Gulf and Caribbean Research

Volume 35 | Issue 1

2024

Recruitment of Juvenile Snapper (Lutjanidae) in the Middle Florida Keys: Temporal Trends and Fine-Scale Habitat Associations

Jack C. Olson
Florida Fish and Wildlife Conservation Commission, Fish and Wildlife Research Institute,
jack.olson@myfwc.com

Ariel Tobin
Florida Fish and Wildlife Conservation Commission, Fish and Wildlife Research Institute,
ariel.tobin@myfwc.com

Mareike D. Duffing Romero
North East Fisheries Science Center, marapp15@gmail.com

Alejandro Acosta
Florida Fish and Wildlife Conservation Commission, Fish and Wildlife Research Institute,
alejandro.acosta@myfwc.com

Recommended Citation

Olson, J. C., A. Tobin, M. D. Duffing Romero and A. Acosta. 2024. Recruitment of Juvenile Snapper (Lutjanidae) in the Middle Florida Keys: Temporal Trends and Fine-Scale Habitat Associations. Gulf and Caribbean Research 35 (1): GCFI1-GCFI13.
Retrieved from https://aquila.usm.edu/gcr/vol35/iss1/5
DOI: https://doi.org/10.18785/gcr.3501.05

GULF AND CARIBBEAN
RESEARCH

Volume 35
2024
ISSN: 2572-1410

Published by
THE UNIVERSITY OF
SOUTHERN MISSISSIPPI.

GULF COAST RESEARCH LABORATORY
Ocean Springs, Mississippi

Gulf and Caribbean Research Vol 34, GCFI 1- GCFI 13, 2024
DOI: 10.18785/gcr.3501.05

Manuscript received, July 14, 2023; accepted, January 26, 2024

GULF AND CARIBBEAN FISHERIES INSTITUTE PARTNERSHIP

RECRUITMENT OF JUVENILE SNAPPER *(LUTJANIDAE)* IN THE MIDDLE FLORIDA KEYS: TEMPORAL TRENDS AND FINE—SCALE HABITAT ASSOCIATIONS[§]

Jack C. Olson[1*], Ariel Tobin[1], Mareike D. Duffing Romero[2,3], and Alejandro Acosta[1]
[1]*Florida Fish and Wildlife Conservation Commission, Fish and Wildlife Research Institute, 2796 Overseas Highway, Suite 119, Marathon, FL 33050, USA;* [2]*North East Fisheries Science Center, National Oceanic and Atmospheric Administration, 166 Water Street, Woods Hole, MA 02543, USA;* [3]*Integrated Statistics, 16 Summer Street, Woods Hole, MA 02543, USA; *Corresponding author, email: jack.olson@myfwc.com*

ABSTRACT: Juvenile recruitment is a major factor in the establishment and maintenance of local population structures of coral reef fishes. An understanding of the factors that affect juvenile recruitment and survival help explain spatial and temporal patterns in adult abundance, especially of commercially and recreationally fished species. Here, we examined the distribution and juvenile recruitment of 5 snapper species: Mutton Snapper *(Lutjanus analis),* Lane Snapper *(L. synagris),* Schoolmaster *(L. apodus),* Gray Snapper *(L. griseus),* and Yellowtail Snapper *(Ocyurus chrysurus)* collected in 1,314 seine samples conducted between 2007 and 2019 in the Middle Florida Keys. We use a generalized linear modeling routine to assess juvenile recruitment of each species as a function of temporal, environmental, and benthic habitat variables. Interannual variability in juvenile recruitment ranged between 2 and 15—fold differences in mean predicted abundance between the highest and lowest producing years by species. Predicted recruitment varied dramatically by species in 2010 following a historic cold spell in south Florida. Three of the 5 species (Lane Snapper, Yellowtail Snapper, and Schoolmaster) exhibited the lowest observed yearly recruitment in that year, while Gray Snapper recruitment peaked. For all species, recruitment indices exhibited strong seasonal trends with peak abundances observed in the fall. Aquatic vegetation type, aquatic vegetation cover, distance from shore, and water temperature were the most important predictors of abundance. Results of this study highlight species—specific preferences for settlement habitat, demonstrate the importance of local—scale recruitment processes, and provide updated, management—relevant juvenile abundance indices for shallow water snapper in the Middle Florida Keys.

KEY WORDS: fishery—independent monitoring, seagrass, nursery habitat, juvenile abundance

INTRODUCTION

Populations of commercially and recreationally targeted fishes can be significantly affected by larval or early juvenile processes (Armsworth 2000, Steele and Forrester 2002, Brosset et al. 2020). Given that small inter—annual differences in juvenile recruitment can lead to pronounced downstream effects in adult populations (Rothschild 1986) and may provide early indication of overfishing (Myers and Barrowman 1996, Richards and Rago 1999), it is important to understand the factors that affect juvenile recruitment and survival (Brosset et al. 2020). Shallow nearshore habitats (e.g., seagrass beds, mangroves) are often utilized as nursery grounds that support larvae and juveniles of many reef fish species, including shallow—water snappers (Lutjanidae; Nagelkerken et al. 2000, Beck et al. 2001). Thus, long—term surveys in such habitats can yield management—relevant information on year—class strength and juvenile demographics.

Shallow—water snapper are targeted by large commercial and recreational fisheries in the South Atlantic region of Florida (Addis et al. 2021). Along the east coast of Florida, Gray Snapper (*Lutjanus griseus*), Mutton Snapper (*Lutjanus analis*), Yellowtail Snapper (*Ocyurus chrysurus*), Schoolmaster (*Lutjanus apodus*), and Lane Snapper (*Lutjanus synagris*) are some of the most common reef—dwelling snapper species and represented the bulk of shallow—water snapper landings between 2007 and 2019 (Lindeman et al. 2000; National Marine Fisheries Service, Fisheries Statistics Division, personal communication). Amongst these species, Gray Snapper, Mutton Snapper, and Yellowtail Snapper accounted for 93% of total landings during this period (52%, 22%, 18%, respectively). In the Florida Keys, specifically, there is a large commercial and recreational snapper fishery dominated by landings of Yellowtail and Gray Snapper (Addis et al. 2021).

For shallow water Lutjanids, pelagic larval duration is about 3—4 weeks post—fertilization (Lindeman 1997, Shulzitski et al. 2009, Claro et al. 2014). Along the Florida Keys reef tract, locally spawned larvae are thought to be retained by cyclonic gyres and eddies propagating within the Straits of Florida (Lee et al. 1994, Limouzy—Paris et al. 1997, Shulzitski et al. 2015, 2018). Retention to nearshore habitats may also be aided by predominant southeasterly winds producing Ekman currents (Lee et al. 1994). However, a percentage of locally produced larvae are also carried out of the Florida Keys by the eastward

---

[§] *This article is based on a virtual presentation given in November 2021 at the 74th meeting of the Gulf and Caribbean Fisheries Institute.*

Florida Current (Domeier 2004, D'Alessandro et al. 2010, Bryan et al. 2015, Shulzitski et al. 2015). Thus, variability in recruitment strength of reef fishes in the Florida Keys appears to be partially a function of the strength and timing of oceanographic and meteorological forces and the degree of synchrony with reproduction events (Lee et al. 1994, Shulzitski et al. 2015).

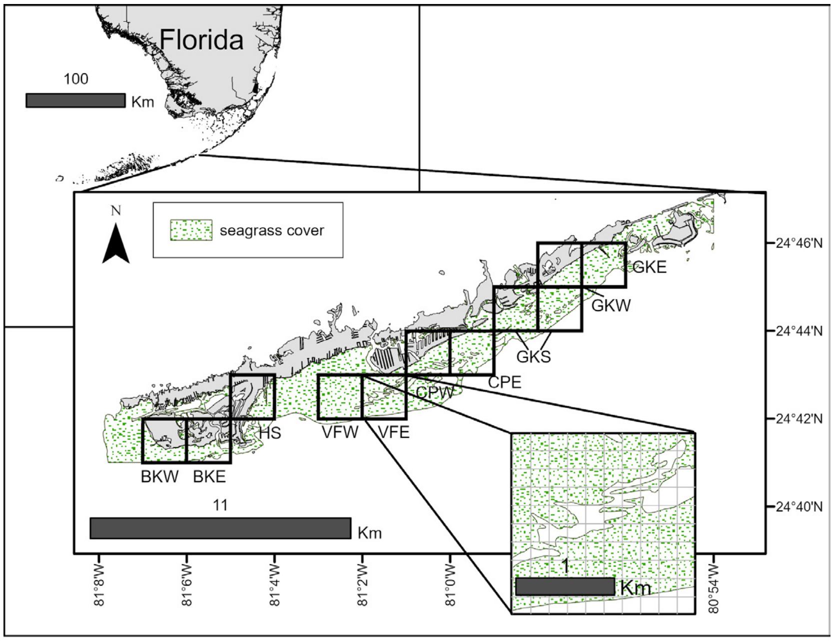

Figure 1. *Sampling frame showing the locations of one-latitudinal by one-longitudinal minute grid cells representing fixed sampling sites in the Middle Florida Keys. Each site was defined by one cell except for Grassy Key South (GKS) which was comprised of 2 cells due to habitat availability constraints. Smallest inset panel shows example of 0.1nm^2 "microgrid" cells used for sample location selection. Site names indicated by abbreviations: BKW—Boot Key West; BKE—Boot Key East; HS—High School; VFW—Vaca Flat West; VFE—Vaca Flat East; CPW—Coco Plum West; CPE—Coco Plum East; GKS—Grassy Key South; GKW—Grassy Key West; GKE—Grassy Key East.*

Tropical and subtropical seagrass beds serve as juvenile settlement habitat for shallow— water snappers across the Western Atlantic region, providing protection from predation and foraging habitat through ontogeny (Stoner 1983, Orth et al. 1984, Nagelkerken et al. 2000, 2002). The Florida Keys National Marine Sanctuary (FKNMS) encompasses extensive seagrass beds in Florida Bay and along the Atlantic side of the archipelago (Fourqurean and Zieman 2002). Prior surveys in the study area have shown that the seagrass beds in the Middle Florida Keys function as settlement habitat for juvenile snappers (Springer and McErlean 1962, Bartels and Ferguson 2006). Bartels and Ferguson (2006) found elevated abundances of settlement—stage snapper in shoal grass (*Halodule wrightii)* beds, likely reflecting the protective value of high blade densities characteristic of the thin—stemmed seagrass (Stoner 1983). However, preference for settlement habitats appears to differ by species; juvenile Yellowtail Snapper prefer turtle grass (*Thalassia testudinum)* over other habitats (Watson et al. 2002, Pollux et al. 2007). In contrast, Lane Snapper and Schoolmaster are thought to be more opportunistic, settling alternatively to hard bottom, mangrove roots, or seagrass beds (Lindeman et al. 1998, Pollux et al. 2007).

