



# Comparative predation rates on larval snappers (Lutjanidae) in oceanic, reef, and nearshore waters

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## ABSTRACT

The life cycle of most reef fishes involves pelagic larvae entering the nearshore environment to settle to benthic substrates. Settlement is considered to be highly risky as larvae encounter high rates of predation mortality associated with shallow nearshore habitats. This potential bottleneck may be particularly significant for many tropical snapper (Lutjanidae) species which bypass the reef to settle to very nearshore seagrass areas. To test the hypothesis that predation-related mortality increases as naïve late-stage fish larvae leave the offshore oceanic environment and enter the nearshore to settle, relative nocturnal predation rates on tethered late-stage snapper larvae were measured in oceanic, coral reef, and nearshore surface waters of the lower Florida Keys, USA. Both relative predation rate and probability of predation in oceanic areas seaward of the reef was significantly greater than over reef or nearshore seagrass/hardbottom habitats. This surprising result may be due to differences in the density or spatial distribution of potential predators between deep offshore (near flotsam at the surface) and shallow nearshore environments (demersal). These findings suggest that successful late-stage snapper larvae should avoid surface waters in deep oceanic areas and move upward in the water column as they pass over the reef and other shallow nearshore environments prior to settlement.

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## 1. Introduction

Most coral reef organisms have complex life histories, whereby relatively sedentary adults produce pelagic eggs or larvae. These larvae often spend days to weeks in the open ocean before returning to reef and/or nearshore environments to settle as juveniles. The pelagic larval phase is a period of extremely high mortality (Houde, 1987), and has been recognized over the last century as a major contributor to fluctuations in recruitment. A widely held assumption is that the evolutionary basis for this pelagic phase in reef fishes is to allow eggs and larvae to develop and grow in an environment away from the abundance of predators that typically occupy coral reef habitats (Johannes, 1978; Strathmann et al., 2002).

More recently, attention has been directed to the brief (usually occurring during a single night) shift from pelagic larva to bottom-associated juvenile — a transition referred to as “settlement.” During this process, settling larvae that are relatively naïve to the juvenile habitat are exposed to a new suite of challenges including different predators, prey, and physical environmental factors. Settlement is often accompanied by very high mortality rates, suggesting that a “predation gauntlet” occurs during and shortly after settlement that may act as a bottleneck for adult populations (Almany and Webster, 2006; Doherty et al., 2004; Osman and Whitlatch, 2004). Despite the importance of this transition, little is

known about the processes involved due in large part to the difficulty involved in unobtrusively tracking and observing larvae at night (when most larval settlement occurs; Dufour and Galzin, 1993; Little, 1977; Reyns and Sponaugle, 1999; Victor, 1991) through sometimes large expanses of open water (but see Acosta and Butler, 1999).

Many shallow water snapper (family: Lutjanidae) species and other ecologically and economically important reef fishes and invertebrates (barracuda, groupers, grunts, and spiny lobsters) use nearshore back-reef areas as settlement and juvenile habitats before moving to reefs as adults. These larvae must therefore traverse at least the shallow fringing reef tract before reaching nearshore seagrass, algal, and/or hardbottom habitats. This additional time in nearshore waters may impose particularly high mortality pressure on settling larvae. The overall objective of this study was to examine relative nocturnal mortality rates of late-stage snapper larvae in surface waters of three different cross-shelf habitats. Specifically, we tested the hypothesis that relative predation rates in surface waters differ among oceanic, reef, and nearshore seagrass/hardbottom habitats, with predation intensifying as relatively naïve larvae leave the deep oceanic environment and encounter increasing predator densities in shallow nearshore waters.

