

Effects of seascape context on condition, abundance, and secondary production of a coral reef fish, *Haemulon plumierii*

Lauren A. Yeager*, Christina L. Acevedo, Craig A. Layman

Marine Sciences Program, Department of Biological Sciences, Florida International University, 3000 NE 151st St., North Miami, Florida 33181, USA

ABSTRACT: Variation in seascape composition has the potential to impact habitat quality for fishes, and characteristics of the surrounding seascape have been correlated with abundance of organisms in many systems. Less studied is how seascape context may affect other aspects of habitat quality including growth, condition, or production of focal species. Juvenile white grunts *Haemulon plumierii* are known to rest on patch reefs during the day and move into seagrass habitat at night to feed, linking multiple habitats through these daily foraging migrations. We created artificial reefs across a gradient of seagrass cover and determined how juvenile white grunt condition, growth, abundance, and secondary production were related to seagrass cover within the seascape. White grunt abundance was positively correlated with the cover of seagrass within the seascape, while condition (relative condition factor, K_n) and growth rate (measured using the ratio of RNA to DNA) did not vary among reefs within different seascapes. Secondary production of white grunts was found to be highest on reefs in seascapes with more seagrass. Our results are consistent with the hypothesis that increased food resources associated with higher seagrass cover contribute to increased grunt production. Differences in habitat quality among reefs in different seascapes were manifest at the population (abundance) and ecosystem function (secondary production) levels and not at the individual level (individual growth rate or condition factor). These results highlight the importance of considering multiple levels of individual and population responses in assessments of habitat quality, and add evidence that seascape composition should be considered in spatially explicit management strategies.

KEY WORDS: Artificial reef · Fitness · *Haemulon plumierii* · Landscape · Predator-prey dynamics · RNA:DNA · Seagrass

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INTRODUCTION

Landscape ecology is a useful framework for examining the consequences of spatial heterogeneity on aspects of ecosystem structure and function (Turner 1989, 2005), and the same approaches are increasingly applied in marine systems. In marine systems, a seascape may be defined as an area of heterogeneous habitat that can be viewed at a range of spatial scales, and the seascape context of a focal patch is the position of the patch relative to surrounding seascape ele-

ments (Grober-Dunsmore et al. 2009). The surrounding seascape has the potential to influence access to resources, exposure to predators, or connectivity among habitats, and therefore can be a central driver of local habitat quality (Sheaves & Johnston 2009). Many studies have used this framework to link variation in organismal abundance and diversity in focal patches to the seascape context (Robbins & Bell 1994, Irlandi et al. 1995, Hovel & Lipcius 2001, Grabowski et al. 2005, Pittman et al. 2007b, Grober-Dunsmore et al. 2008, Yeager et al. 2011).

*Email: lyeag001@fiu.edu

While the importance of seascape context is increasingly acknowledged in the evaluation of habitat quality, few studies have evaluated the impacts of the surrounding seascape on measures of habitat value beyond structural characteristics of fish communities (i.e. beyond fish abundance and community composition). The surrounding seascape can affect access to food resources or predators, possibly resulting in differences in habitat quality of focal habitat types at an individual level (i.e. in terms of condition or growth). For example, patchiness of temperate seagrass systems has been shown to affect growth of bay scallop *Argopecten irradians* (Irlandi et al. 1995). In mangrove tidal creeks, habitat fragmentation results in decreased food availability and slower growth rates in gray snapper *Lutjanus griseus* (Rypel & Layman 2008). Animals that experience faster growth rates, or are in better condition, may experience decreased predation risk (Sogard 1997, Booth & Hixon 1999, Booth & Beretta 2004, Johnson 2008) or higher reproductive output (Hutchings 1993, Fox 1994, Slotte & Fiksen 2000, Neff & Cargnelli 2004). Therefore, understanding how the surrounding seascape affects individual-based measures of habitat quality, like condition or growth, may provide useful information regarding optimal fish habitat.