In this study, we describe fine—scale patterns of juvenile recruitment for Yellowtail Snapper, Gray Snapper, Lane Snapper, Schoolmaster, and Mutton Snapper from monthly seine surveys conducted between 2007 and 2019 in the Middle Florida Keys. Our specific objectives were to (1) relate recruitment patterns to existing information about spawning seasonality and early life history processes, and (2) characterize juvenile recruitment as a function of environmental and habitat variables to elucidate biophysical processes influencing the location and timing of larval settlement in the Middle Florida Keys.

MATERIALS AND METHODS

Data collection

Monthly seine samples were conducted between 2007 and 2019 in nearshore seagrass habitats along the Atlantic shoreline of Marathon, FL. A random survey design was employed based upon a benthic habitat map of the Florida Keys (FDEP 1998). The survey design used a grid of 1—latitudinal by 1—longitudinal minute cells (~1 nautical mile^2) stretching from Grassy Key (24.77N, —80.94W) to Boot Key (24.70N, —81.11W; Figure 1). Ten cells containing roughly equivalent coverage of shallow (< 1m) seagrass beds were chosen for permanent monthly sampling over the duration of the study (Figure 1). From this original list of 10 cells (1 cell/site), an additional cell was added to Grassy Key South (GKS) shortly into the project due to insufficient shallow seagrass cover in the originally selected cell. This resulted in a survey domain of 10 sites covering 11, 1—minute by 1—minute cells (Figure 1). Once per month at each fixed site, one seine sampling location was randomly selected from a nested grid of 100, 0.01 nm^2 "migrogrid" cells, yielding 10 seine samples collected per month. Seining was conducted at the center of each randomly selected "microgrid" cell.

Fish were collected with a 21.3 m center—bag seine following the methods of Bartels and Ferguson (2006). Seine hauls were conducted during daylight hours at mid to high tide whenever possible. All snappers were counted and their standard lengths (SL) measured in millimeters. Water temperature (^{o}C), salinity, and dissolved oxygen concentration (mg/L) were measured during each survey using a YSI water—quality sonde. Due to equipment malfunction, in—situ water quality data were not collected from September 2018 to March 2019. To fill this gap in the sea surface temperature record, we used the National Aeronautics and Space Administration's Multi—Scale Ultra—High Resolution Sea Surface Temperature data (NASA MUR; https://podaac.jpl.nasa.gov/MEaSUREs—MUR). This dataset provided daily sea surface temperatures for the dates in question at 1 km resolution for use in abundance models.

Four randomly selected 1 m^2 submerged aquatic vegetation

TABLE 1. *Modified Braun-Blanquet cover class codes and associated percent cover bins, and SAV type codes and taxonomic categories used for benthic cover estimates at each seining location.*

Braun-Blanquet code	Cover
5	>75%
4	50-75%
3	25-50%
2	5-25%
1	<5%
0.5	<1%, few stems
0.1	<1%, solitary stem

SAV code	Taxonomic category
TT	*Thalassia testudinum*
HW	*Halodule wrightii*
SF	*Syringodium filiforme*
CG	Calcareous green algae
HE	*Halophila engelmannii*
CA	*Caulerpa* spp.
RO	Red algae other
BO	Brown algae
HM	*Halimeda* spp.
GO	Green algae other (i.e., non-calcareous)
DR	Drift red algae
OA	Other algae

(SAV) quadrats were sampled at every seine location. The SAV cover was estimated using a modified Braun—Blanquet technique (Braun—Blanquet 1932), wherein cover types were chosen from 12 taxonomic categories (Table 1) and cover assigned into one of 7 categorical cover classes (Table 1). For analyses, percent cover by SAV type was taken as the midpoint of the cover class bins for each quadrat (e.g., Raposa et al. 2020). The midpoint method for converting categorical cover classes to percent cover was chosen over log—linear transformations (e.g., Van Der Maarel 2007) given that such transformations can yield cover estimates above 100%, thereby presenting difficulties for ecological interpretations of habitat use. Midpoint estimates of percent SAV cover were averaged by survey (i.e., across the 4 replicate quadrats) and SAV type (Table 1).

Statistical Analyses

Environmental and temporal patterns in settlement—stage snapper abundance (i.e., number of individuals ≤ 40 mm SL) from 1,314 seine hauls were examined using generalized linear regression. Analyses were restricted to settlement—stage individuals with SL ≤ 40 mm SL to better estimate variation in abundance near the time of larval settlement. Prior to analyses, surveys from 2008 and 2017 were excluded due to incomplete sampling during peak recruitment months because of logistical difficulties in October 2008 and the passage of Hurricane Irma in September 2017. Given a lack of availability of salinity and dissolved oxygen data from other sources and preliminary analyses showing that temperature, salinity, and dissolved oxygen we are all strongly correlated, only temperature was included in abundance models. Wind speed and direction were calculated as the mean of hourly readings taken over the preceding month at the Marathon airport, Florida Keys (24.72583°N, —81.05167°W; retrieved from https://www.ncei.noaa.gov). A 1 mo period was chosen to encompass the wind conditions during an assumed settlement window for snapper.

Prior to analysis, multicollinearity amongst continuous predictor variables was assessed with a correlation matrix. In several instances, variables were highly correlated with one another (e.g., % *T. testudinum* and distance to shore), however, no pairs of variables returned correlation coefficients > r = 0.6, and thus associated variance inflation was deemed inconsequential (Dormann et al. 2013). In contrast, preliminary analysis indicated large and significant differences in the mean distance to shore between sites (ANOVA; $F_{9,1304} = 537$; $p < 0.0001$), necessitating that distance to shore be nested within sampling site for formal analyses. Site—wise differences in other continuous variables (e.g., % *H. wrightii*; % *T. testudinum*) were negligible, and as a result, no other variables were nested within site. Considering seasonal oscillations in physical variables and the seasonality of snapper recruitment, temperature, wind speed, wind direction, and percent lunar illumination were nested within month in abundance models.

Generalized linear abundance models were fit for each species in R using the packages glmmTMB (Brooks et al. 2017), DHARMa (Hartig 2020), and MuMIn (Barton 2023) to develop temporal abundance indices and predict relationships with physical and environmental covariates. Global models with Poisson, quasi—Poisson, and negative binomial error distributions were compared for each species according to goodness—of—fit, dispersion, and zero—inflation parameters. After selection of appropriate model family, all possible combinations of variables were assembled into candidate models and ranked by Akaike's Information Criterion for small sample sizes (AICc) using the *dredge* function in the MuMIn package. Temporal and spatial autocorrelation of residuals in top—ranked models was assessed graphically using the *acf* function in the Stats package (R Core Team 2023).

In some cases, multiple models received similar support and fell within 2 AICc of the top model. For these instances, we implemented criteria whereby variables were deemed uninformative if their inclusion in a candidate model did not result in a net reduction of > 2 AICc relative to a nested, best—fitting model (Arnold 2010). Model convergence issues were encountered in the case of top ranked models for several species. For Schoolmaster and Yellowtail Snapper, all models containing lunar illumination as a predictor failed to converge. Likewise, for Mutton Snapper, non—convergence occurred for all models containing wind direction. As a remedy, model selection using the *dredge* function was re—executed for these species without the problematic variables. Additional instances of non—convergence in top models were handled by selecting the next best fitting model according to AICc. Model selection tables showing candidate models for each species are provided in the supplementary materials (Tables S1—S5).

