Ecology, 81(8), 2000, pp. 2227–2240

ECOLOGICAL PROCESSES UNDERLYING ONTOGENETIC HABITAT SHIFTS IN A CORAL REEF FISH

CRAIG P. DAHLGREN[1] AND DAVID B. EGGLESTON

North Carolina State University, Department of Marine, Earth, and Atmospheric Sciences, Raleigh, North Carolina 27695-8208 USA

Abstract. Distribution of mobile animals may reflect decisions on how to balance conflicting demands associated with foraging and avoiding predators. A simple optimality model predicts that mobile animals should respond to changes in mortality risk (μ) and growth rate (g) by shifting habitats in a way that maximizes net benefits. In this study, field caging and tethering experiments quantified habitat-specific growth rates and mortality risk, respectively, for three different sizes of a coral reef fish, Nassau grouper (*Epinephelus striatus*), during its juvenile tenure in off-reef nursery habitats. These sizes bracketed the size at which this species undergoes an ontogenetic habitat shift from the interstices of macroalgal clumps ("algal habitat") to areas outside, or adjacent to, macroalgae and other physically complex microhabitats ("postalgal habitats"). Experimental results were used in a cost–benefit analysis to test the following alternative (but not mutually exclusive) hypotheses: (1) juvenile grouper shift habitats in a way that maximizes growth rates (g); (2) juveniles shift habitats in a way that minimizes mortality (predation) risk (μ); and (3) if trade-offs exist between maximizing growth rate and minimizing mortality risk, juveniles shift habitats in a way that minimizes the ratio of mortality risk to growth rate (μ/g).

Results suggested that small fish face a trade-off between living in the relatively safe algal habitat and achieving high growth rates in postalgal habitats. The value of μ/g was significantly lower in the algal than postalgal habitats for small fish, which typically reside in the algal habitat, and significantly lower in postalgal habitats for medium and large fish, which typically reside in postalgal habitats. Thus, habitat use by juvenile Nassau grouper was consistent with the "minimize μ/g hypothesis." These results highlight how behavioral responses to ecological processes, such as changing predation risk with body size, determine distribution patterns of mobile animals.

Key words: *Bahamas; caging experiments;* Epinephelus striatus; *growth rate; habitat;* Laurencia; *macroalgae; Nassau grouper; ontogenetic; optimization models; predation risk; refuge.*

INTRODUCTION

Population dynamics of many mobile animals are influenced by behavioral responses to ecological processes (Lomnicki 1988). For example, habitat use often reflects behavioral decisions associated with the demands of foraging, avoiding predators, or reproducing (Sutherland 1996). Because foraging needs, predation risk, and reproductive conditions change during ontogeny (e.g., due to increases in body size), animals often shift habitats in ways that meet their changing needs (Werner and Gilliam 1984, McNamara and Houston 1986, Werner 1988, Ludwig and Rowe 1990).

Cost–benefit analysis and optimality models can help to identify ecological processes underlying habitat shifts, by examining an animal's decision to shift habitats in terms of fitness-maximizing strategies (Stephens and Krebs 1986). In the case of nonreproductive individuals, increasing the probability of survival to the next size class maximizes fitness (Werner and Gilliam 1984, Mangel and Clark 1986, McNamara and Houston 1986). Thus, a strategy that maximizes energy gains (growth rates) or one that minimizes predation risk may be optimal under certain circumstances (Werner et al. 1983*b*, Holbrook and Schmitt 1988, Nonacs and Dill 1990; review by Persson [1990] and references therein). In many cases, however, there are trade-offs in which the habitat offering the higher potential growth rate also possesses a greater risk of predation (e.g., reviews by Lima and Dill [1990] and Sogard [1994]). For example, when predators are absent from ponds, juvenile sunfish (*Lepomis macrochirus*) occupy the habitat that allows them the highest growth (or foraging) rate (Werner et al. 1983*b*). When predators are present, small sunfish forgo achieving high growth rates and reside in safer, vegetated habitats. However, large sunfish are relatively invulnerable to predation and remain in the better foraging habitat (Werner et al. 1983*a*). Under such trade-offs, animals are predicted to live in the habitat that minimizes the ratio of mortality risk to growth rate (i.e., minimize μ/g) at each size (Werner and Gilliam 1984). Gilliam and Fraser (1987) demonstrated how a variation of this simple

Manuscript received 10 August 1998; revised 5 April 1999; accepted 27 May 1999; final version received 21 July 1999.

[1] Present address: Perry Institute for Marine Science/Caribbean Marine Research Center, 250 Tequesta Drive, Tequesta, Florida 33469 USA. E-mail: cdahlgren@cmrc.org

model (substituting foraging rate for growth rate), could be used to predict habitat shifts by stream fishes.

Ontogenetic habitat shifts are common for mobile marine species whose postlarvae settle from the pelagic environment to benthic habitats that serve as early juvenile nurseries. For example, in temperate systems, the juveniles of many species use vegetated or other complex benthic habitats as nursery areas before moving into adult habitats (e.g., Orth and von Montfrans 1987, Holbrook et al. 1990, Ross and Moser 1995, Arsenault and Himmelman 1996, Gillanders and Kingsford 1996). Several coral reef-associated fish and invertebrates also utilize off-reef habitats (e.g., seagrass, mangroves, and macroalgae) as nursery areas (review by Parrish [1989]; also Marx and Herrnkind 1985, Shulman and Ogden 1987, Eggleston 1995, and Büttner 1996), or utilize on-reef juvenile microhabitats before moving to on-reef adult habitats (Beets and Hixon 1994, Lirman 1994, Light and Jones 1997).

Despite the prevalence of ontogenetic habitat shifts by marine organisms, there is limited information on the ecological processes underlying these shifts (Schmitt and Holbrook 1985, Holbrook and Schmitt 1988, Utne et al. 1993), or whether these shifts are consistent with the predictions of simple optimization models such as the "minimize μ/g hypothesis" (Salvanes et al. 1994, Utne and Aksnes 1994). While the minimize μ/g hypothesis can explain short-term patch use by mobile animals, and is often assumed to explain ontogenetic habitat shifts, the predictions of this model have rarely been tested quantitatively for ontogenetic habitat shifts in any system (Werner and Hall 1988). Moreover, information on why organisms exhibit ontogenetic habitat shifts and the functional role of nursery habitats (e.g., prey refuges or foraging areas) is important for understanding of the dynamics of many populations. In this study, we assessed the role of nursery habitats for a coral reef fish that initially recruits off-reef, and identified how predation risk and growth rates varied as a function of fish size and habitat type. This information allowed us to test whether observed ontogenetic habitat shifts by early juvenile Nassau grouper, *Epinephelus striatus*, were consistent with predictions of the minimize μ/g hypothesis or alternative optimality models (i.e., maximize g or minimize μ).

Methods

Nassau grouper

The Nassau grouper (*Epinephelus striatus*) is a large (≤20 kg) tropical western Atlantic serranid, and it is one of the most important commercial fish in the Caribbean, Bahamas, and Gulf of Mexico (Jory and Iverson 1989, Colin 1992). Moreover, Nassau grouper are important piscivores and benthic carnivores in coral reef systems (Hixon and Beets 1993, Eggleston et al. 1997, 1998). Although adult Nassau grouper inhabit offshore reefs, late larval or early juvenile Nassau grouper (25–35 mm total length, TL) recruit in distinct, wintertime pulses (Shenker et al. 1993) to macroalgal beds (Eggleston 1995). Early juveniles live within the interstices of macroalgal clumps and macroalgal covered coral clumps, primarily *Porites porites*, (hereafter referred to as the "algal habitat") for ~2 mo postsettlement, until they reach a size of ~50 mm TL (Eggleston 1995, Dahlgren 1998). The macroalgae may provide early juveniles with a source of food (e.g., small benthic crustaceans such as amphipods and harpacticoid copepods; Grover et al. 1998), a refuge from predation, or both. At ~50 mm TL, they shift microhabitats and reside outside of and adjacent to macroalgal covered coral clumps or other structurally complex microhabitats (e.g., coral, rubble, solution holes, and sponges; hereafter referred to as "postalgal habitats") within the macroalgal beds (Eggleston 1995, Dahlgren 1998). Subsequent habitat shifts include a "late juvenile" shift from postalgal habitats to patch reefs (Eggleston 1995), followed by an eventual shift to deeper offshore reefs.

Approach

We used field caging and tethering experiments to quantify habitat-specific growth rates and mortality risk, respectively, for three different sizes of early juvenile Nassau grouper. These sizes bracketed the size at which this species undergoes an ontogenetic shift from algal to postalgal habitats. Several additional field and laboratory experiments tested experimental assumptions of diurnal and nocturnal habitat associations, and evaluated potential sampling biases or experimental artifacts associated with the caging and tethering techniques. We then used size- and habitat-specific growth rates and mortality risk in a cost–benefit analysis to test the following alternative (but not mutually exclusive) hypotheses: (1) early juveniles shift habitats in a way that maximizes growth rates (g); (2) early juveniles shift habitats in a way that minimizes mortality (predation) risk (μ); and (3) assuming tradeoffs exist between maximizing growth rate and minimizing mortality risk, early juveniles shift habitats in a way that minimizes the ratio of mortality risk to growth rate (μ/g).

