

# Selective mortality during the larval and juvenile stages of snappers (*Lutjanidae*) and great barracuda *Sphyraena barracuda*

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**ABSTRACT:** Selective mortality during the early life stages in marine organisms can affect the magnitude and composition of recruitment, yet these processes have not been examined in economically important predatory coral reef fishes. Utilizing 3 different stage-specific sampling techniques (shipboard plankton tows, larval light traps, juvenile surveys/seines), we repeatedly sampled multiple cohorts of 3 lutjanid (*Ocyurus chrysurus*, *Lutjanus synagris*, and *L. griseus*) and 1 sphyraenid (*Sphyraena barracuda*) species through time in the Florida Keys (USA). Comparisons of daily growth and size-at-age (from otolith microstructure analysis) for early- and late-stage larvae and young and older juveniles revealed that size- and growth-selective processes operate during the larval stage, while after settlement, growth-selective mortality occurred in the absence of significant size differences. In all 3 lutjanid species, larvae and juveniles that were larger at hatch preferentially survived. In *O. chrysurus* and *L. synagris*, selective mortality of smaller, slower-growing individuals during the larval stage reduced variability in these traits such that larvae were of similar sizes at settlement. Following settlement, patterns of growth-selective mortality were initially opposite (favoring faster juvenile growth in *L. synagris*, and slower growth in *O. chrysurus*), but ultimately survivors of both species grew faster, leading eventually to a size advantage. In contrast, patterns of selective mortality were not evident until settlement in *L. griseus* and *S. barracuda*, and favored larger and smaller sizes-at-settlement, respectively. Overall, our results reveal important patterns of selective mortality and variability between even closely related species.

**KEY WORDS:** *Ocyurus chrysurus* · *Lutjanus synagris* · *Lutjanus griseus* · Growth-mortality hypothesis · Coral reef fishes

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## INTRODUCTION

Most marine fishes are characterized by a dispersive pelagic larval stage followed by metamorphosis into the juvenile form, often accompanied by settlement out of the plankton to the benthos. Mortality rates in this early stage are extremely high (Bailey & Houde 1989, Leggett & Deblois 1994), owing to predation, starvation, and expatriation away from suitable juvenile habitat. Predation is now widely accepted as the ultimate cause of most mortality,

while other factors make larvae more or less susceptible to this endpoint (Bailey & Houde 1989). Small variations in this larval mortality rate can lead to large fluctuations in the size of juvenile and adult populations (Houde 1989). However, high mortality rates in conjunction with variation in larval traits (McCormick 1998), ranging from genetic identity (Vigliola et al. 2007) and environmentally-mediated variation (Sponaugle et al. 2006) to experience with predators (McCormick & Holmes 2006), often lead to non-random mortality and preferential survival of

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certain individuals. The growth-mortality hypothesis (Anderson 1988) has provided a conceptual framework to examine selective loss in larval fishes and contends that larvae that grow faster ('growth rate' hypothesis; Ware 1975), complete the precarious larval stage faster ('stage duration' hypothesis; Houde 1987), and/or are larger at given ages ('bigger is better' hypothesis; Miller et al. 1988) will preferentially survive. Although some experimental (Fuiman 1989, Litvak & Leggett 1992, Pepin et al. 1992) and field studies (Sponaugle et al. 2011) have found the opposite, or no selective patterns (Bertram & Leggett 1994, Robert et al. 2010), this theory has been supported by a number of temperate (e.g. Hovenkamp 1992, Meekan & Fortier 1996, Hare & Cowen 1997) and tropical studies (e.g. Meekan et al. 2006). Thus, high non-random mortality in the planktonic stage of marine fishes suggests that even small changes in larval traits (e.g. size and growth) during the larval phase can lead to large fluctuations in both the size and trait composition of juvenile and adult populations.

High non-random mortality continues through metamorphosis and settlement for benthic marine fishes (Sogard 1997, Almany & Webster 2006). A number of studies have tested whether faster growth and larger size continue to enhance survival (Searcy & Sponaugle 2001, Vigliola & Meekan 2002, McCormick & Hoey 2004, Hawn et al. 2005, Meekan et al. 2006, Hamilton et al. 2008, Durieux et al. 2009, Johnson & Hixon 2010, Rankin & Sponaugle 2011). However, the switch to a more demersal, site-attached lifestyle, including confounding effects of habitat heterogeneity, competition, and density dependence (which are largely avoided by larvae in the diffuse planktonic environment), may mediate or even mask selective processes (Brunton & Booth 2003, Holmes & McCormick 2006, McCormick & Meekan 2007, Samhuri et al. 2009, Johnson et al. 2012).

While selective mortality has been examined in the early life stages of many temperate commercial and recreational fisheries species (Hovenkamp 1992, Meekan & Fortier 1996, Hare & Cowen 1997, Takasuka et al. 2003), most studies examining selective processes in tropical reef species have focused on small, short-lived, and easily sampled fishes (Searcy & Sponaugle 2001, Vigliola & Meekan 2002, McCormick & Hoey 2004, Meekan et al. 2006). Among the findings of these studies is that selective patterns are non-static, changing with ontogeny (Gagliano et al. 2007a) and environmental variability (Grorud-Colvert & Sponaugle 2011, Rankin & Sponaugle 2011). Such changes cannot be detected

without repeated sampling of life stages and inclusion of multiple cohorts. This is a challenging task in the study of reef fishes, as life stages are spatially disparate, with young larvae located offshore at low densities, and late-stage larvae and juveniles located near the reef or other shallow nearshore environments. For commercially and recreationally important predatory reef fishes, this difficulty is compounded by the relative rarity of both early larvae and post-settled juveniles (S. Sponaugle unpubl. data). For this reason, most studies of selective mortality in reef fishes have focused on settlement-stage larvae and/or settled juveniles, and used otoliths (ear stones) to glean information from the early larval stage. While these studies provide insights into the larval traits important for survival to and during the juvenile stage, without larval samples it is not possible to examine selective mortality within the larval stage and to determine how these patterns may change at settlement.

The objective of this study was to examine selective mortality across multiple life stages in commercially and recreationally important coral reef associated lutjanine snappers (family Lutjanidae) and barracudas (family Sphyraenidae). We used 4 different sampling techniques to track and repeatedly sample multiple cohorts of these species ranging from early larvae, through to settlement, and into the juvenile stage. Specifically, we sought to test the growth-mortality hypothesis within the larval stage in terms of size-at-hatch, larval growth, and larval size-at-age, and in the juvenile stage in terms of the aforementioned larval traits as well as pelagic larval duration (PLD), size-at-settlement, juvenile growth, and juvenile size-at-age.

