson et al. 2001; Patterson and Cowan 2003; Stelcheck et al. 2007, this volume). Alternatively, high fishing mortality rates at platforms and artificial reefs may remove snapper very quickly from the population once fish recruit to the commercial or recreational fisheries (Nieland and Wilson 2003).

### Direct Estimates of Post Settlement Movement

More important to population connectivity than the distribution of fish at single points in space or time is the degree of site fidelity (philopatry) individuals display and the spatial scale over which movement occurs. Some inference can be drawn about red snapper movement due to seasonal occurrence of fish in certain habitats and ontogenetic habitat shifts described above, but movement on multiple temporal and spatial scales has been estimated directly in several studies. The two main approaches that have been applied to estimate red snapper site fidelity and movement are conventional and, more recently, ultrasonic tagging. Benefits of conventional tagging include tags being inexpensive and relative-

ly unobtrusive to fish; individual tagged fish can be identified; and, nonscientists can be trained to apply tags (Patterson et al. 2001; Diamond et al. 2007, this volume). However, movement can only be estimated as straight-line distances between release and recapture locations, and reporting rates by fishers often are low in heavily regulated fisheries (Fable 1990). Tag loss also can be problematic (Patterson et al. 2001). With ultrasonic tagging, individuals can be tracked nearly continuously within the range of receivers. Depending on the types of tags deployed, individual tags (fish) can be identified based on their frequency or ping rate, but the ability to track individuals is affected by receiver range and tag battery life. If functionality of tags is compromised, then a fish present but not detected would be perceived as having left the study area (Westmeyer et al. 2007, this volume).

Szedlmayer (1997) conducted the first ultrasonic tagging experiment on red snapper at artificial reef sites off Alabama (Table 1). He concluded from study results that red snapper displayed "high" site fidelity to artificial reefs, yet the mean time fish were detected in his study area was only 150 d for a species with maximum longevity >50 years (Wilson and Nieland 2001). While one tagged individual was detected for 597 d, several others ( $n = 6$  of 23) were lost from the study area. Both "stayers" and "movers" (from Diamond et al. 2007, this volume) have important implications for population connectivity and structure (Dieckmann et al. 1999; Doebeli and Ruxton 1997; Fraser et al. 2001), but movers can no longer be tracked with ultrasonic receivers once they move beyond the range of receivers. Hence, emphasis in red snapper ultrasonic tagging analysis and interpretation has tended to be weighted toward the stayers. For example, Schroepfer and Szedlmayer (2006) concluded that ultrasonically tagged red snapper displayed high site fidelity to artificial reef sites because 87% (13 of 15) of fish were detected within 200 m of study sites 99% of the time they were detected. However, the probability that fish remained resident at reef sites after a year was only approximately 50% (i.e., 50% annual site fidelity). Westmeyer et al. (this volume) reported even lower probability of detection at petroleum platforms off Louisiana after one year, but tag battery failure and thermocline

**Table 1.** Results from ultrasonic tagging studies of sub-adult and adult red snapper in the northern Gulf of Mexico.

Study	Location and Habitat	Area of Detection per Hydrophone	Hydrophones per Site	Number Tagged	Mean TL at Tagging mm	Mean Days Detected in Study Area	Max Days Detected in Study Area
Szedlmayer (1997)	Alabama; artificial reefs	3.1 km <sup>2</sup>	1; roving	23	349	150	597
Szedlmayer and Schroepfer (2005)	Alabama; artificial reefs	≤ 8.0 km <sup>2</sup>	3–4; fixed	54	589	212	595
Schroepfer and Szedlmayer (2006)	Alabama; artificial reefs	≤ 8.0 km <sup>2</sup>	3–4; fixed	77	542	179	597
Westmeyer et al. (this volume)	Louisiana; petroleum platforms	0.02 km <sup>2</sup>	7 within a 35 km <sup>2</sup> area	125	360	64	202

<sup>a</sup> Area of detection was estimated based on maximum detection radii from hydrophones reported in each study.

effects on receivers likely negatively affected their estimates of site fidelity.

Ultrasonic tagging data are useful for examining short-term movements in resident individuals (stayers), but understanding population connectivity and structure is perhaps more dependent on estimating dispersion distances and rates of movers (Doebeli and Ruxton 1997). Conventional tagging studies are better suited for that purpose, despite the limitations cited above, and several large-scale conventional tagging studies have been conducted on GOM red snapper since the 1960s (Table 2). Among the various studies, fish were captured at natural reefs, artificial reefs (including petroleum platforms), or both. However, most of the existing movement data available from conventional tagging studies are from studies conducted over artificial reef sites in the north-central GOM (e.g., Szedlmayer and Shipp 1994; Patterson and Cowan 2003; Strelcheck et al. 2007, this volume). An exception to that are data from the Schlitz Tagging Program conducted off Florida in the 1960s by Florida Department of Natural Resources personnel. Fish in that program were captured and tagged over natural reef sites,

most of which occurred off northwest Florida (Beaumariage 1969). Fable (1980) also reported movement data from fish captured and tagged over a variety of natural and artificial habitats off Texas, as did Diamond et al. (this volume).

Several consistent trends exist in the movement data among conventional tagging studies, although considerable variability also exists in results among them. Most tagged individuals have been small, young fish, with mean TL between 299 and 363 mm across studies (Table 2). Patterson et al. (2001) reported fish size significantly affected the likelihood and distance of movement away from release sites, and Diamond et al. (this volume) reported larger fish had a higher probability of movement than had smaller ones. Red snapper can attain sizes of nearly 1 m TL (Wilson and Nieland 2001); thus, movement estimates based on a sample of small, young individuals may be conservative when applied to larger, older fish in the population.