Effects of the seascape on individual-level traits and population-wide parameters can be combined to provide insight into overall ecosystem function. For example, secondary production, the accumulation of animal biomass over time, is a valuable measure of ecosystem function because it integrates density, growth, and survival into a single metric (Krebs 1994, Benke 2010). A previous study by Valentine-Rose et al. (2011) found that secondary production estimates may be the most informative variable for evaluating the effects of habitat fragmentation in tidal creek wetlands in The Bahamas. Irlandi et al. (1995) found that spatial patterning of seagrass within the seascape determined the transfer of secondary production to higher trophic levels by affecting foraging success of invertebrate predators. Secondary production integrates multiple underlying processes and provides quantitative, functional information about effects of seascape on relative habitat value.

Grunts (Haemulidae) are common coral reef fishes that may be highly dependent on the attributes of the surrounding seascape because of their feeding strategy. During the day, juveniles and adults of many species of grunts are known to shelter in structured habitats, such as patch reefs and mangroves (Starck & Davis 1966, Ogden & Ehrlich 1977, Verweij &

Nagelkerken 2007). At dusk, grunts migrate to feed into nearby soft bottom habitats, such as sand and seagrass (Starck & Davis 1966, Ogden & Ehrlich 1977, Robblee & Zieman 1984, Burke 1995, Nagelkerken et al. 2000). Through these daily foraging migrations, grunts link multiple habitat types and represent important nutrient vectors to coral reef ecosystems (Meyer & Schultz 1985). The nature of these habitat linkages may be dependent on the spatial juxtaposition of resting and foraging habitats (Nagelkerken et al. 2008). As a result, access to preferred, nocturnal foraging grounds within the seascape has the potential to affect the quality and function of focal habitats for grunts.

Our overall objective was to identify how the seascape surrounding artificial reefs affects their relative value as habitat. By using experimental patch reef units, we controlled for patch habitat size and quality, so any differences among sites were expected to be a function of aspects of the surrounding seascape. We evaluated whether the amount of seagrass within the seascape surrounding these artificial patch reefs affected various metrics of grunt habitat quality measured at the individual level (condition and growth), population level (abundance), and the ecosystem function level (secondary production). Specifically, we expected that increased cover of seagrass in the seascape surrounding artificial reefs would result in higher fish condition, faster growth rates, increased fish abundance, and increased secondary production of white grunts.

MATERIALS AND METHODS

Study area

The study was conducted in the Bight of Old Robinson, Abaco, Bahamas (Fig. 1). The Bight of Old Robinson is a semi-enclosed bay that has a complex benthic mosaic comprised of sand, seagrass, hard-bottom and patch reef habitat, as well as tidal creeks with mangrove-lined shorelines. The depth of the Bight ranges from <1 to 4 m. We used a series of 9 artificial patch reefs created in March 2009 to test the importance of seascape factors on reef fish communities (Yeager et al. 2011). Forty concrete cinder blocks were used to create each artificial reef (122 × 76 × 81 cm, length × height × depth; Fig. 1c). Benthic habitats surrounding the reefs were composed of sandy bottom and *Thalassia testudinum*-dominated seagrass beds. Artificial reefs were located at least 500 m from natural patch reefs.