## 2. Materials and methods

### 2.1. Study area

The study area encompassed a ~13 km cross-shelf corridor on the Atlantic side (south–southeast) of Summerland Key, lower Florida

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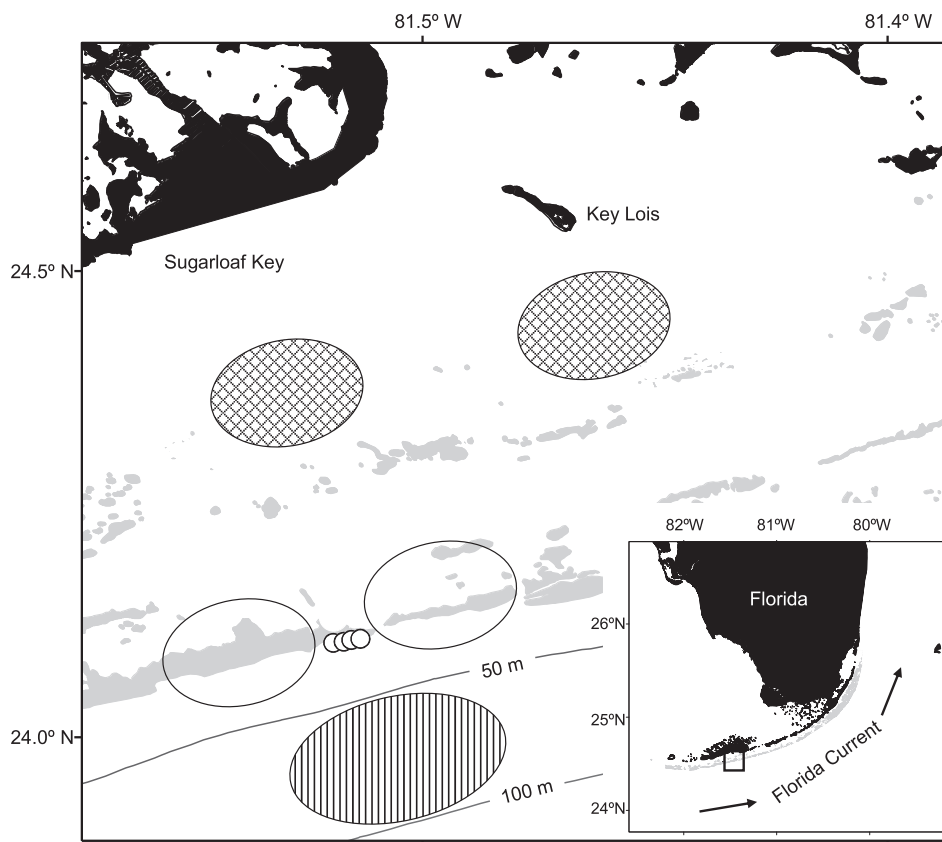
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Keys (FK), USA (Fig. 1). This corridor included three distinct habitats: 1) oceanic waters (OC) between the 50 and 100 m isobaths ~13 km from shore; 2) reef waters (RF) located over or directly adjacent to the fringing reef crest (~10.5 km from shore in 3–7 m of water); and 3) nearshore waters (NR) over seagrass/algae/sand/hardbottom ~3.5 km from shore in ~5–7 m of water (Fig. 1). The marine environment surrounding the lower FK is a dynamic area affected by tides, seasonal winds, and the Florida Current (FC) and its associated meanders and eddies. The net westward water movement inshore of the fringing reef is driven by the prevailing westward winds that persist for most of the year (Pitts, 1994). The combination of these winds and the east–west orientation of the coastline in the lower FK also causes downwelling along the coast, with onshore flow in the upper layers (Lee et al., 1992). On the outer shelf and often over the fringing reef tract, local wind forcing has little influence on the alongshore flow regime, which is dominated by the FC. In the lower FK, variability in the currents over this area occurs on a 30–60 day time scale due to the passage of mesoscale cyclonic eddies that form along the boundary of the Loop Current as it flows south along the west Florida shelf (Fratantoni et al., 1998; Lee et al., 1994).