The scale of observed movement generally increased with sample size and the temporal scale of tagging studies. Movement data presented by Diamond et al. (this volume) from tag returns of fish tagged off Texas represents one

departure from that trend. Substantially more fish were tagged in their study ( $n = 5,614$ ) than in any other, yet only modest levels of movement were observed. However, some of their samples came from deep water (to 100 m); thus, acute or chronic effects of barotrauma may have affected their functional sample size (Patterson et al. 2002; Rummer 2007, this volume) and overall tag return rate (2.8% versus ~6–35% among other studies). Furthermore, the mean and maximum times that recaptured fish were free in their study (564 d) were only about a third of those reported by others (Table 2).

Perhaps the most striking characteristic of red snapper movement data that is consistent among tagging studies is that data tend to be positively skewed and are characterized by a negative binomial distribution (Patterson et al. 2001). That consistent pattern results from a high percentage of zeros in the data (stayers) and the fact that most movers moved only small (<10 km) rather than large (>50 km) distances prior to recapture [e.g., Table 8 in Beaumariage (1969); Figure 5 in Szedlmayer and Shipp (1994); Figure 5 in Patterson and Cowan (2003)].

Fraser et al. (2001) reported similar movement distributions are common across many taxa, and sought to explain the ecological and evolutionary significance of dispersing phenotypes in populations. They demonstrated movers (their “dispersers”) within populations of giant rivulus, *Rivulus hartii*, in Trinidadian streams were individuals who displayed boldness versus fearfulness in traversing open spaces in test tanks prior to tagging. Once tagged and released back into the wild, bold individuals not only moved greater distances in streams, but also had higher individual growth rates. Diamond et al. (this volume) also reported tagged red snapper that moved away from tagging sites off Texas grew at faster rates than ones that stayed. Fraser et al. (2001) concluded that bold behavior traits contributed to greater fitness of surviving movers versus stayers, although the cost of boldness, hence movement, was greater exposure to predation risk.

Currently, it is unknown what the cost of movement away from reef structure is for red snapper. Observed postsettlement movement has been lower in juveniles than in sub-adults,

**Table 2.** Movement and site fidelity estimates from conventional tagging studies of sub-adult and adult red snapper conducted in the northern Gulf of Mexico.

Study	Location and Habitat	Number Tagged	Mean TL at Tagging mm	Number Recaptured	Mean/Max Days Free	Mean/Max km Moved	Site Fidelity <sup>a</sup>
Beaumariage (1969)	West Florida; natural reefs	1,126	NA	384	113/ 2,049	NA/ 279	90% recaptured within 5 km of release site
Fable (1980)	Texas; natural reefs and oil platforms	299	286	17	112/ 253	0.3/ 5	94% recaptured at release site
Szedlmayer and Shipp (1994)	Alabama; artificial reefs	1,155	287	146	137/ 430	4.6/ 32	74% recaptured within 2 km of release site
Patterson and Cowan (2003) <sup>b</sup>	Alabama; artificial reefs	2,932	335	599	404/ 1,501	30.9/ 558	25–27% per year
Strelcheck et al. this volume	Alabama; artificial reefs	4,317	335	629	401/ 1,587	2.1/ 202	48–50% per year
Diamond et al. this volume (TTU Tagging)	Texas; artificial and natural reefs	5,614	363	130	166/ 564	9.8/ 58.3	52.4% recaptured at release site

<sup>a</sup>Site fidelity to release site was directly estimated as an annual rate by Patterson and Cowan (2003) and Strelcheck et al. (this volume) from the decline in recaptures made by researchers at unreported study sites over time.

<sup>b</sup>Data presented in Patterson and Cowan (2003) include data presented in Patterson et al. (2001) plus additional recaptures.

and the scale of movement generally increased with size in the adult life stage (Patterson et al. 2001; Workman et al. 2002; Diamond et al. 2007, this volume). Lorenzen (2000, 2006) demonstrated the existence of an allometric relationship between natural mortality ( $M$ ) and fish body weight. He demonstrated  $M$  declines with increasing body size, which in turn most likely results from a concomitant decrease in predation risk (Sogard 1997; Murakami et al. 2005). Therefore, adult red snapper site fidelity to reefs may decrease, and their movement distances increase, with increasing size and/or age due to a relaxation of predation risk as fish attain larger sizes. But despite the potential for interpopulational genetic mixing resulting from extreme (>100 km) movement observed in some tagged fish (e.g., Beaumariage 1969; Patterson et al. 2002; Strelcheck et al. 2007, this volume), Pruett et al. (2005) reported evidence of evolutionarily recent isolation by distance was apparent in mtDNA haplotype frequencies, and Saillant and Gold (2006) reported significant differences in red snapper genetic effective population size among northern GOM regions. Therefore, although some selection pressure may exist to maintain mover phenotypes in red snapper populations (Fraser et al. 2001), competing pressures must also exist else selection likely would have driven red snapper populations to display even greater movement than what has been observed (Jonsson and Jonsson 1994; Doebeli and Ruxton 1997). Perhaps selection pressures for movement versus philopatry are stage-dependent in red snapper, as has been demonstrated in other marine and anadromous species that maintain divergent migratory tactics (reviewed in Secor 1999). For small, young fish, fitness tradeoffs existing between growth and defense (Sibly et al. 1985) likely favor high site fidelity to reef structure (thigmotaxis) as a refuge from predation (Overholtzer-McLeod 2005), even when high fish density compromises growth (Strelcheck et al. 2005; Lindberg et al. 2006). Predation pressure likely is lower for larger, older fish, for which large size alone may convey fitness, especially in females (Munch and Conover 2003; Andersen et al. 2007); therefore, reef dependency is relaxed (Patterson et al. 2001; McCawley et al. 2007, this volume). It is

unknown, however, what factors may contribute to extreme (>100 km) movement observed in some red snapper. Patterson et al. (2001) reported tagged fish at liberty during hurricanes moved significantly farther than ones which were not exposed to storms. However, Beaumariage (1969) did not report storm effects and several fish recently tagged off northwest Florida have moved extreme distances in the absence of storms (Patterson, unpublished data).

