

## HABITAT FRAGMENTATION DECREASES FISH SECONDARY PRODUCTION IN BAHAMIAN TIDAL CREEKS

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### ABSTRACT

We provide an example of how fish secondary production can be used to assess effects of anthropogenic stress on ecosystem function. Specifically, we demonstrate that fragmentation of hydrologic connectivity in small tidal creeks on Andros Island, Bahamas, decreases secondary production by as much as an order of magnitude for five economically important fish species: gray snapper (*Lutjanus griseus* Linnaeus, 1758), schoolmaster snapper (*Lutjanus apodus* (Walbaum, 1792)), cubera snapper (*Lutjanus apodus cyanopterus* (Cuvier, 1828)), blue striped grunt (*Haemulon sciurus* (Shaw, 1803)), and sailor's choice (*Haemulon parra* (Desmarest, 1823)). We conducted more than 800 individual quadrat surveys, in eight creeks that varied in degree of habitat fragmentation, to estimate total biomass for the focal species. Biomass values were multiplied by in situ or published growth rates to calculate annual secondary production. Differences in estimates of secondary production among creeks were attributable to fewer species, fewer individuals, and smaller individuals in fragmented creeks. Secondary production estimates are a useful way to measure responses of ecosystem function to anthropogenic stress because they are a composite value that incorporates many important aspects of ecosystem function.

Habitat degradation and alteration is a fundamental cause of global declines in biodiversity and loss of critical ecosystem services (Naeem et al., 1994; Heywood and Watson, 1995; Chapin et al., 1997, 1998; Vitousek et al., 1997; Tilman, 1999). Habitat fragmentation, or the sub-division of natural ecosystems (Saunders et al., 1991; Fahrig, 2002, 2003), is one of the most common forms of habitat alteration. In aquatic systems, fragmentation of hydrologic connectivity, i.e., blocking water-mediated transfer of matter, energy, or organisms within or between elements of the hydrologic cycle (Pringle, 2001, 2003a,b), is one of the most common anthropogenic impacts (Holmquist et al., 1998; Benstead et al., 1999; March et al., 2003).

In estuarine ecosystems, habitat fragmentation is wide-spread and particularly damaging to ecological integrity of the systems (Ray, 2005). Tidal flow is a primary physical driver in estuaries, and restricting tidal flow alters physicochemical parameters as well as floral and faunal community structure (Roman et al., 1984; Warren et al., 2002). While there are many studies on effects of fragmentation in rivers (Forman and Alexander, 1998; Trombulak and Frissell, 1999; Pringle, 2003b; Taylor et al., 2006) and in temperate estuaries (Burdick et al., 1997; Eertman et al., 2002; Roman et al., 2002; Tanner et al., 2002; Raposa and Roman, 2003; Ray, 2005), there has been little research in tropical systems (but see Holmquist et al., 1998; Benstead et al., 1999; March et al., 2003; Layman et al., 2004b). Layman et al. (2004b) reported that > 80% of mangrove-lined tidal creek ecosystems on the east coast of Andros Island (the largest island in the Bahamas archipelago) were fragmented to some degree, causing substantial shifts in fish assemblage structure. Whereas this and other studies conducted in tropical coastal systems have documented aspects of altered community structure following fragmentation, effects on composite measures of ecosystem *function* (i.e., ecosystem processes) remain poorly understood (but see Mallin and Lewitus, 2004).

Secondary production, the accumulation of animal biomass over time, is one composite measure of ecosystem function (Benke, 1993). Secondary production is an ideal measure in assessing the nursery function of coastal ecosystems, i.e., ability to support large densities of juvenile marine biota and export these biota to offshore habitats, as it is a comprehensive measure of biomass, growth, and survival of organisms—three of the four core criteria for a nursery area (Beck et al., 2001; Dahlgren et al., 2006). Secondary production estimates recently have been used to assess the functional value of putative nursery habitats, e.g., oyster reefs (Peterson et al., 2003), artificial patch reefs (Powers et al., 2003), seagrass (Edgar and Shaw, 1995c; McCay and Rowe, 2003), and salt marshes (McCay and Rowe, 2003). For example, Peterson et al. (2003) used secondary production to show that oyster reef restoration could increase fish biomass values by as much as  $5 \text{ g m}^{-2} \text{ y}^{-1}$  over 30 yrs. In similar fashion, secondary production studies may be an excellent way to quantify effects of estuarine habitat fragmentation, as fragmentation may result in decreased organism abundance and size (Valentine-Rose et al., in press), two core components of production. In the present study, we describe differences in secondary production between unfragmented and fragmented tidal creeks on Andros Island, Bahamas. We discuss underlying reasons why fragmentation affected secondary production of these systems, and how these data can be used to attribute monetary value to a specific ecosystem service provided by these creek systems. This is the first attempt to estimate secondary production for fishes in mangrove habitat (Faunce and Serafy, 2006).