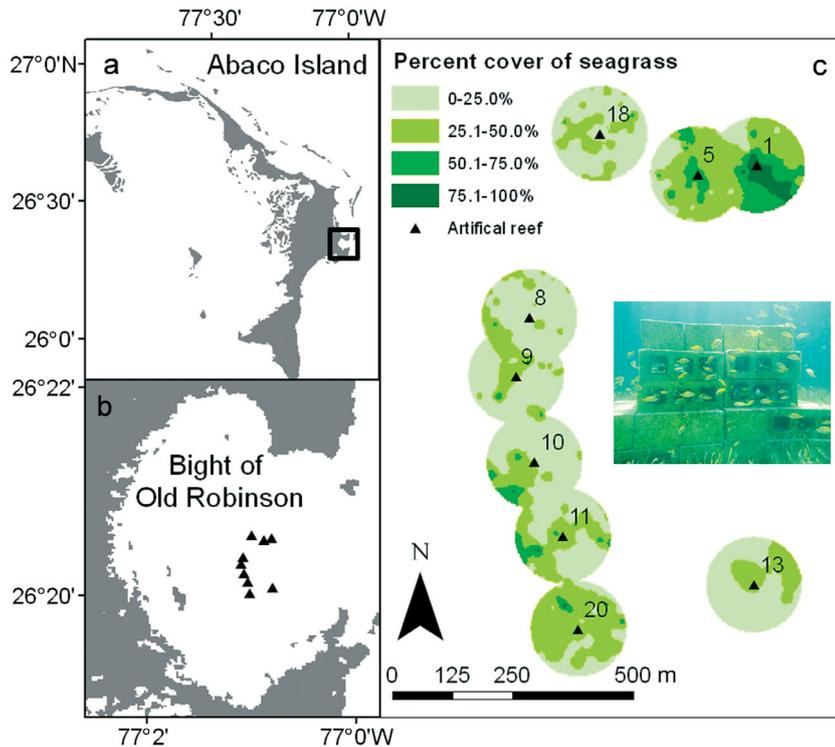


Fig. 1. (a) Study location on Abaco Island in The Bahamas. (b) Location of artificial reef sites used to test the importance of seascape factors on reef fish communities. (c) Percent cover of seagrass in the seascape surrounding each artificial reef. Inset photo shows an artificial reef with a fish assemblage dominated by white grunts

The percent cover of seagrass within the study area was mapped in August 2009. These maps were based on estimates of percent cover within 1 m² quadrats at 609 haphazardly selected points within the study area. The distribution of seagrass around the reefs was mapped using the measured percent cover of seagrass at these fixed points and interpolating these coverages to a 31 000 m² area (circle with 100 m radius) around each reef with an Inverse Distance Weighted interpolation in ArcGIS (Lirman & Cropper 2003).

Study species

In this study, we focused on white grunt *Haemulon plumieri*, one of the most important species driving differences in community structure on the experimental reefs across the seascape gradient (Yeager et al. 2011). Juvenile white grunts are known to form large, daytime, resting schools on patch reef habitats and show high site fidelity for periods of months (Ogden & Ehrlich 1977, Helfman et al. 1982, Appeldoorn et al. 1997, 2009). At dusk, individuals of these schools make nightly migrations into surrounding

soft-bottom habitat (Ogden & Ehrlich 1977, Helfman et al. 1982, Appeldoorn et al. 2009), cued by decreased light levels after sunset (McFarland et al. 1979). Once in the soft-bottom habitat, these schools begin to spread out until they become solitary individuals, which feed within a small area throughout the night (Ogden & Ehrlich 1977, Helfman et al. 1982, Robblee & Zieman 1984, Burke 1995). Juvenile white grunts may migrate up to 300 m, although many individuals may stay within 100 m of the reef if seagrass beds are in close proximity (Ogden & Ehrlich 1977, Burke 1995, Appeldoorn et al. 2009). Prior to sunrise, these schools re-aggregate and return to the same reef, where they spend the day primarily resting (Ogden & Ehrlich 1977, McFarland et al. 1979, Appeldoorn et al. 2009). White grunts feed mainly on benthic invertebrates (Randall 1967, Appeldoorn et al. 1997, 2009, Clark et al. 2009), and seagrass habitats are known to support increased densities of benthic invertebrates when compared to unvegetated bottom (Orth et al. 1984, Ansari et al. 1991, Heck et al. 1997, Nakamura & Sano 2005). Furthermore, previous studies have reported observations of white grunts feeding in seagrass habitat, as opposed to unvegetated bottom, during their nightly foraging migrations (Ogden & Zieman 1977, Appeldoorn et al. 1997).

Data collection

The cover of seagrass within the seascape was evaluated within 100 m of each artificial reef, representing the presumed core foraging area of juvenile grunts. The mean percent cover based on previous seagrass mapping was calculated in ArcGIS (ESRI 2008). Previous studies have found that congeneric species of grunts (*Haemulon flavolineatum* and *H. scirus*) respond most strongly to the seascape within 100 m of their daytime resting habitats (Kendall et al. 2003, Pittman et al. 2007a). Furthermore, differences in seagrass cover at this scale were previously found to be a better predictor of fish community structure on this artificial reef array than seagrass cover at smaller scales (4 or 50 m; Yeager et al. 2011).

