Journal of Experimental Marine Biology and Ecology 440 (2013) 22–28

Contents lists available at SciVerse ScienceDirect

Journal of Experimental Marine Biology and Ecology

journal homepage: www.elsevier.com/locate/jembe

# Elevated habitat quality reduces variance in fish community composition

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ARTICLE INFO

*Article history:*
Received 26 June 2012
Received in revised form 7 November 2012
Accepted 14 November 2012
Available online 21 December 2012

*Keywords:*
Basin Model
Eelgrass
Fish community
Habitat quality
Variance

ABSTRACT

Understanding the intrinsic variability of habitat-specific faunal communities is important to species conservation and ecosystem management. Community variability is driven by many environmental factors, including density-dependent habitat selection. Extensions of MacCall's Basin Model of density dependent habitat selection indicate that variance of a species' density is generally expected to be independent of habitat quality while variance in community composition is expected to decrease with habitat quality. We used these expectations to investigate variability of nearshore fish communities. Fish collections were conducted biweekly in eelgrass (high quality) and unvegetated (low quality) habitats from early summer to late autumn from 1996 to 2009. Higher fish density and biomass, taxa richness, and elevated variability of these measures were associated with the higher quality habitat. Seasonality explained the greatest variance in the fish community followed by habitat quality and year. Consistent with expectation, variability in community composition was less in the high quality habitat. In addition to differences in variability, cyclical seasonal transitions were less predictable and directional multi-year shifts in community structure were more pronounced in the low quality habitat. Our results show that community variability is associated with suboptimal or degraded habitats; a finding of significance given the increased prevalence of anthropogenic disturbance in ecosystems globally.

## 1. Introduction

Understanding the intrinsic variability of habitat-specific faunal communities is important to ecosystem management (Ives et al., 2003; MacCall, 1990; Micheli et al., 1999) as this knowledge can shape decisions concerning harvest strategies (Swain and Wade, 1993), risk analysis (Ives et al., 2003), habitat protection (Sullivan et al., 2006) and study design (Blanchard et al., 2008). Unfortunately, studies of sufficient duration to permit examination of concepts of population and community variation at ecologically meaningful temporal scales are rare (Cody, 1996).

Fluctuating environmental conditions create considerable variation in survival, recruitment (e.g. Cushing, 1975, 1990) and movement patterns (Simms et al., 2004) of animal populations. Such external influences have the ability to drastically alter the composition and abundance of biotic communities (Stenseth et al., 2002). The affinity of organisms to particular habitat conditions can further result in disparate densities (Fretwell and Lucas, 1970). MacCall's (1990) extension of the theory of density dependent habitat selection (Fretwell and Lucas, 1970) casts density-change as a function of local habitat suitability; where habitat suitability can be reduced through among-habitat increases in abundance. Research relative to MacCall's (1990) Basin Model has focused primarily on testing of one prediction, expansion in range with increase in population abundance. However, patterns of variance can also be predicted under this model (Schneider and Cote, submitted for publication). First, variance in density of individual species is expected to be independent of habitat quality, provided density does not fall to zero. In years of low abundance, when populations contract away from poor habitat (density falls to zero), variance in density of individual species is expected to be less in lower quality than higher quality habitat. In contrast, similarity in community structure is expected to increase with habitat suitability.

Nearshore eelgrass (*Zostera marina*) ecosystems provide an opportunity to evaluate habitat-related expectations of community variability. Nearshore marine environments contain a broad range of habitat quality to which fish communities respond (Connolly, 1994; Hughes et al., 2002; Joseph et al., 2006), often in a manner consistent with density-dependent processes (Grant and Brown, 1998; Laurel et al., 2004; Swain and Wade, 1993). They are also habitats of high conservation value (Bell and Pollard, 1989; Orth et al., 1984; Waycott et al., 2009) that are threatened throughout much of their range (Orth et al., 2006; Waycott et al., 2009). Eelgrass habitats have relatively high primary productivity (Waycott et al., 2009), and by providing shelter from predation (e.g. Gorman et al., 2009), are expected to support higher densities and biomass of marine fish than unvegetated habitat. We utilized a 14 year dataset (1996–2009) from Newman Sound, Newfoundland Canada to: 1) establish differences in habitat quality in this study system; 2) quantify variability in density and

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http://dx.doi.org/10.1016/j.jembe.2012.11.006

community composition; and 3) compare observed patterns of spatial and temporal variability in density and community composition to those expected under MacCall's Basin Model (MacCall, 1990).

## 2. Methods

Our study was conducted in Newman Sound, Newfoundland, Canada (Fig. 1); adjacent to Terra Nova National Park. Fjords with rocky headlands, convoluted shorelines and boreal forest characterize the coastline. Despite global trends of decline, eelgrass beds in our study area have been naturally expanding since 2001. Eight eelgrass and four unvegetated sites were established for monitoring in 1996, with eelgrass sites defined as ≥10% areal cover (Laurel et al., 2003). The habitat state of all sites was monitored annually by visual inspection for the presence of eelgrass or more rigorously using aerial, scuba/snorkel, and boat surveys (Table 1) (Warren et al., 2010). In 1999 and 2000, two eelgrass (DS and BC, Fig. 1) and two unvegetated sites (CC and MS, Fig. 1) underwent habitat manipulations, where 500 $m^2$ of eelgrass was removed from the eelgrass sites and 80 $m^2$ of artificial eelgrass was added to the unvegetated sites (Laurel et al., 2003; Table 1). During these manipulations, areal cover of eelgrass remained above 10% and therefore these sites were classified as eelgrass for those years. After 2000, artificial eelgrass structures were removed from the water and subsequent habitat availability was based entirely on natural habitat processes.