### Implications for Population Structure

Postsettlement movement observed in red snapper has significant implications for population structure. Traditionally, population, or stock, structure in GOM red snapper has been evaluated with population genetics techniques. Results of studies designed to examine genetic population structure consistently have shown that interregional variability in selectively-neutral genetics markers, such as mtDNA and nuclear DNA microsatellites, is low. Thus, significant differences among regions in haplotype frequencies have not been found (Gold et al. 1997; Saillant and Gold 2006; Gold and Saillant 2007, this volume). However, Saillant and Gold (2006) reported 10-fold differences in genetic effective population size estimates among southwest, northwest, and north-central regions of the U.S. GOM, which they inferred likely reflected interregional differences in patterns and intensity of migration. Pruett et al. (2005) reported results of nested clade analysis performed on region-specific mtDNA haplotype frequencies were consistent with the hypothesis that red snapper populations were semi-isolated within regions, despite the lack of significant interregional genetic heterogeneity found in selectively neutral markers. Even in the absence of significant gene flow due to oceanographic transport of eggs and larvae, it is possible that extreme (>100 km) movement observed in some adults is sufficient to facilitate genetic mixing among regions (Nolan et al. 1991), yet also so rare as to be inconsequential to the maintenance of persistent interregional differences in population demographics (Policansky and Magnuson 1998). This may be especially true currently as relatively few large fish that are more likely to

be movers exist in the truncated age distribution of the overfished stock (Porch 2007, this volume).

Previously narrow definitions of genetic stock structure in marine fishes have been replaced in recent years with metapopulation concepts due to issues similar to those raised above for red snapper (Thorrold et al. 2001; Kritzer and Sale 2004, 2005). Kritzer and Sale (2005) stated that in order to invoke metapopulation dynamics, subpopulations must be distinct, have dispersal mechanisms among them, and display asynchrony in population dynamics; Levins' (1969) earlier emphasis on extinction risk was abandoned. Pruett et al. (2005) concluded that results of nested clade analysis, in light of asynchronous population dynamics parameters among GOM regions, were consistent with the interpretation that GOM red snapper constituted a metapopulation. I submit that red snapper movement data, presented here in their various forms, also are consistent with that interpretation. Movement sufficient to affect mixing of genetic resources among regions has been demonstrated, but not on scales that would be likely to diminish regional differences in population demographics, such as those demonstrated by Fischer et al. (2004) and Jackson et al. (this volume).

Pruett et al. (2005) indicated precise estimates of movement among regions are required in order to test whether GOM red snapper constitute a metapopulation. Other authors also have recognized that estimates of interpopulational mixing rates on ecological versus evolutionary time scales are required to assess metapopulation structure in fishes (Secor 1999; reviewed in Sale et al. 2005). Perhaps the most powerful tool yet found for that purpose is the use of otolith chemistry as a natural tag to track movement of fish among regions (Begg et al. 2005; Campana 2005). Since Thorrold et al.'s (2001) groundbreaking work employing otolith chemistry as a natural tag to examine weakfish, *Cynoscion regalis*, natal homing and population connectivity, several authors have likewise drawn inferences about population structure in marine fishes via natural tags based on otolith elemental signatures (e.g., Geffen et al. 2003; Miller and Shanks 2004; Hamer et al. 2005; Jonsdottir et al. 2006).

Application of otolith chemistry as a natural tag also has been applied to examine population structure in GOM red snapper. Patterson et al. (1998) reported otolith elemental signatures of age-0 red snapper were significantly different among north-central, northwestern, and southwestern regions of the U.S. GOM. Patterson et al. (in press) reported region-specific otolith elemental signatures (Ba, Mg, Mn, and Sr concentrations) of age-0 fish were significantly different among five successive (1996–2000) year classes, and that classification success in most ( $n = 4$  of 5) years was sufficient to employ signatures as natural tags (e.g., jackknifed classification success of linear discriminant function models approached 80%). Analysis of the core elemental chemistry of otoliths collected from members of the 1996–2000 year classes sampled among study regions in 2001 revealed red snapper displayed strong intraregional philopatry in the first year of life (Cowan et al. 2002). Almost no mixing was estimated to have occurred between the north-central and northwestern GOM as fish aged, which is consistent with data from conventional tagging studies that have not demonstrated mixing between areas east and west of the Mississippi River. Mixing between the northwestern and southwestern regions, however, was greater, with a net subsidy of recruits apparently provided to the southwestern region from the northwestern region.

Overall, postsettlement movement data presented herein are consistent with the inference that GOM red snapper constitute a metapopulation. However, as suggested by Pruett et al. (2005) and despite the resources already invested in estimating movement in red snapper, more precise estimates of movement and exchange rates are required to assess interpopulational connectivity. For example, conventional tagging studies conducted to date have been designed to estimate movement away from tagging sites in a given GOM region, but not necessarily to estimate connectivity among regions. Coordination among ongoing tagging programs would prove beneficial for that purpose. Otolith chemistry has shown great promise as a tool to examine population structure and connectivity in GOM red snapper, but misclassification error (~20%) of age-0 fish is

problematic. Furthermore, not all regions of the GOM where red snapper occur have been studied. Future otolith elemental chemistry research should examine elemental signatures from age-0 fish across the entire GOM Basin, as well as examine the potential for increased region-specific classification accuracies of age-0 fish by addition of other elements and stable isotope values of C and O to otolith signatures.

