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Degree of aquatic ecosystem fragmentation predicts population characteristics of gray snapper (*Lutjanus griseus*) in Caribbean tidal creeks

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Abstract: Ecosystem fragmentation is one of the most damaging anthropogenic impacts to aquatic and terrestrial ecosystems worldwide. In this study, we analyzed population-level characteristics of a resilient top predator, the gray snapper (*Lutjanus griseus*), across a gradient of fragmentation in Bahamian tidal creeks. Analysis of hydrologic connectivity (the inverse of fragmentation) and site-specific population parameters revealed that varying degrees of connectivity translated into predictable characteristics in fish populations. Less-fragmented systems produced fast-growing snapper with high condition factors, whereas more fragmented tidal creeks yielded slow-growing snapper with low condition factors. Underlying reasons for growth rate differences likely originated from structural and functional shifts in tidal creek ecosystems following fragmentation. Such ecosystem-level shifts were reflected by low per-individual volumes of consumed prey, as well as increased parasite infestations. Results indicated that aquatic ecosystem fragmentation may affect long-term fitness and viability of resilient species capable of persisting in fragmented habitats. Our results from estuarine tidal creeks compare well with studies on fragmentation of freshwater streams by dams and suggest that population-level consequences following ecosystem fragmentation may be generalizable between seemingly disparate aquatic environments.

Résumé : La fragmentation des écosystèmes est à l'échelle globale l'un des impacts anthropiques les plus nocifs pour les écosystèmes aquatiques et terrestres. Nous analysons dans notre étude les caractéristiques à l'échelle de la population chez un prédateur résilient de niveau supérieur, le vivaneau sandre gris (*Lutjanus griseus*), le long d'un gradient de fragmentation dans des cours d'eau à marées des Bahamas. L'analyse de la connectivité hydrologique (l'inverse de la fragmentation) et des paramètres démographiques spécifiques aux sites montre que les divers degrés de connectivité se reflètent dans des caractéristiques prévisibles des populations de poissons. Les systèmes moins fragmentés produisent des vivaneaux à croissance rapide et à coefficient de condition élevé, alors que les cours d'eau à marées plus fragmentés contiennent des vivaneaux à croissance lente et à coefficient de condition bas. Ces différences dans la croissance s'expliquent vraisemblablement par des changements structuraux et fonctionnels dans les écosystèmes des cours d'eau à marées après la fragmentation. De tels changements à l'échelle de l'écosystème se traduisent par une consommation individuelle de faibles volumes de proies et des taux accrus d'infestations parasitaires. La fragmentation des écosystèmes aquatiques peut ainsi affecter la fitness à long terme et la viabilité des espèces résilientes capables de survivre dans les habitats fragmentés. Nos résultats obtenus dans les cours d'eau à marées se comparent bien à ceux d'études sur la fragmentation des cours d'eau par les barrages en milieu d'eau douce; cela laisse espérer que les conséquences de la fragmentation des écosystèmes à l'échelle des populations puissent être généralisables pour des environnements aquatiques à première vue disparates.

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Ecosystem fragmentation is one of the core drivers of biodiversity loss and erosion of ecosystem function at local, regional, and global scales (Fahrig 2003). Conceptual and theoretical discussions of fragmentation have been dominated by a focus on terrestrial ecosystems, yet aquatic ecosystem fragmentation is also widespread and can substantially affect biodiversity and ecosystem function (Poff et al. 1997). Aquatic ecosystem fragmentation is defined as the disruption of hydrologic connectivity (i.e., disruption of the water-mediated transfer of matter, energy, or organisms within or between elements of the hydrologic cycle; Pringle 2001). The study of aquatic ecosystem fragmentation has been dominated by a focus on effects of dams in freshwater streams (e.g., Poff et al. 1997). Maintaining connectivity of estuarine and marine ecosystems is similarly important, but has received much less emphasis in the literature (but see e.g., Montague et al. 1987). Here, we examine effects of fragmentation on a resilient top predator species (e.g., a species that can tolerate disturbance but not collapse) in estuarine tidal creeks of the Bahamas, and in doing so, expand the scope of ecosystem fragmentation in estuaries to the population level.