## METHODS

**SITE DESCRIPTION.**—Secondary production estimates were calculated for eight tidal creeks located on the eastern shore of Andros Island, Bahamas. Tidal amplitude in these creeks is ~1 m, with water depths at high tide flooding extensive, shallow intertidal flats. At low tide, water is restricted to the main creek channels providing permanent habitat for fishes (i.e., fishes remain in the main creek channels even on the lowest tides). As an example, inundated area of two surveyed tidal creeks (Somerset and Bowen) at mean high tide level were 270.32 ha and 82.77 ha, while main channel areas inundated at the mean low tide level were 1.60 ha and 0.24 ha, respectively. Main channel areas may contain multiple habitat types (e.g., mangrove, rock, seagrass, or sand), and vary substantially in microtopography among systems. Intertidal flats typically have a sandy substrate with interspersed dwarf red (*Rhizophora mangle* Linnaeus), black (*Avicennia germinans* Linnaeus), white (*Laguncularia racemosa* (Linnaeus) Gaertn. f.), and buttonwood (*Conocarpus erectus* Linnaeus) mangroves.

In the Bahamas, estuary fragmentation frequently results from construction of roads lacking flow conveyance structures (e.g., bridge or culverts) across some portion of the system, which decreases habitat quality and alters floral and faunal assemblage structure (Layman et al., 2004b, Valentine-Rose et al. in press). Following Dynesius and Nilsson (1994), we have identified four categories of estuary fragmentation, ranging from unfragmented systems with uninterrupted tidal flow to totally fragmented systems in which no tidal flow occurs (Layman et al., 2004b). Degree of fragmentation of hydrologic connectivity in creeks was defined a priori (following Layman et al., 2004b) as unfragmented (U), minimally fragmented (MF), partially fragmented (PF), or completely fragmented (CF). For the purposes of this study, in MF, PF, and CF systems, “upstream” refers to areas with restricted tidal flow, while “downstream” refers to areas on the ocean side of the road or causeway. Creek main-channel area, maximum channel depth at low tide, habitat area at low tide, and degree of fragmentation for each surveyed system are provided in Table 1.

**GENERAL SURVEY METHODOLOGY.**—Secondary production estimates were derived from quantitative measures of density, biomass, and in situ or published growth rates for five ec-

Table 1. Summary characteristics of surveyed tidal creeks. U = unfragmented, PF = partially fragmented, CF = completely fragmented (sensu Layman et al., 2004b). D = downstream areas of fragmented tidal creeks and Up = upstream areas of fragmented tidal creeks.

Creek	Degree of fragmentation	Main channel area (m <sup>2</sup> )	Max. channel depth at low tide (m)	Proportion of total creek habitat area			
				Rock	Mangrove	Sand/Silt	Seagrass
White Bight	U	1,008	1	0.59	0.18	0.23	0.01
Somerset	U	16,245	0.5	0.10	0.14	0.03	0.74
Buryin Peace	U	1,810	0.5	0.60	0.25	0.06	0.10
Love Hill	PF-D	8,350	3	0.38	0.20	0.33	0.09
	PF-Up	831	0.5	0.45	0.18	0.36	0.01
Davis	PF-D	10,020	0.5	0.04	0.10	0.84	0.02
	PF-Up	384	0.5	0	0.54	0.46	0
Man o War	PF-D	11,718	0.25	0.39	0.02	0.59	0
	PF-Up	1,650	0.25	0.04	0.10	0.87	0
Conch Sound	PF-D	1,415	0.05	0.68	0.11	0.21	0
	PF-Up	150	0.25	0.33	0.67	0	0
Bowen	CF-D	2,439	2	0.30	0.33	0.10	0.27
	CF-Up	n/a	0.1	n/a	0	n/a	0