## MATERIALS AND METHODS

### Study area and focal species

The lower Florida Keys (FK), USA, consist of a chain of islands running northeast–southwest along the Straits of Florida. Here, shallow (<3 m) nearshore seagrass, hardbottom, and mangrove environments lie just offshore (south/southeast) and are separated from the fringing reef tract (5–10 km offshore) by Hawk Channel (~1 km offshore and up to 10 m deep; Fig. 1). While water within Hawk Channel is influenced mainly by wind and tides (Pitts 1997), currents near and seaward of the fringing reef are dominated by the fast-moving (up to 2 m s<sup>-1</sup>), northeasterly-flowing Florida Current. Periodically, flow in these

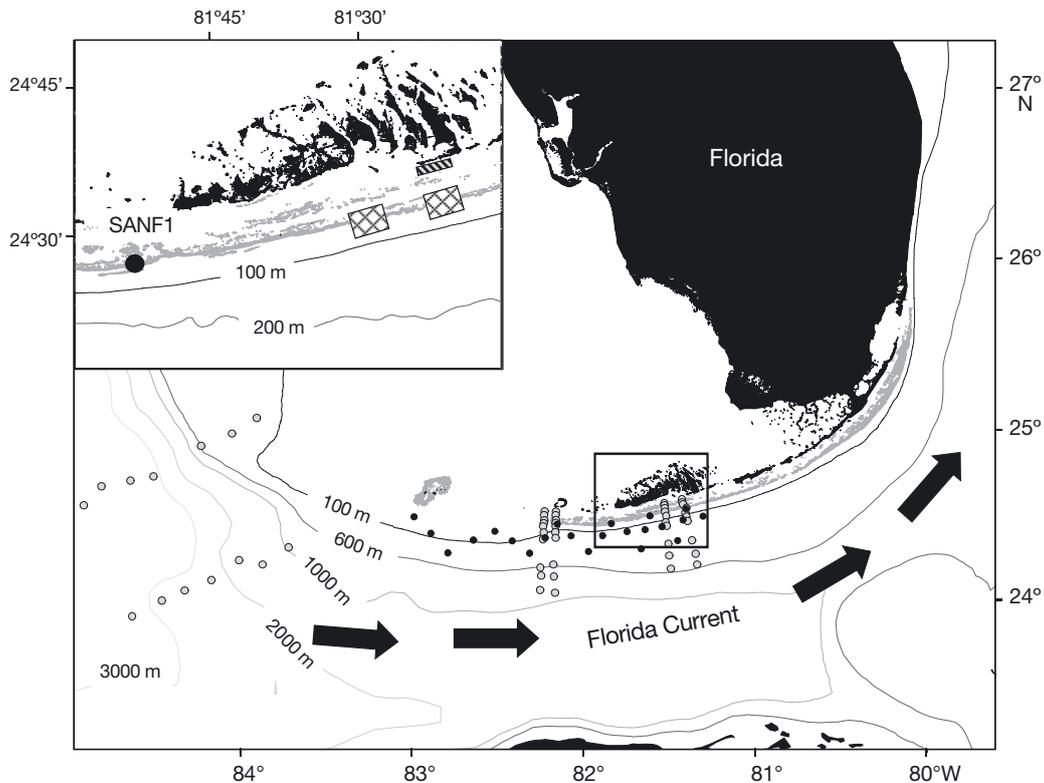


Fig. 1. Study area. Black represents land and gray represents coral reef. Gray circles (54 fixed stations) and black points (22 supplementary stations) represent the 76 stations sampled by MOCNESS during 2007 and 2008. In the inset, the large black circle indicates the location of the NOAA C-MAN station SANF1 where temperature data were obtained, crosshatched boxes are the sites of light trap deployment, and the striped box is the location of the diver surveys and seine sampling targeting juveniles

areas is reversed by large cyclonic mesoscale eddies that influence the oceanography offshore of the lower FK on a time scale of several months, and have been implicated in the retention and nearshore delivery of larvae of reef fishes and invertebrates, including economically important species (Lee & Williams 1999, Lindeman et al. 2001, Yeung & Lee 2002, Sponaugle et al. 2005).

Snappers and barracudas are an important component of commercial and recreational fisheries in the southeast US and the Caribbean. Like many coral reef fishes, their early life history is characterized by a dispersive pelagic larval stage. This stage lasts between 31 and 42 d in several reef-associated snapper species (summarized by Lindeman et al. 2001), while the PLD of *Sphyraena barracuda* has been estimated as 17.6 d (range 15–21) from light trap caught late-stage larvae assumed to be competent to settle (Sponaugle et al. 2005). Although seemingly disparate families, coral-reef associated lutjanids and sphyraenids both settle to shallow nearshore back-

reef habitats instead of reefs (hardbottom, seagrass, and mangroves; Lindeman et al. 1998, Nagelkerken et al. 2001). In the FK, these habitats are vast, and densities of newly settled individuals are low (S. Sponaugle unpubl. data). For several years following settlement, these fishes undergo a seaward ontogenetic migration culminating in large reproductive adults inhabiting and spawning at the fringing coral reef and other deeper shelf slope habitats (Cocheret de la Morinière et al. 2002, Serafy et al. 2003, Eggleston et al. 2004). In both families, the majority of spawning and thus availability of larvae in the FK is restricted to warm summer months (D'Alessandro et al. 2007, 2010, 2011, Kadison et al. 2010).

#### Sample collection and identification

Four sampling methods were employed to target the different ontogenetic stages of lutjanids and sphyraenids. Shipboard plankton tows targeted

pelagic larvae and were carried out at 76 stations during daylight hours on 3 separate cruises: 29 May to 15 June 2007, 30 July to 13 August 2007, and 17 June to 1 July 2008 (Fig. 1). At each station, a multiple opening closing net and environmental sampling system (MOCNESS) and frame net were used to make oblique tows of 20 m depth bins from the surface to 100 m, and horizontal tows of the top ~0.5 m of the water column, respectively. Both net systems were towed at a speed of  $1 \text{ m s}^{-1}$ , were outfitted with continuously recording flow meters and depth and temperature sensors, and had  $4 \text{ m}^2$  (MOCNESS) and  $2 \text{ m}^2$  (Neuston) openings in the 1 mm mesh nets (see Guigand et al. 2005). An important assumption in studying selective mortality is that repeated samples are from the same population (Meekan & Fortier 1996). While recent studies of reef fish population structure within the FK revealed little genetic structure (Purcell et al. 2009, Shulzitski et al. 2009), suggesting that the area comprises 1 well-mixed population on an evolutionary time scale, this does not exclude the possibility of structure on an ecological time scale. As a conservative approach, the locations of the sampling stations (54 fixed transect and 22 supplementary stations) offshore and upstream of the lower FK (Fig. 1) were selected to correspond spatially with the majority of late-stage larval and juvenile snappers collected in the lower FK in both years (see 'Results').

To target late-stage larvae in the process of settlement, 4 replicate larval light traps (modified from a design by Sponaugle & Cowen 1996) were deployed nightly at each of 2 sites over the fringing reef crest in the lower FK for 2 wk encompassing the new and third-quarter moons in June (8 to 22 June 2007 and 27 May to 10 June 2008), July (7 to 21 July 2007 and 26 June to 10 July 2008), and August (5 to 19 August 2007 and 25 July to 8 August 2008) of 2007 and 2008. Traps consisted of a 1.07 m long, 0.43 m diameter cylinder of 500  $\mu\text{m}$  Nitex netting (Sea Gear), surrounding a 30 cm submersible 5 W fluorescent light (Bellamare). The net cylinders had six 15 cm funnel shaped openings on the sides, and tapered on the bottom to a 1 l plastic cod-end. Traps were attached to semi-permanent moorings shortly before sunset and retrieved the following morning just after sunrise.

Juvenile snappers and barracuda were captured opportunistically in shallow (<2 m) nearshore seagrass and hardbottom habitats during June, July, and August of 2007 and 2008 in the vicinity of Big Munson Key using hand nets and the anesthetic Quinaldine or a 21 m (3.2 mm mesh) seine. In addition, winter collections utilizing only the 21 m seine were

carried out in both 2007 and 2008 (20 to 22 December 2007 and 5 to 7 December 2008) in this same area to target older juvenile snappers. Although each sampling method can introduce bias into the samples (e.g. towed nets tend to under-sample larger, older, more agile larvae), utilizing both active and passive sampling techniques enabled the capture of a nearly complete larval age/size range, and minimized this bias (see Table 1 for collected samples).