Study site

All experiments were conducted in the vicinity of the Caribbean Marine Research Center (CMRC) on Lee Stocking Island, Bahamas (23°45′ N, 76°10′ W; Fig.1) during 1995, 1996, and 1998. Field experiments were conducted in tidal creeks at the north end of Great Exuma Island (Sites B3 and B4; Fig. 1). These tidal creeks serve as important settlement and early juvenile nursery habitats for Nassau grouper (Eggleston 1995). Tidal creeks were 1–4 m deep, fringed by mangroves, and contained expansive (>7 200 m^2) shallow areas dominated by macroalgae (*Laurencia* sp.). Other microhabitats within the tidal creeks included small corals

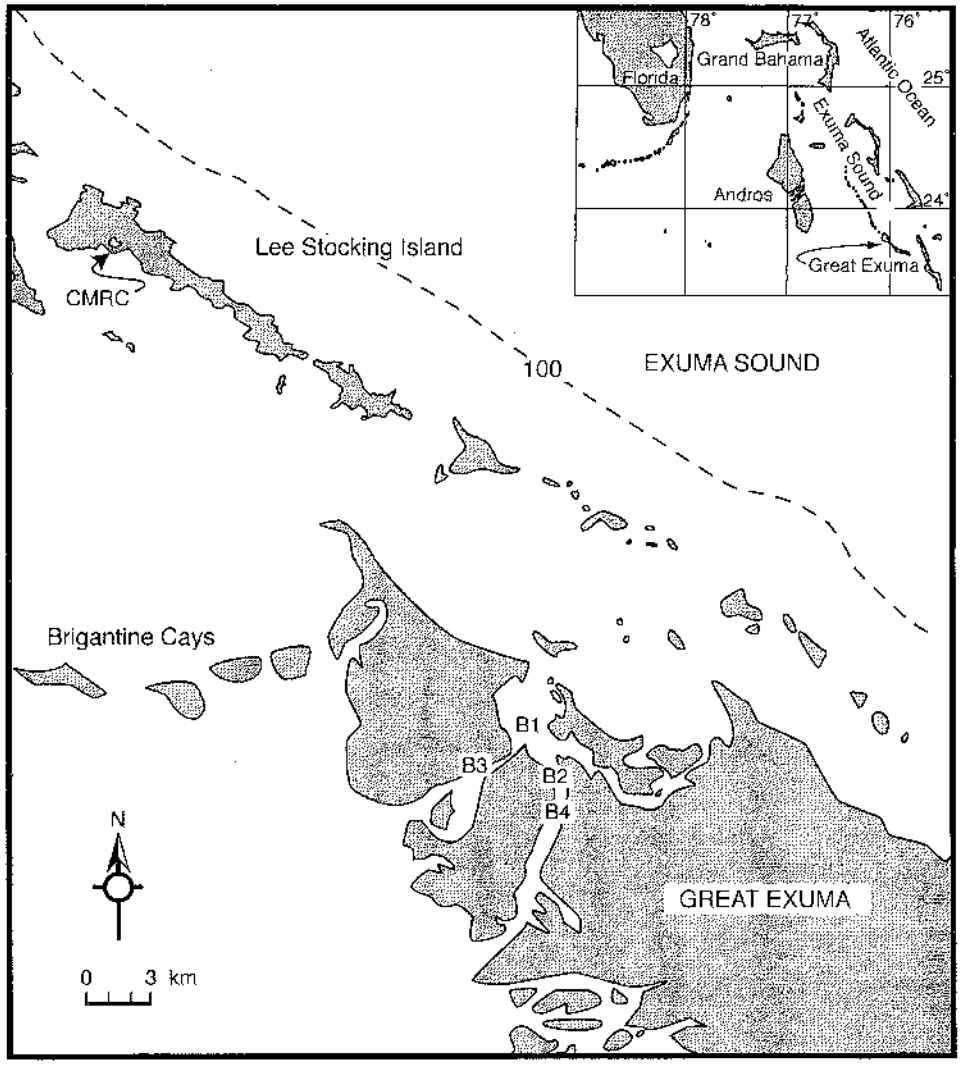

FIG. 1. Study sites B3 and B4 at Great Exuma Island near the Caribbean Marine Research Center (CMRC), Lee Stocking Island, Bahamas. Sites B1 and B2 are included as reference points to be consistent with site labeling of other studies (Eggleston 1995, Dahlgren 1998).

(mostly *Porites porites*), seagrass (*Thalassia testudinum*), sponges, rock ledges, crevices, and solution holes (Dahlgren 1998). Water temperatures at these sites ranged from 20° to 35°C during field experiments. Laboratory experiments were conducted at the CMRC in aquaria in an indoor wet laboratory facility, with controlled water temperature and photoperiod.

Ecological processes underlying habitat shifts

To determine whether early juvenile Nassau grouper shift habitats in a way that maximizes growth rates (g), minimizes mortality risk (μ), or minimizes the ratio μ/g, mortality risk and growth rates were quantified in the field for three size classes of early juveniles (small: 35–40 mm TL; medium: 50–55 mm TL; and large: 70–75 mm TL) in both algal and postalgal habitats. The small and large size classes corresponded to the size of fish found in algal and postalgal habitats, respectively, whereas the medium size class corresponded to the smallest size of fish commonly found in the postalgal habitat (Eggleston 1995, Dahlgren 1998). All field estimates of μ and g were made on juveniles from a cohort that recruited in January 1996. Experiments with each size class were conducted sequentially such that mortality risk and growth rates were estimated at the time that each size class was observed in the natural population. Thus, estimates of mortality risk, growth rate, and μ/g were compared between habitats for each size class separately.

Nocturnal vs. diurnal distribution patterns

Previous documentation of the ontogenetic habitat shift by early juvenile Nassau grouper from algal to postalgal microhabitats was based on daytime obser-

vations (Eggleston 1995, Dahlgren 1998). It was necessary to confirm that size-specific habitat use is similar during the day and night because the experimental approach by which we measured size- and habitat-specific growth rates restricted fish to living in either the algal or postalgal habitat day and night. Differing nocturnal and diurnal habitat use could bias estimates of growth rates.

Because it was impossible to observe small fish in the field at night, we quantified diurnal and nocturnal use of algal vs. postalgal habitats in laboratory aquaria. In this experiment, clumps of macroalgae (*Laurencia* sp.; 400-mL displacement volume) were rinsed under flowing seawater to remove all potential prey items, placed in the middle and against the rear wall of a 154-L aquarium, and spread to 20 cm in diameter and 15 mm high to resemble naturally occurring clumps of this volume (Eggleston 1995). Five macroalgal clumps were carefully examined to ensure that the rinsing technique removed all prey items, which was the case. Despite the fact that prey distribution may influence nocturnal habitat use, it was necessary to remove all prey from the macroalgae because it was impossible to provide fish with postalgal prey assemblages in the laboratory. Therefore, allowing prey to remain only in the algal habitat in the laboratory would have clearly confounded habitat and food supply. A single fish was added to each aquarium in the evening or morning (for day and night observations, respectively) and allowed to acclimate for 12 h before we observed habitat use. Several days prior to an experiment and during an experiment, fish were conditioned to a 12:12 light:dark photocycle and 23–24°C water temperature. Observations were made from behind a partition to avoid disturbing fish. Fish position relative to the algal clump was recorded hourly from 0800 to 1800 during daytime observations, and every hour from 2000 to 0600 during nighttime observations. Nighttime observations were made by shining a red light into each aquarium just long enough to thoroughly search the entire aquarium (<20 s) without eliciting an escape response in fish (C. Dahlgren, *personal observation*). To be consistent, daytime observations were also limited to <20 s per aquarium. If a fish was not seen during an observation, it was assumed to be in or under an algal clump. Ten separate fish were observed during the day and at night for each size class, with each size class observed sequentially under identical conditions. The frequency of observations in which fish were outside of (>5 cm away from) algae was compared between day and night for each size class separately using a loglinear G test (Sokal and Rohlf 1995).

Do size-specific habitat shifts maximize growth rate (g)?

To estimate size- and habitat-dependent growth rates of early juvenile Nassau grouper, three separate caging experiments were conducted in the field at sites B3 and B4 (Fig. 1) during the winter, spring, and summer of 1996 (for small, medium, and large size classes, respectively). The use of cages was necessary to prevent movement of juveniles between microhabitats, and exclude potential predators. Circular cages, 0.6 m radius and 0.7 m tall, consisted of a steel frame covered with 6.35-mm vexar plastic mesh on top and the sides, with the bottom left open. Each cage was secured to the substrate with steel spikes, and sealed with a nylon mesh skirt (6.35-mm mesh) that was weighted with chain to conform to substrate topography. Each cage encompassed an area (1.2 m^2) more than twice the average area used by early juveniles during daily movement (see *Results: Assessment of potential caging artifacts*). Because previous observations indicated that early juveniles did not occupy areas with <30% macroalgal cover (Eggleston 1995), cages were deployed in areas with 40–60% macroalgal cover and placed >10 m apart to ensure that replicates were independent.

One fish was randomly assigned to each cage, and each cage was randomly assigned to one of three experimental treatments: (1) an "algal" treatment, which confined a fish to foraging within the interstices of macroalgal clumps; (2) a "postalgal" treatment, which prevented fish from accessing the interstices of macroalgal clumps, but allowed fish to use postalgal microhabitats (e.g., coral, rubble, sponges, the edge of *Laurencia* clumps, and seagrass); and (3) a control, where fish had access to both algal and postalgal habitats. In algal and postalgal treatments, access to algal clumps was controlled by placing all *Laurencia* sp. found within a cage inside a large, nylon-mesh bag (6.35-mm mesh size). Each fish in the algal treatment was placed inside the bag, thereby restricting it to foraging within the macroalgae. Each fish in the postalgal treatment was placed in the large, circular cage, but was excluded from the interstices of the algal clump by the mesh bag. Clumps of macroalgae within mesh exclusion/inclusion bags covered 50% of the area enclosed by the cage in both enclosures and exclosures; therefore, algal and postalgal treatments presented fish with equal foraging areas. Control cages also contained ~50% cover of unbagged macroalgae at the start of the experiment. During each 6–7-wk experimental period, cages were checked on a weekly basis for fish escape, cleaned of silt and fouling organisms, and, if necessary, repaired. Six replicates of each treatment were deployed at each study site for a total of 36 cages (algal: $n = 6$ replicates; postalgal: $n = 6$; control: $n = 6$; × two sites) for each size class.