Terms included in global abundance models were year,

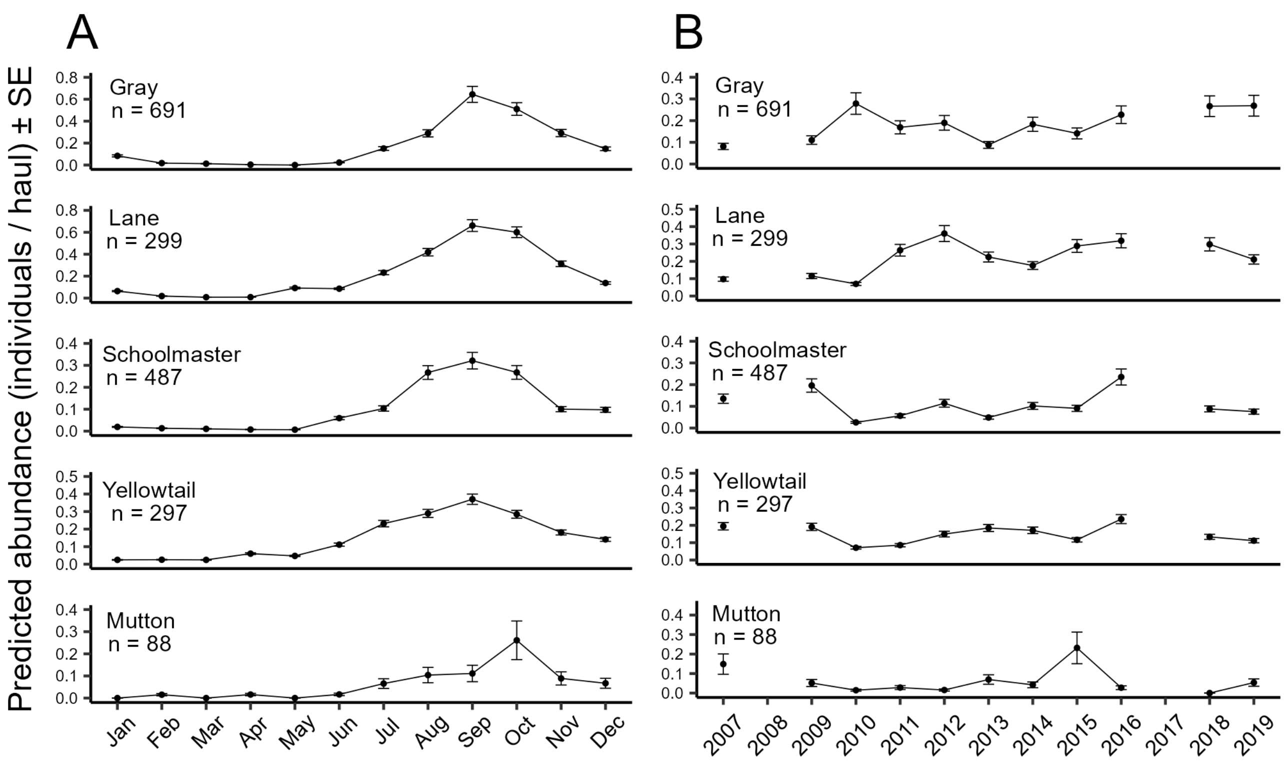

Figure 2. *Predicted abundance indices (individuals per haul) from the best-fitting models for settlement-stage snapper (≤ 40 mm SL). Data collected in 2008 and 2017 were not included in models due to sampling gaps during peak recruitment months. Note that y-axis scales differ between plots. A. Monthly. B. Yearly.*

month, site, distance to shore, water temperature, % *T. testudinum* cover, % *H. wrightii* cover, % *Syringodium filiforme* (manatee grass) cover, % calcareous green algae cover, Shannon diversity of aquatic vegetation types, % lunar illumination, wind speed, wind direction, and the interaction terms, year:site, year:month, and site:month. Given that study goals included developing temporal abundance indices, terms year and month were included as fixed effects in all models. Estimated marginal mean predictions were calculated by year, month, and SAV cover variables from the best—fitting abundance model, by species. Yearly and monthly abundance predictions were used to calculate mean between—month abundance variance by species to estimate the relative degree of spawning seasonality. Peak spawning months were estimated from mean lengths of settlement—stage fish caught, published larval growth rates, and peak recruitment months.

Results

A total of 1,862 settlement—stage snapper were caught during 1,314 seines conducted along the shore of Marathon, FL between 2007 and 2019. Gray Snapper were caught most frequently (16% occurrence), followed by Lane Snapper (11%), Schoolmaster (10%), Yellowtail Snapper (10%), and Mutton Snapper (3%). Abundances were highest in the fall for all species with peak recruitment in September and October (Figure 2A). Among annual trends, model—estimated abundance was lowest in 2010 for 3 of 5 species with the notable exception of Gray Snapper, whose settlement—stage abundance peaked during that year (Figure 2B). In 2010, mutton abundance (*n* = 1) was second lowest behind 2018 (*n* =0). Model—predicted recruitment variability between the lowest and highest producing years by species ranged from 200% to 1500%.

Snapper abundance by species was differentially predicted by temporal and locational factors (year, month, site) as well as environmental variables (% *H. wrightii*, % *T. testudinum*, % *S. filiforme*, % calcareous green algae, distance to shore, and water temperature) in best—fitting models. Three of 5 species' models included % *H. wrightii* cover as a positive predictor of abundance, however the strength of associations varied by snapper species (Figure 3, Table 2). At sites with a discernible effect of distance to shore, Schoolmaster and Gray Snapper abundance was negatively predicted by distance from the shoreline, while Yellowtail Snapper abundance increased with distance (Figure 4). Neither lunar illumination, wind speed, wind direction, SAV diversity, nor interactions between site, month, and year, were predictors in any best—fitting model (Tables S1—S5).

Across years, mean between—month variance in abundance ranged from 0.02 ± 0.01 (fish/haul) for Yellowtail Snapper, to a high of 0.21 ± 0.02 (fish/haul) for Gray Snapper (Table 3). Mean standard lengths of settlement—stage individuals (< 40 mm SL) were smallest for Lane Snapper (28.19 ± 1.03 mm SL) and greatest for Schoolmaster (30.15 ± 0.56 mm SL). Based upon mean lengths at capture and peak predicted recruitment months, mean peak spawning was estimated to have occurred in July for Schoolmaster, Gray Snapper, and Yellowtail Snapper, and in August for Mutton Snapper and Lane Snapper (Table 3).

Among SAV types, *T. testudinum* was the dominant species across all sites (mean coverage: 45.8 ± 8.70%). The highest estimated cover for the species was found at Boot Key West (67.14

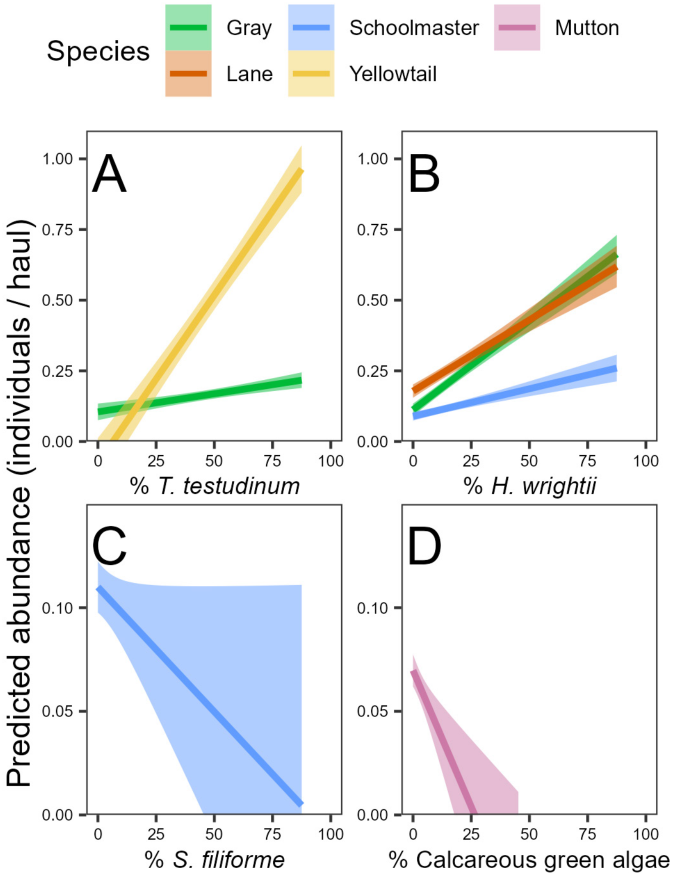

Figure 3. *Predicted abundance (individuals / haul) of settlement-stage snapper by percent cover of vegetation. Relationships shown for SAV types included in the best fitting abundance model by species. Shaded regions indicate 95% confidence intervals. Note that y-axis scales differ among plots. A. Thalassia testudinum. B. Halodule wrightii. C. Syringodium filiforme. D. Calcareous green algae.*

± 2.20%). *Halodule wrightii* cover averaged 11.8 ± 6.10% and was greatest at Grassy Key West, Coco Plum East, and High School (27.14 ± 2.59%, 21.01 ± 2.40%, 17.57 ± 2.45%, respectively). Other SAV types were comparatively sparse at all locations; overall, *S. filiforme* cover averaged 1.9 ± 0.26%, while calcareous green algae cover averaged 2.2 ± 0.14%.

Gray Snapper

Across all samples, 691 settlement–stage Gray Snapper were caught. Terms in the best fitting model of Gray Snapper abundance were year, month, site, site/distance to shore, % *T. testudinum* cover, % *H. wrightii* cover, and month/water temperature (Table 2, Table S1). Among years, the lowest predicted abundance for Gray Snapper occurred in 2007 (0.08 ± 0.01 fish/haul) and the greatest in 2010 (0.28 ± 0.05 fish/haul; Figure 2B), amounting to a 243% difference. The highest predicted monthly abundance occurred in September (0.64 ± 0.07 fish/haul), and the lowest in May, when no settlement–stage Gray Snapper were found throughout the entirety of the study (Figure 2A). Across sites, Gray Snapper predicted abundance was highest at the High School sampling site (0.57 ± 0.05 fish/haul) and lowest at Vaca Flat East (0.03 ± 0.003 fish/haul). Gray Snapper abundance was positively predicted by *H. wrightii* and *T. testudinum* cover (Figure 3A, Figure 3B); however, abundance was most sensitive to changes in *H. wrightii* cover. Distance to shore was also determinant of abundance for the species, however effect sizes differed by sampling site. Abundance decreased with distance to shore most sharply at Boot Key West and Grassy Key South (Figure 4). The effect of water temperature on predicted Gray Snapper abundance varied by month with discernible, positive effects found in October and to a lesser degree, December (Figure 5).

Lane Snapper

In total, 299 settlement–stage Lane Snapper were caught over the study period. Terms in the best fitting abundance model were year, month, site, and *H. wrightii* cover (Table 2, Table S2). Yearly effects were characterized by lowest predicted abundance in 2010 (0.07 ± 0.009 fish/haul) and highest abundance in 2012 (0.36 ± 0.05 fish/haul; Figure 2B), a difference of 415%. Among months, Lane Snapper abundance peaked in September (0.66 ± 0.05 fish/haul) and fell to its lowest predicted value in April (0.009 ± 0.0007 fish/haul; Figure 2A). Among SAV types, Lane Snapper abundance was positively predicted by *H. wrightii* cover (Figure 3B). Predicted site–wise abundance was greatest at Vaca Flat West (0.57 ± 0.06 fish/haul) and lowest at Vaca Flat East (0.06 ± 0.006 fish/haul).