Upon collection, all larvae and juveniles were immediately fixed in 95% ETOH and later measured to the nearest 0.1 mm notochord length (NL; pre-flexion larvae) or standard length (SL; post-flexion larvae and juveniles) and identified to species either morphologically using standard larval fish guides (e.g. Richards 2006), or molecularly (all young snapper larvae captured in pelagic tows except *Rhomboplites aurorubens*) following the protocols of D'Alessandro et al. (2010). Most late-stage larvae captured in light traps could be readily identified morphologically; however, 1 group of snapper species containing *Lutjanus griseus*, *L. jocu*, *L. apodus*, and *L. cyanopterus*, hereafter referred to as 'type G,' could not be distinguished confidently without molecular confirmation. Due to the large numbers of type G snapper larvae collected in light traps (see 'Results') and the high cost of molecular identification, only those type G larval snappers selected for otolith analysis were identified to species.

### Otolith analysis

Otoliths were removed from all juveniles and a random subset of pelagic and light-trap larvae. One sagitta (snappers) or lapillus (barracuda) from each individual was imbedded in crystal-bond thermoplastic glue on a glass microscope slide. Snapper otoliths were polished to a thin transverse section containing the otolith primordium, while barracuda otoliths were laid flat and polished to the primordium on only 1 side. A 1000 $\times$  digital image of each otolith was taken using a Leica DMLB microscope equipped with an Infinity 2 digital camera. Otolith increments were enumerated and measured along the longest axis from the primordium to the outer edge using Image Pro 7.0 software (Media Cybernetics). In sectioned otoliths of snapper larvae and juveniles, the longest otolith axis shifted progressively with growth. To maintain consistency among individuals of different ages, a non-linear reading axis was created by tracing the longest axis of growth every 4 increments. Increments were enumerated and meas-

ured twice (without knowledge of prior readings) for each otolith by the same person, and if counts differed by  $\leq 5\%$ , 1 count was randomly selected for analysis. If replicate counts differed by  $>5\%$ , the otolith was read a third time. If this third read differed by  $\leq 5\%$  from 1 of the other 2 reads, 1 of these was randomly chosen for analysis. Otherwise, the otolith was excluded from further analysis.

Daily increments have been previously validated in juvenile *Sphyraena barracuda* (D'Alessandro et al. 2011), *Lutjanus griseus* (Ahrenholz 2000), *L. synagris* (Mikulas & Rooker 2008), and *Ocyurus chrysurus* (Lindeman 1997). Therefore, age in days post hatch (DPH) was the total number of increments between the otolith primordium and otolith edge, plus a 2 d correction for time to first increment formation in snapper species (e.g. D'Alessandro et al. 2010). No such correction was necessary for *S. barracuda* (D'Alessandro et al. 2011). The spawn date of each individual snapper and barracuda, estimated as the DPH age plus 1 d to account for incubation time (e.g. D'Alessandro et al. 2010, 2011), was used to delineate monthly cohorts (see Table 2). Daily increments are known to change markedly in width and optical contrast at the time of settlement to juvenile habitat, usually beginning with a conspicuously dark settlement mark in snappers (Lindeman 1997, Allman & Grimes 2002, Zapata & Herrón 2002, Victor et al. 2009) and this appeared to hold true for *S. barracuda* as well. Juvenile age in days post settlement (DPS) was the number of increments between the settlement mark and otolith edge. Regression analyses of SL and otolith radius, SL and age, as well as between residuals of an otolith radius-at-age regression and residuals of a SL-at-age regression (Hare & Cowen 1995), were used to verify the otolith growth–somatic growth relationship. However, to avoid introducing error in back-calculating somatic growth from otoliths (Chambers & Miller 1995), the distance between consecutive increments was used as a relative measure of daily larval growth while otolith radius-at-age was used as a proxy for relative size-at-age.

### Data analysis

To examine selective loss through ontogeny, larvae were grouped together according to their DPH age as initial larvae (comprised entirely of larvae captured in MOCNESS samples; Li) or surviving larvae (comprised of MOCNESS larvae older than the species-specific cutoff age [see Table 2] and light trap larvae;

Ls), and juveniles (captured post-settlement in juvenile habitat) by their juvenile age in DPS as initial juveniles (Ji) or surviving juveniles (Js). Specific ranges of ages for these groups varied among species due to sample size constraints (see Table 2). To identify whether selective loss occurred among ontogenetic groups, we evaluated the samples in terms of size-at-hatch (radius of the primordium), daily larval growth (otolith increment width), and size-at-age (otolith radius-at-age), including size-at-settlement and PLD for juveniles. Late-stage larvae captured in light traps comprised the majority of Ls, but were assumed to be traversing the reef to settle in nearshore environments; thus their DPH age was considered to be their PLD, and their total otolith radius was assumed to be their size-at-settlement. While analyses of PLD and size-at-settlement include Ls, only light trap captured late-stage larvae were included. Differences in traits among age groups were initially evaluated on a cohort-by-cohort basis, but this stratification of the data did not change overall trends, and all larvae and juveniles were pooled across cohorts (for a cohort-by-cohort analysis of the 2 most abundant species, see Fig. S1 in the supplement at [www.int-res.com/articles/suppl/m474p227\\_supp.pdf](http://www.int-res.com/articles/suppl/m474p227_supp.pdf)).

Previous studies have established the strong effect of temperature on larval growth of tropical coral reef fish larvae (McCormick & Molony 1995, Sponaugle et al. 2006). To account for this effect, differences in traits among age groups were tested at specific points using analysis of covariance (ANCOVA; Systat 11) with temperature as a covariate (e.g. Rankin & Sponaugle 2011). Temperature data were obtained from the National Oceanic and Atmospheric Administration (NOAA) Coastal-Marine Automated Network (C-MAN) station SANF1 due to its location upstream of light trap and juvenile collections, near the east–west center of the MOCNESS stations. Data were first tested for normality and homogeneity of variance (and log transformed where necessary), as well as for significant interactions between temperature and age group (homogeneity of slopes test; Systat 11). When data failed to meet the assumptions of parametric statistics, ANCOVA was used on rank-transformed data (Conover & Iman 1982). To examine whether growth and size-at-age differed among age groups, larval growth and size-at-age trajectories were plotted and statistically tested at Increments 5, 10, and 15 of the otolith. The  $\alpha$  values were Bonferroni corrected to control for Type 1 error associated with repeated tests. These tests as well as tests of size-at-hatch among age groups used the mean

temperature on the date of increment formation and the date of hatch as covariates, respectively. When differences were detected, Tukey-type post hoc tests were used to identify specific patterns. The presence of linear or non-linear selection on size-at-hatch was illustrated by generating non-parametric cubic splines of the fitness function for this trait (Sinclair et al. 2002). These were calculated using a binomial distribution with initial and survivor age groups to obtain relative survival over time (e.g. Gagliano et al. 2007a, Grorud-Colvert & Sponaugle 2011).

To evaluate whether differences in juvenile growth and size among age groups were apparent relative to settlement, growth and size-at-age trajectories of late-stage larvae and juveniles were also aligned by their settlement marks (assumed to be the next daily increment that would have formed in late-stage light trap caught larvae), plotted, and tested as above. Growth was tested at 5 and 15 DPS where possible; size was tested at the last increment for which there were at least 5 individuals in each age group. As with tests of larval trajectories, these tests used mean temperature on the dates of increment formation as a covariate. Tests of PLD and size-at-settlement in these late-stage larvae and juveniles used mean temperature experienced during the entire larval duration as a covariate. The presence of linear or non-linear selection on these traits was illustrated with cubic splines. Temperature data were obtained from the NOAA C-MAN station SAN-F1 (Fig. 1) as daily means, and were assigned to each increment for each individual based on the day of increment formation (date of capture – [total age – increment number]). Although location-specific temperature data at the time of capture were available for MOCNESS-collected larvae, these data were not available for juveniles or light trap captured larvae, and fixed station temperature data were chosen to capture relative changes in temperature over time.