Fish were measured (millimeters total length) immediately before placement in cages and upon removal. Total growth over the experiment was divided by the time (in days) that each fish was caged to determine its average daily growth rate. To test whether juveniles shifted habitats in a way that maximizes growth, average daily growth rates were compared between habitats (algal and postalgal) for each size class separately

using a randomized complete block design ANOVA, with Site (site B3 vs. site B4) treated as a fixed blocking factor, and Habitat ("algal", "postalgal", and "control") as the main factor. The assumption of homogeneity of variances was confirmed for each size class using an F_{max} test (Sokal and Rohlf 1995). For each size class, differences in growth rates among specific habitats were tested using paired orthogonal contrasts to test the a priori hypotheses that (1) the mean growth rates of fish in control treatments did not differ from those in the habitat treatment in which each size class occurred naturally, but (2) both the control and preferred natural habitat had greater mean growth rates than the other habitat treatment for each size class (i.e., small fish: $g_{control} = g_{algal} > g_{postalgal}$; medium and large fish: $g_{control} = g_{postalgal} > g_{algal}$).

Assessment of potential caging artifacts

To ensure that the caging manipulation did not interact with or confound experimental treatments (sensu Peterson and Black 1994), additional analyses and experiments were conducted. Because previous studies indicated that habitat characteristics such as macroalgal cover and volume are important determinants of both fish habitat use and prey abundance (Eggleston 1995, Dahlgren 1998), both factors were quantified to ensure that they did not vary among habitat treatments during the experiment. At the end of experiments, the percent cover of macroalgae was estimated within each cage, and several randomly selected cages of each habitat treatment (n = three cages per treatment at both sites) were sampled to determine the displacement volume of macroalgae. For algal and postalgal treatments, macroalgal volume was based on the volume present in mesh inclusion/exclusion bags, whereas all of the macroalgae within control cages were suction sampled to quantify macroalgal volume (see Eggleston 1995 for suction sampling details). Displacement volume and percent cover of macroalgae were compared between habitat treatments (algal, postalgal, and control) from each site using a randomized complete block design ANOVA, with site as the fixed blocking factor. Differences among habitat treatment levels were detected with a Ryan's Q test, as recommended by Day and Quinn (1989). The assumption of homogeneity of variances was confirmed with an F_{max} test (Sokal and Rohlf 1995).

Experimental artifacts may have also resulted from the use of mesh bags for enclosures and exclusions. Since we used identical mesh sizes for both the mesh bag enclosures and exclosures within the large cages, as well as the large cages themselves, prey could pass through each equally well. Nevertheless, because confining fish in bagged macroalgae may have artificially reduced fish growth rates in the algal treatment (but not the others) by decreasing their ability to forage, foraging rates in bagged and unbagged macroalgae were compared in the laboratory. In this experiment, one liter of rinsed macroalgae (*Laurencia* sp.) was placed into each of three bags identical to those used in the field, which were then positioned in each of three 154-L aquaria. In three identical aquaria, the same volume of unbagged, rinsed macroalgae was added. Forty amphipods (*Cymadusa* sp.) were added as prey to each aquarium, 12 h prior to the release of a single Nassau grouper (43–45 mm TL) inside each bagged macroalgal clump in the experimental treatment, or next to each clump of macroalgae in the unbagged control. Amphipods were used because they are the most abundant prey item in the guts of juvenile grouper over the size range used in this study (Grover et al. 1998). The grouper were starved for 12 h prior to release, and allowed 72 h to forage. After 72 h, the grouper were removed; all algae and debris collected with hand-nets and sorted to remove all remaining prey, and the number of surviving amphipods in each aquarium was counted. The mean number of prey eaten per 72 h was compared between bagged (n = 3 aquaria) and unbagged (n = 3 aquaria) treatments using a t test.

Do size-specific habitat shifts minimize mortality risk, μ?

To test whether the habitat shift by juvenile Nassau grouper from the algal to postalgal habitat minimized mortality risk, relative predation risk was estimated for each size class of fish in each habitat. Because mortality rates in predator exclusion cages with unmanipulated macroalgae were essentially zero, predation was assumed to be the main source of mortality. Relative predation risk was estimated by tethering juvenile grouper of each size class (small, medium, and large) in both algal and postalgal habitats in the field at site B3 (Fig. 1). Fish were tethered through the lower jaw with 30 cm of 0.009-mm diameter monofilament fishing line (0.8 kg test) attached to a spike driven into the substrate. This length of tether gave the fish a 2 800-cm^2 area in which to move. Twenty grouper were randomly assigned to algal (n = 10 fish) and postalgal (n = 10 fish) treatments and tethered 10 m apart in an area where macroalgal cover ranged from 40 to 50%. Algal treatment fish were tethered within naturally occurring macroalgal clumps (*Laurencia* sp.). Postalgal treatment fish were tethered so that they could take refuge adjacent to macroalgae, or utilize a number of other postalgal microhabitats (e.g., living and dead coral, rock ledges, solution holes, and sponges), but could not use the interstices of the macroalgal clump. All tethered fish were deployed by 1000 in the morning and checked by snorkelers every 2 h to ensure that the tethers were not tangled or in danger of breaking. During each check of tethered fish, their habitat use and the presence of any potential predators or juvenile conspecifics was also recorded. The experiment was terminated 15 min after sunset (1815–1915), and the presence or absence of tethered fish was recorded. Absence of fish at the end of the experiment was assumed to result from mor-

tality due to predation (see *Results*: *Assessment of potential tethering artifacts*). Each 12-h tethering experiment was done twice within a five-day period for each size class of fish (small = 39.0 ± 3.0 mm TL; medium = 53.5 ± 2.3 mm TL; large = 73.0 ± 2.9 mm TL [means ± 1 SE]). To test the hypothesis that juvenile Nassau grouper shift habitats in a way that minimizes mortality risk, the number of fish missing at the end of the experiment was compared between algal and postalgal treatments using separate loglinear G tests for each size class (Sokal and Rohlf 1995).

Assessment of potential tethering artifacts

Despite the fact that tethering has been used effectively as a tool for examining relative predation risk of fish (Shulman 1985, McIvor and Odum 1988, Rozas and Odum 1988, Ruiz et al. 1993, Connell 1997, Curran and Able 1998), there may be "simple" or "higher order" artifacts associated with the manipulation (sensu Peterson and Black 1994). Examples of simple artifacts include any changes in health, behavior, or encounters with predators due to tethering that result in an increase or decrease in survivorship of tethered vs. untethered fish. Artifacts of higher order involve an interaction between the technique of tethering and the treatment (e.g., escape from tethers or behavioral changes due to tethering are dependent on habitat). Because tethering was used in this study as a relative estimate of size- and habitat-specific predation risk, tethering artifacts that are constant among habitat treatments (i.e., simple artifacts) do not bias results (e.g., Aronson and Heck 1995 and references therein), but should be minimized to increase the accuracy of results (Zimmer-Faust et al. 1994). Experimental techniques that interact with treatments (i.e., artifacts of higher order) confound experimental results and must be avoided (Peterson and Black 1994).

To identify simple artifacts, laboratory behavioral observations were conducted to determine how fish were affected by tethering. The first experiment noted any qualitative changes in the condition (e.g., injury, infection, or death) or behavior (e.g., failure to feed or use refuges) of 10 tethered fish compared to 10 untethered fish (30–34 mm) kept in the laboratory and observed daily for 1.5 wk. Changes in behavior due to tethering were also examined in the field by quantifying the behavior of four tethered and four untethered fish released next to haphazardly selected clumps of macroalgae. Fish were released >10 m apart to ensure statistical independence, and a stationary diver (or snorkeler depending on water depth and visibility) observed each tethered or untethered fish from a distance of >1 m. After a 10-min acclimation period divers recorded the type, time, and duration of every activity of the fish (e.g., movement into or out of macroalgal clumps or feeding) and estimated the distance moved during the activity with the assistance of a 40-cm PVC (polyvinyl chloride plastic) pipe marked with centimeter increments. Observations lasted 2.5–3.5 h in the afternoon and included evening crepuscular times when foraging activity was expected to be greatest. Observations were terminated 20–30 min after sunset, before darkness made the fish impossible to relocate. Because the type of activity of such small fish was often difficult to distinguish from >1 m away, activities that were short in duration (<20 s) and involved movement over short distances (<2 body lengths), were grouped for statistical analysis. Because observation times varied in length, mean individual movement rates were standardized to 1-h increments and compared statistically between tethered and untethered fish using a t test.

To ensure that tethered fish could not escape from or break tethers, an experiment was conducted in which seven fish were tethered in algal and seven in postalgal habitats inside caged enclosures that excluded predators. Because predators were excluded, any fish missing from tethers were assumed to have broken or pulled off of their tethers. The largest size class of fish was chosen for this experiment because they were expected to have the greatest potential for breaking or pulling off of the tethers (smaller fish were not observed to have pulled off of or broken tethers during earlier laboratory observations). Because both algal and postalgal treatments were used in this experiment, we were able to detect tethering artifacts of higher order (sensu Peterson and Black 1994) by comparing the potential for escape from tethers between algal and postalgal habitat treatments.