In freshwater streams, growth of lotic fishes can be substantially altered by ecosystem fragmentation (Rypel et al. 2006). Altered growth rates likely originate from large-scale shifts and discontinuities in the structure and function of flow-regulated systems (Ward and Stanford 1983). More specifically, in fragmented freshwater streams, floodplain connectivity is lost, prey diversity and abundance is lowered, and physiochemical conditions are considerably altered (Ward and Stanford 1983) — all of which can affect fish growth rate (Campana and Thorrold 2001). In Caribbean tidal creeks, similar shifts in ecosystem structure and function have been observed in systems with poorly constructed flow conveyance structures (i.e., bridges or culverts) at road crossings, thereby inhibiting hydraulic exchange between upstream and downstream reaches (Layman et al. 2007; Valentine-Rose et al. 2007). We examined the effect of aquatic ecosystem fragmentation on growth rate of gray snapper (*Lutjanus griseus*), an ecologically and economically important fish species in Bahamian tidal creeks, as a model of how fragmentation of estuarine ecosystems may affect population-level characteristics of critical fishery species.

Our study systems were 13 clear-water, mangrove-lined tidal creeks located on Abaco and Andros islands, Bahamas. These estuarine creeks are important to the ecology, economy, and culture of the Bahamas because of their critical role as fish and invertebrate nurseries, feeding areas, and their support of popular recreational and commercial fisheries (see Layman et al. 2007 for more detailed site descriptions). Tidal flow is the principle organizing factor of the ecology in these systems, driving floral and faunal composition and affecting key biotic interactions such as predation rates (Rypel et al. 2007; Valentine-Rose et al. 2007). Our study systems were chosen to reflect a complete gradient of fragmentation, from creeks with no tidal exchange to those with a maximum mean daily tidal range of ~0.8 m. Degree of fragmentation was estimated using HOBO® water-level loggers. Percent fragmentation was determined as the reduction in mean daily tidal amplitude at each creek site relative to the maximum possible amplitude (Layman et al. 2007). Hydrologic connectivity and fragmentation are used interchangeably in this paper and are assumed to be direct inverses. High-fragmentation tidal creeks were defined as sites with ≤50% of the natural tidal range, whereas creeks with ≥50% of the natural range were classified as low-fragmentation creeks.

We collected 271 gray snapper from the 13 tidal creeks from May to November 2006 using a combination of different methods (gill nets, hook and line, cast nets, and fish traps). We attempted to sample all size and age classes present in each tidal creek. Captured fish were measured (standard length, SL) and weighed (wet weight), and their otolith sagittae extracted for age determinations. Stomach contents were examined visually and gravimetrically using standard methodology. Presence or absence of common gray snapper trematode parasites was categorically scored for each fish (0 = parasites absent, 1 = parasites present). Otoliths were prepared and their ages determined using common methodology (Rypel et al. 2006). Age assignments were blindly replicated and verified by a second reader. A third reader settled any disagreements between readers one and two (discrepancies represented only 3% of all fish). Condition factor (K) was calculated according to Le Cren (1951).

In low-fragmentation tidal creeks, population age structures of gray snapper were diverse, represented most age classes, and suggested strong recruitment of snapper across years. In high-fragmentation creeks, age structures were composed of only one or two age classes. For example, in Double Block Creek, a highly fragmented (3% connectivity) system, 20 of 21 fish were age-4 and in Indian River (another high-fragmentation system, 15% connectivity) all fish were age-4. These scenarios are indicative of acute and highly episodic recruitment of snapper over time. Alternatively, in Camp Abaco Down, a low-fragmentation (87% connectivity) system, age classes 1–7 were represented, a pattern that was repeated in other low-fragmentation systems. We observed significant differences in the size distributions of snapper, with low-fragmentation systems having size distributions significantly biased toward larger fish (Fig. 1*a*, Kolmogorov–Smirnoff test, $P < 0.0001$). Mean condition factor of snapper was significantly higher (t test, $F = 27.5$, $P < 0.0001$; mean ± standard error (SE) K low-fragmentation = 1.34 ± 0.15, high-fragmentation = 0.68 ± 0.04) and mean parasite score significantly lower at low-fragmentation sites (t test, df = 1, $F = 65.2$, $P < 0.0001$; mean ± SE parasite score low-fragmentation = 0.02 ± 0.02, high fragmentation = 0.69 ± 0.09).