onomically important fish species (gray snapper: *Lutjanus griseus* Linnaeus, 1758; schoolmaster snapper: *Lutjanus apodus* (Walbaum, 1792); cubera snapper: *Lutjanus cyanopterus* (Cuvier, 1828); blue striped grunt: *Haemulon sciurus* (Shaw, 1803); sailor's choice: *Haemulon parra* (Desmarest, 1823)). Density and biomass (based on length-weight regressions) of these species were estimated in 1 m<sup>2</sup> sample plots using underwater visual census (UVC) with mask and snorkel (Brock, 1954; Layman et al., 2004b). Surveys at high tide in creeks are extremely difficult because of the spatial extent of inundated intertidal areas and dispersal of fish throughout these shallow-water areas. Thus, surveys were taken within 2 hrs of low tide, which facilitated estimating fish biomass because focal fish species were constricted to the main channel. While this resulted in superficially high per unit area (m<sup>-2</sup>) estimates in all creeks, extrapolated values of whole-creek production (see below) are more robust than high tide estimates because surveys were conducted when fish biomass was easiest to quantify. Secondary production estimates were based upon UVC samples collected in May 2005. Because secondary production is calculated on an annual time scale, a single-month survey of different size-classes and abundance is often combined with size-specific growth rates to calculate annual production (Huryn, 1996, 1998; Peterson et al., 2003; Powers et al., 2003).

We estimated fish density (N) using 1 m<sup>2</sup> visualized quadrats (i.e., we visually estimated the 1 m × 1 m sample area without actually deploying a quadrat prior to observing fish). We used quadrats instead of belt transects (e.g., Schmitt and Sullivan, 1996; Gust et al., 2001; Thompson and Mapstone, 2002; Mumby et al., 2004) because of specific underlying aspects of the tidal creek habitat template. Creeks included in this study are relatively small and, in most cases, it was not possible to lay out transects > 5 m in length within a single habitat type. Further, both quadrat and transect methods may bias fish density estimates because of induced behavioral responses of the target species by overestimating curious individuals that approach a diver, or underestimating shy individuals that move into refugia (Kulbicki, 1998; Sneddon, 2003). However, since study creeks had relatively shallow low tide water depths (Table 1), swimming along transect lines likely would have induced more behavioral responses in fishes than use of the quadrat method (due to increased disturbance of benthic habitat during continual swimming). Both techniques result in an underestimation of all fishes that utilize creek habitats, as some transient individuals may not remain in the main channel at low tide and only move into creeks at high tide to feed. However, based on observation of hundreds of

individually tagged juvenile snapper (J. E. Allgeier, University of Georgia, unpubl. data) and hundreds of hours of UVC (Layman et al., 2004b, L. Valentine-Rose, University of Alabama, unpubl. data), it is apparent that the overwhelming majority of individuals of the focal species are tidal creek residents, i.e., do not move out of creek systems over a period of days to weeks (although they may undergo ontogenetic habitat shifts out of creeks as adults). Additionally, use of quadrats allowed for extensive within-site replication and a more precise estimate of mean fish densities within habitat types. Although any survey methodology will likely result in biased fish density estimates, we employed a standardized survey protocol among all sites, which allowed for robust among-system comparisons.

**DENSITY ESTIMATION.**—Since fish densities vary significantly among habitat types (Blaber et al., 1989; Sheaves, 1992; Mateo and Tobias, 2001; Eggleston et al., 2004), we conducted surveys separately in each habitat type in each creek (see Table 1). Quadrat areas were visually estimated one minute prior to obtaining densities and lengths because use of actual quadrats resulted in fish behavioral avoidance of the quadrat area. To scale production values for an entire creek, we calculated the total extent of each of four main habitat types (rock, mangrove, sand/silt, and seagrass) in the creek channel. We then divided each habitat into 25 equal sections, and in each sub-section we randomly selected a 1 m<sup>2</sup> area for the UVC. At survey time, one author (L.V.-R.) approached the pre-determined quadrat area within ~2 m, waited 1 min for fish to acclimate, and then noted the density (N) and length (L) of each of the focal species. For fragmented tidal creeks, this protocol was conducted in each habitat type both upstream and downstream of the road blockage.

**AGE CLASS AND BIOMASS ESTIMATION.**—Age class distributions for each species were estimated by running published or in situ derived Von Bertalanffy growth rate parameters (Table 2) in reverse from known lengths estimated in the field:

$$Age = -\ln(L_{\infty} - L_{age})/k + t_0$$

where  $L_{age}$  = field estimated lengths,  $L_{\infty}$  = asymptotic maximum length,  $t_0$  = age at zero length, and  $k$  = Brody growth coefficient. When multiple growth rates were available for a species, growth rates from similar habitats and environmental conditions were averaged and used to calculate age classes. Error in production estimates may have resulted from using the same growth rates for both fragmented and unfragmented tidal creeks for three of the focal species (Table 2). However, since growth rates are likely slower in fragmented creeks due to stressful conditions (see Discussion), differences in secondary production estimates presented here are conservative (i.e., we likely underestimated production differences between fragmented and unfragmented creeks).