Schoolmaster

Over the time series, 487 settlement–stage Schoolmaster were caught in seine samples. The best fitting model of Schoolmaster abundance included the terms year, month, site, % *H. wrightii* cover, % *S. filiforme* cover, and site/distance to shore

TABLE 2. *Terms in the best-fitting generalized linear models of settlement-stage snapper abundance as identified by AICc. Terms abbreviated as follows: TT–% Thalassia testudinum cover; HW–% Halodule wrightii cover; SF–% Syringodium filiforme cover; CG–% calcareous green algae cover. Nested model terms indicated by /.*

Species	**Model terms**	**Error family**
Gray	year + month + site + TT + HW + month / water temp. + site / dist. to shore	quasi-Poisson
Lane	year + month + site + HW	negative binomial
Schoolmaster	year + month + site + HW + SF + site / dist. to shore	quasi-Poisson
Yellowtail	year + month + site + TT + month / water temp. + site / dist. to shore	quasi-Poisson
Mutton	year + month + CG	quasi-Poisson

TABLE 3. *Mean between-month variance in settlement-stage abundance (± se), mean standard length (SL; mm), published larval growth rates (mm/day), mean estimated ages (days; ± se), and estimated peak spawning months. Note that larval and early juvenile growth information for Schoolmaster was lacking and therefore growth rate was taken as the mean of the other species' growth rates.*

Species	Between-month Variance	SL (mm)	Growth rate (mm/day)	Mean est. age (days)	Est. peak spawning month	Growth rate sources
Gray	0.21 (0.04)	29.27 (0.54)	0.69	42.36 (0.78)	July	Richards and Saksena 1980, Allman and Grimes 2002, Denit and Sponaugle 2004
Lane	0.03 (0.01)	28.19 (1.03)	0.73	38.62 (1.41)	August	Clarke et al. 1997
Schoolmaster	0.06 (0.02)	30.15 (0.56)	0.64	46.92 (0.87)	July	–
Yellowtail	0.02 (0.01)	29.75 (0.91)	0.54	55.10 (1.68)	July	Riley et al. 1995, Clarke et al. 1997
Mutton	0.04 (0.04)	29.6 (0.92)	0.61	48.60 (1.5)	August	Clarke et al. 1997

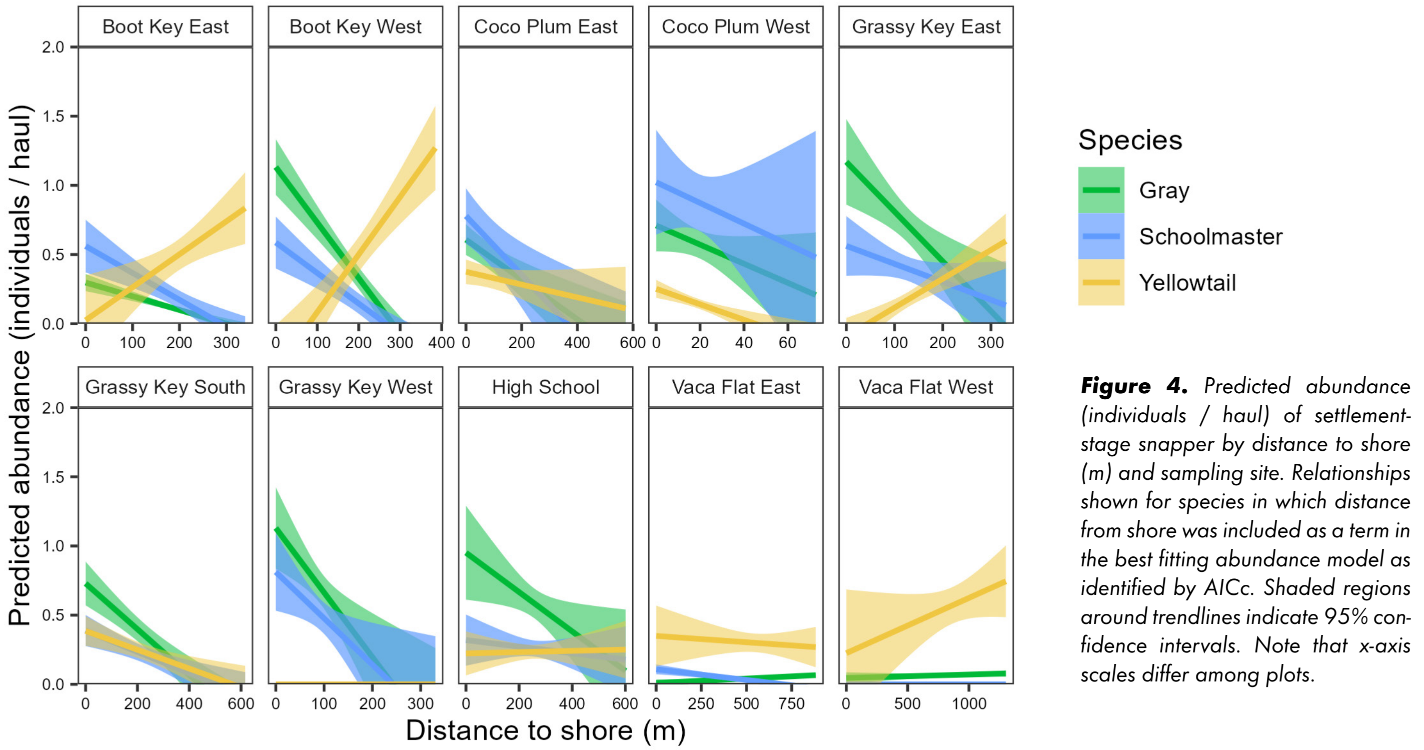

Figure 4. *Predicted abundance (individuals / haul) of settlement-stage snapper by distance to shore (m) and sampling site. Relationships shown for species in which distance from shore was included as a term in the best fitting abundance model as identified by AICc. Shaded regions around trendlines indicate 95% confidence intervals. Note that x-axis scales differ among plots.*

(Table 2, Table S3). Predicted abundance was lowest in 2010 (0.03 ± 0.004 fish/haul) and highest in 2016 (0.24 ± 0.04 fish/haul; + 805%; Figure 2B). Like other species, the highest abundance for Schoolmaster was predicted in September (0.32 ± 0.04 fish/haul), and the lowest in May (0.007 ± 0.001 fish/haul), the month when only one individual was caught over the length of the study (Figure 2A). Schoolmaster abundance was positively predicted by *H. wrightii* cover (Figure 3B), and a weak negative association was identified with *S. filiforme* cover (Figure 3C). Among sites, predicted catches were highest at High School (0.26 ± 0.03 fish/haul), and smallest at Vaca Flat West, where no settlement–stage Schoolmaster was ever caught. At sites where relationships between abundance and distance to shore were identified, Schoolmaster were more abundant closer to the shoreline (Figure 4). Among these sites, the strongest effect of distance to shore was found at Coco Plum East.

Yellowtail Snapper

A total of 297 settlement–stage Yellowtail Snapper were caught in the study. Terms in the best fitting model were year, month, site, % *T. testudinum* cover, month/water temperature, and site/distance to shore (Table 2, Table S4). Across years, Yellowtail Snapper abundance was lowest in 2010 (0.07 ± 0.008 fish/haul) and highest in 2016 (0.24 ± 0.02 fish/haul), amounting to a 233% difference (Figure 2B). Month–wise predicted abundance was equally low in January and March (0.02

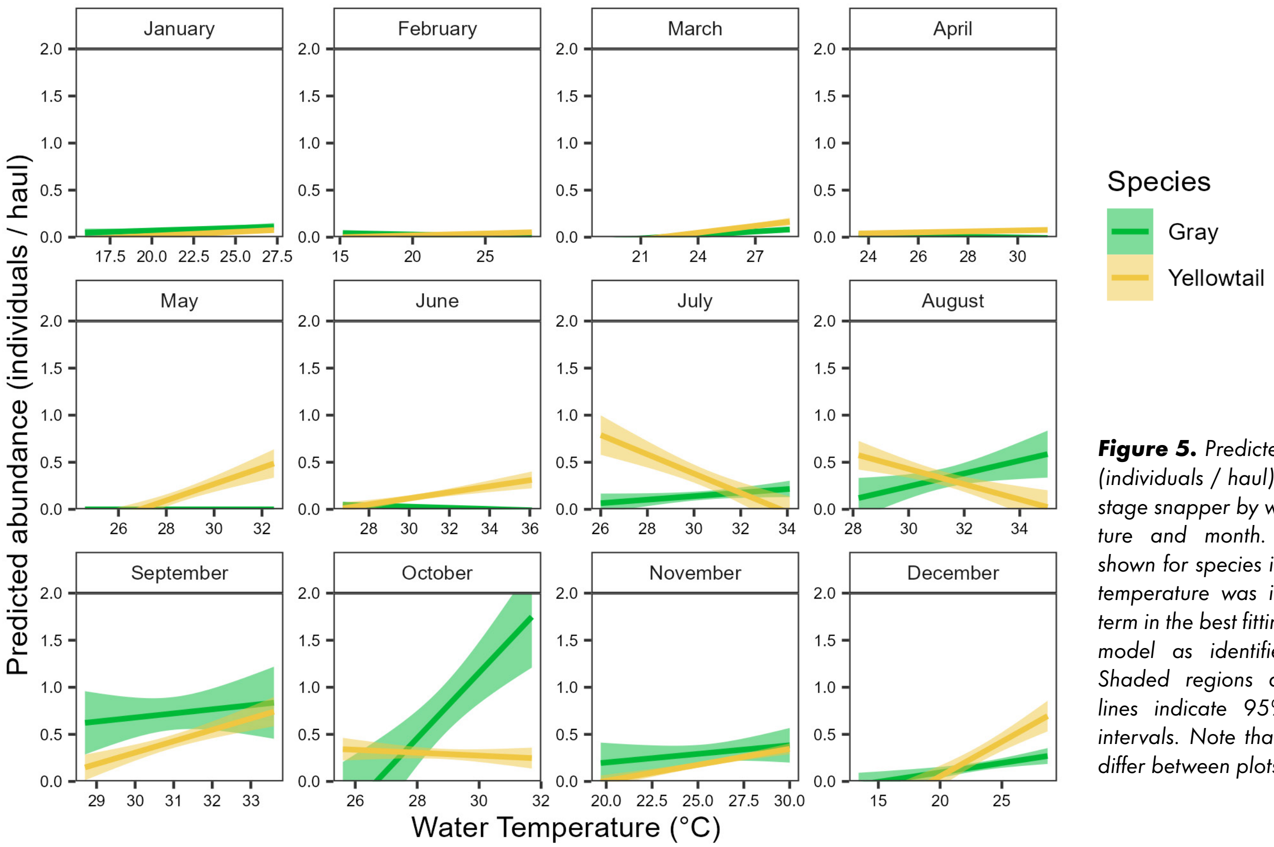

Figure 5. *Predicted abundance (individuals / haul) of settlement-stage snapper by water temperature and month. Relationships shown for species in which water temperature was included as a term in the best fitting abundance model as identified by AICc. Shaded regions around trendlines indicate 95% confidence intervals. Note that x-axis scales differ between plots.*