In order to support the assumption that seagrass density may affect food availability for white grunts, benthic cores were used to evaluate the abundance of white grunt prey items at sites with varying seagrass densities. These sites were located in the general study area, but at least 100 m away from natural or artificial reefs to examine natural densities of invertebrates in the absence of significant predation from reef-associated predators. The percent cover of seagrass within a 1 m² quadrat was estimated for 18 sites using a modified Braun-Blanquet method (Fourqurean et al. 2001). The benthos from each quadrat was sampled using a 10 cm diameter core to collect the top 3 cm of sediment. Sediment samples were stained with Rose Bengal to aid the location of benthic organisms. In the laboratory, benthic sediment samples were sifted using 2 mm and 500 µm sieves. Sieved samples were sorted under a dissecting microscope. All organisms were identified to the lowest feasible taxonomic level and abundance was estimated.

The abundance of white grunts on artificial reefs was estimated using underwater visual census by trained observers (L.A.Y. and C.A.L.). Sizes of all fish were estimated to the nearest cm total length with the aid of a graduated dive slate. Fish communities were surveyed on 15 dates from March 2009 to April 2010 (see Yeager et al. 2011 for more details on fish surveys). We restricted all our analyses to juvenile white grunts <15 cm standard length (SL) (<19 cm total length [TL]) in an attempt to include only juveniles that had settled on the reefs, and not larger individuals that may have migrated from other habitats. Only 15 individuals, representing less than 1% of all individuals observed during the study period, were excluded using this criterion.

Measures of fish condition and growth rate were used to evaluate individual-level metrics of habitat quality. Fish condition was evaluated based on the morphometric relative condition factor (Le Cren 1951). Fish which are heavier than average for their length may be considered to be in better condition. To estimate growth rate, we used the ratio of RNA to DNA in muscle tissue. Examination of RNA:DNA to investigate growth rate is based on the premise that the amount of DNA in cells remains constant, while the amount of RNA increases with growth rate as more protein synthesis is required. This technique has been used successfully as a measure of relative growth in fishes (Buckley 1984, Folkvord et al. 1996, Garcia et al. 1998, Buckley et al. 1999) and has been shown to typically integrate growth rates over a period of weeks (Johnson et al. 2002, Piazza & La Peyre 2010).

White grunts were collected from artificial reefs using mesh wire traps with mesh sizes of 1 and 2 cm in April 2010. Traps were deployed in the benthos surrounding the artificial reefs and were allowed to soak for 2 to 14 h before being retrieved. White grunts were removed from the traps and placed into coolers of fresh ocean water with aerators before being transferred by boat to land to be processed. Fish were euthanized with an overdose of eugenol, a known fish anesthetic (following Florida International University IACUC # A3096-01, 10-013). White grunts were euthanized one at a time to ensure tissues were promptly preserved to prevent degradation of RNA. The SL of each fish was measured to the nearest mm and blotted wet weight was measured to the nearest 0.01 g. A small muscle tissue sample was removed and placed into a 1.5 ml microcentrifuge tube filled with RNAlater[®] (Introgen[™]) to prevent degradation of RNA, then kept frozen until further processing.

Fish muscle samples were processed for RNA and DNA concentrations in the laboratory at Florida International University following the protocol of Bolnick & Lau (2008), with minor modifications. White grunt muscle tissue used weighed between 2 to 8 mg and a homogenized sample of mosquitofish *Gambusia affinis* was used for the control homogenate.

Data analysis

The relationship between the cover of seagrass and the density of benthic invertebrates in core samples was examined using linear regression. Benthic invertebrate densities were fourth-root transformed prior to analysis in order to meet assumptions of normality ($p = 0.1$) and homogeneity of variance ($p = 0.2$).

Fish length and weight were used to calculate the predicted length:weight relationship for white grunts in this system. The relationship between fish length and weight was modeled with the following equation:

$$W = aL^n \quad (1)$$

where W = weight in g, L = SL of fish in mm and a and n are constants. Relative condition factor can be calculated using this empirically derived length:weight relationship as follows (Le Cren 1951):

$$K_n = \frac{W}{aL^n} \quad (2)$$

When the relative condition factor (K_n) > 1, a fish is heavier than expected based on its size (i.e. higher condition), while $K_n < 1$ indicates an individual is lighter than expected for its size (i.e. lower condition). The mean K_n was calculated for each reef. RNA:DNA was first corrected for fish length and

sample run using linear regression procedures (Sokal & Rohlf 1981); the mean of corrected RNA:DNA was then calculated for each reef.