To calculate overall fish biomass, length/weight (L/W) regressions for each species were derived based on individuals ranging over the entire size distribution in creeks for that species. Individuals were collected by seining or hook-and-line from each tidal creek in May 2004 (1 yr prior to survey period). Standard length was measured in the lab with calipers to the nearest 0.1 mm, and wet weight was measured with an electronic scale to the nearest 0.01 g. L/W regressions were derived from this data (Table 3) based on the following formula:

$$\log W = \log a + b \log L$$

with lengths in millimeters, weights in grams, and species-specific constants  $a$  and  $b$ .

Age class biomass ( $B$ ) was calculated by multiplying the  $N$  of each age class by the weights calculated from the L/W regression, and total  $B$  was found by summing age class  $B$  estimates. Biomass m<sup>-2</sup> estimates were calculated for each habitat in each creek to (1) compare fish distributions across habitats within and among creeks, and (2) for secondary production estimates (see below). While L/W relationships may be affected by fragmentation (i.e., individuals of equal length may be different weights in different creeks), using the same regressions for

Table 2. Parameters and sources given for the Von Bertalanfy (VB) growth equation  $L_{age+1} = L_{\infty} (1 - e^{-k(t-t_0)})$  where  $L_{age}$  = field estimated lengths,  $L_{\infty}$  = asymptotic maximum length,  $t_0$  = age at zero length, and  $k$  = Brody growth coefficient with all lengths  $L$  representing standard length (SL) in millimeters. Size range (min-max) given for fish collected in situ are all within size ranges used for published VB equations. Temperatures given for published VB equations used ( $^{\circ}\text{C}$ ), while for those experienced in situ during the sampling month were 33–35  $^{\circ}\text{C}$  in upstream areas of fragmented creeks and 25–30  $^{\circ}\text{C}$  in downstream areas of all creeks. Growth rates for schoolmaster in unfragmented tidal creeks fit a linear model, with the equation  $y = 24.711x + 50.826$ , where  $y$  is standard length in millimeters, and  $x$  is age in years (A. Rypel, University of Alabama, unpubl. data).

Species	$L_{\infty}$	$k$	$t_0$	$^{\circ}\text{C}$	Source
Gray snapper					
UF	947	.036	-2.5		in situ
FD	238	.303	.14		in situ
FU	191	.352	.1		in situ
Schoolmaster					
FD-U	416	.061	-1.9		in situ
Cubera snapper	877	.125		27.2	Valle et al., 1997
Blue striped grunt	305	.22	-1.4	27.2	Valle et al., 1997
	334	.3	0	27.2	Appeldoorn, 1992
Sailors choice	349	.24	-2.7	27.2	Valle et al., 1997

each creek again likely resulted in conservative estimates of differences between fragmented and unfragmented tidal creeks.

SECONDARY PRODUCTION CALCULATION.—For each species, annual secondary production ( $P$ ) was calculated in each habitat for each age class by subtracting field B estimates from B estimates predicted for each individual one year later by Von Bertalanfy growth parameters:

$$L_{age+1} = L_{\infty} (1 - e^{-k(t-t_0)}).$$

In other words,  $P = B_{age+1} - B_{age\ field}$ . Mean  $P\ \text{m}^{-2}$  was calculated for each habitat, and then each habitat was weighted by the proportion of that habitat type in the survey area (Table 1). Weighted habitat  $P\ \text{m}^{-2}$  values were then summed, giving total creek  $P\ \text{m}^{-2}$  (Appendix 1). Secondary production values for each species in unfragmented tidal creeks were statistically compared to those in fragmented tidal creeks using a paired t-test assuming unequal variance.

It is important to note that these  $P$  values are intended to be used for comparisons among tidal creeks within this study. Care should be taken in extending these numbers for comparisons with other systems. Due to the limitations of our sampling method, they are not exact whole-ecosystem values, as they do not include in situ growth, survival, or emigration and immigration rates for all species. The use of published growth rates from similar environmental conditions to estimate secondary production is a common practice when in situ growth rates cannot be obtained (Waters, 1977; Benke, 1993; Peterson et al., 2003; Powers et al., 2003). The lack of survival, mortality, and migration estimates surely affects our production estimates, but these estimates are extremely difficult to obtain in coastal and estuarine ecosystems (Adams et al., 2006). Nonetheless, the goal of this study was to employ a standardized protocol across sites allowing for robust among-system comparisons of secondary production estimates. Therefore, these limitations do not compromise the value of the estimates in this study to indicate ecosystem functional response to fragmentation.