## 2.2. Study organisms and field collection

To study predation during settlement, we focused on snappers (Lutjanidae) that are associated with coral reefs as adults. The occurrence of late-stage larvae and newly settled juveniles of western Atlantic and Caribbean snappers in nearshore waters, as indicated by recruitment surveys (Watson et al., 2002), back-calculation of settlement from juveniles (Allman and Grimes, 2002; Denit and Sponaugle, 2004; Tzeng et al., 2003), channel net (Halvorsen, 1994),

and light trap catches (D'Alessandro et al., 2007; Wilson, 2001), peaks during warm summer months (July–September) between third quarter to new moon periods. Channel net catches have further shown that ingress of snapper larvae to back-reef habitats through tidal channels occurs mostly at night and in the upper 1 m of the water column (Halvorsen, 1994). Therefore, late-stage larval snappers were collected in July–August 2008 and July 2009 between the third quarter and new moons at 1–2 m depth using light traps over the fringing reef crest in the vicinity of American Shoal reef (Fig. 1). Traps were modified from a design by Sponaugle and Cowen (1996) and consisted of a 1.07 m-long, 0.43 m-diameter cylinder of 500  $\mu$ m Nitex netting (Sea Gear Corp.), surrounding a 30 cm submersible 5 W fluorescent light (Bellmare). 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. Upon retrieval, larval snappers were separated from the rest of the sample, placed into a 220-L cooler of aerated seawater, and transported to shore where they were anesthetized, measured to the nearest 0.5 mm, and tethered (see below). A three-species group consisting of the species *Lutjanus apodus* (Walbaum, 1792), *Lutjanus griseus* (Linnaeus, 1758), and *Lutjanus jocu* (Bloch and Schneider, 1801), was utilized in this study. Morphological differentiation of these larvae to the species level is tenuous, and molecular techniques were not feasible in the present study since live larvae were required for the experiment. The tethering procedure consisted of suturing a 20 cm length of polyester-core thread through the dorsal musculature under the dorsal fin, approximately in line with the first anal spine, avoiding the notochord and major blood vessels (Danilowicz and Sale, 1999). Larvae were then allowed to recover in individual 1-L jars of seawater for at least 2 h before experiments began.



**Fig. 1.** Map of the study area offshore of Sugarloaf Key, Florida, showing light trap moorings (open circles) and the three areas where experiments were conducted: blue water (OC; striped oval), reef (RF; open ovals), and nearshore (NR; cross hatched ovals). Land is shown in black and reef is shown in gray.

### 2.3. Experimental protocol

The experimental design was modified from Acosta and Butler (1999). Eight weighted swivels were attached to a 1.5 m square polyvinyl chloride raft by 10 kg-test monofilament line (Fig. 2). Tethered larvae were attached to the swivels upon deployment such that larvae hung 0.5 m below the surface with a 20 cm sphere of free movement. Care was taken to include both relatively large and small individuals during each experiment to ensure that the length distribution of larvae utilized in each habitat represented the light trap catch from the previous night. The raft was equipped with a small mast topped with a light beacon, which flashed every 30 s to facilitate retrieval at night. This beacon sat inside an opaque upward-facing 40 cm diameter funnel to prevent lighting of the area around the experiment (Fig. 2). The raft was deployed from an 8 m vessel which waited at least 100 m away with engines and lights shut off during each trial. The raft was allowed to drift for 30 min in each habitat, at which time it was retrieved and the number of larvae remaining on their tethers was recorded. Deployment and retrieval points were recorded to confirm that the device drifted over the intended habitat and to allow assessment of relationships between relative predation rate and the distance/direction of drift. This procedure was repeated in each of the three habitats in random order throughout the course of a single night and constituted one run of the experiment. To coincide with the most relevant time for natural larval snapper ingress and settlement, all experiments were conducted in full darkness after 2130 h, in the upper 1 m of the water column, and during peak ingress and settlement within the year and lunar cycle. Each fish larva was used only once in one 30 min drift, and experiments were conducted on only relatively calm ( $<5 \text{ ms}^{-1}$  winds) nights to minimize disturbance to the tethered larvae by waves and shear between water currents and wind.