± 0.002 fish/haul) and peaked in September (0.37 ± 0.03 fish/haul; Figure 2A). Site level abundance was greatest at Boot Key East (0.71 ± 0.08 fish/haul), whereas no settlement–stage Yellowtail Snapper were ever encountered at Coco Plum West or Grassy Key West. Yellowtail Snapper abundance was strongly and positively predicted by *T. testudinum* cover, the strongest such relationship for any snapper species assessed (Figure 3A). No other SAV types were predictors in the best–fitting model of Yellowtail Snapper abundance. Distance from shore negatively predicted Yellowtail Snapper abundance at several sites: Boot Key East, Boot Key West, and Grassy Key East (Figure 4). At other sites, the relationship between distance to shore and Yellowtail Snapper abundance was indiscernible. The effect of water temperature on Yellowtail Snapper abundance oscillated between months: In May, June, September, November, and December, abundance was positively predicted by water temperature. In July and August, the relationship was reversed with peak abundances at the lowest observed water temperatures (Figure 5).

Mutton Snapper

In total, 88 settlement–stage Mutton Snapper were caught in this study, the fewest of any snapper species assessed here. The best fitting model for the species included the terms year, month, and % calcareous green algae cover (Table 2, Table S5). Year–wise trends were characterized by low abundance in 2018, when zero individuals were caught, and highest predicted abundance in 2015 (0.23 ± 0.08 fish/haul; Figure 2B). Mutton Snapper caught in 2015 (n = 36) represented nearly half of all individuals caught over the entire 13–year time series. Comparing the lowest producing year when Mutton Snapper were caught (i.e., 2010; mean predicted abundance = 0.01 ± 0.004 fish/haul) and 2015, there was a 1,480% difference. Predicted abundance peaked in October (0.26 ± 0.08 fish/haul) and was lowest in January, March, and May, months when not a single Mutton Snapper was caught during the study (Figure 2A). Mutton Snapper abundance was negatively predicted by calcareous green algae cover (Figure 3D), while no other relationships with SAV types were identified in the best–fitting model.

Discussion

Early life history processes affecting juvenile recruitment have consequences for adult stock size and are therefore a critical component of fisheries research (Szuwalski et al. 2015). We found variation in the strength, timing, and location of snapper recruitment in the Middle Florida Keys attributed primarily to interannual variability, spawning seasonality, species–specific habitat associations, and intra–month water temperature fluctuations. Among interannual trends, predicted abundances in 2010 were lower for 3 of 5 species (Lane Snapper, Schoolmaster, and Yellowtail Snapper), with the notable exception of Gray Snapper whose settlement–stage abundance was greatest during that year. Our results also confirm previously documented juvenile snapper associations with seagrasses *H. wrightii* and *T. testudinum* (Bartels and Ferguson 2006, Pollux et al. 2007) and weaker associations with other SAV types. Spatial distributions of settlement–stage abundance were influenced by both distance to shore and sampling site (i.e., along shore position), indicating heterogenous habitat utilization and/or larval settlement across our sampling domain.

A period of historically cold weather early in 2010 likely influenced the unusual snapper recruitment patterns observed in that year. The January 2010 South Florida cold spell was one of the most severe on record, both for its extreme low water temperatures and persistence (Boucek and Rehage 2014). Mean water temperature in January 2010 was 18.08°C (min: 9.70, max: 25.0), while the January mean for the other years surveyed was 22.20°C (min: 15.60, max: 27.10). The cold event lasted for 12 days and resulted in mass mortality of fish and corals (Lirman et al. 2011, Colella et al. 2012, Santos et al. 2016). Public fish kill reporting data from the Florida Keys submitted during this period includes reports of dead individuals of many common reef—dwelling fish families, including snapper (Florida Fish and Wildlife Conservation Commission 2010). During the recruitment season later that year, abundances of settlement—stage Lane Snapper, Schoolmaster and Yellowtail Snapper were the lowest of the 13—year time series, while Mutton Snapper abundance was also uncharacteristically low. In contrast, Gray Snapper abundance peaked in 2010. Climatic disturbances have been shown to produce lasting changes to the size and demographics of fish populations through direct mortality, reduced fitness from a lack of prey resources, and increased larval mortality, all resulting in reduced recruitment (Drinkwater 2002, Planque et al. 2010, Asch et al. 2019). Reliable information on the lethal low temperature threshold for snapper species is limited; however, based upon geographic range, Gray Snapper is thought to have the highest resistance to cold weather of the snapper assessed here (Wuenschel et al. 2012). Increased Gray Snapper reproduction, early juvenile survival, or both corresponds with findings by Santos et al. (2016), who noted that adult Gray Snapper catch—per—unit—effort in South Florida increased immediately following the January 2010 cold event. The unique severity of the January cold event and the documented, widespread impacts suggest that a combination of direct mortality and indirect ecological effects are responsible for anomalous snapper recruitment observed in 2010.

Spawning seasonality was apparent in monthly abundance indices for all species. Estimated settlement—stage abundances peaked for Gray Snapper, Lane Snapper, Schoolmaster, and Yellowtail Snapper in September, while newly settled Mutton Snapper were most abundant in October. Based upon estimated post—hatch ages and published growth rates (Table 3), peak inferred spawning occurred in late July for Schoolmaster, Gray Snapper, and Yellowtail Snapper, and mid—to—late August for Lane Snapper and Mutton Snapper. Other authors have noted that Yellowtail Snapper and Lane Snapper have longer spawning seasons compared to other Caribbean snapper species, with near year—round spawning observed in some locales (Reshetnikov and Claro 1976, Thompson and Munro 1983, Domeier et al. 1996, Figuerola et al. 1997). Based upon lower recruitment variation across months, a pattern of extended spawning appears to hold true for Yellowtail Snapper and Lane Snapper in the Florida Keys (Zimmermann et al. 2019). Monthly recruitment patterns indicate elevated spawning from March to November for Yellowtail Snapper and April to November for Lane Snapper. Our July peak spawning estimate for Gray Snapper corresponds with other estimates from South Florida (Domeier et al. 1996, Barbieri and Colvocoresses 2003). In contrast, little information exists on the timing of peak Schoolmaster spawning in Florida by which to compare our July estimate. However, in Cuba, elevated Schoolmaster spawning has been observed from April to June (García—Cagide et al. 1994). The lack of basic knowledge regarding the reproductive biology of Schoolmaster in Florida represents an opportunity for future research.

Our August estimate for Mutton Snapper peak spawning is later than observed in previous studies in the Florida Keys (Barbieri and Colvocoresses 2003 (April—May), Burton et al. 2005 (May—July)). Given that the sample size for settlement—stage Mutton Snapper was relatively low (*n* = 88), our peak spawning estimate should be interpreted with caution. However, our evidence of substantial Mutton Snapper spawning in August has implications for the management of spawning aggregation sites in the Florida Keys, notably the recently protected Western Dry Rocks Mutton Snapper spawning site, which is closed to fishing from 1 April to 31 July (Florida Fish and Wildlife Conservation Commission 2021).

Among annual abundance trends by species, the 2015 spike in juvenile Mutton Snapper abundance stands alone for its magnitude: roughly 3 times as many individuals were caught in that year compared to the 2007—2019 mean. Notably, over the same 13—year period, commercial Mutton Snapper landings from the Atlantic coast of Florida (including the Florida Keys) also peaked in 2015 (19,533 kg; National Marine Fisheries Service, Fisheries Statistics Division, pers. comm.). Taken together, these 2 data points suggest that a strong year—class entered the fishery in 2015 and became reproductively mature, thereby generating the strong pulse of juveniles we observed. While we are unable to determine the sources of Mutton Snapper larvae entering our sampling domain, one hypothesized source is Riley's Hump, a regionally important multi—species spawning aggregation site located within the Tortugas South Ecological Reserve. Since receiving fishing protection in 2001, annual Mutton Snapper spawning aggregations there have steadily recovered from depletion and now include thousands of individuals (Burton et al. 2005, Feeley et al. 2018). Given that modeling and drifter studies have demonstrated that the Middle Florida Keys receives fish larvae from the Dry Tortugas region (Bryan et al. 2015, Domeier 2004), it's conceivable that the 2015 recruitment peak was an indirect result of strong recovery of Mutton Snapper spawning aggregations at Riley's Hump.