Do size-specific habitat shifts minimize μ/g?

Mortality risk (μ) and growth rate (g) estimates from the tethering and caging experiments were used to calculate an estimate of μ/g for each size class of fish in both the algal and postalgal habitats. For size classes in which growth rates differed significantly between sites, calculations and analysis of μ/g used habitat-specific growth rates from site B3 only because mortality risk was only quantified at that site. Habitat-specific growth rates from both sites were used to calculate and analyze μ/g for all other size classes.

The hypothesis that μ/g was minimized in the habitat in which juveniles of each size are observed in the field was tested with a one-tailed randomization test (Manly 1997). This test compared the experimentally determined difference in μ/g between algal and postalgal habitats ($\mu/g_{\text{algal}} - \mu/g_{\text{postalgal}}$) to a random distribution of $\mu/g_{\text{algal}} - \mu/g_{\text{postalgal}}$ for each size class of juvenile Nassau grouper. The random values for $\mu/g_{\text{algal}} - \mu/g_{\text{postalgal}}$ were generated using experimentally derived estimates of μ and g for each size class (pooled from both habitats) that were re-assigned to a habitat treatment (algal or postalgal) at random. Randomly assigned μ and g values were used in simulations to determine habitat-specific μ/g values, which allowed us to calculate $\mu/g_{\text{algal}} - \mu/g_{\text{postalgal}}$. The randomization procedure was repeated 5 000 times for each fish size

class to generate a random distribution of values for $\mu/g_{algal} - \mu/g_{postalgal}$. The null hypothesis, that experimentally determined values for $\mu/g_{algal} - \mu/g_{postalgal}$ were random for each size class, was tested by calculating the percentage of the random distribution that was above or below the experimentally determined $\mu/g_{algal} - \mu/g_{postalgal}$. Because μ/g was expected to be minimized in the algal habitat for the small size class ($\mu/g_{algal} < \mu/g_{postalgal}$), the experimentally determined value of $\mu/g_{algal} - \mu/g_{postalgal}$ was expected to be negative. Significance at the $\alpha = 0.05$ level was detected and the null hypothesis was rejected if 95% of the randomly generated $\mu/g_{algal} - \mu/g_{postalgal}$ values were greater than the experimentally determined difference. Because μ/g was expected to be minimized in the postalgal habitat for the medium and large fish ($\mu/g_{algal} > \mu/g_{postalgal}$), experimentally determined values of $\mu/g_{algal} - \mu/g_{postalgal}$ were expected to be positive. Therefore, significance at the $\alpha = 0.05$ level and rejection of the null hypothesis occurred if 95% of the randomly generated values were less than the experimentally determined values.

Results

Nocturnal vs. diurnal distribution patterns

Both diurnal and nocturnal habitat use in the laboratory reflected size-specific habitat use observed in the field during the day. However, small Nassau grouper (mean ± 1 SE = 30 ± 1.0 mm TL) were observed in the macroalgae even more frequently at night (99% of observations) than during the day (87% of observations) ($n = 22$ fish, $G_1 = 13.0$, $P < 0.001$). Other sizes showed no significant difference in habitat use between night and day (medium $n = 19$ fish, $G_1 = 1.76$, $P > 0.05$; large: $n = 17$ fish, $G_1 = 0.98$, $P > 0.05$). As observed in the field, residency within macroalgal clumps decreased as fish size increased (Dahlgren 1998). Medium fish (mean ± 1 SE = 57 ± 1.5 mm TL) were inside (or under) algal clumps in 63% of observations (day = 60%, night = 67%), and large fish (mean ± 1 SE = 73 ± 2.1 mm TL) were within (or under) algal clumps in 40% of observations (day = 44%, night = 36%). Because none of the fish size classes appeared to have switched habitats between day and night, experiments confining fish to algal or postalgal habitats during both day and night were realistic.

Size- and habitat-specific growth rates

Cages used to estimate growth rates were effective enclosures during trials with small and medium size classes of grouper, but strong tidal currents associated with the passage of hurricanes caused many of the cages to flip over at both sites during experiments with large fish, reducing the number of cages sampled (Fig. 2). In addition, a few small fish apparently escaped from cages, and several cages containing medium fish were flipped over or lifted off the bottom by mating nurse sharks (*Ginglymostoma cirratum*) at site B3 (Fig. 2). Despite reduced sample sizes, the statistical comparisons were still powerful enough to detect significant differences in growth rates among treatments for all size classes. Growth rates for all three sizes of fish were significantly higher in the postalgal and control habitat treatments than in the algal treatment (Table 1, Fig. 2). Growth rates differed between sites for small fish only, with growth rates significantly greater at site B3 than site B4 (mean ± 1 SE: B3 = 0.23 ± 0.01 mm/d; B4 = 0.18 ± 0.01 mm/d; Table 1; paired orthogonal contrast).

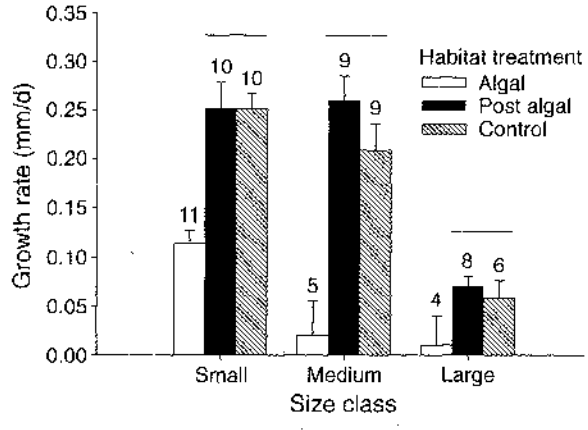

FIG. 2. Habitat-specific growth rates (mean and 1 SE) from caging experiments with small (mean = 38.4 mm TL), medium (mean = 53.7 mm TL), and large (mean = 73.1 mm TL) size classes of juvenile Nassau grouper (*Epinephelus striatus*). The number of fish sampled in each habitat is listed above each histogram bar. Histogram bars spanned by a horizontal line do not differ significantly (paired orthogonal contrasts $P > 0.05$).

Assessment of potential caging artifacts

Significant differences in growth rates among habitat treatments did not appear to be confounded by varying habitat characteristics such as algal volume or percent cover of macroalgae within cages. The percent cover of macroalgae (*Laurencia* sp.) differed among habitat treatments at the end of experiments for the small size class only (Table 1), with higher percent macroalgal cover in controls than algal and postalgal treatments (mean ± 1 SE: algal = 50.2 ± 2.2%; postalgal = 50.0 ± 2.3%; control = 60.5 ± 2.3%; Ryan's Q test, $P < 0.05$). The percent cover of macroalgae only differed between sites in experiments with the medium fish (Table 1). In this case, percent cover was higher in cages at site B3 than at site B4 (Ryan's Q, $P < 0.05$); however, both sites were within the range of naturally occurring macroalgal cover (B3 = 53 ± 3.2%; B4 = 40 ± 3.4%). The volume of macroalgae (*Laurencia* sp.) at the end of the experiments did not differ between habitat treatments for the small and medium fish (cages with large fish were not sampled due to logistical constraints), but differed between sites for both size classes (Table 1). In experiments with small and medium fish, cages at

TABLE 1. Variation in growth rates (in millimeters per day) of juvenile Nassau grouper (*Epinephelus striatus*) in the Bahamas (one-way randomized complete block design ANOVA).

Experiment	Source of variation	df	MS	F
A) Small size class				
Growth rates	Site (Block)	1	0.015	8.58**
	Habitat	2	0.067	30.55***
	Error	27	0.002	
Algal cover	Site (Block)	1	181.9	3.53 NS
	Habitat	2	365.2	7.09**
	Error	27	51.5	
Algal volume	Site (Block)	1	3.11	10.61**
	Habitat	2	0.75	2.58 NS
	Error	25	0.29	
B) Medium size-class				
Growth rates	Site (Block)	1	0.011	1.66 NS
	Habitat	2	0.103	16.02***
	Error	19	0.006	
Algal cover	Site (Block)	1	349.9	7.08*
	Habitat	2	3.6	0.07 NS
	Error	19	49.4	
Algal volume	Site (Block)	1	0.630	7.66*
	Habitat	2	0.308	3.75 NS
	Error	8	0.082	
C) Large size class				
Growth rates	Site (Block)	1	0.000	0.07 NS
	Habitat	2	0.007	4.35*
	Error	14	0.021	
Algal cover	Site (Block)	1	148.5	3.53 NS
	Habitat	2	98.4	2.34 NS
	Error	14	42.1	

Note: Listed are summary statistics for the effects of Site (blocking factor: site B3 vs. B4) and Habitat (algal, postalgal, and control) on mean daily growth rates (mm TL/d), percent cover of macroalgae at the end of an experiment, and macroalgal volume at the end of an experiment for each of three size classes of Nassau grouper (*Epinephelus striatus*). See Fig. 2 for the results of paired orthogonal contrasts between levels of treatments that were significant. NS = not significant ($P > 0.05$).

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

site B3 had a higher mean algal volume than those at site B4 (B3 = 1.47 ± 0.16 L; B4 = 0.78 ± 0.14 L; Ryan's Q test, $P < 0.05$).