Von Bertalanffy growth models (Fig. 1*b*) based on length-at-age data predicted that gray snapper from low-fragmentation tidal creeks would ultimately reach 2.5 times the maximum size (L_∞ = 580.9 mm SL) of the same age fish from high-fragmentation creeks (L_∞ = 232.1 mm SL). Bootstrapped values of L_∞, theoretical mean length at time 0 (T_0), and K for low-fragmentation systems differed significantly from estimates in high-fragmentation systems (Wilcoxon two-sample test: L_∞, $P < 0.0001$; T_0, $P < 0.0001$; K, $P < 0.0001$), and bootstrapped values of Von Bertalanffy predicted length-at-ages were, in all cases, significantly higher in low-fragmentation compared with high-fragmentation systems (Wilcoxon two-sample tests for age classes 1–10, all P values < 0.0001). Intensive sampling

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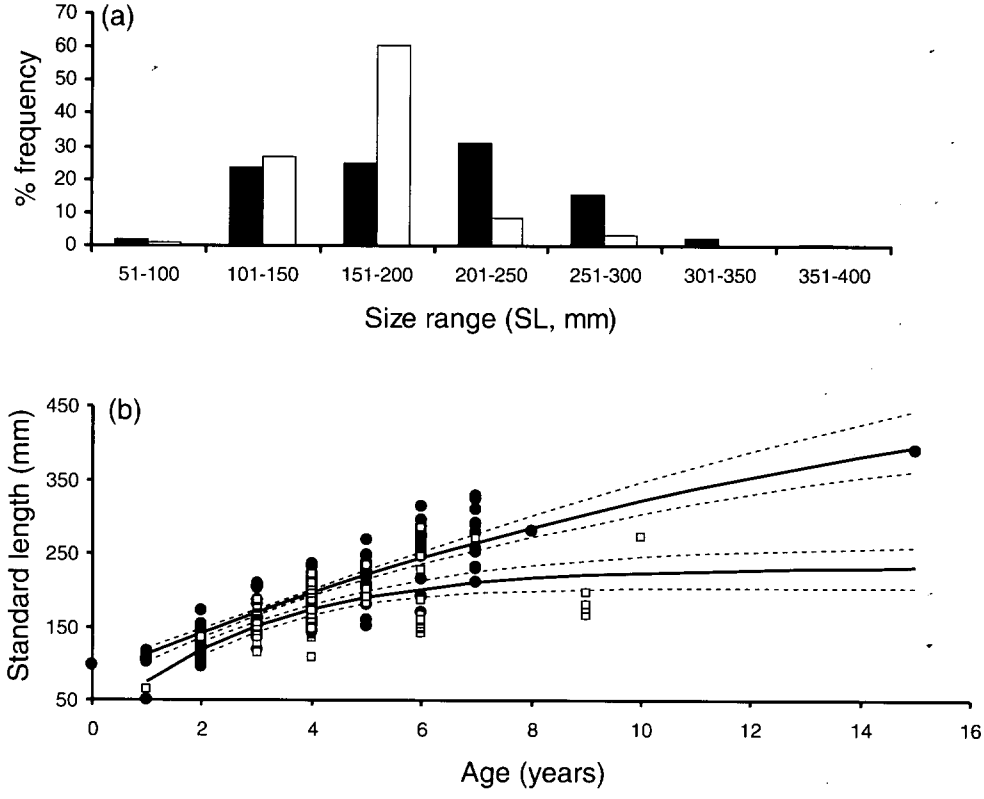
Fig. 1. (*a*) Size frequency distributions of gray snapper (*Lutjanus griseus*) from high-fragmentation (open bars) and low-fragmentation (solid bars) Bahamian tidal creeks, May–November 2006. (*b*) Von Bertalanffy growth curves for gray snapper captured from low-fragmentation (L_∞ = 580.9, T_0 = –2.2, K = 0.07, N = 175, solid circles, top line) and high-fragmentation (L_∞ = 232.1, T_0 = –0.2, K = 0.3, N = 96, open squares, bottom line) creeks. Confidence intervals for each function are denoted by broken lines and were derived using a bootstrapping technique (Rypel 2007).



(see above) and extensive underwater visual census suggested there were no small (e.g., SL < 80 mm) or large (SL > 300 mm) individuals living in any of the high-fragmentation systems; therefore, they do not appear in the high-fragmentation growth curves. However, underwater visual census surveys confirmed that small grey snapper were abundant in low-fragmentation systems. Exclusion of one very large individual from a low-fragmentation creek had nonsignificant effects on all statistical results (for example, growth rates still differed significantly, Wilcoxon two-sample tests all P values < 0.0001), and we therefore report the statistical values that include this particular individual. Significant linear regressions revealed that site-specific values of growth rate (assayed as the slope of length-to-$\log_{10}$ age regression for each site, Rypel et al. 2006), condition factor, and parasite scores were highly predictable based on degree of fragmentation (Fig. 2). These trends were not the result of fish size differences between sites, because each regression was also run with SL as a potential explanatory variable (e.g., a multiple regression), and in no case did size have a significant effect on the model (growth P = 0.95, condition P = 0.92, parasite P = 0.80).