Fish community abundance data were obtained from a long-term nearshore fish-community monitoring program established in Newman Sound in 1996 (Gregory et al., 2006). Fish were collected at all sites biweekly from July to November each year, 1996–2009; there was no sampling in 1997.

Fish were sampled using a 25 m long × 2 m high Danish bag seine net with 19 mm stretched mesh size. The net was deployed from shore by boat to a distance of 55 m, at a typical depth of 5 m, then hauled by two people standing 16 m apart on shore. The net sampled fish up to 2 m above the seabed in an area of 880 $m^2$. Escapement rate is low, on the order of 5%; details of the gear and its efficiency are documented elsewhere (Schneider et al., 1997). Captured fish were counted and measured to standard length (±5 mm SL). Biomass for each species was estimated by applying species-specific, length–weight regressions derived from another nearshore study conducted along the northeast Newfoundland coast (unpublished data, D. Methven University of New Brunswick, Saint John).

**Table 1**
Methods of habitat characterization and numbers of eelgrass and unvegetated sites in 1996–2009[a]. A — aerial surveys from aircraft; S — snorkel or scuba surveys; V — visual inspections only from boat[b].

| Site type | Number of sites | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Year[1] | 96 | 98 | 99 | 00 | 01 | 02 | 03 | 04 | 05 | 06 | 07 | 08 | 09 |
| Survey method[2] | V | A–S | A–S | A | A | A | V | V | V | A | V | V | V |
| Eelgrass | 8 | 8 | 6 | 6 | 9 | 9 | 9 | 10 | 10 | 10 | 10 | 11 | 11 |
| Unvegetated | 4 | 4 | 2 | 2 | 3 | 3 | 3 | 2 | 2 | 2 | 2 | 1 | 1 |
| Eelgrass removal | – | – | 2 | 2 | – | – | – | – | – | – | – | – | – |
| Artificial eelgrass | – | – | 2 | 2 | – | – | – | – | – | – | – | – | – |

[a] No sampling in 1997.
[b] All sites were visually inspected for eelgrass presence in July each year.

### 2.1. Data analysis

#### 2.1.1. Habitat-related differences in community composition

Fish community data from each seine haul were square root transformed (Clarke and Green, 1988) and then averaged for each site within each season and year. We used the Bray–Curtis Index (Bray and Curtis, 1957) to analyze community similarity and dissimilarity in abundance and biomass. Taxa that typified (i.e., contributed most to within-habitat similarity values) specific habitats and discriminated (i.e., contributed most to dissimilarity values) among habitat types were determined using SIMPER (PRIMER 6). The SIMPER method evaluates the contribution of each taxa to Bray–Curtis similarity values for pairs of sites within and among groups. The differences in fish communities across habitat types, years and season were evaluated through PERMANOVA (PERMANOVA + 1.0.3; 9999 permutations), a permutation-based multivariate analog of ANOVA (Anderson, 2001). Site was included in the model as a random effect (nested within habitat) to account for repeat sampling of sites. Interactions (season and year with habitat) were evaluated with Bonferroni-corrected pairwise comparisons of habitat effects within

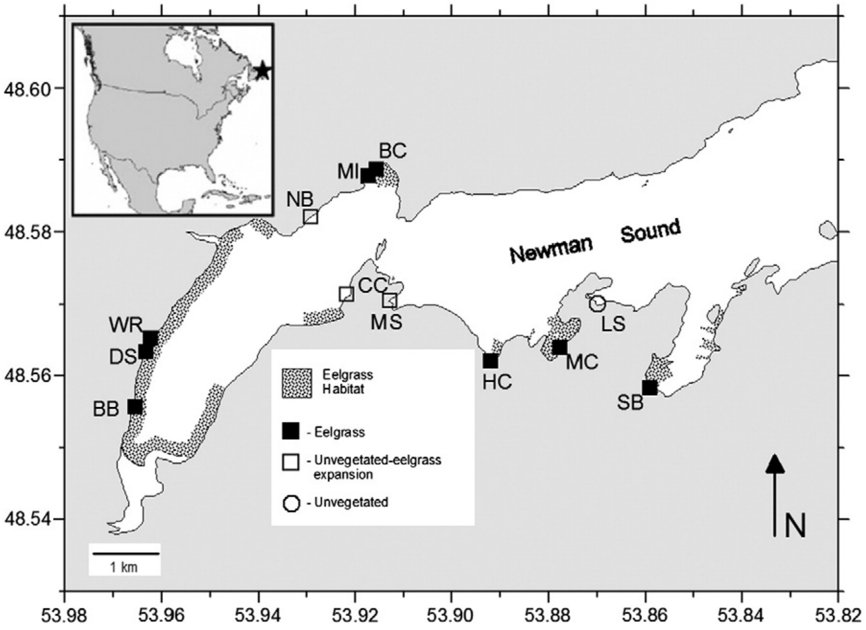

**Fig. 1.** Fish sampling locations July–November 1996–2009, in Newman Sound, Newfoundland. Nearshore eelgrass habitat depicts distribution condition in 1996. Transition from unvegetated to eelgrass habitat occurred in NB, CC and MS beginning in 2001.