Significant differences in growth rates between habitat treatments did not result from confinement artifacts, such as artificially reduced foraging rates in algae due to the mesh bag used to confine fish. Foraging rates (number of prey eaten per 72 h) of Nassau grouper confined to macroalgae by a mesh bag in the laboratory were not significantly different from foraging rates of fish allowed to forage in the macroalgae but not confined by a mesh bag ($t = -0.36$, df = 4, $P > 0.7$). Although statistical power was low (~30%), mean values were similar. After 72 h, a mean of 23.3 amphipods was eaten by grouper in the bagged macroalgae and 25.3 eaten in the natural (unbagged) macroalgae.

Size- and habitat-specific mortality rates

During the main tethering experiment, our observations of tethered fish every 2 h indicated that tethering was effective at keeping juveniles in the assigned (algal or postalgal) habitat. Fish in the postalgal treatment used a number of habitats including: the edge of *Laurencia* sp. clumps (34.0% of observations), rock ledges and holes (22.7%), live and dead coral (20.5%), sponges (11.4%), and other structured microhabitats (11.4%). Most of the fish in the postalgal treatment had access to more than one postalgal habitat type, and there was some movement between postalgal habitats during the experiment (17% of all fish in postalgal treatment). Potential predators that were observed during tethering included larger Nassau grouper (>10 mm TL; $n = 17$ fish in all observations), bar jack (*Caranx ruber*; $n = 10$ fish), schoolmaster snapper (*Lutjanus apodus*; $n = 5$ fish), lizardfish (*Synodus intermedius*; $n = 3$ fish), red hind (*Epinephelus guttatus*; $n = 2$ fish), and gray snapper (*L. griseus*; $n = 1$ fish), most of which have been identified as important predators in our macroalgal nursery system (Coba-Cetina 1995). The combined results from the two field tethering experiments for each size class of fish identified significantly lower relative predation rates in the algal than postalgal habitat for small grouper ($G_1 = 3.96$, $P < 0.05$), and no significant difference between habitats for either medium ($G_1 = 0.50$, $P > 0.05$) or large fish ($G_1 = 0.03$, $P > 0.05$; Fig. 3).

Assessment of potential tethering artifacts

Tethering did not appear to negatively affect Nassau grouper condition or behavior. During a 1.5-wk laboratory assessment of potentially adverse tethering artifacts, all fish remained tethered, and there were no deaths, infections, or injuries (e.g., broken jaws from pulling on tethers). Tethered fish (mean ± 1 SE = 33

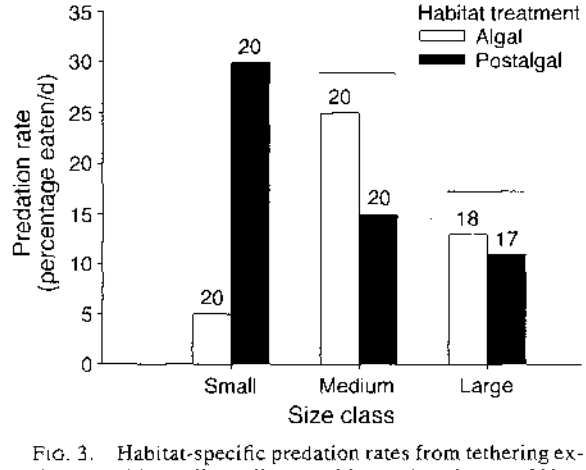

FIG. 3. Habitat-specific predation rates from tethering experiments with small, medium, and large size classes of Nassau grouper (*Epinephelus striatus*) at site B3 (see Fig. 1). Histogram bars spanned by a horizontal line do not differ significantly (loglinear G test, $P > 0.05$).

± 1.0 mm TL) also behaved similarly to untethered fish, residing in clumps of macroalgae and feeding on flake, pellet, and natural foods (amphipods).

Field observations also indicated that the behavior of tethered fish was similar to that of untethered fish. Both tethered and untethered fish (n = 8 fish for both treatments; mean ± 1 SE = 44 ± 2.5 mm TL) immediately entered macroalgal clumps when released. Common behaviors of both tethered and untethered fish included: movement within macroalgal clumps, darting out of a clump and returning immediately, and feeding inside and outside of macroalgae. Tethered fish were observed to occasionally pull on their tether, but never escaped. All of these activities were grouped together for an analysis of total movement rate (number of moves per hour), since they were all short in duration (<20 s), involved movement over short distances (<2 body lengths), and were often indistinguishable from each other. There were only two observations of an untethered grouper moving >30 cm (the length of the tether). A single individual made two moves between macroalgal clumps that were 1 m apart; the first of which appeared to be the result of an interaction with a similar sized conspecific residing within the initial macroalgal clump. There was no detectable difference between movement rates of tethered and untethered fish (t = −2.05, df = 6, P > 0.05). Although statistical power was relatively low (~30%), means were similar (tethered: 10 moves/h; untethered: 14 moves/h).

Tethering inside cages indicated that juveniles were unable to break or escape from tethers under field conditions, regardless of habitat treatment. None of the seven juveniles (mean ± 1 SE = 74.0 ± 1.6 mm TL) was missing from its tether after a 10-h period. Thus, neither simple artifacts nor those of higher order (sensu Peterson and Black 1994) were detected.

Ratio of mortality risk to growth rate (μ/g)

Because site effects were significant for the growth rate of small fish and mortality was estimated only at site B3, calculations of habitat-specific μ/g for small fish used mortality risk and growth rates from that site only. Habitat-specific μ/g for both medium and large fish was calculated using the mortality risk estimates from site B3 (the only site where mortality risk was estimated), and pooled growth rate data from sites B3 and B4, since growth rates did not vary significantly between these sites.

Habitat-specific μ/g ratios calculated from experimental data for each fish size class indicated that μ/g was lower in the algal than the postalgal habitat for small fish ($\mu/g_{algal} < \mu/g_{postalgal}$; Fig. 4) and that μ/g was lower in the postalgal than algal habitat for medium and large fish ($\mu/g_{algal} > \mu/g_{postalgal}$; Fig. 4). Results of the one-tailed randomization test on the differences between μ/g from the algal and postalgal habitats indicated that these differences were significant at $\alpha = 0.05$ for each size class (Fig. 5).

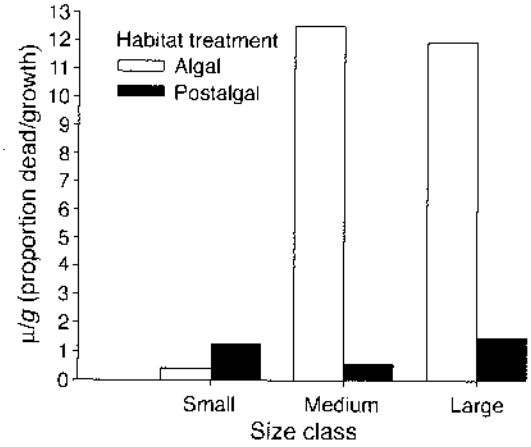

FIG. 4. Habitat-specific values of the mortality-risk/growth-rate ratio (μ/g) calculated for each size class of Nassau grouper (*Epinephelus striatus*).

DISCUSSION

Ontogenetic habitat shifts

Cost–benefit analysis of size- and habitat-specific growth rates and mortality risk indicated that when early juvenile Nassau grouper are small (35–40 mm TL), there are trade-offs between achieving a high growth rate in postalgal habitats and reducing predation risk in the algal habitat. Because small fish are typically found in the algal habitat (Eggleston 1995, Dahlgren 1998), the "maximize growth rate" hypothesis is rejected. In addition, the habitat shift by larger fish out of the interstices of macroalgae did not support the "minimize mortality risk" hypothesis, as mortality risk did not differ between habitats for medium and large fish. When habitat-specific growth rates and mortality risk were examined simultaneously for each size class of fish, the ratio of mortality risk to growth rate (μ/g) was minimized in the habitat in which juveniles of each size class were observed to reside in the field (Eggleston 1995, Dahlgren 1998). Thus, the observed ontogenetic habitat shift by early juvenile Nassau grouper supports the hypothesis that they shift habitats in a way that minimizes μ/g.

In both terrestrial and aquatic systems, a variety of taxa face trade-offs between foraging and avoiding predators. For example, Himalayan snowcocks (*Tetraogallus himalayensis*), a bird that feeds on grasses, forbs, and sedges, are more vulnerable to raptorial predators in areas where they can forage most efficiently (Bland and Temple 1990). The snowcocks respond to this trade-off by using safe but low-efficiency foraging habitats in summer, when raptors are abundant, and reverting to high-efficiency foraging habitats in the winter, when raptors are less common (Bland and Temple 1990). Small colonial web-building spiders face a similar trade-off, where living at the edge of a colony results in higher foraging success, but also