To our knowledge, this is the first study to provide evidence for population-level impacts on fish growth due to ecosystem fragmentation in mangrove-dominated estuarine ecosystems. We observed stunted growth rates of gray snapper in fragmented tidal creeks, and this is likely to reduce reproductive output (e.g., fitness) of snapper. For example, smaller individuals are more susceptible to predation in the juvenile stage, and adults may become sexually mature later in life and (or) produce fewer ova per mature female. A large percentage (>70%) of adult gray snapper (>5 year old) from high-fragmentation systems were not sexually mature, whereas most gray snapper (78%) were sexually mature by 2 years of age in low-fragmentation creeks. We discuss two potential reasons as to why growth rates of gray snapper may be so strongly influenced by ecosystem fragmentation.

First, fragmentation of tidal creeks is known to alter the density and diversity of gray snapper prey (Layman et al. 2007). In the current study, 29% of gray snapper individuals from low-fragmentation sites had empty stomachs compared with 56% of individuals with empty stomachs from high-fragmentation sites. Gray snapper from low-fragmentation creeks also consumed significantly higher mean volumes of prey per individual (mean ± SE = 1.08 ± 0.21 mL) than did fish from high-fragmentation tidal creeks (mean ± SE = 0.48 ± 0.18 mL, t test, df = 1, F = 4.34, P = 0.03). Second, fragmentation is also known to induce major shifts in the physiochemical characteristics of tidal creeks (Valentine-Rose et al. 2007), which likely leads to the increased parasite infestations of snapper in fragmented systems. High parasite infestations (often >100 parasites per individual) were consistently observed for individuals captured from high-fragmentation systems, while snapper were rarely parasitized by trematodes in low-fragmentation systems.

In addition to lowered growth rates, local and regional gray snapper fisheries are likely also affected by disruption

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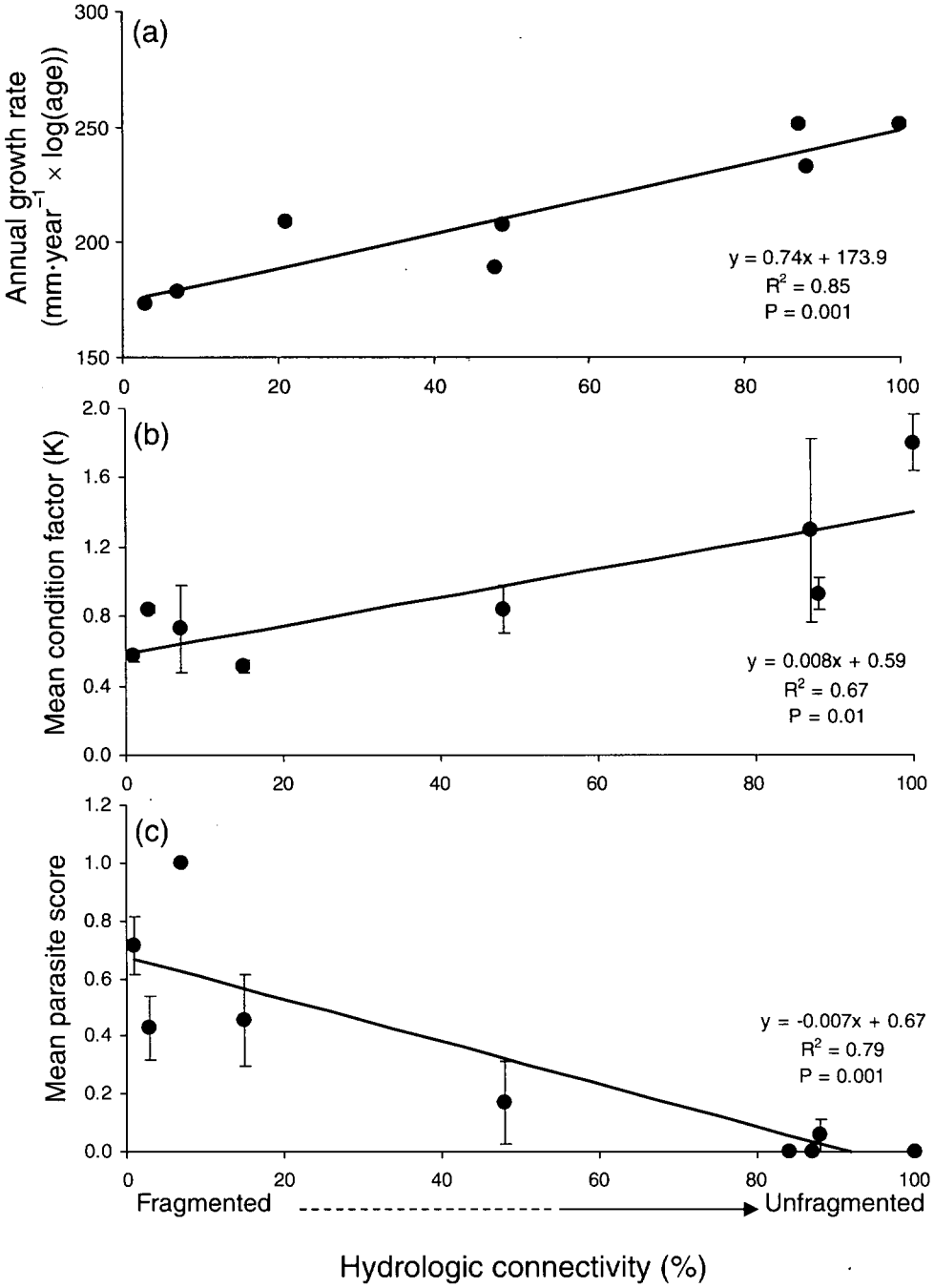
Fig. 2. Mean gray snapper (*Lutjanus griseus*) (*a*) site-specific growth rate (only sites with >3 age classes were used), (*b*) condition factor (*K*) and (*c*) parasite score expressed as linear functions of percent hydrologic connectivity with the ocean. Error bars in panels *b* and *c* represent the mean ± 1 standard error (SE).