Preliminary 30 min daytime trials were carried out at the start of experimentation in 2008 and 2009, during which all tethered larvae were carefully and continuously observed in each habitat type for possible experimental bias and among-treatment artifacts. Larvae were not jerked about by movement of the raft, never became entangled or broke free from their tethers, and could move freely in a 20 cm radius around each weighted swivel. Moreover, in the 2–4 h that newly tethered larvae recovered in individual 1-L jars, they never

broke free from their tethers. Therefore, during experimental runs, larvae missing from their tethers upon retrieval of the drifter were considered lost due to predation.

### 2.4. Data analysis

Before testing differences in relative predation rates among habitats, we analyzed the data for relationships with confounding factors. A simple ANOVA and Tukey–Kramer HSD test was used to identify relationships between the distance the drifter traveled and habitat, and Pearson's product moment correlations were used to examine relationships (within habitats) between predation rate and distance the drifter traveled. Because the sensory distance of the predators and thus the true independence of each larva on the raft could not be determined, relative predation data were analyzed both as proportional (proportion of fish preyed upon during each deployment) and binomial (predation occurred or did not occur) datasets. A Pearson's Chi Square test and Tukey-type multiple comparisons for proportions were used in the former case, and a Cochran's Q and similar Tukey-type multiple comparisons in the latter to determine if relative predation was non-uniform between the three habitat types and identify where differences occurred (Zar, 1999). To test for size selection by predators, t-tests were used to compare the mean lengths of larvae that were preyed upon with those that survived.

## 3. Results

Rafts of tethered larvae were deployed in all three habitats a total of 16 times over 13 nights in July–August 2008 and July 2009. These experiments utilized 384 snapper larvae ranging from 11 to 17 mm SL, 51 of which were preyed upon, resulting in an overall predation rate of 13%. The drifter traveled significantly farther in RF than in OC or NR environments (Fig. 3; ANOVA;  $p = 0.001$ ; Tukey–Kramer HS tests: OC vs RF  $p = 0.026$ ; OC vs NS  $p < 0.001$ ; RF vs NS  $p = 0.341$ ), but no significant relationships were identified between relative predation rates and the distance the drifter traveled within each habitat or for all habitats pooled (Fig. 4). Likewise, the mean lengths of larvae that were preyed upon and those that survived were not significantly different whether pooled over the entire study (Fig. 5; t-test:

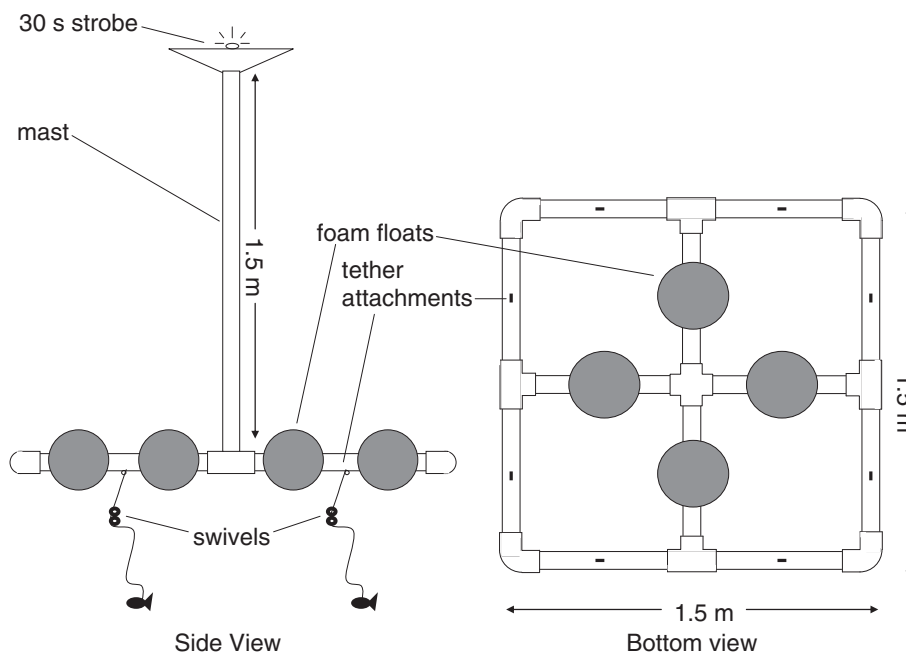


Fig. 2. Schematic of the drifting device to which larval snappers were tethered.