## RESULTS

Extent of habitat type coverage varied among tidal creeks (Table 1). However, unfragmented tidal creeks tended to be characterized by a combination of mangrove, rock, and seagrass habitats, while fragmented creeks had greater proportion of silt/sand flats. In areas inundated at low tide, rock was the most common habitat type in White Bight (58%), Buryin Peace (59%), Love Hill (38%), and Conch Sound (67%), mangrove was the most common in Bowen (67%), seagrass in Somerset (74%), and sand/silt flats in Davis (83%) and Man o War (59%) (Table 1). Both natural variability and human impacts affect the extent of each habitat type. Geology and local hydrology drive the extent of exposed rock and can affect areas most conducive for mangrove and seagrass growth. Human impacts can modify natural habitat coverage, e.g., by altering abiotic conditions such as light and salinity, or edaphic conditions through sedimentation, which renders creeks less than optimal for seagrass and/or mangrove growth and fills in important rock habitat.

Highest fish biomass for each species at low tide was found in association with mangrove or rock habitat, with the exception of seagrass habitat in Bowen Sound for blue striped grunt (Fig. 1). For example, in Somerset, > 85% of gray snapper, schoolmaster snapper, blue striped grunt, and sailor's choice was associated with mangrove habitat. In the three creeks with the most disrupted tidal regime (MOW-partially fragmented, CNC-partially fragmented, BOW-completely fragmented), the highest fish biomass was never associated with mangrove habitat (with the exception of schoolmaster snapper in Bowen). In Man o War, fish were never associated with mangrove habitat, likely because no large-mangroves were found along the main channel areas. Fish typically were not associated with sand and seagrass habitat (0%–2% across all creeks) at low tide, with the exception of blue striped grunt in Bowen seagrass habitat (100%), and for schoolmaster (35%) and cubera snapper (25%) in Buryin Peace seagrass.

Secondary production of fish biomass was significantly higher in unfragmented tidal creeks than fragmented creeks ( $t$ -test  $P < 0.05$  for each species), sometimes as much as an order of magnitude (Fig. 2). For example, for schoolmaster snapper, values ranged from 34 to 107  $\text{g m}^{-2} \text{yr}^{-1}$  in unfragmented creeks, and from 0.2 to 6.5  $\text{g m}^{-2} \text{yr}^{-1}$  in fragmented creeks. Cubera snapper, sailor's choice, and blue striped grunt were not found in the three creeks with highly disrupted tidal flow (MOW, CNC, and BOW) with the exception of cubera snapper in MOW (4  $\text{g m}^{-2} \text{yr}^{-1}$ ) and sailor's choice in BOW (2  $\text{g m}^{-2} \text{yr}^{-1}$ ). Gray and schoolmaster snapper consistently had higher production values than the other three species (maximum 150  $\text{g m}^{-2} \text{yr}^{-1}$  compared

Table 3. Parameters and sources given for the length-weight ( $L/W$ ) conversion equation  $\log W = \log a + b \log L$  where  $a$  and  $b$  are species-specific constants, # = number of individuals used to develop in situ  $L/W$  regressions, with all lengths  $L$  representing standard length (SL) in millimeters and all weights  $W$  representing weight in grams. Size range (min–max) given for fish collected in situ.

Species	$a$	$b$	min–max (mm)	$r^2$	#
Gray snapper	-4.2751	2.8754	40–290	0.9917	115
Schoolmaster	-4.3009	2.9107	50–180	0.9509	100
Cubera snapper	-4.0684	2.7574	74–310	0.997	37
Blue striped grunt	-4.4	2.9437	63–174	0.989	35
Sailors choice	-4.4476	2.9803	50–135	0.9839	31