We focused analysis of grunt abundance on artificial reefs over the time period after which fish communities had become relatively stable (i.e. fish abundance, species richness and community structure changed little over time; Yeager et al. 2011). The mean number of grunts from July 2009 to April 2010 on each reef was calculated.

Secondary production was calculated as the accumulation of new biomass over time (Benke 2010). Growth rates were estimated by following some cohorts on the artificial reefs for periods of months to obtain a mean linear growth rate (G) of 0.03 cm d^{-1} . This rate was within the range of growth rates reported for juvenile French grunts (Grol et al. 2008). A linear growth rate was used to model fish growth, as opposed to an exponential growth model such as the von Bertalanffy growth equation (von Bertalanffy 1938), as the former is more appropriate for modeling growth of juvenile fishes (Faunce & Serafy 2008). Production estimates were calculated for each individual size class (1 cm) for each survey interval using a modified version of the removal-summation method (Waters & Crawford 1973, Benke 1976). Secondary production (in g wet weight $\times t^{-1}$) was calculated as:

$$Ps_{(\Delta t)} = (\bar{B}s_{(t+1)} - \bar{B}s_{(t)}) \times \bar{N}s_{(\Delta t)} \quad (3)$$

where $Ps_{(\Delta t)}$ is the production of individuals belonging to size class s from the start to the end of time interval t . The time interval t varied based on the number of days between surveys. $\bar{B}s(t)$ represented the average biomass for an individual from size class s at the beginning of the time interval t . Biomass (B) was calculated based on the measured length:weight relationship ($\text{Log } W = 3.10 \times \text{Log } L - 4.75$; $R^2 = 0.99$). The TL of an individual from size class s at the end of the time interval t was estimated using G . $\bar{B}s_{(t+1)}$ was then calculated from the estimated TL at the end of t and the length:weight relationship based on Eq. (1). $\bar{N}s_{(\Delta t)}$ is the mean number of individuals in the size class over the time interval. We summed our secondary production estimates across all size classes between 0 and 19 cm TL (corresponding to 0 to 15 cm SL) from July 2009 to April 2010 to estimate total secondary production per reef over the study period.

The relationship between individual (condition and RNA:DNA), population (abundance) and functional (secondary production) based estimates of habitat quality and the mean percent cover of seagrass within 100 m of each reef were tested with separate linear regression models (SAS software v 9.2).

RESULTS

Percent cover of seagrass at patch habitats from which benthic cores were sampled ranged from 0 to 90%. Major taxonomic groupings of invertebrates from benthic cores included (ordered from most to least abundant): Gastropoda (33.3%), Annelida (24.7%), Ostracoda (13.6%), unidentified worms (9.3%), Bivalvia (8.0%), Copepoda (6.2%), Ophiuroidea (1.9%), and Tanaidacea (1.2%), with Decapoda, Mysidacea, and unidentified Crustacea each making up <1% of the total benthic invertebrate abundance. The abundance of benthic invertebrates ranged from 1 to 25 individuals per core (corresponding to density of 1.3 to 31.8 individuals per 100 cm^2). The density of benthic invertebrates (fourth-root transformed) was positively related to the percent cover of seagrass ($y = 1.58 + 0.0052x$, $r^2 = 0.24$, $p = 0.04$; Fig. 2).

The mean percent cover of seagrass within 100 m of the artificial reefs ranged from 16.4 to 49.3%. A total of 221 individual white grunts ranging from 4.1 to 14.9 cm SL were examined for individual-based measures of habitat quality (K_n and RNA:DNA). K_n ranged from 0.58 to 1.21 and mean \pm SE K_n ranged from 0.91 ± 0.02 to 1.07 ± 0.01 among reefs. Mean K_n was not related to the mean percent cover of seagrass within 100 m ($r^2 = 0.04$, $p = 0.6$; Fig. 3a). Corrected RNA:DNA ranged from 0.29 to 2.76 among individuals and mean RNA:DNA ranged from 1.12 ± 0.11 to 1.44 ± 0.06 among reefs. Like K_n , mean RNA:DNA was not related to the mean percent cover of seagrass within 100 m ($r^2 = 0.06$, $p = 0.5$; Fig. 3b).