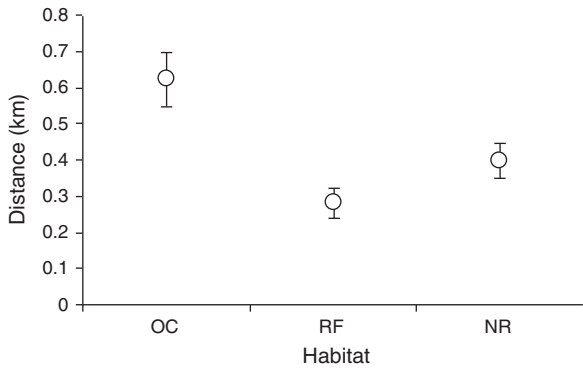


Fig. 3. Mean ( $\pm$  SE) distance (km) the drifter traveled in each of the three habitats (OC = oceanic; RF = reef; NR = nearshore).

$p = 0.710$ ;  $df = 243$ ), or grouped by habitat ( $t$ -test: OC:  $p = 0.980$   $df = 70$ ; RF:  $p = 0.800$   $df = 48$ ; NR:  $p = 0.270$   $df = 11$ ).

Both chi-square (proportional data;  $\chi^2 = 25.53$ ;  $p < 0.010$ ) and Cochran's Q tests (binomial data;  $Q = 9.8$ ;  $p < 0.010$ ) revealed that relative levels of predation differed between the three habitat types. Multiple comparisons of data analyzed binomially indicated that probability of predation was significantly higher in OC than in NR (Table 1; Fig. 6). When data were analyzed as proportions, larvae in OC experienced a significantly higher level of predation than those in either RF or NR (Table 1; Fig. 6).

#### 4. Discussion

It is widely held that reef fish possess a pelagic larval stage to reduce mortality rates on their eggs and larvae by spatially separating them from reef-based predators (Johannes, 1978; Strathmann et al., 2002). Based on this contention we hypothesized that relative nocturnal predation rates on late-stage snapper larvae in surface waters would differ significantly between open water and shallow nearshore environments, and that these rates would be highest over

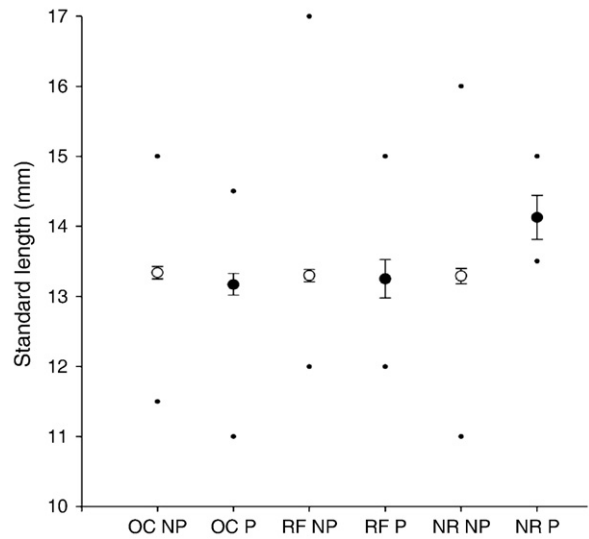


Fig. 5. Mean ( $\pm$  SD) lengths of tethered larvae (large circles) both absent (preyed upon; P; large black circles) and present (not preyed upon; NP; large open circles) after 30 min of drift over the three habitats: oceanic (OC), reef (RF), and nearshore (NR). Range of data is given as black dots.

nearshore reef and seagrass habitats. Our results revealed that relative rates of nocturnal predation on surface larvae differed significantly among habitats, but the pattern was opposite to that predicted. Nocturnal predation on late-stage snapper larvae was highest offshore and decreased closer to shore.