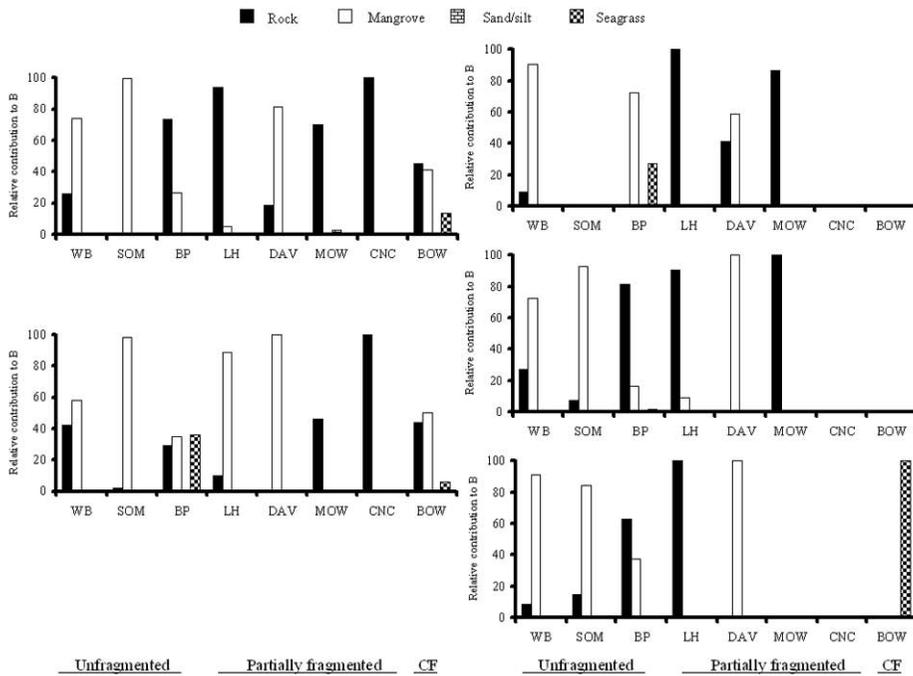


Figure 1. Relative contribution (out of 100%) of habitat to biomass (“B”) of (A) gray snapper, (B) schoolmaster, (C) cubera, (D) blue striped grunt, and (E) sailor’s choice. WB = White Bight, SOM = Somerset, BP = Buryin Peace, LH = Love Hill, DAV = Davis, MOW = Man o War, CNC = Conch Sound, BOW = Bowen. U = Unfragmented, PF = Partially fragmented, CF = Completely fragmented (sensu Layman et al., 2004b).

to maximum values of 12, 80, and 55 g m<sup>-2</sup> yr<sup>-1</sup> for cubera, blue striped grunt, and sailor’s choice, respectively), largely a function of abundance. For example, there were a mean of 2.0 gray snapper m<sup>-2</sup> and 1.5 schoolmaster snapper m<sup>-2</sup> in White Bight, with only 0.08 blue striped grunts m<sup>-2</sup> and 0.5 sailor’s choice m<sup>-2</sup>. Production values in Man o War were more similar to unfragmented creeks than to fragmented creeks for the three snapper species, perhaps a result of restoration efforts 1 yr prior to sampling (see Layman et al., 2004a).

Downstream areas of fragmented tidal creeks always had higher production values than upstream areas (Fig. 3). For example, production values for gray snapper in Love Hill downstream areas were 150 g m<sup>-2</sup> yr<sup>-1</sup> compared to 11 g m<sup>-2</sup> yr<sup>-1</sup> upstream. Upstream areas in Love Hill, Davis, and Bowen consistently had production values close or equal to zero (due to low abundance and small size classes) in upstream areas. Within fragmented creeks, blue striped grunt were never found in upstream areas, sailor’s choice were only found upstream in Love Hill, and cubera snapper were only found upstream in Man o War. Man o War had similar upstream and downstream values of schoolmaster snapper production (33 and 25 g m<sup>-2</sup> yr<sup>-1</sup>, respectively), suggesting that recent restoration of hydrologic connectivity (Layman et al., 2004a) may have mitigated effects of previous fragmentation. Lower production and species numbers in upstream areas may be an artifact of shallow waters associated with low-tide surveys. However, these results also occur in downstream areas, suggesting that this pattern is to some extent a consequence of fragmentation.