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### References

- Allman, R. J., and G. R. Fitzhugh. This volume. Temporal age progressions and relative year-class strength of Gulf of Mexico red snapper. Pages 283–299 in W. F. Patterson, III, J. H. Cowan, Jr., G. R. Fitzhugh, and D. L. Nieland, editors. Red snapper ecology and fisheries in the U.S. Gulf of Mexico. American Fisheries Society, Symposium 60, Bethesda, Maryland.
- Almany, G. R., M. L. Berumen, S. R. Thorrold, S. Planes, and G. P. Jones. 2007. Local replenishment of coral reef fish populations in a marine reserve. *Science* 316:742–744.
- Andersen, K. H., K. D. Farnsworth, U. H. Thygesen, and J. E. Beyer. 2007. The evolutionary pressure from fishing on size at maturation of Baltic cod. *Ecological Modeling* 204:246–252.
- Ayre, D. J., and T. P. Hughes. 2000. Genotypic diversity and gene flow in brooding and spawning corals along the Great Barrier Reef, Australia. *Evolution* 54:1590–1605.
- Bailey, H. K., IV, J. H. Cowan, Jr., and R. L. Shipp. 2001. Experimental evaluation of potential effects of habitat size and presence of conspecifics on habitat association by young-of-the-year red snapper. *Gulf of Mexico Science* 19:119–131.
- Baskett, M. L., S. A. Levin, S. D. Gaines, and J. Dushoff. 2005. Marine reserve design and the evolution of size at maturation in harvested fish. *Ecological Applications* 15:882–901.
- Beaumariage, D. S. 1969. Returns from the 1965 Schlitz tagging program including a cumulative analysis of previous results. Florida Department of Natural Resources Technical Series 59:1–38.
- Begg, G. A., S. E. Campana, A. J. Fowler, and I. A. Suthers. 2005. Otolith research and application: current directions in innovation and implementation. *Marine and Freshwater Research* 56:477–484.
- Bradley, E., and C. E. Bryan. 1975. Life history and fishery of the red snapper (*Lutjanus campechanus*) in the northwestern Gulf of Mexico: 1970–1974. *Proceedings of the Gulf and Caribbean Fisheries Institute* 27:77–106.
- Bryant, H. E., M. R. Dewey, N. A. Funicelli, G. M. Ludwig, D. A. Meineke, and L. J. Mengal. 1989. Movement of five selected sportfish species of fish in Everglades National Park. *Bulletin of Marine Science* 44:515.
- Campana, S. E. 2005. Otolith science entering the 21<sup>st</sup> century. *Marine and Freshwater Research* 56:485–496.
- Collins, L. A., J. H. Finucane, and L. E. Barger. 1980. Description of larval and juvenile red snapper, *Lutjanus campechanus*. *Fishery Bulletin* 77:965–974.
- Collins, L. A., A. G. Johnson, and C. P. Keim. 1996. Spawning and annual fecundity of the red snapper (*Lutjanus campechanus*) from the northeastern Gulf of Mexico. Pages 174–188 in F. Arreguin-Sanchez, J. L. Munro, M. C. Balgos, and D. Pauly, editors. Biology, fisheries and culture of tropical groupers and snappers. ICLARM Conference Proceedings Number 48.
- Cowan, J. H., Jr., M. Woods, W. Patterson, III, and D. Nieland. 2002. Otolith microchemistry (and reproductive biology) portion- Stock structure of red snapper in the northern Gulf of Mexico: is their management as a single stock justified based on spatial and temporal patterns of genetic variation, otolith microchemistry, and growth rates. National Marine Fisheries Service, Marine Fisheries Initiative (MARFIN) Grant NA87FF0425.
- Cowen, R. K., and L. R. Castro. 1994. Relation of coral reef fish larval distributions to island scale circulation around Barbados, West Indies. *Bulletin of Marine Science*. 54:228–244.
- Cowen, R. K., C. B. Paris, and A. Srinivasan. 2006. Scaling of connectivity in marine populations. *Science* 311:522–527.
- Cowen, R. K., K. M. M. Lwiza, S. Sponaugle, C. B. Paris, and D. B. Olson. 2000. Connectivity of marine populations: open or closed? *Science* 287:857–859.
- Diamond, S. L., M. D. Campbell, D. Olson, Y. Wang, J. Zeplin, and S. Qualia. This volume. Movers and stayers: individual variability in site fidelity and movements of red snapper off Texas. Pages 149–170 in W. F. Patterson, III, J. H. Cowan, Jr., G. R. Fitzhugh, and D. L. Nieland, editors. Red snapper ecology and fisheries in the U.S. Gulf of Mexico.