of metapopulation dynamics due to fragmentation. Gray snapper are purported to rely on both nearshore (e.g., tidal creek) and open ocean habitat to complete their life cycle, and thus disruption of hydrologic connectivity may disrupt natural life-history patterns. Whereas low-fragmentation systems contained nearly complete age-structures, only one or two age classes were found in high-fragmentation systems, presumably because juveniles could only colonize these systems on extreme high tides (e.g., corresponding to hurricanes). As such, even presumably intact mangrove-dominated wetlands associated with fragmented tidal creeks may support relatively little fishery production, and they do not serve as important nursery habitat (Valentine-Rose et al. 2007). Fragmented tidal creeks can be viewed as population sinks because fish have restricted (or nonexistent) means of emigrating from suboptimal biological conditions in fragmented creeks.

In a similar study of large freshwater streams, Rypel et al. (2006) found analogous trends in population parameters of freshwater drum (*Aplodinotus grunniens*) within and among large river impoundments in southeastern USA that differed in their degree of hydrologic connectivity (because of dams).

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Reservoirs with shorter hydraulic retention times and lotic stream reaches (e.g., high hydrologic connectivity) yielded progressively higher annual growth rates, lipid, and condition factors. In the present study, gradual losses in hydrologic connectivity produced nearly identical deteriorations in annual growth rates and condition factors to that observed in the Rypel et al. (2006) freshwater study. Moreover, major shifts in the community structure of estuaries due to impoundment (e.g., Montague et al. 1987; Layman et al. 2007) appear similar to those commonly observed in freshwater ecosystems (Poff et al. 1997). Taken together, these studies suggest that population- and community-level responses to ecosystem fragmentation across disparate systems may conform to some general patterns.

Studies of aquatic ecosystem fragmentation have been dominated by a focus on the effects of dams on freshwater streams (Poff et al. 1997). Based on this study, it appears that response of marine-dominated tidal creeks to loss of hydrologic connectivity may be similar to patterns commonly observed in freshwater streams fragmented by dams. This study, therefore, introduces the exciting possibility that ecological patterns and systems' response to aquatic ecosystem fragmentation in freshwater and estuarine environments may be comparable. If supported by additional studies, some well-acknowledged freshwater paradigms (e.g., Ward and Stanford 1983; Poff et al. 1997) might also be applicable to estuarine environments. Additional research should ascertain whether population-level impacts correlate directly to important ecosystem-level modifications because of fragmentation (e.g., secondary production, decomposition, nutrient cycling). If this holds true, population-level metrics commonly employed by fisheries managers, such as those used in this study, might be useful surrogates for assessing larger-scale modifications to aquatic ecosystems. By applying such metrics, it may be possible to bridge some sizeable conceptual gaps among aquatic disciplines to attain a more robust and complimentary understanding of the functioning of intact and altered aquatic ecosystems across the globe.

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