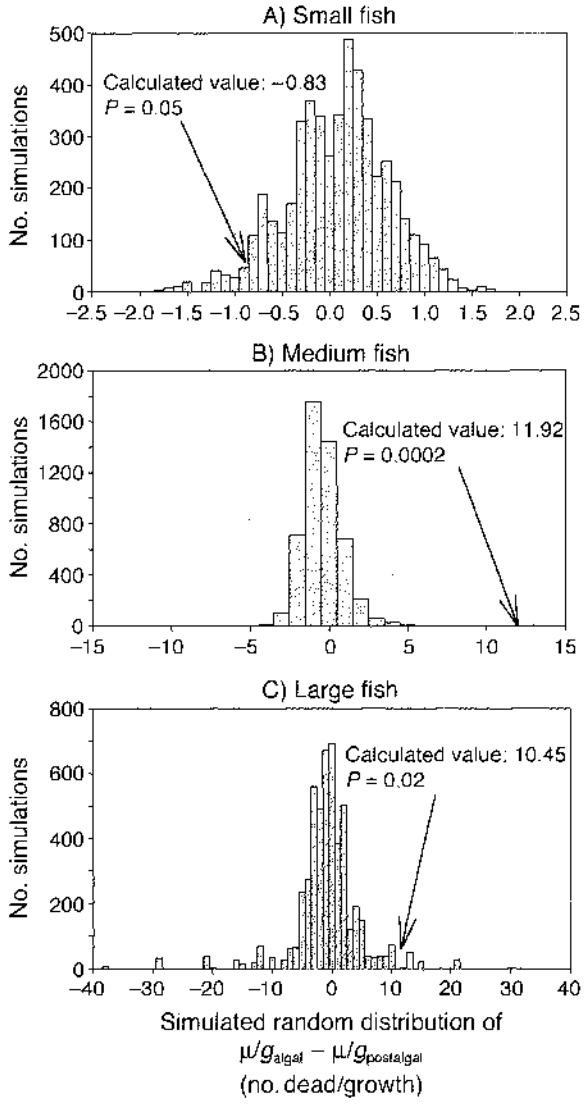

FIG. 5. Comparisons of $\mu/g_{algal} - \mu/g_{postalgal}$ calculated from field experiments with simulated random distribution of $\mu/g_{algal} - \mu/g_{postalgal}$ for three size classes (total lengths in millimeters) of early juvenile Nassau grouper: (A) small, (B) medium, and (C) large. Histograms show the number of simulations (out of 5000) producing each value of $\mu/g_{algal} - \mu/g_{postalgal}$. Arrows indicate where values of $\mu/g_{algal} - \mu/g_{postalgal}$ calculated from field experiments fall in relation to the simulated random distribution.

greater predation risk (Rayor and Uetz 1993). Changes in habitat-dependent foraging rates as spiders grow result in ontogenetic habitat shifts from the edge of the colony towards the center (Rayor and Uetz 1993). In aquatic systems, fish, amphibians, and invertebrates may also adjust foraging behavior or habitat use to account for predation risk (e.g., Skelly and Werner 1990, Diehl and Ecklov 1995, Dill and Fraser 1997). When faced with such trade-offs, short-term behavioral decisions such as discretionary patch use and ontogenetic habitat shifts often follow the predictions of the minimize μ/g hypothesis (e.g., Werner 1986, Gilliam and Fraser 1987, Werner and Hall 1988, Bowers 1990, Nonacs and Dill 1990, Skelly and Werner 1990, Utne and Aksnes 1994). Because such niche shifts in response to changing mortality risk and growth rates can result in complex individual behaviors (Fraser and Gilliam 1987, Rahel and Stein 1988, Anholt and Werner 1995), life histories (Werner and Gilliam 1984, Werner 1986, Ludwig and Rowe 1990, Ebenman 1992), population structure (Power 1984, Gilliam et al. 1993, Fraser et al. 1995), and community dynamics (Huang and Sih 1990, Turner and Mittelbach 1990, Christensen and Persson 1993), understanding the causes and consequences of these shifts is of utmost importance.

Ecological processes underlying the habitat shift

The processes underlying the observed ontogenetic habitat shift out of macroalgal clumps by juvenile Nassau grouper appear to be a decrease in predation risk in the postalgal habitat as fish grow, as well as growth rates that differ among habitats for medium and large fish (Figs. 2 and 3, Table 2). Despite significant differences in habitat-specific growth rates for small fish ($g_{postalgal} > g_{algal}$), greater differences in habitat-specific predation risk ($\mu_{postalgal} > \mu_{algal}$) cause μ/g to be lower in the algal than postalgal habitat (Table 2). Thus, fish forgo achieving a high growth rate outside of algae and take refuge within the safer macroalgal clumps. Medium and large fish have similar mortality rates in both habitats, but large differences in habitat-specific growth rates ($g_{postalgal} > g_{algal}$) cause μ/g to be lower in the postalgal than algal habitat (Table 2).

For small fish, mortality rates are probably lower within algal clumps than outside them because the

TABLE 2. Summary of size- and habitat-specific growth rates (g), mortality rates (μ), and μ/g for juvenile Nassau grouper (*Epinephelus striatus*).

Fish size	Habitat		Algal : Postalgal	Primary mechanism
	Algal	Postalgal		
Small				mortality
μ	0.05	0.30	1:6	
g	0.12	0.24	1:2	
μ/g	0.42	1.25		
Medium				growth
μ	0.25	0.15	NS	
g	0.02	0.26	1:13	
μ/g	12.50	0.58		
Large				growth
μ	0.13	0.11	NS	
g	0.01	0.07	1:7	
μ/g	11.93	1.48		

Notes: Values of μ are the proportion of dead fish per day in tethering experiments, and values of g are mean daily growth rates (mm/d) from the caging experiment. NS indicates that no significant differences were observed (i.e., algal : postalgal ratio ~1:1). The primary mechanism driving habitat use of each size class is identified.

clump's complex structure may reduce the probability that a predator will detect the fish (Mattila 1992) or reduce the efficiency of an attacking predator (e.g., Savino and Stein 1982, Anderson 1984). Although our study did not compare predation risk among fish sizes, some trends were observed. The apparent decrease in size-dependent predation risk in the postalgal habitat as fish grew may result from three factors: (1) changing predator guilds over time (although no such change was noted in observations during tethering experiments); (2) an increase in the value of postalgal habitats as a structural refuge, due to an increase in fish body size (e.g., predation rate decreases as refuges become better scaled to body size; Hixon and Beets 1989, 1993, Eggleston et al. 1990, 1997); and (3) fish may have reached a "refuge in size" (e.g., review by Sogard [1997]). These alternative explanations are not mutually exclusive, and our experiments were not designed to test them. Predation risk within the algal habitat was relatively constant; however, it appears to have initially increased as fish grew, perhaps because fish outgrew the structural refuge provided by the interstices of the clump, then decreased, possibly the result of fish reaching a refuge in size (Fig. 3). Regardless of the size-dependent mechanisms influencing habitat-specific predation risk, the low predation risk in the postalgal habitats for larger size classes contributed to the shift from the less profitable algal habitat to more profitable postalgal habitats.

The observed habitat-specific differences in growth rates may be due to reduced foraging efficiency of juvenile Nassau grouper within macroalgae, despite the common occurrence of preferred prey items within macroalgal clumps (Grover et al. 1998). If this is the case, the foraging efficiency of fish in macroalgae is expected to be dependent on size, with smaller fish better able to forage within the interstices of the macroalgae than large fish. Our results suggest that small fish have a higher growth rate in the algal habitat than large fish (Fig. 2), supporting this hypothesis. In addition, the small size class of Nassau grouper appeared to have a higher foraging rate in the algal habitat than the large size class in a laboratory study (C. Dahlgren, *unpublished data*).

Although the ontogenetic habitat shift out of macroalgae was consistent with the predictions of the minimize μ/g hypothesis, our study did not test whether the shift occurs at a fixed size or is a behavioral adaptation in which fish can estimate habitat-specific growth (or foraging) rate and mortality risk, and make decisions accordingly. Nevertheless, numerous experiments manipulating prey availability and predation risk suggest that fish and other animals are capable of assessing relative rewards and risks, and making short-term habitat choices that minimize the ratio of mortality risk to growth rate (e.g., Gilliam and Fraser 1987, Abrahams and Dill 1989, Nonacs and Dill 1990, Utne et al. 1993, Utne and Aksnes 1994). Even animals with limited perceptual capabilities, such as tube-building polychaetes, can adjust foraging and hiding behavior in response to changes in predation risk and prey availability (Dill and Fraser 1997). Other studies show that decisions on how to balance trade-offs may depend on the physiological condition (e.g., hunger), sex, or life history stage of an individual (Mangel and Clark 1986, McNamara and Houston 1986, Abrahams and Dill 1989, Fraser and Gilliam 1992, Utne and Aksnes 1994). In this study, the results of the caged control treatment, in which fish were free to live in either algal or postalgal habitats in the absence of predation, suggest that juvenile Nassau grouper may be able to adjust the size at which they shift habitats in response to changing perceived predation risk. For example, growth rates of small fish in control treatments were higher than those in the algal treatment but did not differ from those in the postalgal treatment. This pattern suggests that eliminating predation risk in control cages allowed small fish to forage in postalgal habitats. Observations made during weekly cage inspections also indicated that small fish in control treatments would reside outside of the macroalgae (C. Dahlgren, *personal observation*).

Potential consequences to populations

The response of the small size class of early juvenile Nassau grouper to trade-offs between achieving a high growth rate and living in relative safety from predation may influence population dynamics and structure in several important ways. By confining small fish to living in suboptimal foraging habitat, predation may have important sublethal effects on populations. Confinement to suboptimal foraging habitats reduced individual growth rates during this early stage in development, which may affect predator–prey and competitive interactions (Olsen et al. 1995, Olsen 1996). In addition, restricting small juveniles to the interstices of macroalgal clumps may inflate densities, particularly in areas of low algal cover or high recruitment. Under these circumstances, density-dependent processes may be important in limiting the population (Walters and Juanes 1993). Such indirect or sublethal effects of predation may be as important as direct effects in structuring populations (Lima 1998), and may interact synergistically with the direct effects of predation (Hixon and Carr 1997).