- American Fisheries Society, Symposium 60, Bethesda, Maryland.
- Dieckmann, U., B. O'Hara, and W. Weisser. 1999. The ecology of dispersal. *Trends in Ecology & Evolution* 14:88–90.
- Doebeli, M., and G. D. Ruxton. 1997. Evolution of dispersal rates in metapopulation models: branching and cyclic dynamics in phenotype space. *Evolution* 51:1730–1741.
- Doherty, P. J., Planes, S., and P. Mather. 1995. Gene flow and larval duration in seven species of fish from the Great Barrier Reef. *Ecology* 76:2373–2391.
- Drass, D. M., K. L. Bootes, J. Lyczkowski-Shultz, B. H. Comyns, G. J. Holt, C. M. Riley, and R. P. Phelps. 2000. Larval development of red snapper, *Lutjanus campechanus*, with comparisons to co-occurring snapper species. *Fishery Bulletin* 98:507–527.
- Dufrene, T. A., S. J. Bentley, and Y. C. Allen. 2003. Geologic and geoscoustic study of surficial deposits, north-central Gulf of Mexico continental shelf. *Transactions of the Gulf Coast Association of Geological Societies* 53:210–216.
- Fable, W. A., Jr. 1980. Tagging studies of red snapper (*Lutjanus campechanus*) and vermilion snapper (*Rhomboplites aurorubens*) off the south Texas coast. *Contributions in Marine Science* 23:115–121.
- Fable, W. A., Jr. 1990. Summary of king mackerel tagging in southeastern USA: mark-recapture techniques and factors influencing tag returns. Pages 161–167 in N. C. Parker, editor. *Fish Marking Techniques*. American Fisheries Society, Symposium 7, Bethesda, Maryland.
- Fischer, A. J., M. S. Baker, C. A. Wilson. 2004. Red snapper (*Lutjanus campechanus*) demographic structure in the northern Gulf of Mexico based on spatial patterns in growth rates and morphometrics. *Fishery Bulletin* 102:593–603.
- Fitzhugh, G. R., C. C. Koenig, F. C. Coleman, C. B. Grimes, and W. Sturges. 2005. Spatial and temporal patterns in fertilization and settlement of young gag (*Mycteroperca microlepis*) along the West Florida Shelf. *Bulletin of Marine Science* 77:377–396.
- Franks, J. S., J. R. Hendon, and N. M. Garber. 2004. Red snapper (*Lutjanus campechanus*) associated with a small artificial structure in the Mississippi Sound, a northern Gulf of Mexico estuary. *Proceedings of the Gulf and Caribbean Fisheries Institute* 55:853–864.
- Fraser, D. F., J. F. Gilliam, M. J. Daley, A. N. Le, and G. T. Skalski. 2001. Explaining leptokurtic movement distributions: Intrapopulation variation in boldness and exploration. *American Naturalist* 158:124–135.
- Futch, R. B., and G. E. Bruger. 1976. Age, growth, and reproduction of red snapper in Florida waters. Pages 165–184 in H. R. Bullis and A. C. Jones, editors. *Proceedings: Colloquium on snapper-grouper fishery resources for the western central Atlantic Ocean*. Florida Sea Grant College Report 17.
- Geary, B. W., J. J. Mikulas, Jr., J. R. Rooper, A. M. Landry, Jr. and T. M. Dellapenna. This volume. Patterns of habitat used by newly settled red snapper in the northwestern Gulf of Mexico. Pages 23–35 in W. F. Patterson, III, J. H. Cowan, Jr., G. R. Fitzhugh, and D. L. Nieland, editors. *Red snapper ecology and fisheries in the U.S. Gulf of Mexico*. American Fisheries Society, Symposium 60, Bethesda, Maryland.
- Geffen, A. J., K. Jarvis, J. P. Thorpe, R. T. Leah, and R. D. M. Nash. 2003. Spatial differences in the trace element concentrations of Irish Sea plaice *Pleuronectes platessa* and whiting *Merlangius merlangus* otoliths. *Journal of Sea Research* 50:247–256.
- Gilg, M. R., and T. J. Hilbish. 2003. Patterns of larval dispersal and their effect on the maintenance of a blue mussel hybrid zone in southwestern England. *Evolution* 57:1061–1077.
- Gledhill, C., and A. David. 2004. Survey of fish assemblages and habitat within two marine protected areas on the west Florida shelf. *Proceedings of the Gulf and Caribbean Fisheries Institute* 55:614–625.
- Gold, J. R., E. Pak, and L. R. Richardson. 2001. Microsatellite variation among red snapper (*Lutjanus campechanus*) from the Gulf of Mexico. *Marine Biotechnology* 3:293–304.
- Gold, J. R., and E. Saillant. This volume. Population structure of red snapper in the northern Gulf of Mexico. Pages 181–195 in W. F. Patterson, III, J. H. Cowan, Jr., G. R. Fitzhugh, and D. L. Nieland, editors. *Red snapper ecology and fisheries in the U.S. Gulf of Mexico*. American Fisheries Society, Symposium 60, Bethesda, Maryland.
- Gold, J. R., F. Sun, and L. R. Richardson. 1997. Population structure of red snapper from the Gulf of Mexico as inferred from analysis of mitochondrial DNA. *Transactions of the American Fisheries Society* 126:386–396.
- Goodyear, C. P. 1988. Recent trends in the red snapper fishery of the Gulf of Mexico. National Marine Fisheries Service, Southeast Fisheries Science Center, Miami Laboratory Report CRD-87/88–16, Miami, Florida.
- Goodyear, C. P. 1995. Red snapper stocks in U.S. waters of the Gulf of Mexico. National Marine Fisheries Service, Southeast Fisheries Center, Miami Laboratory, CRD 95/96–05, Miami, Florida.
- Hamer, P. A., G. P. Jenkins, and B. M. Gillanders. 2005. Chemical tags in otoliths indicate the importance of local and distant settlement areas to populations of a temperate sparid, *Pagrus auratus*. *Canadian Journal of Fisheries and Aquatic Sciences* 62:623–641.
- Hanisko, D. S., J. Lyczkowski-Shultz, and G. W. Ingram. This volume. Indices of larval red snapper occurrence and abundance for use in stock assessment. Pages 257–271 in W. F. Patterson, III, J. H. Cowan, Jr., G. R. Fitzhugh, and D. L. Nieland, editors. *Red snapper ecology and fisheries in the U.S. Gulf of Mexico*. American Fisheries Society, Symposium 60, Bethesda, Maryland.
- Hanisko, D. S., J. Lyczkowski-Shultz. 2003. Occurrence and pelagic habitat of reef fish larvae in the Gulf of Mexico. Pages 205–224 in D. R. Stanley and A. Scar-