Several factors specific to this study and inherent to tethering studies in general have the potential to bias experimental results. The most obvious is that tethering otherwise mobile organisms introduces experimental artifacts that usually inflate natural predation rates. However, these are cancelled out when applied equally to all treatments as they were here. In contrast, current speeds could not be controlled for and differed among habitats (due in large part to the

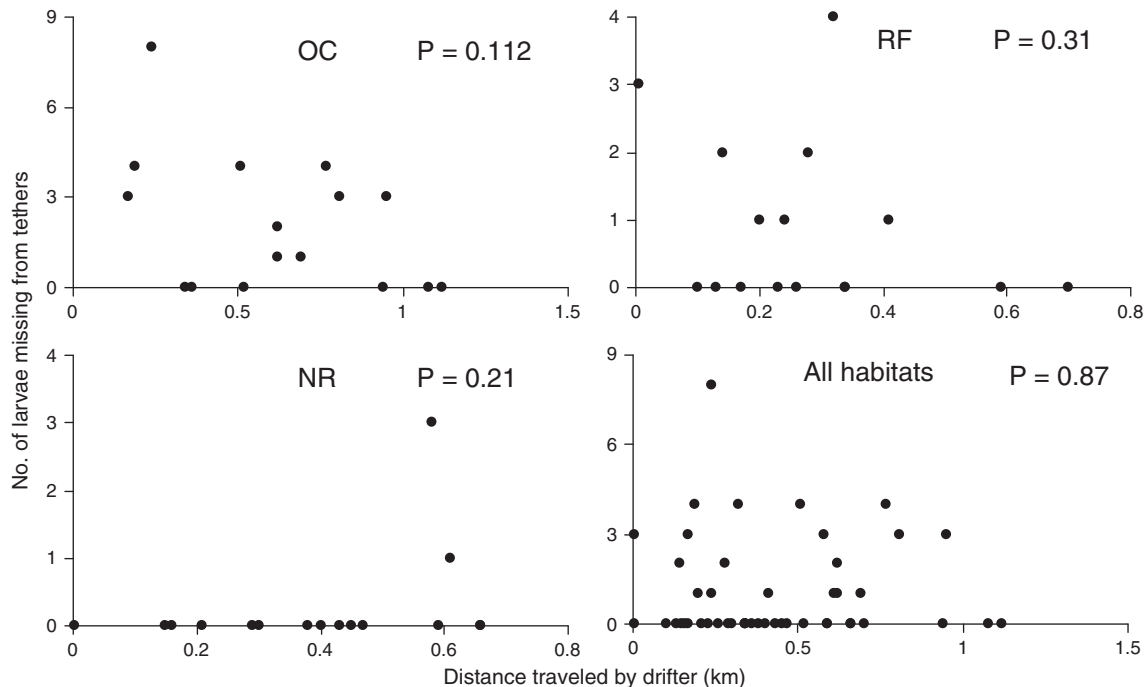


Fig. 4. Plots of distance traveled by the drifter vs number of larvae missing from tethers in each of three habitats (OC = oceanic; RF = reef; NR = nearshore) and all three habitats combined (all habitats).