## RESULTS

Of the 532 randomly selected MOCNESS- and frame net-captured snapper larvae, 440 (83%) were identified to species (Table 1). MOCNESS-captured sphyraenid larvae were monotypic and consisted of 90 *Sphyraena barracuda*. Light trap catches yielded 10 562 lutjanid larvae dominated by *Lutjanus synagris* and type G and 1884 sphyraenid larvae dominated by *S. barracuda* (Table 1). Summer juvenile collections in nearshore environments yielded 208 juvenile snappers and 24 juvenile barracuda, while

winter juvenile collections in both years yielded a total of 59 *Ocyurus chrysurus* juveniles.

Sample sizes of 4 species, *Ocyurus chrysurus*, *Lutjanus synagris*, *L. griseus*, and *Sphyraena barracuda*, contained enough individuals overlapping in at least 2 of the 3 ontogenetic stages to be analyzed. A total of 647 snapper (3 species combined) and 292 barracuda otoliths were sectioned and read. Of these, 551 of the snapper (85%) and 273 of the barracuda (93%) had reliable otolith reads and were retained for analysis; however, a further 45 snappers and 49 barracuda fell outside of the monthly cohort delineations and were excluded from the final analysis. This left a total of 217 *O. chrysurus*, 182 *L. synagris*, 107 *L. griseus*, and 175 *S. barracuda* individuals to be broken into 4 age groups (only 3 age groups for *L. griseus* as only newly settled juveniles <2 DPS were captured; Table 2).

All otolith radius–SL regressions ( $r^2 = 0.88–0.98$ ;  $p < 0.001$ ), SL–age regressions ( $r^2 = 0.77–0.94$ ;  $p < 0.001$ ), and regressions of residuals from both ( $p < 0.01$ ), were highly significant, indicating that otolith size is a good proxy for fish size in early life stages of these species. Significant patterns in size-at-hatch across age groups were identified in all 3 snapper species such that individuals surviving to the juvenile stage (Ji) were significantly larger at hatch than either initial (Li) or surviving (Ls) larvae, and relative fitness increased with increasing size-at-hatch

Table 1. Species composition and sample size of larvae and juveniles collected off the Florida Keys. Type G refers to a 4-species group (*Lutjanus griseus*, *L. jocu*, *L. apodus*, and *L. cyanopterus*) that could not be identified to species morphologically. The number of *Ocyurus chrysurus* juveniles is broken into summer (S) and winter (W) collections

Species	MOCNESS/ frame net larvae	Light trap larvae	Hand net/ seine juveniles
<i>Rhomboplites aurorubens</i>	188		
<i>Ocyurus chrysurus</i>	108	1089	153 (94 S; 59 W)
<i>Lutjanus synagris</i>	66	5039	56
<i>Lutjanus griseus</i>	40	4020 (type G)	35
<i>Lutjanus analis</i>	27	218	
<i>Lutjanus apodus</i>	6		
<i>Lutjanus mohogoni</i>		4	
<i>Lutjanus vivanus</i>	3		
<i>Lutjanus campechanus</i>	2		
Unidentified Lutjanidae	92	157	
<i>Sphyraena barracuda</i>	90	1883	24
<i>Sphyraena guachancho</i>		1	
Total sphyraenids	90	1884	24
Total lutjanids	440	10527	244

Table 2. *Ocyurus chrysurus*, *Lutjanus synagris*, *L. griseus*, and *Sphyraena barracuda*. Temporal spawning range, mean water temperature from the NOAA C-MAN station SANF1, mean pelagic larval duration (PLD), and sample sizes of initial pelagic larvae (Li), surviving pelagic larvae (Ls), initial post-settled juveniles (Ji), and surviving post-settled juveniles (Js) of each species studied by cohort. Cut-off ages for each age group designation for each species are given in parentheses: Li and Ls in days post hatch; Ji and Js in days post settlement. Dates are given as m/dd/yy

	Spawn date range	Mean temp (°C)	Li	Ls	Ji	Js	PLD (d)
<i>Ocyurus chrysurus</i>							
			(<22)	(>22)	(<50)	(>50)	
Cohort 1	5/13/07–6/12/07	27.9	15	45	14	0	26.8
Cohort 2	7/3/07–8/3/07	30.4	25	26	8	5	23.9
Cohort 3	5/18/08–6/17/08	28.6	29	31	5	14	24.6
Sample totals			<b>69</b>	<b>102</b>	<b>27</b>	<b>19</b>	<b>25.3</b>
<i>Lutjanus synagris</i>							
			(<22)	(>22)	(<10)	(>10)	
Cohort 1	5/29/07–6/15/07	28.4	0	25	17	6	26.8
Cohort 2	7/1/07–7/29/07	30.4	30	31	12	0	24.2
Cohort 3	5/31/09–6/23/09	29.1	0	24	24	13	25.6
Sample totals			<b>30</b>	<b>80</b>	<b>53</b>	<b>19</b>	<b>25.6</b>
<i>Lutjanus griseus</i>							
			(<22)	(>22)			
Cohort 1	7/2/07–7/27/07	30.3	27	31	0	0	25.7
Cohort 2	7/21/08–7/30/08	29.6	0	27	22	0	25.7
Sample totals			<b>27</b>	<b>58</b>	<b>22</b>	<b>0</b>	<b>25.7</b>
<i>Sphyraena barracuda</i>							
			(<20)	(>20)	(<4)	(>4)	
Cohort 1	5/12/07–5/29/07	26.9	24	27	7	7	25.4
Cohort 2	7/14/07–7/28/07	30.4	29	31	0	1	22.4
Cohort 3	6/2/08–6/24/08	28.6	31	17	1	0	22.2
Sample totals			<b>84</b>	<b>75</b>	<b>8</b>	<b>8</b>	<b>23.3</b>

(Fig. 2). However, no significant differences in this parameter were identified among any age groups in *Sphyraena barracuda*.

Larval growth and size-at-age trajectories in 2 of 3 examined snapper species (*Ocyurus chrysurus*, *Lutjanus synagris*) revealed that Li were smaller-at-age and grew more slowly than older age groups (Fig. 3, Table 3). For *O. chrysurus*, this pattern was consistent for both larval growth and size-at-age, beginning early in larval life (Increment 5, except Js), and lasting until the maximum age of Li (Fig. 3, Table 3). Larval growth and size-at-age trajectories of *L. synagris* were similar to *O. chrysurus*, although the slower growth rate of Li than other age groups took longer to appear (by Increment 10, except Js). Differences among age groups in growth and size on Day 10 in *L. griseus* indicated that Ji grew more quickly than Ls, but growth of Li fluctuated between the 2 (Table 3). Similarly inconsistent patterns of larval growth were