The effects of SAV cover and offshore distance varied by snapper species, implying differential early juvenile habitat preferences. Near—shore vegetated habitats are well known to be ontogenetically important for snapper in South Florida and the Florida Keys (Springer and McErlean 1962, Starck 1971, Bartels and Ferguson 2006, Faunce and Serafy 2007). While Bartels and Ferguson (2006) found a negative correlation between total snapper abundance (all species) and *T. testudinum* cover, our results indicate that *T. testudinum* beds do in fact serve as preferred settlement habitat for Gray and Yellowtail Snapper. However, in the case of Gray Snapper, *H. wrightii* beds harbored higher densities of settlers. High blade densities found in *H. wrightii* beds (> 10,000 blades/m^2) are thought to provide enhanced shelter and foraging opportunities for some early juvenile fishes (Stoner 1983). While stomach content analyses of juvenile Yellowtail Snapper are lacking for the Florida Keys, Watson et al. (2002) observed that settlement–stage individuals fed primarily on plankton drifting above and within *T. testudinum* beds before switching to benthic invertebrate prey as larger juveniles. The comparatively lower stem densities found in *T. testudinum* beds (Stoner 1983) and their position further from shore may provide better access to planktonic prey. In contrast, *H. wrightii*– associated species (Gray Snapper, Schoolmaster, and Lane Snapper) appear to rely more heavily upon benthic crustacean prey early in their development (Hettler 1989, Rooker 1995, Duarte and García 1999, Franks and VanderKooy 2000), which have been found in higher abundances in *H. wrightii* beds (Stoner 1983, Lewis 1984).

Fluctuations in the availability and quality of nursery habitat have been shown to strongly influence the recruitment of other demersal species (Aburto–Oropeza et al. 2007, 2010, Wilson et al. 2017, Schloesser and Fabrizio 2019). The Florida Keys region has experienced widespread seagrass die–offs and community shifts intermittently since 1987, thought to stem primarily from anoxic conditions created by high temperature and salinity events (Hall et al. 2016). Nearshore seagrass beds along the archipelago also face threats from sewage–derived nutrient enrichment (Lapointe et al. 2004) and physical damage from boat propellers (Kenworthy et al. 2002), both of which can facilitate species–shifts, macroalgal blooms, and habitat fragmentation. Given our finding that juvenile snapper abundance covaried with seagrass cover, future research efforts should seek to quantify how seagrass losses and shifts in nearshore SAV communities affect the abundance of snapper recruits in the Florida Keys.

Relationships between juvenile snapper abundance and in–situ water temperature differed by species and sampling month. Yellowtail Snapper and Gray Snapper abundance were predicted by month–wise water temperatures, yet the strength and direction of effects differed widely between sampling months. For instance, Yellowtail Snapper abundance increased with water temperature in May, June, September, and December, and decreased with higher temperatures in July and August. Likewise, Gray Snapper abundance was positively predicted by higher temperatures in October and to a lesser extent December. Given that sampling days were not fixed within months, contrasting relationships with water temperature in adjacent months likely reflect seasonal fluctuations in temperature and juvenile abundance rather than month–specific environmental preferences. Nevertheless, our results confirm that juveniles of both species can tolerate a range of water temperatures in the summer and early fall (26 – 34 °C) (Wallace 1977, Flaherty et al. 2014). Such tolerances have been suggested as evolutionary means of maximizing the tradeoff between the energetic costs of inhabiting extreme environments and reduced predation risk in areas less hospitable to predators (Wuenschel et al. 2004, Grol et al. 2011).

Neither moon phase, wind speed, nor wind direction predicted the recruitment of juvenile snapper in any best–fitting model. Given that snapper are known to spawn according to moon phase in the Florida Keys (Domeier et al. 1996), the lack of a lunar signal in our model predictions likely indicates a disconnection of spawned larval supply from settlement–stage abundance due to planktonic processes (Sponaugle and Pinkard 2004, Pineda et al. 2010), that our survey methods lacked the precision to detect a true lunar recruitment signal, or both. Wind–driven surface currents can deliver pelagic larvae to nursery habitats (Basterretxea et al. 2012, Goikoetxea and Irigoien 2013, Schlaefer et al. 2018), and have been hypothesized as an onshore transport mechanism for larval fishes in the Middle Florida Keys (Lee et al. 1994, 1992). Given that our modeling methods did not permit recruit–specific examination of wind conditions preceding settlement (e.g., Schlaefer et al. 2018), and individual surveys often captured conspecifics of a variety of lengths (and inferred settlement dates), a true wind effect may have gone undetected. Likewise, variation in spawning output, larval mortality, and/or post–settlement mortality could have obscured potential wind effects by contributing unexplained abundance variation. Future analyses incorporating oceanographic data offshore of the Florida Keys (e.g., water temperature, current speed) into settlement–stage abundance models would help to more directly address the influence of pre–settlement processes on juvenile abundance.

Shallow–water snappers remain an important recreational and commercial fishery resource in South Florida and the Florida Keys. The 13–year recruitment time series analyzed here provides updated, management–relevant information on juvenile habitat associations, patterns of interannual recruitment variation, and spawning seasonality. Long–term monitoring efforts like this one are invaluable to fisheries managers, particularly in the context of a changing climate. As extreme weather events such as the 2010 cold spell are predicted to become increasingly common, continued monitoring will be necessary to document related trends in juvenile recruitment and adult population dynamics. Furthermore, questions remain regarding the influence of interacting biophysical factors on snapper recruitment in the Florida Keys. Within this framework, the appropriate management of snapper fisheries along the Florida Reef Tract will greatly benefit from additional research linking pre– and post–settlement mortality, juvenile recruitment, and stock size.

ACKNOWLEDGEMENTS

We are grateful for technical and logistical assistance provided by D. Morley, P. Barbera, J. Keller, J. Renchen, J. Herbig, and C. Howe. This manuscript was greatly improved by helpful comments from G. Delgado, J. Peake, and 2 anonymous reviewers. This research was funded by State of Florida recreational saltwater fishing license fees.

LITERATURE CITED

Aburto–Oropeza, O., E. Sala, G. Paredes, A. Mendoza, and E. Ballesteros. 2007. Predictability of reef fish recruitment. Ecology 88:2220–2228. https://doi.org/10.1890/06–0857.1

Aburto–Oropeza, O., G. Paredes, I. Mascareñas–Osorio, and E. Sala. 2010. Climatic influence on reef fish recruitment and fisheries. Marine Ecology Progress Series 410:283–287. https://doi.org/10.3354/meps08695.

Addis, D., S. Allen, R.G. Muller, J. Munyandorero, J. O'Hop, C. Swanson, H. O'Farrell, and M. Tyler–Jedlund. 2021. Florida's inshore and nearshore species: 2020 status and trends. Final Report, Florida Fish and Wildlife Conservation Commission, Fish and Wildlife Research Institute, St. Petersburg, FL, USA. 315 p.

Allman, R.J. and C.B. Grimes. 2002. Temporal and spatial dynamics of spawning, settlement, and growth of gray snapper (*Lutjanus griseus*) from the West Florida shelf as determined from otolith microstructures. Fisheries Bulletin 100:391–403.

Armsworth, P.R. 2000. Modelling the swimming response of late stage larval reef fish to different stimuli. Marine Ecology Progress Series 195:231–247. https://doi.org/10.3354/meps195231.

Arnold, T.W. 2010. Uninformative parameters and model selection using Akaike's Information Criterion. Journal of Wildlife Management 74:1175–1178. https://doi.org/10.2193/2009–367.

Asch, R.G., C.A. Stock, and J.L. Sarmiento. 2019. Climate change impacts on mismatches between phytoplankton blooms and fish spawning phenology. Global Change Biology 25:2544–2559. https://doi.org/10.1111/gcb.14650.

Barbieri, L.R. and J.A. Colvocoresses. 2003. Southeast Florida reef fish abundance and biology: Five–year performance report. Final Report, Florida Fish and Wildlife Conservation Commission. St. Petersburg, FL, USA. 118 p.

Bartels, C.T. and K.L. Ferguson. 2006. Preliminary observations of abundance and distribution of settlement–stage snappers in shallow, nearshore seagrass beds in the Middle Florida Keys. Proceedings of the Gulf and Caribbean Fisheries Institute 67:235–247.

Barton, K. 2023. MuMIn: Multi–Model Inference. R package version 1.47.5. https://CRAN.R–project.org/package=MuMIn (viewed on 2/1/24)

Basterretxea, G., A. Jordi, I.A. Catalán, and A. Sabats. 2012. Model–based assessment of local–scale fish larval connectivity in a network of marine protected areas. Fisheries Oceanography 21:291–306. https://doi.org/10.1111/j.1365–2419.2012.00625.x.

Beck, M.W., K.L. Heck, Jr., K.W. Able, D.L. Childers, D.B. Eggleston, B.M. Gillanders, B. Halpern, C.G. Hays, K. Hoshino, T.J. Minello, R.J. Orth, P.F. Sheridan, and M.P. Weinstein. 2001. The identification, conservation, and management of estuarine and marine nurseries for fish and invertebrates. BioScience 51:633–641. https://doi.org/10.1641/0006–3568(2001)051%5B0633:TICAMO%5D2.0.CO;2

Boucek, R.E. and J.S. Rehage. 2014. Climate extremes drive changes in functional community structure. Global Change Biology 20:1821–1831. https://doi.org/10.1111/gcb.12574.

Braun–Blanquet, J. 1932. Plant Sociology. The Study of Plant Communities. McGraw Hill, New York, NY, USA, 439 p.

Brooks, M.E., K. Kristensen, K.J. van Benthem, A. Magnusson, C.W. Berg, A. Nielsen, H.J. Skaug, M. Mächler, and B.M. Bolker. 2017. GlmmTMB balances speed and flexibility among packages for zero–inflated generalized linear mixed modeling. The R Journal 9:378–400. https://doi.org/10.32614/rj–2017–066.

Brosset, P., A.D. Smith, S. Plourde, M. Castonguay, C. Lehoux, and E. Van Beveren. 2020. A fine–scale multi–step approach to understand fish recruitment variability. Scientific Reports 10:16064. https://doi.org/10.1038/s41598–020–73025–z.