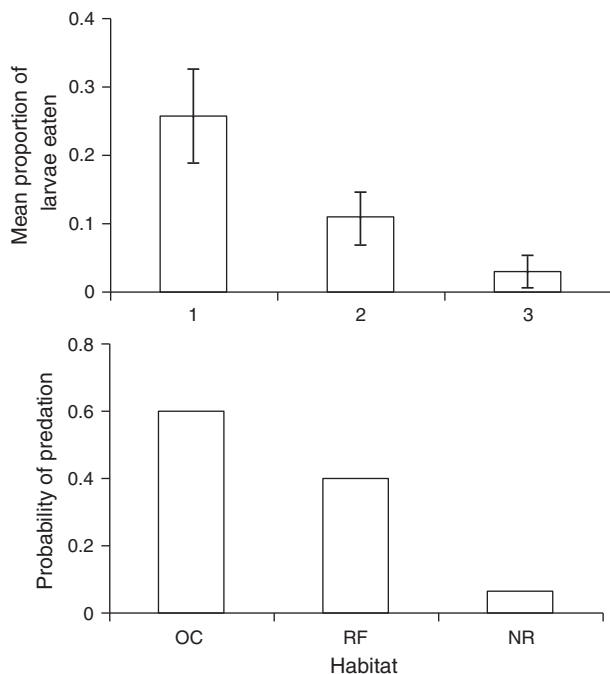
**Table 1**

Test statistics from multiple comparisons of relative predation between the three habitat types analyzed binomially (probability of predation; Probability) and as proportions (percent of larvae preyed upon; Proportion). Critical values at the  $\alpha = 0.01$  level are given in parentheses. Bold type indicates significant differences.

Site	Probability ( $S_{\alpha=0.01} = 3.035$ )	Proportion ( $q_{\alpha=0.01} = 4.12$ )
OC v RF	1.16	<b>4.38</b>
OC v NR	<b>3.10</b>	<b>7.77</b>
RF v NR	1.94	3.39

proximity of OC treatments to the FC), resulting in significantly different distances traveled (and potential exposure to predators) between habitats. However, no significant relationship between distance the drifter traveled and predation rate was identified for the entire study or within any of the three habitats. Thus, it is unlikely that the distance traveled by the drifter was a causative factor in the observed pattern of relative predation.

It is likely that predator guilds in the three environments (treatments) in this study differed in their compositions, opening the possibility for unequal interactions between predators and tethered larvae among treatments, deemed “second order artifacts” (Aronson and Heck, 1995; Haywood et al., 2003; Peterson and Black, 1994). For example, the late-stage larvae utilized in this study were presumably at or close to competency to settle, when morphological changes (e.g., development of juvenile pigmentation in snappers) make them less conspicuous in the shallow nearshore juvenile environment. If such changes had already begun, moving them back into the oceanic environment and exposing them to oceanic predators would inflate the predation rate in this area. However, the larvae utilized had not yet settled and were still part of the pelagic planktonic community. Because of the large size range (6 mm SL) of these larvae, lack of size selection amongst preyed upon larvae in any of the examined environments, and largely transparent state of most of the utilized larvae, it seems unlikely that this potential second order



**Fig. 6.** Mean ( $\pm$  SE) proportion of larval snappers preyed upon per drifter deployment (out of eight; top panel), and overall probability of at least one predation event occurring (binomial representation of data; bottom panel), over each of the three habitats: oceanic (OC), reef (RF), and nearshore (NR).

artifact significantly affected the results, though this cannot be definitively concluded. To rule out or control for all second order artifacts, the identity and reaction to tethered larvae of all potential predators in each habitat are needed, and this was beyond the scope of this study. Two other studies to date have tethered planktonic organisms to measure relative predation rates in different nearshore environments of the FK, and these utilized preliminary trials, behavioral observations, and experimental assays to evaluate experimental biases and second order artifacts (Acosta and Butler, 1999; Bullard and Hay, 2002). In both cases, none were identified and tethering was determined to be a valid means of measuring relative predation rates. Ours is the first study to tether larval fish, and while all second order artifacts cannot be ruled out, preliminary trials did not indicate any among-treatment bias or experimental artifacts.