- borough-Bull, editors. Fisheries, reefs, and offshore development. American Fisheries Society, Symposium 36, Bethesda, Maryland.
- Hjort, J. 1914. Fluctuations in the great fisheries of Northern Europe. *Conseil Permanent International pour L'Explorations de la Mer* 20:1–228.
- Holland, D. S., and R. J. Brazeel. 1993. Marine reserves for fisheries management. *Marine Resource Economics* 11:157–171.
- Hood, P. B., A. J. Strelcheck, and P. Steele. This volume. A history of red snapper management in the Gulf of Mexico. Pages 241–256 in W. F. Patterson, III, J. H. Cowan, Jr., G. R. Fitzhugh, and D. L. Nieland, editors. Red snapper ecology and fisheries in the U.S. Gulf of Mexico. American Fisheries Society, Symposium 60, Bethesda, Maryland.
- Ingram, G. W., and W. F. Patterson, III. 2001. Movement patterns of red snapper (*Lutjanus campechanus*), greater amberjack (*Seriola dumerili*), and gray triggerfish (*Balistes capriscus*) in the Gulf of Mexico and the utility of marine reserves as management tools. *Proceedings of the Gulf and Caribbean Fisheries Institute* 52:686–699.
- Jackson, M. W., J. H. Cowan, Jr., and D. A. Nieland. This volume. Demographic differences in northern Gulf of Mexico red snapper reproductive maturation: implications for the unit stock hypothesis. Pages 197–206 in W. F. Patterson, III, J. H. Cowan, Jr., G. R. Fitzhugh, and D. L. Nieland, editors. Red snapper ecology and fisheries in the U.S. Gulf of Mexico. American Fisheries Society, Symposium 60, Bethesda, Maryland.
- James, M. K., P. R. Armsworth, L. B. Mason, and L. Bode. 2002. The structure of reef fish metapopulations: modelling larval dispersal and retention patterns. *Proceedings of the Royal Society of London, Series B: Biological Sciences* 269:2079–2086.
- Johnson, M. S., and R. Black. 2006. Islands increase genetic subdivision and disrupt patterns of connectivity of intertidal snails in a complex archipelago. *Evolution* 60:2498–2506.
- Jones, G. P., S. Planes, and S. R. Thorrold. 2005. Coral reef fish larvae settle close to home. *Current Biology* 15:1314–1318.
- Jones, G. P., M. J. Milicich, M. J. Emslie, and C. Lunow. 1999. Self-recruitment in a coral reef fish population. *Nature (London)* 402:802–804.
- Jonsdottir, I. G., S. E. Campana, and G. Mareinsdottir. 2006. Stock structure of Icelandic cod *Gadus morhua* L. based on otolith chemistry. *Journal of Fish Biology* 69:136–150.
- Jonsson, B., and J. Jonsson. 1993. Partial migration: niche shift versus sexual maturation in fishes. *Reviews in Fish Biology and Fisheries* 3:348–365.
- Kraus, R. T., R. L. Hill, J. R. Rooper, and T. M. Dellapenna. 2006. Preliminary characterization of a mid-shelf bank in the northwestern Gulf of Mexico as essential habitat of reef fishes. *Proceedings of the Gulf and Caribbean Fisheries Institute* 57:621–632.
- Kritzer, J. P., and P. F. Sale. 2004. Metapopulation ecology in the sea: From Levins' model to marine ecology and fisheries science. *Fish and Fisheries* 5:131–140.
- Kritzer, J. P., and P. F. Sale. 2005. The metapopulation ecology of coral reef fishes. Pages 31–68 in J. P. Kritzer and P. F. Sale, editors. *Marine Metapopulations*. Academic Press, Boston, Massachusetts.
- Laswell, J. S., W. W. Sager, W. W. Schroeder, R. Rezak, K. S. Davis, and E. G. Garrison. 1990. Atlas of high-resolution geophysical data, Mississippi-Alabama marine ecosystem study. OCS Study/MMS 90–0000. U.S. Department of the Interior, Minerals Management Service, Gulf of Mexico OCS Regional Office, New Orleans, Louisiana.
- Levins, R. 1969. Some demographic and genetic consequences of environmental heterogeneity for biological control. *Bulletin of the Entomological Society of America* 15:237–240.
- Lindberg, W. J., T. K. Frazer, K.M. Portier, F. Vose, J. Loftin, D. J. Murie, D. M. Mason, B. Nagy, and M. K. Hart. 2006. Density-dependent habitat selection and performance by a large mobile reef fish. *Ecological Applications* 16:731–746.
- Lorenzen, K. 2000. Allometry of natural mortality as a basis for assessing optimal release size in fish-stocking programmes. *Canadian Journal of Fisheries and Aquatic Sciences* 57:2374–2381.
- Lorenzen, K. 2006. Population management in fisheries enhancement: Gaining key information from release experiments through use of a size-dependent mortality model. *Fisheries Research* 80:19–27.
- Lyczkowski-Shultz, J., and D. S. Hanisko. This volume. A time series of observations on red snapper larvae from SEAMAP surveys, 1982–2003: seasonal occurrence, distribution, abundance and size. Pages 3–22 in W. F. Patterson, III, J. H. Cowan, Jr., G. R. Fitzhugh, and D. L. Nieland, editors. Red snapper ecology and fisheries in the U.S. Gulf of Mexico. American Fisheries Society, Symposium 60, Bethesda, Maryland.
- Marko, P. B., S. C. Lee, A. M. Rice, J. M. Gramling, T. M. Fitzhenry, J. S. Mcalister, G. R. Harper, and A. L. Moran. 2004. Fisheries: mislabelling of a depleted reef fish. *Nature (London)* 430:309–310.
- McCawley, J. R., and J. H. Cowan, Jr. This volume. Seasonal and size specific diet and prey demand of red snapper on Alabama artificial reefs. Pages 71–96 in W. F. Patterson, III, J. H. Cowan, Jr., G. R. Fitzhugh, and D. L. Nieland, editors. Red snapper ecology and fisheries in the U.S. Gulf of Mexico. American Fisheries Society, Symposium 60, Bethesda, Maryland.
- Meyer, C. G., K. N. Holland, and Y. P. Papastamatiou. 2007. Seasonal and diel movements of giant trevally *Caranx ignobilis* at remote Hawaiian atolls: implications for the design of marine protected areas. *Marine Ecology Progress Series* 333:13–25.
- Miller, J. A., and A. L. Shanks. 2004. Evidence for limited larval dispersal in black rockfish (*Sebastes melanops*): implications for population structure and marine-reserve design. *Canadian Journal of Fisheries and Aquatic Sciences* 61:1723–1735.