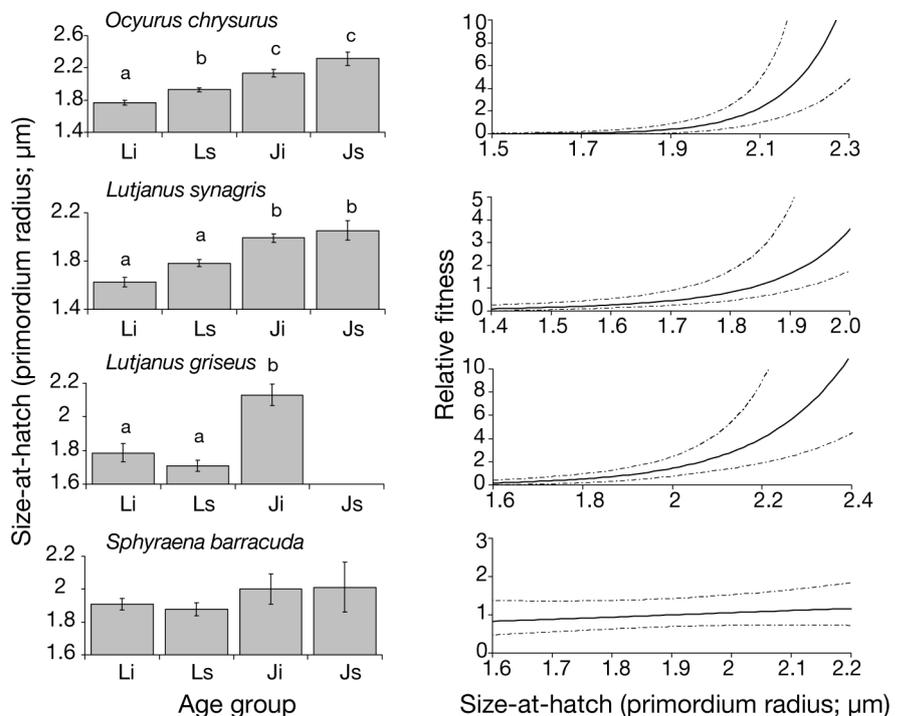


Fig. 2. *Ocyurus chrysurus*, *Lutjanus synagris*, *L. griseus*, and *Sphyraena barracuda*. Left panels: mean  $\pm$  SE size-at-hatch of examined species illustrating differences among initial larvae (Li), surviving larvae (Ls), initial juveniles (Ji), and surviving juveniles (Js). Letters indicate significant differences (ANCOVA  $p < 0.05$ ). Right panels: Fitness functions created using cubic splines. (---): 95% confidence bands

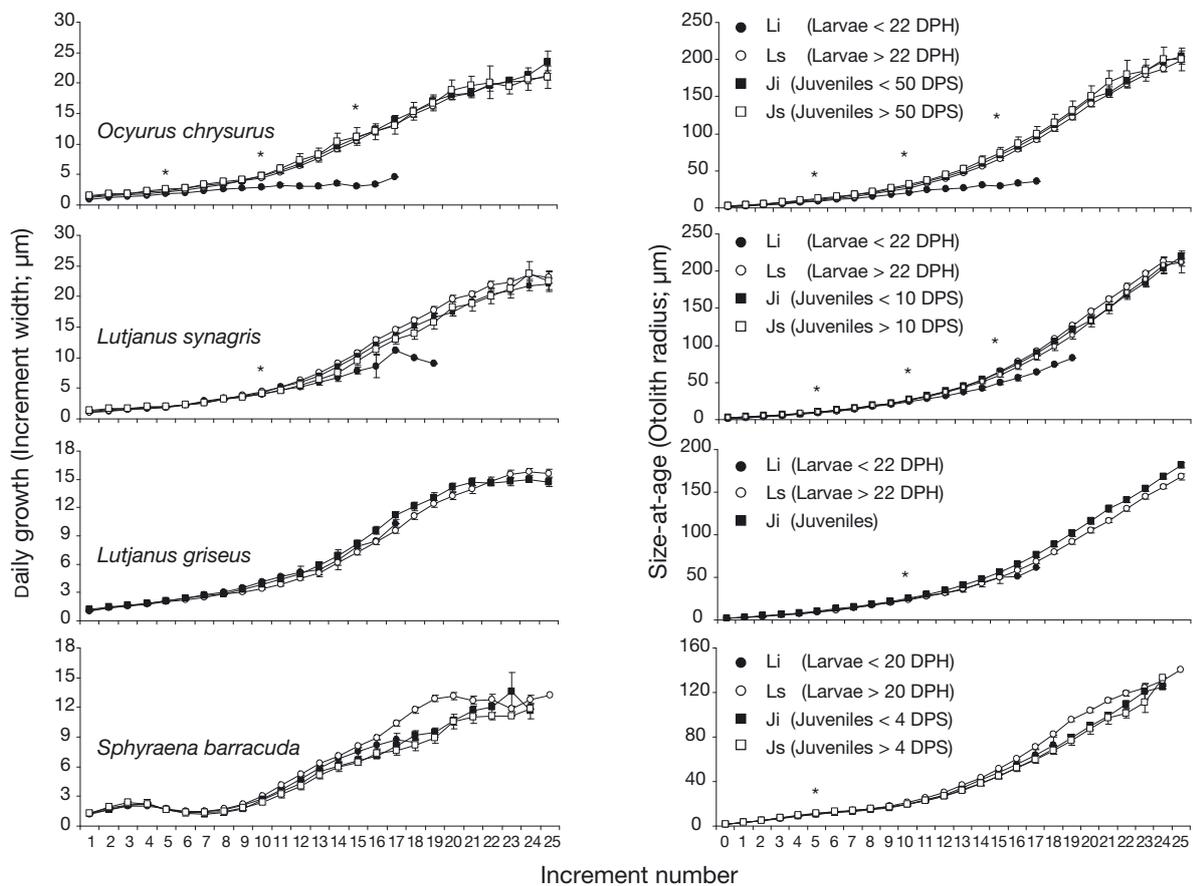


Fig. 3. *Ocyurus chrysurus*, *Lutjanus synagris*, *L. griseus*, and *Sphyaena barracuda*. Larval growth (left panels) and size-at-age (right panels) trajectories of initial larvae (Li), surviving larvae (Ls), initial juveniles (Ji), and surviving juveniles (Js) of the 4 studied reef fish species. Increments 5, 10, and 15 in both larval growth and size-at-age were tested using ANCOVA, and significant differences ( $p < 0.05$ ; Bonferroni correction applied) among groups are indicated with \*. Specific p-values and patterns among groups are given in Table 3. DPH: days post hatch, DPS: days post settlement. Error bars are  $\pm$ SE

apparent for *Sphyaena barracuda* larvae and juveniles, resulting in few significant differences in size-at-age (only Ls was larger at Increment 5 than Li; Fig. 3, Table 3).

Among Ls (only those captured in light traps and assumed to be settling) and juveniles, there were no significant differences in PLD among age groups for any species examined (ANCOVA  $p > 0.05$ ). Among the snappers, size-at-settlement was significantly greater in Ji than Ls only in *Lutjanus griseus* (Fig. 4). *Sphyaena barracuda* survivors exhibited the opposite pattern, whereby Js were smaller at settlement than Ls (Fig. 4). Despite the lack of differences in PLD or size-at-settlement among age groups in *Ocyurus chrysurus* and *L. synagris*, differences in juvenile growth quickly appeared following settlement (Fig. 5). For *O. chrysurus*, these patterns were initially opposite to earlier patterns such that surviving juveniles grew significantly slower than Ji

(5 DPS), but this reversed by 15 DPS (Fig. 5, Table 4), and by 29 DPS, size-at-age was significantly larger in Js (Fig 5, Table 4). In *L. synagris*, Js grew faster than Ji, and this difference became apparent in size-at-age by 9 DPS (Fig. 5, Table 4). Juvenile *L. griseus* only as old as 2 DPS were captured in this study, so juvenile groups could not be compared. Similarly, sample sizes of *S. barracuda* juveniles limited the extent to which differences in juvenile growth could be tested, though the single point that was tested (Increment 3) revealed no significant differences in growth or size-at-age between Ji and Js (Fig. 5, Table 4).

In addition to these patterns in growth and size-at-age among age groups, temperature had a significant effect on larval growth and size-at-age for all 4 species up until the point of settlement (Table 3). In contrast, no tests of juvenile growth revealed temperature to be a significant covariate (Table 4).