Bryan, D.R., J. Luo, J.S. Ault, D.B. McClellan, S.G. Smith, D. Snodgrass, and M.F. Larkin. 2015. Transport and connectivity modeling of larval permit from an observed spawning aggregation in the Dry Tortugas, Florida. Environmental Biology of Fishes 98:2263–2276. https://doi.org/10.1007/s10641–015–0445–x.

Burton, M.L., K.J. Brennan, R.C. Muñoz, and R.O. Parker. 2005. Preliminary evidence of increased spawning aggregations of mutton snapper (*Lutjanus analis*) at Riley's Hump two years after establishment of the Tortugas South Ecological Reserve. Fishery Bulletin 103:404–410.

Clarke, M.E., M.L. Domeier, and W.A. Laroche. 1997. Development of larvae and juveniles of the mutton snapper (*Lutjanus analis*), lane snapper (*Lutjanus synagris*) and yellowtail snapper (*Lutjanus chrysurus*). Bulletin of Marine Science 61:11–37.

Claro, R., K.C. Lindeman, and L.R. Parenti, eds. 2014. Ecology of the Marine Fishes of Cuba. Smithsonian Institution Press, Washington D.C., USA, 478 p.

Colella, M.A., R.R. Ruzicka, J.A. Kidney, J.M. Morrison, and V.B. Brinkhuis. 2012. Cold–water event of January 2010 results in catastrophic benthic mortality on patch reefs in the Florida Keys. Coral Reefs 31:621–632. https://doi.org/10.1007/s00338–012–0880–5.

D'Alessandro, E.K., S. Sponaugle, and J.E. Serafy. 2010. Larval ecology of a suite of snappers (family: Lutjanidae) in the Straits of Florida, Western Atlantic Ocean. Marine Ecology Progress Series 410:159–175. https://doi.org/10.3354/meps08632.

Denit, K. and S. Sponaugle. 2004. Growth variation, settlement, and spawning of gray snapper across a latitudinal gradient. Transactions of the American Fisheries Society 133:1339–1355. https://doi.org/10.1577/t03–156.1.

Domeier, M.L. 2004. A potential larval recruitment pathway originating from a Florida marine protected area. Fisheries Oceanography 13:287–294. https://doi.org/10.1111/j.1365–2419.2004.00287.x.

Domeier, M.L., C.C. Koenig, and F.C. Coleman. 1996. Reproductive biology of the gray snapper with notes on spawning for other Western Atlantic snapper. Proceedings of an EPOMEX/ICLARM International Workshop on Tropical Snappers and Groupers, Campeche, Mexico, 26–29 October 1993, p. 189–201.

Dormann, C.F., J. Elith, S. Bacher, C. Buchmann, G. Carl, G. Carré, J.R.G. Marquéz, B. Gruber, B. Lafourcade, P.J. Leitão, T. Münkemüller, C. Mcclean, P.E. Osborne, B. Reineking, B. Schröder, A.K. Skidmore, D. Zurell, and S. Lautenbach. 2013. Collinearity: A review of methods to deal with it and a simulation study evaluating their performance. Ecography 36:27–46. https://doi.org/10.1111/j.1600–0587.2012.07348.x.

Drinkwater, K. F. 2002. A review of the role of climate variability in the decline of northern cod. In: N.A. McGinn, ed. Fisheries in a Changing Climate, The American Fisheries Society, Bethesda, MD, USA, p. 113–109

Duarte, L.O. and C.B. García. 1999. Diet of the lane snapper, *Lutjanus synagris* (Lutjanidae), in the Gulf of Salamanca, Colombia. Caribbean Journal of Science 35:54–63.

Faunce, C.H. and J.E. Serafy. 2007. Nearshore habitat use by gray snapper (*Lutjanus griseus*) and bluestriped grunt (*Haemulon sciurus*): Environmental gradients and ontogenetic shifts. Bulletin of Marine Science 80:473–495.

FDEP. 1998. Benthic habitats of the Florida Keys. Technical Report, Florida Marine Research Institute, St. Petersburg, FL, USA. 53 p.

Feeley, M.W., D. Morley, A. Acosta, P. Barbera, J. Hunt, T. Switzer, and M. Burton. 2018. Spawning migration movements of mutton snapper in Tortugas, Florida: Spatial dynamics within a marine reserve network. Fisheries Research 204:209–223. https://doi.org/10.1016/j.fishres.2018.02.020.

Figuerola, M., D. Matos–Caraballo, and W. Torres. 1997. Maturation and reproductive seasonality of four reef fish species in Puerto Rico. Proceedings of the Gulf and Caribbean Fisheries Institute 50:938–968.

Flaherty, K.E., T.S. Switzer, B.L. Winner, and S.F. Keenan. 2014. Regional correspondence in habitat occupancy by gray snapper (*Lutjanus griseus*) in estuaries of the southeastern United States. Estuaries and Coasts 37:206–228. https://doi.org/10.1007/s12237–013–9652–x.

Florida Fish and Wildlife Conservation Commission. 2010. Fish Kill Database Directory 2010. https://myfwc.com/research/saltwater/health/abnormalities/#

Florida Fish and Wildlife Conservation Commission. 2021. FWC protects multi–species spawning aggregations near Western Dry Rocks. 2021. https://myfwc.com/news/all–news/wdr–comm–221

Fourqurean, J.W. and J.C. Zieman. 2002. Nutrient content of the seagrass *Thalassia testudinum* reveals regional patterns of relative availability of nitrogen and phosphorous in the Florida Keys, USA. Biogeochemistry 61:229–245. https://www.jstor.org/stable/1469799

Franks, J.S. and K.E. VanderKooy. 2000. Feeding habits of juvenile lane snapper *Lutjanus synagris* from Mississippi coastal waters, with comments on the diet of gray snapper *Lutjanus griseus*. Gulf and Caribbean Research 12:11–17. https://doi.org/10.18785/gcr.1201.02.

García–Cagide, A.R., R. Claro, and B.V. Koshelev. 1994. Reproduction. In: R. Claro, K.C. Lindeman, and L.R. Parenti, eds. Ecology of the Marine Fishes of Cuba. Smithsonian Institution Press, Washington, D.C., USA, p. 187–262.

Goikoetxea, N. and X. Irigoien. 2013. Links between the recruitment success of northern European hake (*Merluccius merluccius* l.) and a regime shift on the NE Atlantic continental shelf. Fisheries Oceanography 22:459–476. https://doi.org/10.1111/fog.12033.

Grol, M.G.G., I. Nagelkerken, A.L. Rypel, and C.A. Layman. 2011. Simple ecological trade–offs give rise to emergent cross–ecosystem distributions of a coral reef fish. Oecologia 165:79–88. https://doi.org/10.1007/s00442–010–1833–8.

Hall, M.O., B.T. Furman, M. Merello, and M.J. Durako. 2016. Recurrence of *Thalassia testudinum* seagrass die–off in Florida Bay, USA: Initial observations. Marine Ecology Progress Series 560:243–249. https://doi.org/10.3354/meps11923.

Hartig, F. 2020. DHARMa: Residual Diagnostics for Hierarchical (Multi–Level/Mixed) Regression Models. R package version 0.4.6. https://CRAN.R–project.org/package=DHARMa

Hettler, W.F. 1989. Food habits of juveniles of spotted seatrout and gray snapper in Western Florida Bay. Bulletin of Marine Science 44:155–162.

Kenworthy, W., M.S. Fonseca, P.E. Whitfield, and K.K. Hammerstrom. 2002. Analysis of seagrass recovery in experimental excavations and propeller–scar disturbances in the Florida Keys National Marine Sanctuary. Journal of Coastal Research 37:75–85. https://www.jstor.org/stable/25736344

Lapointe, B.E., P.J. Barile, and W.R. Matzie. 2004. Anthropogenic nutrient enrichment of seagrass and coral reef communities in the Lower Florida Keys: Discrimination of local versus regional nitrogen sources. Journal of Experimental Marine Biology and Ecology 308:23–58. https://doi.org/10.1016/j.jembe.2004.01.019

Lee, T.N., C. Rooth, E. Williams, M. McGowan, A.M. Szmant, and M.E. Clarke. 1992. Influence of Florida current, gyres, and wind–driven circulation on transport of larvae and recruitment in the Florida Keys coral reefs. Continental Shelf Research 12:971–1002. https://doi.org/10.1029/1998jc900101.

Lee, T.N., 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. Bulletin of Marine Science 54:621–646.

Lewis, F. 1984. Distribution of macrobenthic crustaceans associated with *Thalassia*, *Halodule* and bare sand substrata. Marine Ecology Progress Series 19:101–113. https://doi.org/10.3354/meps019101.

Limouzy—Paris, C.B., H.C. Graber, D.L. Jones, A.W. Röpke, and W.J. Richards. 1997. Translocation of larval coral reef fishes via sub—mesoscale spin—off eddies from the Florida current. Bulletin of Marine Science 60:966–983.

Lindeman, K.C. 1997. Development of grunts and snappers of Southeast Florida: Cross—shelf distributions and effects of beach management alternatives. Ph.D. thesis. University of Miami, Coral Gables, FL, USA, 419 p.

Lindeman, K.C., G.A. Diaz, J.E. Serafy, and J.S. Ault. 1998. A spatial framework for assessing cross—shelf habitat use among newly settled grunts and snappers. Proceedings of the Gulf and Caribbean Fisheries Institute 50:385–416.

Lindeman, K.C., R. Pugliese, G.T. Waugh, and J.S. Ault. 2000. Developmental patterns within a multispecies reef fishery: Management applications for essential fish habitats and protected areas. Bulletin of Marine Science 66:929–956. https://sedarweb.org/documents/sedar—51—rd—05—developmental—patterns—within—a—multispecies—reef—fishery—management—applications—for—essential—fish—habitats—and—protected—areas/

Lirman, D., S. Schopmeyer, D. Manzello, L.J. Gramer, W.F. Precht, F. Muller—Karger, K. Banks, B. Barnes, E. Bartels, A. Bourque, J. Byrne, S. Donahue, J. Duquesnel, L. Fisher, D. Gilliam, J. Hendee, M. Johnson, K. Maxwell, E. McDevitt, J. Monty, D. Rueda, R. Ruzicka, and S. Thanner. 2011. Severe 2010 cold—water event caused unprecedented mortality to corals of the Florida Reef tract and reversed previous survivorship patterns. PLoS ONE 6:23047. https://doi.org/10.1371/journal.pone.0023047.