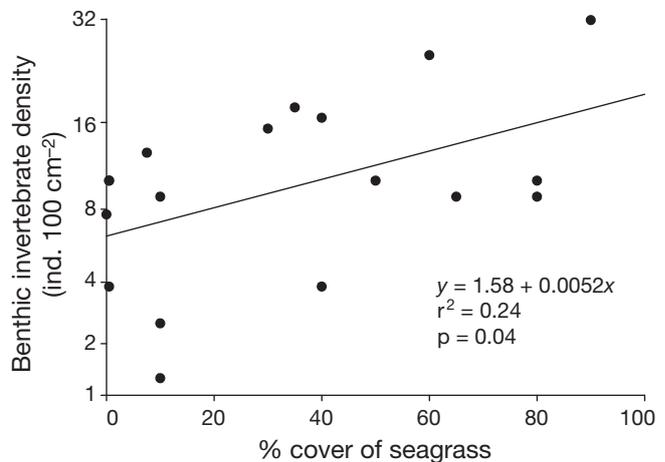


Fig. 2. Density of benthic invertebrates in benthic cores versus the percent cover of seagrass, sampled in 1 m^2 quadrats ($n = 18$). Note that the density of benthic invertebrates is plotted on a fourth-root scale, but the y-axis labels show untransformed densities