So why then would predation at the surface become less intense as larvae move shoreward? The answer may lie in differences in the distribution of predators between the three habitats such that more predators were concentrated near the surface (and near the experimental drifter) in OC and closer to the bottom in RF and NR. Juveniles and adults of many fish species (potential predators of late-stage larval snappers) commonly aggregate near the surface around flotsam and floating algae in deep oceanic waters (Casazza and Ross, 2008; Hunter and Mitchell, 1967; Kingsford and Choat, 1985). Such drifting communities were abundant and frequently in proximity to the experimental raft in OC during the present study. In contrast, on coral reefs, predators of settling larval fish may be more concentrated near the bottom. Planktivorous fish can cause a near-bottom depletion of zooplankton on some reefs (Heidelberg et al., 2010; Holzman et al., 2007), and much of the mortality associated with settlement of fish larvae is attributed to the actions of small reef-associated predatory fish (Carr and Hixon, 1995; Holbrook and Schmitt, 2002). In fact, seven of nine families of reef fishes known to consume larval reef fish in the Caribbean are small bottom dwellers (Randall, 1967). In a recent study which involved observation of larval snappers (*Lutjanus carponotatus*) settling during the day, predation and aggressive interactions were only observed when larvae attempted to settle to the benthos and not when swimming over the reef (Quere and Leis, 2010), suggesting that predators in this environment stay close to the bottom. Such reef-based predation on small fishes is higher at night (Danilowicz and Sale, 1999) when most larval fish settlement occurs. Although transient predators that may hunt above the reef are also an important component of reef-based predation (Hixon and Carr, 1997), the extent to which they feed on settling fish larvae is unknown. Back reef habitats are often cited as nursery areas and may offer a lower predation risk than shallow reef environments (Chittaro et al., 2005), however, in our study, relative predation rates and probabilities between RF and NR were similar. This may be due to the similar depth ranges and thus potential vertical distribution of predators between these two nearshore habitats. Therefore, larvae tethered to within 1 m of the surface likely encountered an increased abundance of predators in OC and fewer in RF and NR where they were separated from the bottom (and presumably the majority of predators). Alternatively, the patterns in relative predation may have simply arisen from differences in the density of relevant predators between the three habitats. Unfortunately, too few data exist as to the identity of major larval fish predators in the study area or relative densities among habitats to confirm or refute this possibility.

Higher predation on surface larvae offshore suggests that to reduce predation mortality, wild settlement stage larvae should remain at depth offshore, and move into surface waters as they enter reef and nearshore waters. An upward shift in the vertical distribution of snapper larvae during ingress is consistent with several other studies. In tethering post-larval spiny lobsters at varying distances above the bottom along a typical offshore–inshore transport path in the FK (coral reef, coastal lagoon, and bay), Acosta and Butler (1999) also

identified a reduction in relative predation with distance inshore and concluded that these organisms likely utilize the surface waters during the darkest lunar phase to reduce risk of predation during inshore migration. Utilizing the upper water column in the shallow nearshore habitats of the lower FK would also allow these post-larvae to take advantage of onshore movement of surface waters typical of this region (Lee and Williams, 1999; Lee et al., 1992). While less is known about the ingress of late-stage larval snappers (especially in offshore oceanic waters), younger and smaller (mostly 3–9 mm SL) larvae of reef-associated western Atlantic and Caribbean snappers in deep waters of the FC are concentrated in the upper 25 m of the water column, move to shallower depths with development, and are rarely captured at the surface by neuston nets nocturnally or diurnally (D'Alessandro et al., 2010; Huebert et al., 2010). Direct observation of settling late-stage *L. carponotatus* larvae revealed that in near-reef areas, larvae preferred the upper half of the water column, but avoided the upper 2.5 m (Quere and Leis, 2010). In contrast, depth-stratified light trapping over reefs (Hendriks et al., 2001) and channel netting in nearshore tidal passages (Halvorsen, 1994) indicated that most late-stage snapper larvae are near the surface in these shallow water areas. Combined with these studies, results of our tethering experiments suggest that during the settlement process, successful larval snappers avoid the surface in deep oceanic waters until they encounter a water column constrained by the shallow fringing reef crest. To avoid near-bottom predators in these shallow environments, larvae should move to shallower depths. By following this cross-shelf migration strategy, larvae could minimize encounters with the highest concentrations of predators and capitalize on onshore transport mechanisms. The unexpected results of this study underscore our lack of a full understanding of the processes functioning during this critical time. Future efforts should be directed at obtaining a more three dimensional understanding of predation risk for a diversity of species as they near the end of their pelagic existence and seek juvenile habitat.

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