Table 3. *Ocyurus chrysurus*, *Lutjanus synagris*, *L. griseus*, and *Sphyraena barracuda*. ANCOVA results (p-values) for differences in larval growth rates (otolith increment widths) and larval size-at-age (otolith radii) at selected increments among age groups (A), with temperature (T) as a covariate, and the nature of the significant differences (Pattern) between initial larvae (Li), surviving larvae (Ls), initial juveniles (Ji), and surviving juveniles (Js). Significant values are **bold** (reflects Bonferroni correction applied to  $\alpha = 0.05$ ). FST indicates that the relationship between the covariate and dependent variable differed between the 2 groups, and ANCOVA was not possible

	Daily growth (increment widths)			Size-at-age (otolith radii)		
	p (A)	p (T)	Pattern	p (A)	p (T)	Pattern
<i>Ocyurus chrysurus</i>						
Increment 5	< <b>0.001</b>	<b>0.001</b>	(Li<Ls<Ji) = Js	< <b>0.001</b>	<b>0.002</b>	(Li<Ls<Ji) = Js
Increment 10	< <b>0.001</b>	< <b>0.001</b>	Li < (Ls=Ji=Js)	< <b>0.001</b>	< <b>0.001</b>	Li < (Ls=Ji=Js)
Increment 15	< <b>0.001</b>	< <b>0.001</b>	Li < (Ls=Ji=Js)	<b>0.001</b>	<b>0.001</b>	Li < (Ls=Ji=Js)
<i>Lutjanus synagris</i>						
Increment 5	0.232	<b>0.003</b>		< <b>0.001</b>	0.167	(Li,Ls) < (Ji,Js)
Increment 10	<b>0.016</b>	< <b>0.001</b>	(Li<Ls=Ji) = Js	<b>0.002</b>	< <b>0.001</b>	Li < (Ls,Ji,Js)
Increment 15	0.062	< <b>0.001</b>	Li < (Ls=Ji=Js)	<b>0.013</b>	< <b>0.001</b>	Li < (Ls=Ji=Js)
<i>Lutjanus griseus</i>						
Increment 5	FST			FST		
Increment 10	<b>0.002</b>	0.037	Ls < (Li,Ji)	<b>0.004</b>	<b>0.002</b>	(Li,Ls) < Ji
Increment 15	0.149	0.866	Li = Ls = Jy	0.040	0.181	(Ls<Ji) = Li
<i>Sphyraena barracuda</i>						
Increment 5	0.346	0.067	Li=Ls=Ji=Js	<b>0.007</b>	0.337	(Li<Ls) = Ji,Js
Increment 10	FST			FST		
Increment 15	0.256	< <b>0.001</b>	Li=Ls=Ji=Js	0.167	< <b>0.001</b>	Li=Ls=Ji=Js

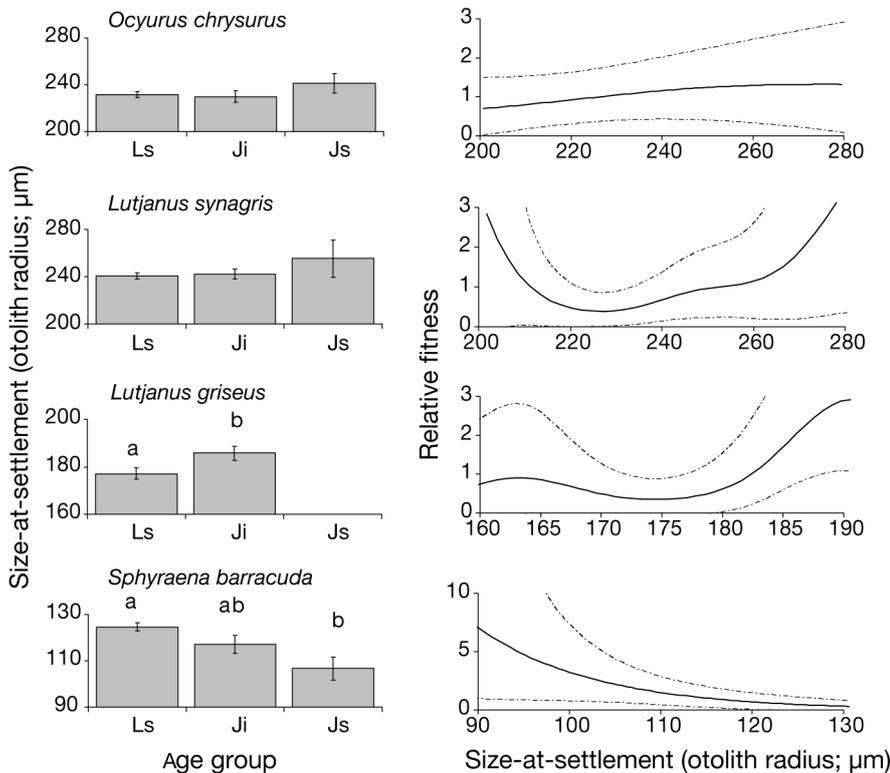


Fig. 4. *Ocyurus chrysurus*, *Lutjanus synagris*, *L. griseus*, and *Sphyraena barracuda*. Left panels: mean  $\pm$  SE size-at-settlement of examined species for surviving larvae (Ls), initial juveniles (Ji), and surviving juveniles (Js). Letters indicate significant differences (ANCOVA p < 0.05). Right panels: fitness functions created using cubic splines. (---): 95% confidence bands

## DISCUSSION

This study is among the first attempts to link pelagic larvae of tropical reef fishes with surviving juveniles. By tracking and repeatedly sampling young cohorts of 4 economically important species through time, we identified species-specific patterns of size- and growth-selective mortality in the larval and juvenile stages. Selective mortality began at the initiation of the larval period based on size-at-hatch, as evidenced by a significant trend of larger sizes-at-hatch in successively older (survivor) groups in all 3 snapper species. Although larval quality (i.e. size of energy reserves) may also play an important role at this early stage (Gagliano et al. 2007a), our results suggest a more direct link between size-at-hatch and fitness and are consistent with findings for several other species (Vigliola & Meekan 2002, Macpherson & Raventos 2005, Meekan et al. 2006, Islam et al. 2010). Because size-at-hatch can be affected by egg size (Chambers 1997) and