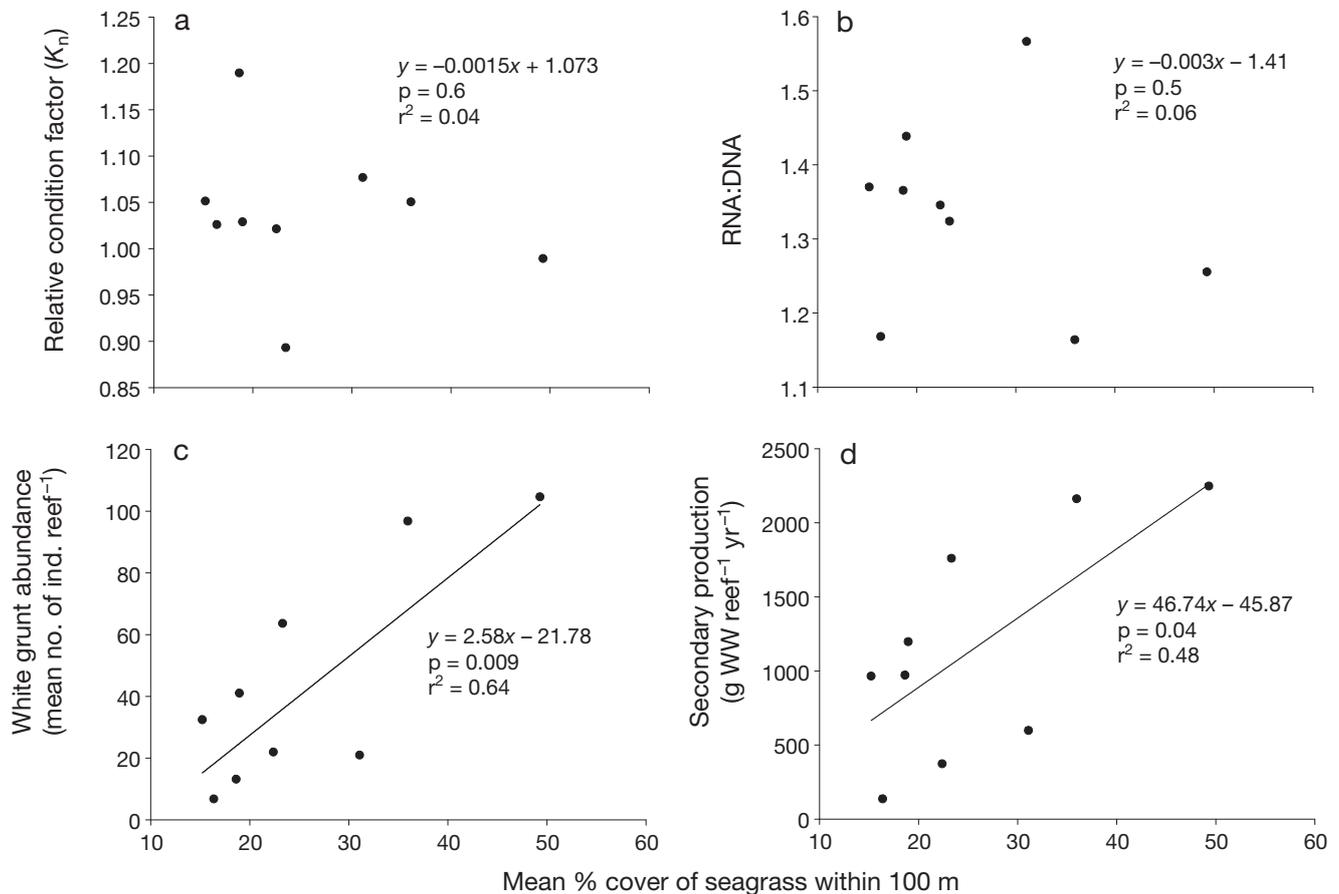


Fig. 3. Relationship between the mean percent cover of seagrass within the seascape and (a) mean relative condition factor (K_n), (b) mean RNA:DNA, (c) abundance, and (d) secondary production of white grunts. A trend line is shown for the relationships where $p < 0.05$

The mean number of white grunts per reef from July 2009 to April 2010 ranged from 6.7 ± 1.1 to 104.6 ± 27.6 individuals per reef. The mean number of grunts per reef was positively related to the mean percent cover of seagrass within 100 m ($r^2 = 0.64$, $p = 0.007$; Fig. 3c). White grunt secondary production ranged from 135 to 2246 g wet weight per reef yr⁻¹. Secondary production was positively related to the mean percent cover of seagrass within 100 m ($r^2 = 0.48$, $p = 0.04$; Fig. 3d).

DISCUSSION

Our experiment, employing a set of artificial reefs, provided evidence that seascape context affects aspects of habitat quality and ecosystem function. However, seascape effects on habitat quality for white grunts appeared to be limited to population level and functional responses; increased cover of seagrass within the seascape resulted in higher

abundance of white grunts on reefs and increased secondary production. We did not find any relationship between seascape context and individual-based traits. Combining measures of individual fitness with population and functional measures may reveal a more complex view of the relationship between organisms and the seascape.

Increased cover of seagrass within the seascape likely provides grunts with higher quality foraging habitat by increasing prey availability. While we did not map prey availability around the reefs explicitly, our benthic core sampling results support the hypothesis that seagrass represents higher quality foraging habitat, as densities of benthic invertebrates increased with seagrass cover. White grunts have been reported in previous studies to feed preferentially in seagrass at night, as opposed to on sandy bottoms (Ogden & Zieman 1977, Appeldoorn et al. 1997); this behavior is likely a response to increased resource availability. Additionally, seagrass may provide increased shelter from predators compared to sandy

bottom, reducing the risk of predation to grunts during their foraging bouts. Increased prey availability and structural complexity likely explain the positive effects of seagrass availability within the seascape on white grunt habitat quality.

While there was no clear relationship between seascape context and individual-based measures of habitat quality, more grunts were found on artificial reefs in seascapes with higher seagrass cover. This pattern could be explained in part by an ideal free distribution model, where individuals distribute themselves proportionally to the suitability (e.g. resource availability) of various habitat patches (Fretwell & Lucas 1970). Under this scenario, all habitat patches are similar in terms of suitability at the individual level because the ratio of consumers to resources is similar across patches. In this study, reefs with more seagrass in the seascape likely represent the most suitable foraging habitat, mediated in at least part through increased availability of grunt prey items, causing more grunts to utilize those reefs in close proximity to preferred foraging areas. However, increased abundance of grunts on reefs with more seagrass may have led to greater competition for prey, making per capita resource availability similar across reefs. As a result, reefs in different seascape contexts may represent similar habitat quality at an individual level; this would explain why the benefit of increased resource availability associated with higher seagrass seascapes was manifest only at the population level in our study.