- Mitchell, K. M., T. Henwood, G. R. Fitzhugh, and R. J. Allman. 2004. Distribution, abundance, and age structure of red snapper (*Lutjanus campechanus*) caught on research longlines in U.S. Gulf of Mexico. *Gulf of Mexico Science* 22:164–172.
- Moseley, F. N. 1966. Biology of the red snapper, *Lutjanus aya Bloch*, of the northwestern Gulf of Mexico. *Publication of the Institute of Marine Science* 11:90–101.
- Munch, S. B., and D. Conover. 2003. Rapid growth results in increased susceptibility to predation in *Menidia menidia*. *Evolution* 57:2119–2127.
- Murakami, T., K. Yoshioka, S. Aida, T. Unimo, and H. Nakagawa. 2005. Relation of size at release of hatchery-reared black rockfish *Sebastes inermis* to survival in a *Zostera* belt around Ikuno Island, Hiroshima Prefecture, Japan. *Bulletin of the Japanese Society of Scientific Fisheries* 71:354–362.
- Nieland, D. L., and C. A. Wilson. 2003. Red snapper recruitment to and disappearance from oil and gas platforms in the northern Gulf of Mexico. Pages 73–82 in D. R. Stanley and A. Scarborough-Bull, editors. *Fisheries, reefs, and offshore development*. American Fisheries Society, Symposium 36, Bethesda, Maryland.
- Nolan, K., J. Grossfield, and I. Wirgin. 1991. Discrimination among Atlantic coast populations of American shad (*Alosa sapidissima*) using mitochondrial DNA. *Canadian Journal of Fisheries and Aquatic Sciences* 48:1724–1734.
- Ogle, J. T., and J. M. Lotz. 2006. Characterization of an experimental indoor larval production system for red snapper. *North American Journal of Aquaculture* 68:86–91.
- Overholtzer-McLeod, K. L. 2005. Post-settlement emigration affects mortality estimates for two Bahamian wrasses. *Coral Reefs* 24:283–291.
- Papanikos, N., R. Phelps, K. Williams, A. Ferry, and D. Maus. 2003. Egg and larval quality of natural and induced spawns of red snapper, *Lutjanus campechanus*. *Fish Physiology and Biochemistry* 28:487–488.
- Parker, R. O., Jr., D. R. Colby, and T. D. Willis. 1983. Estimated amount of reef habitat on a portion of the U.S. south Atlantic and Gulf of Mexico continental shelf. *Bulletin of Marine Science* 33:935–940.
- Patterson, W. F., III and J. H. Cowan, Jr. 2003. Site fidelity and dispersion of tagged red snapper, *Lutjanus campechanus*, in the northern Gulf of Mexico. Pages 181–194 in D. R. Stanley and A. Scarborough-Bull, editors. *Fisheries, Reefs, and Offshore Development*. American Fisheries Society, Symposium 36, Bethesda, Maryland.
- Patterson, W. F., III, J. H. Cowan, Jr., E. Y. Graham, and W. B. Lyons. 1998. Otolith microchemical fingerprints of age-0 red snapper, *Lutjanus campechanus*, from the northern Gulf of Mexico. *Gulf of Mexico Science* 16:83–91.
- Patterson, W. F., III, G. W. Ingram, Jr., R. L. Shipp, and J. H. Cowan, Jr. 2002. Indirect estimation of red snapper (*Lutjanus campechanus*) and gray triggerfish (*Balistes capricus*) release mortality. *Proceedings of the Gulf and Caribbean Fisheries Institute* 53:526–536.
- Patterson, W. F., III, J. H. Cowan, Jr., C. A. Wilson, and Z. Chen. In press. Temporal and spatial variability in juvenile Gulf of Mexico red snapper otolith elemental signatures. *Transactions of the American Fisheries Society*.
- Patterson, W. F., III, J. C. Watterson, R. L. Shipp, and J. H. Cowan, Jr. 2001. Movement of tagged red snapper in the northern Gulf of Mexico. *Transactions of the American Fisheries Society* 130:533–545.
- Patterson, W. F., III, C. A. Wilson, J. H. Cowan, Jr., S. J. Bentley, T. A. Henwood, Y. C. Allen, and T. A. Dufrene. 2005. Delineating essential juvenile red snapper habitat in the north central Gulf of Mexico. Pages 277–288 in P. W. Barnes and J. P. Thomas, editors. *Effects of fishing on benthic habitats*. American Fisheries Society, Symposium 41, Bethesda, Maryland.
- Policansky, D. and J. J. Magnuson. 1998. Genetics, metapopulations, and ecosystem management of fisheries. *Ecological Applications* 8(1):S119–S123.
- Porch, C. E. This volume. An assessment of the red snapper fishery in the U.S. Gulf of Mexico using a spatially-explicit age-structured model. Pages 325–351 in W. F. Patterson, III, J. H. Cowan, Jr., G. R. Fitzhugh, and D. L. Nieland, editors. *Red snapper ecology and fisheries in the U.S. Gulf of Mexico*. American Fisheries Society, Symposium 60, Bethesda, Maryland.
- Pothoff, T., S. Kelly, and L. A. Collins. 1988. Osteological development of the red snapper, *Lutjanus campechanus*. *Bulletin of Marine Science* 43:1–40.
- Pruett, C. L., E. Saillant, and J. R. Gold. 2005. Historical population demography of red snapper (*Lutjanus campechanus*) from the northern Gulf of Mexico based on analysis of sequences of mitochondrial DNA. *Marine Biology* 147: 593–602.
- Rooker, J. R., A. Landry, Jr., B. W. Geary, and J. A. Harper. 2004. Assessment of a shell bank and associated substrates as nursery habitat of postsettlement red snapper. *Estuarine, Coastal and Shelf Science* 59:653–661.
- Rummer, J. L. This volume. Factors affecting catch and release (CAR) mortality in fish: insight into CAR mortality in red snapper and the influence of catastrophic decompression. Pages 113–132 in W. F. Patterson, III, J. H. Cowan, Jr., G. R. Fitzhugh, and D. L. Nieland, editors. *Red snapper ecology and fisheries in the U.S. Gulf of Mexico*. American Fisheries Society, Symposium 60, Bethesda, Maryland.
- Saillant, E., and J. R. Gold. 2006. Population structure and variance effective size of red snapper (*Lutjanus campechanus*) in the northern Gulf of Mexico. *Fishery Bulletin* 104:136–148.
- Sale, P. F., R. K. Cowen, B. S. Danilowicz, G. P. Jones, J. P. Kritzer, K. C. Lindeman, S. Planes, N. V. C. Polunin, G. R. Russ, Y. J. Sadovy, and R. S. Steneck. 2005. Critical science gaps impede use of no-take fishery reserves. *Trends in Ecology & Evolution* 20:74–80.
- Schroeder, W. W., A. W. Shultz, and J. J. Dindo. 1988.