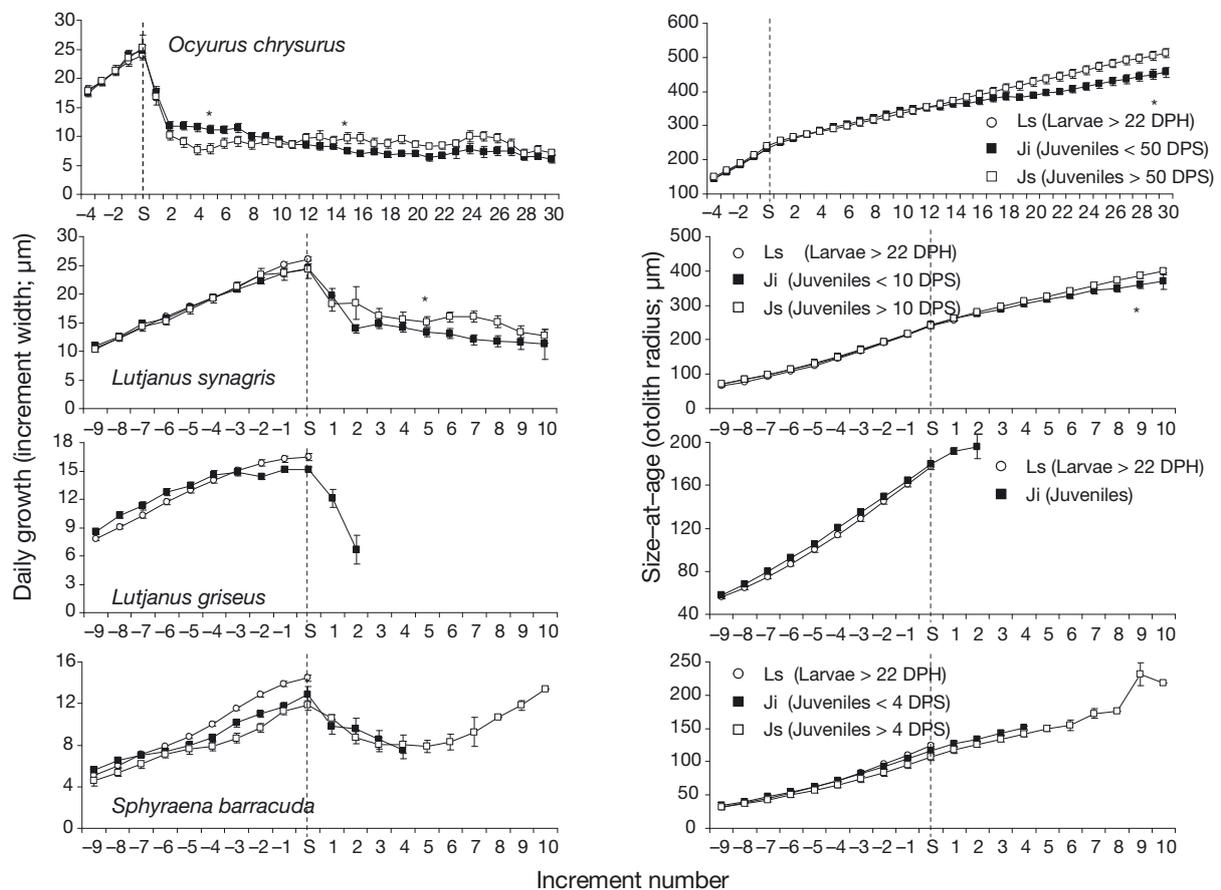


Fig. 5. *Ocyurus chrysurus*, *Lutjanus synagris*, *L. griseus*, and *Sphyaena barracuda*. Late larval and early juvenile growth (left panels) and size-at-age (right panels) trajectories aligned by settlement (S) of surviving larvae (Ls), initial juveniles (Ji), and surviving juveniles (Js) of the 4 study species. ANCOVAs were used to test for significant differences between juvenile groups at 5 and 15 d post settlement (DPS) when possible, and the last increment for which at least 5 individuals remained in each group. Significant differences ( $p < 0.05$ ; Bonferroni correction applied where necessary) are indicated by \*, and specific p-values and patterns are given in Table 4. Dashed lines represent settlement. DPH: days post hatch. Error bars are  $\pm$ SE

energy provisions within eggs (Kerrigan 1997, Gagliano & McCormick 2007), which themselves are influenced by maternal quality, age, size, and condition (Martensdottir & Steinarrson 1998, McCormick 1999, Raventos & Planes 2008), this result may indicate that maternal input had a significant effect on the survival of these fishes past the point of juvenile population replenishment.

Although a survival advantage for larger size-at-hatch was not identified for *Sphyaena barracuda* in this study, larger size-at-hatch of *S. barracuda* larvae in the Straits of Florida in 2003 and 2004 conveyed a growth, size-at-age, and presumably survival advantage (D'Alessandro et al. 2011). However, this earlier study sampled larvae monthly for 2 yr, encompassing more seasonal and inter-annual variability in selective processes. Such variability in the intensity of size-selective mortality has been identified in the FK

(Grorud-Colvert & Sponaugle 2011, Rankin & Sponaugle 2011) as well as in several other systems (Meekan & Fortier 1996, Shoji et al. 2005, Robert et al. 2007) and may explain these contrasting results.

Reconstructed larval growth and size-at-age trajectories showed that both growth- and size-selective mortality was present in all species examined. The most common pattern was selective loss of larvae with the slowest growth and smallest sizes-at-age, as evidenced by the significant difference in these parameters between Li and all other groups in *Ocyurus chrysurus* and *Lutjanus synagris*. This selectivity, which acted in the first few weeks of larval life, both inflated and homogenized mean larval growth of the surviving population by removing smaller, slower-growing larvae. Selective mortality favoring fast growth early in the larval period was also found in Atlantic mackerel *Scomber scombrus*, where it

Table 4. *Ocyurus chrysurus*, *Lutjanus synagris*, and *Sphyraena barracuda*. ANCOVA results (p-values) for differences in juvenile growth rates (otolith increment widths) and juvenile size-at-age (otolith radii) at selected increments between age groups (A), with temperature (T) as a covariate, and the nature of the significant differences (Pattern) between initial juveniles (Ji) and surviving juveniles (Js). Daily growth was tested at increments 5 and 15 d post settlement or the last day where sample sizes were sufficient; size-at-age was tested at the last increment with at least 5 individuals. Significant values are **bold** (reflects Bonferroni correction to  $\alpha = 0.05$  where applicable)

	Daily growth (increment widths)			Size-at-age (otolith radii)			
	p (A)	p (T)	Pattern	p (A)	p (T)	Pattern	
<i>Ocyurus chrysurus</i>				<i>Ocyurus chrysurus</i>			
Increment 5	<b>0.016</b>	0.090	Ji > Js	Increment 29	<b>0.018</b>	0.284	Ji < Js
Increment 15	<b>0.022</b>	0.106	Ji < Js				
<i>Lutjanus synagris</i>				<i>Lutjanus synagris</i>			
Increment 5	<b>0.030</b>	0.593	Ji < Js	Increment 9	<b>0.031</b>	0.786	Ji < Js
<i>Sphyraena barracuda</i>				<i>Sphyraena barracuda</i>			
Increment 3	0.983	0.248	Ji = Js	Increment 3	0.223	0.503	Ji = Js

homogenized growth rate of survivors, and obscured the relationship between fast larval growth and recruitment (Robert et al. 2007).

Selective sampling has the potential to produce similar effects as predator-mediated selective mortality. For example, plankton net sampling typically under-samples larger, faster-swimming larvae, which could have the effect of apparent selective survival of slow growers (i.e. the surviving larvae tend to be smaller and slower-growing). However, our analysis produced the opposite finding, that surviving larvae were those that grew fast and achieved larger sizes-at-age, suggesting that sampling bias is not the cause of the observed pattern. It is possible that light traps preferentially collect strong swimmers; however, divers collected every juvenile detected on the benthos, and seines were used to further augment those collections. The use of multiple collection techniques with differential biases may have contributed to the minimal sampling bias across the early life history of these species.

Directional size-selective mortality in *Sphyraena barracuda* and *Lutjanus griseus* did not appear until the transition from the larval to juvenile phase (size-at-settlement), and was opposite between the 2 species. While *L. griseus* displayed a size-selective advantage for larger individuals at settlement (consistent with the growth-mortality hypothesis), this pattern was reversed in *S. barracuda*. Several studies of temperate species identified survival advantages for smaller larvae (Fuiman 1989, Litvak & Leggett 1992, Pepin et al. 1992, Takasuka et al. 2004), and suggested that the mechanism behind this pattern of selectivity is a size-mediated decrease in encounter rate, a primary component of predation events (reviewed by Bailey & Houde 1989). Predator selec-

tion for larger prey is also consistent with optimal foraging theory, because larger prey provide more energy when the costs are equivalent (reviewed by Takasuka et al. 2004). Grorud-Colvert & Sponaugle (2006) found that smaller, high condition *Thalassoma bifasciatum* escaped predators more readily and exhibited less risk-taking behavior shortly after settlement. The conflicting patterns in size-at-settlement between *L. griseus* and *S. barracuda* and the difference in timing of size-selective mortality between these 2 species and *L. synagris* and *Ocyurus chrysurus* (the latter lacking differences in size-at-settlement) highlight important species-specific variability among these fishes as well as selective pressures acting on them.