These population-level differences in abundance led to increased secondary production on reefs within seascapes with more seagrass. Because growth rates were assumed to be similar among reefs, differences in secondary production were driven by differences in fish abundance and size structure over time, as opposed to differences in growth rates. If our assumption of similar growth rates was not reasonable, this could have affected trends in secondary production. However, we did not find a trend between our proxy for growth (RNA:DNA) and seascape context. Furthermore, it has been suggested that differences in secondary production among sites is likely driven by fish abundance and size structure when these metrics vary greatly among sites, as opposed to small differences in growth (Rypel & Layman 2008, Valentine-Rose & Layman 2011, Valentine-Rose et al. 2011). Increased fish secondary production on reefs with more seagrass within the seascape probably translates to an increased contribution to the adult population. Similarly, because juvenile grunts are important prey for many top predators (Randall 1967), increased production of grunts will likely result in increased transfer of

secondary production to higher trophic levels. For these reasons, secondary production may be a useful tool to evaluate effects of seascape context on habitat quality.

While artificial reefs have been found to be good experimental representations of natural patch reef habitats (Alevizon et al. 1985, Hixon & Beets 1989, 1993, Yeager et al. 2011), there are a few limitations that should be considered when applying the results of this study to natural systems. First, reefs in this study were relatively small compared to many natural patch reefs. The additional structure provided by larger reefs would likely support more individuals, potentially resulting in increased interspecific competition for resources. Also, the close proximity of some reefs may lead to overlap in nighttime foraging areas, although the mean overlap was only 14% (range 0 to 29%) in a seascape area of 31 000 m². Furthermore, in this study, individual-based measures of habitat quality (condition and RNA:DNA) were assessed only once, providing a snapshot of these metrics. This single sampling event was necessary to avoid affecting grunt assemblages during the course of the study.

How these measures vary temporally is unknown. Additionally, while not our objective, it was not possible to definitively differentiate between 'new' secondary production of white grunts versus attraction of fish from surrounding habitat. However, we observed continual recruitment of the fish to these reefs, as early juveniles (1 to 2 cm in size), and the artificial reefs were relatively isolated from natural, structured habitats (at least 500 m away from the nearest natural reef) from which larger grunts could have moved. Moreover, a previous study found that juvenile grunts are not recruitment limited and availability of post-settlement, structured habitat appears to control population sizes (Shulman & Ogden 1987). These factors support the notion that secondary production of juvenile white grunts associated with these artificial reefs likely represents new production.

Results of our study highlight the importance of considering higher order response variables when attempting to evaluate habitat quality. Data needed to evaluate the importance of nursery areas for marine species are typically divided into hierarchical levels: (1) presence/absence, (2) density, (3) growth or predation risk, and (4) production (Able et al. 1999, Beck et al. 2001, Dahlgren et al. 2006). Examinations of habitat quality based on individual traits in isolation may lead to inaccurate estimates of habitat value, if density dependence, selective mortality and connectivity are not considered (Searcy et al. 2007).

Higher order estimates of habitat quality, such as production, are often considered to be the most rigorous estimators and integrate across other metrics (Searcy et al. 2007, Faunce & Serafy 2008, Valentine-Rose et al. 2011). In this study, had we chosen to focus on metrics of growth and condition alone, we would have failed to detect differences in habitat quality. Incorporation of abundance and secondary production provided for a more complete view of habitat quality for white grunt populations.

Integrating habitat variables across ecologically relevant scales is critical for effective conservation and management programs (Mumby 2006, Sheaves 2009, Edwards et al. 2010). Incorporating various individual- and population-based measures of habitat value is crucial for advancing our understanding of the importance of seascape characteristics in determining the suitability of focal habitat types for populations of marine organisms. Populations of fisheries species, such as white grunts, may suffer multiple threats, including loss/alteration of habitat and overfishing. The results of this study support the notion that even relatively minor changes in the surrounding seascape have the potential to affect ecosystems function (i.e. secondary production). Since reefs with more seagrass in the surrounding seascape support greater production of white grunts, a loss of seagrass cover could result in overall declines in production in such systems.

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