Despite the potential negative effects of confinement to macroalgae, enhanced survivorship of small fish within macroalgae suggests that it plays an important role in mediating the direct effects of predation on newly settled fish. This may be particularly important in determining population size and structure because juvenile fish may suffer high size-dependent predation (Sogard 1997). For example, many reef fish show Type III survivorship, where juveniles suffer up to 90% mortality during the first month after settlement (Shulman and Ogden 1987, Hixon 1991). Despite high size-dependent predation risk outside of macroalgae, relatively

low predation risk for small Nassau grouper living within the structural refuge provided by macroalgae may increase early juvenile survivorship. Eggleston (1995) found Nassau grouper populations in algal beds decreased by only 25% across several macroalgal nursery areas during the first month after settlement. In contrast, Nassau grouper settling into other habitats suffered higher morality rates (Beets and Hixon 1994). Nevertheless, settlement and early juvenile stages may still represent a potential population bottleneck at much larger spatial scales, since macroalgae occupies a small percentage of the shallow-water habitats in this region of the Bahamas (Lipcius et al. 1997), and only a small percentage of settlement-stage fish may be transported to these high quality juvenile habitats. Because macroalgal habitats are relatively rare, examining the role of macroalgal beds within the framework of a source–sink metapopulation model (Pulliam 1988) may greatly enhance our understanding of Nassau grouper population dynamics, and our ability to conserve this species.

ACKNOWLEDGMENTS

We thank the staff of the Caribbean Marine Research Center, particularly G. Dennis and T. Bailey, for logistical support. We are also very grateful to T. Wolcott, S. Ratchford, H. Stewart, L. Etherington, M. Sutyak, M. Huggler, D. Nadeau, L. Mullins, C. H. Dunn, and C. McKinney-Richards and numerous Earthwatch volunteers for field assistance. Field experiments benefited from constructive input from M. Hixon. S. Ellner provided advice on the use of randomization tests. The manuscript was improved through the comments of J. Gilliam, M. Posey, J. Rice, M. Hixon, and two anonymous reviewers. This research was made possible through a grant-in-aid-of-research from Sigma Xi; NOAA's National Undersea Research Program and the Perry Foundation's Caribbean Marine Research Center; the University of North Carolina at Wilmington/North Carolina State University Interinstitutional Ph.D. program; Earthwatch—The Center for Field Research; and the National Science Foundation (OCE97-34472).

LITERATURE CITED

Abrahams, M. V., and L. M. Dill. 1989. A determination of the energetic equivalence of the risk of predation. Ecology **70**:999–1007.

Anderson, O. 1984. Optimal foraging by largemouth bass in structured environments. Ecology **65**:851–861.

Anholt, B. R., and E. E. Werner. 1995. Interaction between food availability and predation mortality mediated by adaptive behavior. Ecology **76**:2230–2234.

Aronson, R. B., and K. L. Heck Jr. 1995. Tethering experiments and hypothesis testing in ecology. Marine Ecology Progress Series **121**:307–309.

Arsenault, D. J., and J. H. Himmelman. 1996. Size-related changes in vulnerability to predators and spatial refuge use by juvenile Iceland scallops *Chlamys islandica*. Marine Ecology Progress Series **140**:115–122.

Beets, J., and M. A. Hixon. 1994. Distribution, persistence, and growth of groupers (Pisces: Serranidae) on artificial and natural patch reefs in the Virgin Islands. Bulletin of Marine Science **55**:470–483.

Bland, J. D., and S. A. Temple. 1990. Effects of predation-risk on habitat use by Himalayan Snowcocks. Oecologia **82**:187–191.

Bowers, M. A. 1990. Exploitation of seed aggregates by Merriam's kangaroo rat: harvesting rates and predation risk. Ecology **71**:2334–2344.

Büttner, H. 1996. Rubble mounds of sand tilefish *Malacanthus plumieri* (Bloch 1787) and associated fishes in Colombia. Bulletin of Marine Science **58**:248–260.

Christensen, B., and Persson, L. 1993. Species-specific antipredatory behaviours: effects on prey choice in different habitats. Behavioral Ecology and Sociobiology **32**:1–9.

Coba-Cetina, L. 1995. Immigration variability and post-settlement processes of the spiny lobster, *Panulirus argus*, in the Exuma Cays, Bahamas. Thesis. Virginia Institute of Marine Science, College of William and Mary, Williamsburg, Virginia, USA.

Colin, P. L. 1992. Reproduction of the Nassau grouper, *Epinephelus striatus* (Pisces:Serranidae) and its relationship to environmental conditions. Environmental Biology of Fishes **34**:357–377.

Connell, S. D. 1997. The relationship between large predatory fish and recruitment and mortality of juvenile coral reef-fish on artificial reefs. Journal of Experimental Marine Biology and Ecology **209**:261–278.

Curran, M. C., and K. W. Able. 1998. The value of tethering fishes (winter flounder and tautog) as a tool for assessing predation rates. Marine Ecology Progress Series **163**:45–51.

Dahlgren, C. P. 1998. Population dynamics of early juvenile Nassau grouper: an integrated modeling and field study. Dissertation. North Carolina State University, Raleigh, North Carolina, USA.

Day, R. W., and G. P. Quinn. 1989. Comparisons of treatments after an analysis of variance in ecology. Ecological Monographs **59**:433–463.

Diehl, S., and P. Ecklov. 1995. Effects of piscivore-mediated habitat use on resources, diet, and growth of perch. Ecology **76**:1712–1726.

Dill, L. M., and A. H. G. Fraser. 1997. The worm re-turns: hiding behavior of a tube-dwelling marine polychaete, *Serpula vermicularis*. Behavioral Ecology **8**:186–193.

Ebenman, B. 1992. Evolution in organisms that change their niches during their life cycle. American Naturalist **139**: 990–1021.

Eggleston, D. B. 1995. Recruitment in Nassau grouper *Epinephelus striatus*: post-settlement abundance, microhabitat features, and ontogenetic habitat shifts. Marine Ecology Progress Series **124**:9–22.

Eggleston, D. B., J. J. Grover, and R. N. Lipcius. 1998. Ontogenetic diet shifts in Nassau grouper: trophic linkages and predatory impact. Bulletin of Marine Science **63**:111–126.

Eggleston, D. B., R. N. Lipcius, and J. J. Grover. 1997. Predator and shelter size effects on coral reef fish and spiny lobster prey. Marine Ecology Progress Series **149**:43–59.

Eggleston, D. B., R. N. Lipcius, D. L. Miller, and L. Coba-Cetina. 1990. Shelter scaling regulates survival of juvenile Caribbean spiny lobster *Panulirus argus*. Marine Ecology Progress Series **62**:70–88.

Fraser, D. F., and J. F. Gilliam. 1987. Feeding under predation hazard: response of the guppy and Hart's rivulus from sites with contrasting predation hazard. Behavioral Ecology and Sociobiology **21**:203–209.

Fraser, D. F., and J. F. Gilliam. 1992. Nonlethal impacts of predator invasion: facultative suppression of growth and reproduction. Ecology **73**:959–970.

Fraser, D. F., J. F. Gilliam, and T. Yip-Hoi. 1995. Predation as an agent of population fragmentation in a tropical watershed. Ecology **76**:1461–1472.

Gillanders, B. M., and M. J. Kingsford. 1996. Elements in otoliths may elucidate the contribution of estuarine recruitment to sustaining coastal reef populations of a tem-

perate reef fish. Marine Ecology Progress Series **141**:13–20.

Gilliam, J. F., and D. F. Fraser. 1987. Habitat selection under predation hazard: test of a model with foraging minnows. Ecology **68**:1856–1862.

Gilliam, J. F., D. F. Fraser, and M. Alkins-Koo. 1993. Structure of a tropical stream fish community: a role for biotic interactions. Ecology **74**:1856–1870.

Grover, J. J., D. B. Eggleston, and J. M. Shenker. 1998. Transition from pelagic to demersal phase in early-juvenile Nassau grouper, *Epinephelus striatus*: pigmentation, squamation, and ontogeny of diet. Bulletin of Marine Science **62**:97–113.

Hixon, M. A. 1991. Predation as a process structuring coral reef fish communities. Pages 475–508 *in* P. F. Sale, editor. The ecology of fishes on coral reefs. Academic Press, San Diego, California, USA.

Hixon, M. A., and J. P. Beets. 1989. Shelter characteristics and Caribbean fish assemblages: experiments with artificial reefs. Bulletin of Marine Science **44**:666–680.

Hixon, M. A., and J. P. Beets. 1993. Predation, prey refuges, and the structure of coral-reef fish assemblages. Ecological Monographs **63**:77–101.

Hixon, M. A., and M. H. Carr. 1997. Synergistic predation, density dependence and population regulation in marine fish. Science **277**:946–949.

Holbrook, S. J., M. H. Carr, R. J. Schmitt, and J. A. Coyer. 1990. Effect of giant kelp on local abundance of reef fishes: the importance of ontogenetic resource requirements. Bulletin of Marine Science **47**:104–114.

Holbrook, S. J., and R. J. Schmitt. 1988. The combined effects of predation risk and food reward on patch selection. Ecology **69**:125–134.

Huang, C., and A. Sih. 1990. Experimental studies on behaviorally mediated indirect interactions through a shared predator. Ecology **71**:1515–1522.

Jory, D. E., and E. S. Iverson. 1989. Species profiles: life histories and environmental requirements of coastal fishes and invertebrates (South Florida), black, red, and Nassau groupers. U.S. Fish and Wildlife Service, Biological Report **82**.