Despite the small amount of variability in growth and size at the time of settlement of *Ocyurus chrysurus* and *Lutjanus synagris*, patterns of juvenile growth-selective mortality were evident quickly after settlement. This pattern of mortality was independent of size, as significant differences in size between age groups emerged only after 1 to 3 wk. Such a rapid appearance of growth-selective loss following settlement, as well as rapid reversals in the direction of selection, must have been due to some component within the juvenile habitat affecting growth itself. Temperature variability, although important to selective processes across life stages, is generally small during summer months in shallow waters of the FK. Predation may be a more likely explanation for the observed patterns, as the days following settlement to juvenile habitat are extremely dangerous for young reef fish as they encounter a suite of new predators (reviewed by Almany & Webster 2006). However, it is unlikely that a predator has any means of evaluating differences in growth among individu-

als independent of size. The most parsimonious explanation is that growth was affected by feeding success, as a function of individual behavior. Feeding (or lack thereof) can have immediate and lasting effects on growth (Shoji et al. 2005) as well as swimming speed, responsiveness to predatory attacks, and overall survival (Booth & Hixon 1999, Chick & Van Den Avyle 2000). This suggests that in *L. synagris*, individuals that fed most successfully and/or frequently preferentially survived, consistent with the paradigm that faster-growing individuals gain a survival advantage over slower-growing ones. Within 1 wk, this growth advantage translated into a size advantage, consistent with many recent studies (Searcy & Sponaugle 2001, Durieux et al. 2009, Grorud-Colvert & Sponaugle 2011) and with conventional ecological theory that faster-growing and thus larger individuals should be susceptible to fewer predators due to gape limitation, be better able to escape predation, resist starvation, and tolerate physiological extremes (reviewed by Sogard 1997).

Although juvenile *Ocyurus chrysurus* ultimately shared this pattern of advantageous fast growth, slower growth was favored during the first 10 d following settlement. Slower juvenile growth by survivors is exhibited by another reef fish, the bicolor damselfish *Stegastes partitus*, in the FK (Rankin & Sponaugle 2011) and in the Bahamas (Johnson & Hixon 2010), due to increased energy expenditure in territorial defense by larger settlers. Thus, a trade-off may exist in recently settled *O. chrysurus* juveniles, whereby avoiding predation during this vulnerable stage (by sheltering more than feeding, or associating with habitats with lower predation risks, but sub-optimal feeding) is more beneficial to overall survival (e.g. Werner & Hall 1988). Opposite patterns in growth-selective mortality shortly after settlement in 2 closely related species (a natural hybrid between *O. chrysurus* and *Lutjanus synagris* occurs; Loftus 1992) that settle to similar habitat at similar sizes (based on sizes of late-stage larvae in light traps; S. Sponaugle & E. D'Alessandro unpubl. data), suggests that they are under different selective pressures. Differences in selective processes for closely related species occupying similar habitats have also been found for 2 tropical wrasses, *Thalassoma bifasciatum* and *Halichoeres bivittatus*, where the latter exhibited a survival advantage for fast larval growth while the former did not, possibly due to contrasting ecologies and exposure to different predator guilds, rates of predation, and selective pressures (Searcy & Sponaugle 2001). Differences in predators were also found to influence patterns of selective mortality of a

newly settled damselfish (McCormick & Hoey 2004). Thus, despite being closely related and settling to the same habitats, some aspect of morphology or behavior of *O. chrysurus* and *L. synagris* causes them to experience different patterns in selective mortality.

Although it is frequently difficult to disentangle the relative effects of the 3 major components of the growth-mortality hypothesis because they are all highly correlated and likely act synergistically (Hare & Cowen 1997, Takasuka et al. 2004), some efforts have pointed to the importance of growth rate, even in the absence of size and PLD differences (Takasuka et al. 2003, 2004, Islam et al. 2010). Such selection was evident in our study of *Ocyurus chrysurus* and *Lutjanus synagris*, where significant differences between age groups were identified in juvenile growth but not size-at-age. However, the opposite trend was occasionally apparent in the larval stage, where larval size-at-age (including size-at-hatch) differed among age groups but growth did not (Increment 5 in *Sphyræna barracuda* and *L. synagris*, and size-at-settlement in *S. barracuda*). There was no evidence in our study of the advantages of a short PLD (i.e. stage duration hypothesis), as no significant differences in PLD were found between age groups for any species. Thus, size-selective mortality may have played a dominant role in the larval life of *S. barracuda*, and *L. synagris*, but growth-selective mortality seemed to be the major selective force in juvenile *O. chrysurus* and *L. synagris*. Our results illustrate how selective processes may switch between stages, and survivors may ultimately face conflicting pressures over time.

Despite the relatively small seasonal temperature variation in the sub-tropical FK, and small temperature range within the seasonal scope of our study (1–3°C), temperature was often a significant covariate in tests of larval growth rate and size-at-age, a result consistent with previous findings of temperature-mediated larval growth in *Thalassoma bifasciatum* in the FK (Sponaugle et al. 2006). In contrast, during the early juvenile phase for the 3 species examined, temperature was never a significant covariate. The effect of temperature may have been tempered by a decrease in trait variability resulting from selective mortality in the larval stage (at least for *Ocyurus chrysurus* and *Lutjanus synagris*), or dampened by increased importance of other factors such as resource availability and competition in the juvenile environment. Temperature can serve as a mediating factor of selective mortality in reef fishes, changing the intensity (Gagliano et al. 2007b) and pattern of selective loss of individuals (Grorud-

Colvert & Sponaugle 2011, Rankin & Sponaugle 2011). However, it is unlikely that patterns or direction of selective loss were significantly affected by temperature in our study, as this typically occurs over seasonal timescales and all of our cohorts were from summer.

## CONCLUSIONS

This study is the first examination of selective processes in fishery-targeted tropical reef fish species. By examining otolith-based growth and size-at-age throughout the pelagic larval and early juvenile stages of 3 species of snapper and 1 species of barracuda, we demonstrated that selective mortality plays an important role in determining which individuals survive both the pelagic larval and early juvenile stages. The implications for our overall understanding of the ecology and management of these species are as follows: (1) Regardless of taxonomic relatedness, different species can exhibit variability in selective patterns, pointing to the differentially important roles of particular ecological processes. (2) Despite this species-specific variability, some consistent patterns of selection for faster growth and larger sizes-at-age in both the larval and juvenile stages of 2 snappers may translate into enhanced survival during recruitment, possibly leading to larger juvenile and adult populations, as has been shown for other species (e.g. Vigliola & Meekan 2002, McCormick & Hoey 2004, Sponaugle & Pinkard 2004, Jenkins & King 2006, Sponaugle et al. 2006, Tanaka et al. 2006, Robert et al. 2007). Such consistent patterns in selective mortality may have predictive value for future recruitment if used in conjunction with larval surveys. (3) Lastly, the significance of size-at-hatch, and possibly maternal contribution, to survival through the larval and into the juvenile stage in *Ocyurus chrysurus*, *Lutjanus synagris*, and *L. griseus* has important implications for the management of these heavily fished species. Current single-species management relies on the minimum size at sexual maturity to apply size limits to the exploitable stage in most fishes, and assumes that every spawning female is equivalent. Studies of other species have shown that larger, older, or higher condition females produce larger eggs and larvae (Marteinsdottir & Steinarsson 1998, Berkeley et al. 2004, Raventos & Planes 2008). If this correlation exists in the snapper species examined here, then current size limits should be adjusted to protect not only immature fish that have not had a

chance to spawn, but also larger, older fishes that would effectively contribute more offspring to the juvenile population.

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