- Inner-shelf hardbottom areas, northeastern Gulf of Mexico. *Transactions of the Gulf Coast Association of Geological Societies* 38:535–541.
- Schroepfer, R. L., and S. T. Szedlmayer. 2006. Estimates of residence and site fidelity for red snapper *Lutjanus campechanus* on artificial reefs in the northeastern Gulf of Mexico. *Bulletin of Marine Science* 78:93–101.
- Secor, D. H. 1999. Specifying divergent migrations in the concept of stock: the contingent hypothesis. *Fisheries Research* 43:13–34.
- Secor, D. H. 2002. Historical roots of the migration triangle. *ICES Marine Science Symposia* 215:229–335.
- Secor, D. H. 2006. The year-class phenomenon and the storage effect in marine fishes. *Journal of Sea Research* 57:91–103.
- Sibly, R. M., P. Calow, and N. Nichols. 1985. Are patterns of growth adaptive? *Journal of Theoretical Biology* 112:553–574.
- Sogard, S. M. 1997. Size-selective mortality in the juvenile stage of teleost fishes: a review. *Bulletin of Marine Science* 60:1129–1157.
- Strelcheck, A., J. H. Cowan, Jr., and W. F. Patterson, III. This volume. Site fidelity, movement, and growth of red snapper: Implications for artificial reef management. Pages 135–148 in W. F. Patterson, III, J. H. Cowan, Jr., G. R. Fitzhugh, and D. L. Nieland, editors. *Red snapper ecology and fisheries in the U.S. Gulf of Mexico*. American Fisheries Society, Symposium 60, Bethesda, Maryland.
- Strelcheck, A. J., J. H. Cowan, Jr., and A. Shah. 2005. The influence of reef location on artificial reef fish assemblages in the north-central Gulf of Mexico. *Bulletin of Marine Science* 77:425–440.
- Swearer, S. E., J. S. Shima, M. E. Hellberg, S. R. Thorrold, G. P. Jones, D. R. Robertson, S. G. Morgan, K. A. Selkoe, G. M. Ruiz, and R. R. Warner. 2002. Evidence of self-recruitment in demersal marine populations. *Bulletin of Marine Science* 70:251–271.
- Szedlmayer, S. T. 1997. Ultrasonic telemetry of red snapper, *Lutjanus campechanus*, at artificial reef sites in the northeast Gulf of Mexico. *Copeia* 1997:846–850.
- Szedlmayer, S. T., and J. Conti. 1999. Nursery habitats, growth rates, and seasonality of age-0 red snapper, *Lutjanus campechanus*, in the northeast Gulf of Mexico. *Fishery Bulletin* 97:626–635.
- Szedlmayer, S. T., and J. C. Howe. 1997. Substrate preference in age-0 red snapper, *Lutjanus campechanus*. *Environmental Biology of Fishes* 50:203–207.
- Szedlmayer, S. T., and J. D. Lee. 2004. Diet shifts of juvenile red snapper (*Lutjanus campechanus*) with changes in habitat and fish size. *Fishery Bulletin* 102:366–375.
- Szedlmayer, S. T., and R. L. Schroepfer. 2005. Long-term residence of red snapper on artificial reefs in the northeastern Gulf of Mexico. *Transactions of the American Fisheries Society* 134:315–325.
- Szedlmayer, S. T., and R. L. Shipp. 1994. Movement and growth of red snapper, *Lutjanus campechanus*, from an artificial reef area in the northeastern Gulf of Mexico. *Bulletin of Marine Science* 55:887–896.
- Thorrold, S. R., C. Latkoczy, P. K. Swart, and C. M. Jones. 2001. Natal homing in a marine fish metapopulation. *Science* 291:297–299.
- Trexler, J. C., and J. Travis. 2000. Can marine protected areas restore and conserve stock attributes of reef fishes? *Bulletin of Marine Science* 66:853–873.
- Wells, R. J. D. 2007. The effects of trawling and habitat use on red snapper and the associated community. Doctoral dissertation. Louisiana State University, Baton Rouge, Louisiana.
- Westmeyer, M. P., C. A. Wilson, and D. L. Nieland. This volume. Fidelity of red snapper to petroleum platforms in the northern Gulf of Mexico. Pages 97–111 in W. F. Patterson, III, J. H. Cowan, Jr., G. R. Fitzhugh, and D. L. Nieland, editors. *Red snapper ecology and fisheries in the U.S. Gulf of Mexico*. American Fisheries Society, Symposium 60, Bethesda, Maryland.
- Wilson, C. A., and D. L. Nieland. 2001. Age and growth of red snapper, *Lutjanus campechanus*, from the northern Gulf of Mexico off Louisiana. *Fishery Bulletin* 99:653–664.
- Wilson, C. A., and D. L. Nieland. 2004. The role of oil and gas platforms in providing habitat for northern Gulf of Mexico red snapper, *Lutjanus campechanus*. *Proceedings of the Gulf and Caribbean Fisheries Institute* 55:757–764.
- Workman, I. K., and D. G. Foster. 1994. Occurrence and behavior of juvenile red snapper, *Lutjanus campechanus*, on commercial shrimp fishing grounds in the northeastern Gulf of Mexico. *Marine Fisheries Review* 56:9–11.
- Workman, I., A. Shah, D. Foster, and B. Hataway. 2002. Habitat preferences and site fidelity of juvenile red snapper (*Lutjanus campechanus*). *ICES Journal of Marine Science* 59:S43–S50.