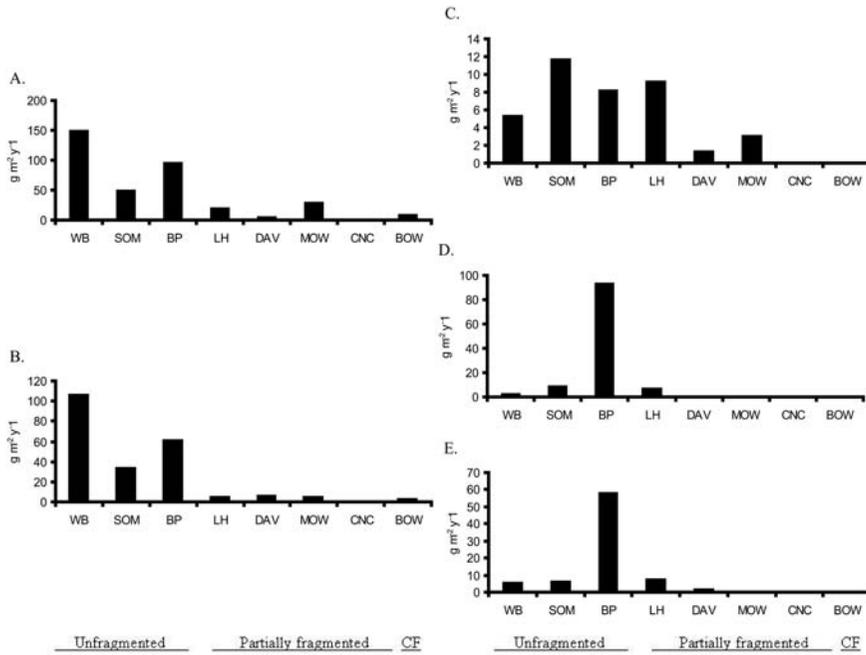


Figure 2. Estimated annual production values ( $\text{g m}^{-2} \text{ yr}^{-1}$ ) for (A) gray snapper, (B) schoolmaster, (C) cubera, (D) blue striped grunt, and (E) sailor's choice. Note different y-axis values for each species. WB = White Bight, SOM = Somerset, BP = Buryin Peace, LH = Love Hill, DAV = Davis, MOW = Man o War, CNC = Conch Sound, BOW = Bowen. U = Unfragmented, PF = Partially fragmented, CF = Completely fragmented (sensu Layman et al., 2004b).

## DISCUSSION

Our study suggests that fragmentation of tidal creeks significantly reduces secondary production of five economically important fish species in the Bahamas. Lower production values in fragmented systems resulted from a combination of fewer species, lower densities of those species, and smaller size classes of fishes. Secondary production is directly related to food quality and quantity (Benke et al., 1988; Benke, 1993; Edgar and Shaw, 2004a,b,c) which is likely reduced in fragmented creeks (Valentine-Rose et al. in press). Higher salinity and temperature in upstream areas of fragmented tidal creeks (Valentine-Rose et al. in press) may decrease productivity by increasing energy costs in juvenile fishes (Wuenschel et al., 2004, 2005), as well as by influencing their survival and viability (Green and Fisher, 2004). Recruitment of post-settlement fishes may be lower in fragmented creeks due to reduction in supply rates and connectivity to larval sources (Gaines and Roughgarden, 1985; Cowen et al., 2006) or reduced quantity and quality of preferred habitat (Carr, 1994; Jordan et al., 1998; Adams and Ebersole, 2004; Mumby et al., 2004; Dorenbosch et al., 2005). In our study, highest fish production typically was associated with creeks with the most available mangrove and rock habitat, suggesting habitat complexity likely is a major factor affecting the levels of secondary production. The correlation between habitat complexity and fish production also has been observed in freshwater stream studies (Benke et al., 1988).

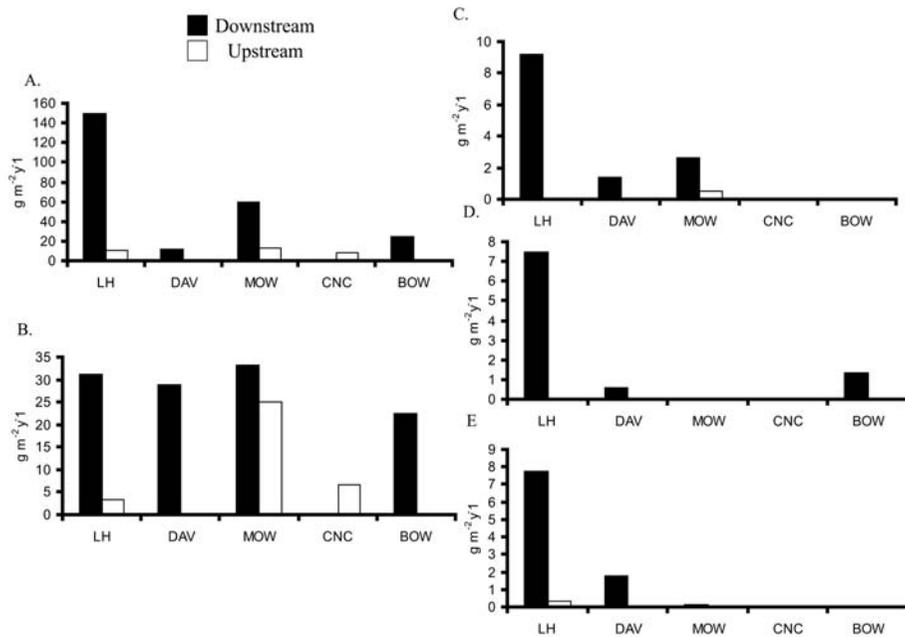


Figure 3. Estimated annual production values ( $\text{g m}^{-2} \text{yr}^{-1}$ ) for (A) gray snapper, (B) schoolmaster, (C) cubera, (D) blue striped grunt, and (E) sailor's choice in downstream (filled bars) and upstream (unfilled bars) areas of fragmented tidal creeks. LH = Love Hill, DAV = Davis, MOW = Man o War, CNC = Conch Sound, BOW = Bowen.