Light, P. R., and G. P. Jones. 1997. Habitat preference in newly settled coral trout (*Plectropomus leopardus*, Serranidae). Coral Reefs **16**:117–126.

Lima, S. L. 1998. Nonlethal effects in the ecology of predator–prey interactions. BioScience **48**:25–34.

Lima, S. L., and L. M. Dill. 1990. Behavioral decisions made under the risk of predation: a review and prospectus. Canadian Journal of Zoology **68**:619–640.

Lipcius, R. N., W. T. Stockhausen, D. B. Eggleston, L. S. Marshall, Jr., and B. Hickey. 1997. Hydrodynamic decoupling of recruitment, habitat quality and adult abundance in the Caribbean spiny lobster: source–sink dynamics? Marine and Freshwater Research **48**:63–72.

Lirman, D. 1994. Ontogenetic shifts in habitat preferences in the three-spot damselfish, *Stegastes planifrons* (Cuvier), in Roatan Island, Honduras. Journal of Experimental Marine Biology and Ecology **180**:71–81.

Lomnicki, A. 1988. Population ecology of individuals. Princeton University Press, Princeton, New Jersey, USA.

Ludwig, D., and L. Rowe. 1990. Life-history strategies for energy gain and predator avoidance under time constraints. American Naturalist **135**:686–707.

Mangel, M., and C. W. Clark. 1986. Towards a unified foraging theory. Ecology **67**:1127–1138.

Manly, B. F. J. 1997. Randomization, bootstrap and Monte Carlo methods in biology. Second edition. Chapman and Hall, London, UK.

Marx, J. M., and W. F. Herrnkind. 1985. Macroalgae (Rhodophyta: *Laurencia* spp.) as habitat for young juvenile spiny lobsters, *Panulirus argus*. Bulletin of Marine Science **36**:423–431.

Mattila, J. 1992. The effect of habitat complexity on predation efficiency of perch *Perca fluviatilis* L. and ruffe *Gymnocephalus cernuus* (L.). Journal of Experimental Marine Biology and Ecology **157**:55–67.

McIvor, C. C., and W. E. Odum. 1988. Food, predation risk, and microhabitat selection in a marsh fish assemblage. Ecology **69**:1341–1351.

McNamara, J. M., and A. I. Houston. 1986. The common currency for behavioral decisions. American Naturalist **127**:358–378.

Nonacs, P., and L. M. Dill. 1990. Mortality risk vs. food quality trade-offs in a common currency: ant patch preferences. Ecology **71**:1886–1892.

Olsen, M. H. 1996. Ontogenetic niche shifts in largemouth bass: variability and consequences for first-year growth. Ecology **77**:179–190.

Olsen, M. H., G. G. Mittelbach, and C. W. Osenberg. 1995. Competition between predator and prey: resource-based mechanisms and implications for stage-structured dynamics. Ecology **76**:1758–1771.

Orth, R. J., and J. van Montfrans. 1987. Utilization of a seagrass meadow and tidal marsh creek by blue crabs *Callinectes sapidus*. I. Seasonal and annual variations in abundance with emphasis on post-settlement juveniles. Marine Ecology Progress Series **41**:283–294.

Parrish, J. D. 1989. Fish communities of interacting shallow-water habitats in tropical oceanic regions. Marine Ecology Progress Series **58**:143–160.

Persson, L. 1990. Predicting ontogenetic niche shifts in the field: what can be gained by foraging theory. Pages 303–321 *in* R. N. Hughes, editor. Behavioral mechanisms of food selection. Springer-Verlag, Berlin, Germany.

Peterson, C. H., and R. Black. 1994. An experimentalist's challenge: when artifacts of intervention interact with treatments. Marine Ecology Progress Series **111**:289–297.

Power, M. E. 1984. Depth distribution of armored catfish: predator-induced resource avoidance? Ecology **65**:523–528.

Pulliam, H. R. 1988. Sources, sinks, and population regulation. American Naturalist **132**:652–661.

Rahel, F. J., and R. A. Stein. 1988. Complex predator–prey interactions and predator intimidation among crayfish, piscivorous fish, and small benthic fish. Oecologia **75**:94–98.

Rayor, L. S., and G. W. Uetz. 1993. Ontogenetic habitat shifts within the selfish herd: predation risk and foraging trade-offs change with age in colonial web-building spiders. Oecologia **95**:1–8.

Ross, S. W., and M. L. Moser. 1995. Life history of juvenile gag, *Mycteroperca microlepis*, in North Carolina estuaries. Bulletin of Marine Science **56**:222–237.

Rozas, L. P., and W. E. Odum. 1988. Occupation of submerged aquatic vegetation by fishes: testing the roles of food and refuge. Oecologia **77**:101–106.

Ruiz, G. M., A. H. Hines, and M. H. Posey. 1993. Shallow water as a refuge habitat for fish and crustaceans in non-vegetated estuaries: an example from Chesapeake Bay. Ecology **99**:1–16.

Salvanes, A. G. V., J. Giske, and J. T. Nordeide. 1994. Life-history approach to habitat shifts for coastal cod, *Gadus morhua* L. Aquaculture and Fisheries Management **25**:215–228.

Savino, J. F., and R. A. Stein. 1982. Predator-prey interaction between largemouth bass and bluegills as influenced by simulated submersed vegetation. Transactions of the American Fisheries Society **111**:255–266.

Schmitt, R. J., and S. J. Holbrook. 1985. Patch selection by juvenile black surfperch (Embiotocidae) under variable

risk: interactive influence of food quality and structural complexity. Journal of Experimental Marine Biology and Ecology **85**:269–285.

Shenker, J. M., E. D. Maddox, E. Wishinski, A. Pearl, S. R. Thorrold, and N. Smith. 1993. Onshore transport of settlement-stage Nassau grouper *Epinephelus striatus* and other fishes in Exuma Sound, Bahamas. Marine Ecology Progress Series **98**:31–43.

Shulman, M. J. 1985. Recruitment of coral reef fishes: effects of distribution of predators and shelter. Ecology **66**:1056–1066.

Shulman, M. J., and J. C. Ogden. 1987. What controls tropical reef fish populations: recruitment or benthic mortality? an example in the Caribbean reef fish *Haemulon flavolineatum*. Marine Ecology Progress Series **39**:233–242.

Skelly, D. K., and E. E. Werner. 1990. Behavioral and life historical responses of larval American toads to an odontonate predator. Ecology **71**:2313–2322.

Sogard, S. M. 1994. Use of suboptimal foraging habitats by fishes: consequences to growth and survival. Pages 103–131 *in* D. J. Stouder, K. L. Fresh, and R. J. Feller, editors. Theory and application in fish feeding ecology. Belle Baruch Marine Institute Series, University of South Carolina Press, Columbia, South Carolina, USA.

Sogard, S. M. 1997. Size-selective mortality in the juvenile stage of teleost fishes: a review. Bulletin of Marine Science **60**:1129–1157.

Sokal, R. R., and F. J. Rohlf. 1995. Biometry. Third Edition. Freeman, New York, New York, USA.

Stephens, D. W., and J. R. Krebs. 1986. Foraging theory. Princeton University Press, Princeton, New Jersey, USA.

Sutherland, W. J. 1996. From individual behaviour to population ecology. Oxford University Press, Oxford, UK.

Turner, A. M., and G. G. Mittelbach. 1990. Predator avoidance and community structure: interactions among piscivores, and plankton. Ecology **71**:2241–2254.

Utne, A. C. W., and D. L. Aksnes. 1994. An experimental study on the influence of feeding vs. predation risk in the habitat choice of juvenile and adult two- spotted goby *Gobiusculus flavescens* (Fabricius). Journal of Experimental Marine Biology and Ecology **179**:69–79.

Utne, A. C. W., D. L. Aksnes, and J. Giske. 1993. Food, predation risk and shelter: an experimental study on the distribution of adult two-spotted goby *Gobiusculus flavescens* (Fabricius). Journal of Experimental Marine Biology and Ecology **166**:203–216.

Walters, C. J., and F. Juanes. 1993. Recruitment limitation as a consequence of natural selection for use of restricted feeding habitats and predation risk taking by juvenile fishes. Canadian Journal of Fisheries and Aquatic Science **50**: 2058–2070.

Werner, E. E. 1986. Amphibian metamorphosis: growth rate, predation risk, and the optimal size at transformation. American Naturalist **128**:319–341.

Werner, E. E. 1988. Size, scaling, and the evolution of complex life cycles. Pages 60–81 *in* B. Ebenman and L. Persson, editors. Size-structured populations. Springer-Verlag, Berlin, Germany.

Werner, E. E., and J. F. Gilliam. 1984. The ontogenetic niche and species interactions in size-structured populations. Annual Review of Ecology and Systematics **15**:393–425.

Werner, E. E., J. F. Gilliam, D. J. Hall, and G. G. Mittelbach. 1983*a*. An experimental test of the effects of predation risk on habitat use in fish. Ecology **64**:1540–1548.

Werner, E. E., and D. J. Hall. 1988. Ontogenetic habitat shifts in bluegill: the foraging rate–predation risk trade-off. Ecology **69**:1352–1356.

Werner, E. E., G. G. Mittelbach, D. J. Hall, and J. F. Gilliam. 1983*b*. Experimental tests of optimal habitat use in fish: the role of relative habitat profitability. Ecology **64**:1525–1539.

Zimmer-Faust, R. K., D. R. Fielder, K. L. Heck Jr., L. D. Coen, and S. G. Morgan. 1994. Effects of tethering on predatory escape response by juvenile blue crabs. Marine Ecology Progress Series **111**:299–303.