Myers, R.A. and N.J. Barrowman. 1996. Is fish recruitment related to spawner abundance? Fishery Bulletin 94:707–724.

Nagelkerken, I., G. Van Der Velde, M.W. Gorissen, G.J. Meijer, T. Van't Hof, and C. Den Hartog. 2000. Importance of mangroves, seagrass beds and the shallow coral reef as a nursery for important coral reef fishes, using a visual census technique. Estuarine, Coastal and Shelf Science 51:31–44. https://doi.org/10.1006/ecss.2000.0617.

Nagelkerken, I., C.M. Roberts, G. Van der Velde, M. Dorenbosch, M.C. Van Riel, E. Cocheret de la Morinière, and P.H. Nienhuis. 2002. How important are mangroves and seagrass beds for coral—reef fish? The nursery hypothesis tested on an island scale. Marine Ecology Progress Series 244:299–305. https://doi.org/10.3354/meps244299.

Orth, R.J., K.L. Heck, and J. Van Montfrans. 1984. Faunal communities in seagrass beds: A review of the influence of plant structure and prey characteristics on predator: prey relationships. Estuaries 7:339–350. https://www.jstor.org/stable/1351618

Pineda, J., F. Porri, V. Starczak, and J. Blythe. 2010. Causes of decoupling between larval supply and settlement and consequences for understanding recruitment and population connectivity. Journal of Experimental Marine Biology and Ecology 392:9–21. https://doi.org/10.1016/j.jembe.2010.04.008.

Planque, B., J.M. Fromentin, P. Cury, K.F. Drinkwater, S. Jennings, R.I. Perry, and S. Kifani. 2010. How does fishing alter marine populations and ecosystems sensitivity to climate? Journal of Marine Systems 79:403–417. https://doi.org/10.1016/j.jmarsys.2008.12.018.

Pollux, B.J.A., W.C.E.P. Verberk, M. Dorenbosch, E. Cocheret De La Morinière, I. Nagelkerken, and G. Van Der Velde. 2007. Habitat selection during settlement of three Caribbean coral reef fishes: Indications for directed settlement to seagrass beds and mangroves. Limnology and Oceanography 52:903–907. https://doi.org/10.4319/lo.2007.52.2.0903.

R Core Team. 2023. R: A Language and Environment for Statistical Computing. Vienna, Austria. https://www.R—project.org/

Raposa, K.B., T.E. Kutcher, W. Ferguson, R.A. McKinney, K. Miller, and C. Wigand. 2020. Evaluation of plot—scale methods for assessing and monitoring salt marsh vegetation composition and cover. Northeast Naturalist 27:151–167. https://doi.org//10.1656/045.027.0113.

Reshetnikov, Y.S. and R. Claro. 1976. Cycles of biological processes in tropical fishes with reference to *Lutjanus synagris*. Journal of Ichthyology 16:711–722.

Richards, R.A. and P.J. Rago. 1999. A case history of effective fishery management: Chesapeake Bay striped bass. North American Journal of Fisheries Management 19:356–375. https://doi.org/10.1577/1548—8675(1999)019<0356:achoef>2.0.co;2.

Richards, W.J. and V.P. Saksena. 1980. Description of larvae and early juveniles of laboratory—reared gray snapper, *Lutjanus griseus* (Linnaeus)(Pisces, Lutjanaidae). Bulletin of Marine Science 30:515–521.

Riley, C.M., G.J. Holt, and C.R. Arnold. 1995. Growth and morphology of larval and juvenile captive bred yellowtail snapper, *Ocyurus chrysurus*. Fisheries Bulletin 93:179–185.

Rooker, J.R. 1995. Feeding ecology of the schoolmaster snapper, *Lutjanus apodus* (Walbaum), from Southwestern Puerto Rico. Bulletin of Marine Science 56:881–894.

Rothschild, B.J. 1986. Dynamics of Marine Fish Populations. Harvard University Press, Cambridge, MA, USA. 277 p.

Santos, R.O., J.S. Rehage, R. Boucek, and J. Osborne. 2016. Shift in recreational fishing catches as a function of an extreme cold event. Ecosphere 7:1–16. https://doi.org/10.1002/ecs2.1335.

Schlaefer, J.A., E. Wolanski, J. Lambrechts, and M.J. Kingsford. 2018. Wind conditions on the Great Barrier Reef influenced the recruitment of snapper (*Lutjanus carponotatus*). Frontiers in Marine Science 5:1–20. https://doi.org/10.3389/fmars.2018.00193.

Schloesser, R.W. and M.C. Fabrizio. 2019. Nursery habitat quality assessed by the condition of juvenile fishes: not all estuarine areas are equal. Estuaries and Coasts 42:548–566. https://doi.org/10.1007/s12237–018–0468–6.

Shulzitski, K., M.A. McCartney, and M.L. Burton. 2009. Population connectivity among Dry Tortugas, Florida and Caribbean populations of mutton snapper (*Lutjanus analis*), inferred from multiple microsatellite loci. Fishery Bulletin 107:501–509.

Shulzitski, K., S. Sponaugle, M. Hauff, K. Walter, E.K. D'Alessandro, and R.K. Cowen. 2015. Close encounters with eddies: Oceanographic features increase growth of larval reef fishes during their journey to the reef. Biology Letters 11:20140746 https://doi.org/10.1098/rsbl.2014.0746.

Shulzitski, K., S. Sponaugle, M. Hauff, K.D. Walter, E.K. D'Alessandro, and R.K. Cowen. 2018. Patterns in larval reef fish distributions and assemblages with implications for local retention in mesoscale eddies. Canadian Journal of Fisheries and Aquatic Sciences 75:180–192. https://doi.org/10.1139/cjfas—2016—0304

Sponaugle, S. and D. Pinkard. 2004. Lunar cyclic population replenishment of a coral reef fish: Shifting patterns following oceanic events. Marine Ecology Progress Series 267:267–280. https://doi.org/10.3354/meps267267.

Springer, V.G. and A. McErlean. 1962. Seasonality of fishes on a South Florida shore. Bulletin of Marine Science 12:39–60.

Starck, W.A.I. 1971. Biology of the gray snapper *Lutjanus griseus* (Linneaus) in the Florida Keys. In: W.A. Starck II and R.E. Schroeder, eds. Investigations on the Gray Snapper, *Lutjanus griseus.* Studies in Tropical Oceanography, Volume 10. University of Miami Press, Coral Gables, FL, USA. p. 11—150.

Steele, M.A. and G.E. Forrester. 2002. Early post—settlement predation on three reef fishes: effects on spatial patterns of recruitment. Ecology 83:1076–1091. https://www.jstor.org/stable/3071915

Stoner, A.W. 1983. Distribution of fishes in seagrass meadows: Role of macrophyte biomass and species composition. Fishery Bulletin 81:837–846.

Szuwalski, C.S., K.A. Vert—Pre, A.E. Punt, T.A. Branch, and R. Hilborn. 2015. Examining common assumptions about recruitment: A meta—analysis of recruitment dynamics for worldwide marine fisheries. Fish and Fisheries 16:633–648. https://doi.org/10.1111/faf.12083.

Thompson, R. and J.L. Munro. 1983. The biology, ecology and bionomics of the snappers, Lutjanidae. In: J.L. Munro, ed. Caribbean Coral Reef Fishery Resources, ICLARM Studies and Reviews, Manila, Philippines. p. 94—109.

Van Der Maarel, E. 2007. Transformation of cover—abundance values for appropriate numerical treatment — alternatives to the proposals by Podani. Journal of Vegetation Science 18:767–770. https://doi.org/10.1111/j.1654—1103.2007.tb02592.x

Wallace, R.K. 1977. Thermal acclimation, upper temperature tolerance, and preferred temperature of juvenile yellowtail snappers, *Ocyurus chrysurus* (Bloch)(Pisces: Lutjanidae). Bulletin of Marine Science 27:292–298.

Watson, M., J.L. Munro, and F.R. Gell. 2002. Settlement, movement and early juvenile mortality of the yellowtail snapper *Ocyurus chrysurus*. Marine Ecology Progress Series 237:247–256. https://doi.org/10.3354/meps237247.

Wilson, S.K., M. Depczynski, T.H. Holmes, M.M. Noble, B.T. Radford, P. Tinkler, and C.J. Fulton. 2017. Climatic conditions and nursery habitat quality provide indicators of reef fish recruitment strength. Limnology and Oceanography 62:1868–1880. https://doi.org/10.1002/lno.10540.

Wuenschel, M.J., A.R. Jugovich, and J.A. Hare. 2004. Effect of temperature and salinity on the energetics of juvenile gray snapper (*Lutjanus griseus*): Implications for nursery habitat value. Journal of Experimental Marine Biology and Ecology 312:333–347. https://doi.org/10.1016/j.jembe.2004.07.007

Wuenschel, M.J., J.A. Hare, M.E. Kimball, and K.W. Able. 2012. Evaluating juvenile thermal tolerance as a constraint on adult range of gray snapper (*Lutjanus griseus*): A combined laboratory, field and modeling approach. Journal of Experimental Marine Biology and Ecology 436–437:19–27. https://doi.org/10.1016/j.jembe.2012.08.012.

Zimmermann, F., M. Claireaux, and K. Enberg. 2019. Common trends in recruitment dynamics of Northeast Atlantic fish stocks and their links to environment, ecology and management. Fish and Fisheries 20:518–536. https://doi.org/10.1111/faf.12360.