Production values in fragmented tidal creeks were typically lower, often substantially so, than in unfragmented tidal creeks. Nonetheless, differences between fragmented and unfragmented creeks may have been more pronounced had we not used the same growth rates in all creeks for three of the five species. It is likely that many fish species' growth rates are slower in fragmented creeks due to loss of preferential food sources (Cocheret de la Morinière, 2004b; Kieckbusch et al., 2004; Nemerson and Able, 2004), inadequate refuge habitat (Cocheret de la Morinière et al., 2004a), or adverse environmental conditions (Green and Fisher, 2004; Wuenschel et al., 2004, 2005). Furthermore, fish in fragmented creeks were generally smaller and may have lower survival rates (Fuiman and Werner, 2002). In sum, our methodology did not employ in situ growth rates for all species or mortality estimates for any species, and we believe these measures would further the discrepancy between secondary production estimates for fragmented and unfragmented tidal creeks.

Because secondary production encompasses three of the four criteria defining a nursery, i.e., density, growth, and survival (Benke, 1993; Beck et al., 2001; Dahlgren et al. 2006), secondary production is a first step in assessing nursery function of estuaries. Complemented with direct evidence of export of juveniles from fragmented estuaries to off-shore adult habitats (i.e., neighboring back reef and coral reef ecosystems (Dahlgren and Marr, 2004; Mumby et al., 2004; Dorenbosch et al., 2005), nursery function of these systems could be quantitatively estimated. The species in this study are believed to experience ontogenetic habitat shifts from juvenile to adult habitats (Cocheret de la Morinière et al., 2003a,b, 2004; Serafy et al., 2003), and therefore decreases in productivity in important juvenile nursery habitat through fragmentation most likely results

in decreased contribution of individuals to offshore adult habitats (Mumby et al., 2004; Dorenbosch et al., 2005).

Secondary production values may be helpful in putting an economic value on ecosystem services, which is often crucial for prioritizing management and conservation efforts (Costanza et al., 1997). Based on economic value of commercially important species, secondary production estimates can be directly translated into a dollar value of one service (i.e., production of consumable animal protein) provided by these creek systems. For example, an extensive survey of local fisherman and restaurants on Andros Island revealed the average price for the five focal species sold by fishermen is \$18/kg for all species 15 cm or longer, while Androsian restaurants charge an average of \$7/fish 15 cm or longer. Applying these numbers to fish secondary production estimates from our study creeks, hydrologic fragmentation (even of our small creeks) can result in a loss of up to \$9000 of value (for the five focal species). Differences between estimates of secondary production and loss of economic worth of fish biomass between unfragmented and fragmented creeks may be even more pronounced in larger creek systems. In our study, we examined differences in secondary production between small creeks (< 2 ha). However, some tidal creek systems in the Bahamas are thousands of hectares in size, such as Fresh Creek, Andros (~4100 ha). Larger creek systems have a higher abundance of fish, a higher number of species (L. Valentine, University of Alabama, unpubl. data), and generally have larger individuals (pers. obs.), all of which would serve to increase secondary production estimates and economic value. Our study systems appear to be ideal "natural" systems in which to work, because they are small enough to thoroughly sample in a quantitative manner and they can be physically manipulated (e.g., restored) at the ecosystem-scale (e.g., Gribsholt et al., 2005). Therefore, they can serve as natural experimental units with which to make comparisons, as well as to scale-up responses to much larger wetland systems throughout the Bahamas and Caribbean.

In conclusion, we provide a survey methodology to assess the effects of anthropogenic stress on an ecosystem function: secondary production. This is the first attempt to estimate secondary production for mangrove fishes (Faunce and Serafy, 2006). We suggest secondary production may be an appropriate measure of ecosystem functional responses to other anthropogenic stresses, as it is a single, composite value that incorporates many factors within an ecosystem. Other studies can build upon this framework to provide more accurate production estimates, e.g., by determining in situ growth for all species. Although in almost all situations in situ survival and migration will be difficult to estimate, secondary production estimates without these measures still provide for a powerful tool to make among-system comparisons. Comparative studies of secondary production may provide insight into patterns of ecosystem functional response following environmental change, and may also be useful in applying monetary values to ecosystem responses to anthropogenic stress or habitat restoration.

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