



# Fractal measures of habitat structure: maximum densities of juvenile cod occur at intermediate eelgrass complexity

Maria E. Thistle<sup>1,6,\*</sup>, David C. Schneider<sup>2</sup>, Robert S. Gregory<sup>3,4</sup>, Nadine J. Wells<sup>5,7</sup>

<sup>1</sup>Cognitive and Behavioural Ecology Programme, Memorial University of Newfoundland, St. John's, Newfoundland and Labrador A1B 3X7, Canada

<sup>2</sup>Ocean Sciences Centre, Memorial University of Newfoundland, St. John's, Newfoundland and Labrador A1C 5S7, Canada

<sup>3</sup>Ecological Sciences Section, Fisheries and Oceans Canada, 80 E. Whitehills Road, PO Box 5667, St. John's, Newfoundland and Labrador A1C 5X1, Canada

<sup>4</sup>Department of Biology, Memorial University of Newfoundland, St. John's, Newfoundland and Labrador A1B 3X9, Canada

<sup>5</sup>Environmental Science Programme, Memorial University of Newfoundland, St. John's, Newfoundland and Labrador A1B 3X9, Canada

<sup>6</sup>Present address: Department of Biological Sciences, University of Alberta, Edmonton, Alberta T6G 2E9, Canada

<sup>7</sup>Present address: Science Branch, Fisheries and Oceans Canada, 80 E. Whitehills Road, PO Box 5667, St. John's, Newfoundland and Labrador A1C 5X1, Canada

**ABSTRACT:** Habitat patchiness is known to alter the relation of a population to both its predators and its prey. We developed a biologically interpretable measure of habitat complexity to test whether juvenile fish density depends on degree of patchiness. In Newfoundland coastal waters, juvenile fish species, including Atlantic cod *Gadus morhua*, are associated with eelgrass *Zostera marina*. However, the association of density with eelgrass cover is dependent upon site and the scale of analysis. We tested for non-monotonic relationships (with an intermediate optimum) between 5 spatial characteristics of eelgrass and density of 3 juvenile (Age-0) fish species: Atlantic cod, Greenland cod *G. ogac*, and white hake *Urophycis tenuis*. We used aerial photography to determine eelgrass perimeter and area measurements at multiple scales, fractal dimensions of perimeter ( $D_P$ ) and area ( $D_A$ ), and a measure that combines perimeter and area complexity at these scales ( $\beta_{P/A}$ ). Fish densities were estimated at each site using a seine net. We found parabolic relationships between  $\beta_{P/A}$  and density for all 3 species, indicating highest fish densities at sites of intermediate patchiness and edge regularity. Furthermore, we determined that  $\beta_{P/A}$  provided a less ambiguous estimate of spatial configuration than other measures. This intermediate maximum may reflect a trade-off, whereby eelgrass sites of intermediate spatial complexity provide juvenile fish with both optimal protective cover and opportunity to feed. This pattern may apply to any species requiring open areas in which to forage as well as shelter to offset predation risk.

**KEY WORDS:** Habitat patchiness · Landscape ecology · Eelgrass · Fractal · Multiple scales · Habitat use · Atlantic cod · Greenland cod · White hake

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## INTRODUCTION

Over-exploitation has decimated marine ecological communities worldwide (Tegner & Dayton 1999, Hutchings 2000, Myers & Worm 2003), including Atlantic cod *Gadus morhua* populations (Hutchings &

Myers 1994). Recovery of a population from collapse requires increased recruitment, which depends upon year-class strength (Swain & Sinclair 2000). There is increasing evidence that the critical period (Hjort 1914) that determines year-class strength in marine fish is not restricted to planktonic life-history stages

(Sissenwine 1984, Bailey 2000, Ciannelli et al. 2005). In the northwest Atlantic, year-class strength of Atlantic cod *G. morhua* at settlement ceased to predict subsequent strength of that cohort (Schneider et al. 1997a), although it did prior to collapse in 1992 (Ings et al. 1997). The failure of this population to recover substantially since that time has placed increasing emphasis on understanding those factors that govern mortality after settlement.

Age 0 and 1 Atlantic cod and its congener, Greenland cod *Gadus ogac*, exhibit habitat-mediated mortality in coastal environments (Linehan et al. 2001, Laurel et al. 2003a, Gorman et al. 2009). This suggests that the availability of appropriate habitat may increase survival during this life-history stage. In Newfoundland, post-settled juvenile cod utilise eelgrass *Zostera marina* beds (e.g. Gotceitas et al. 1997, Laurel et al. 2003b), an important nursery habitat susceptible to human disturbance (Fonseca 1992). However, cod densities measured at eelgrass versus non-eelgrass sites are only significantly higher in every 2 out of 3 paired comparisons (Gotceitas et al. 1997). Wells (2002) proposed that cod density is related to eelgrass spatial complexity, such that the increased risk of predation with increasing habitat patchiness is balanced against a corresponding increased access to food—the Intermediate Optimum Hypothesis (IOH).

Eelgrass extends throughout the northern coastal zones of the Atlantic and Pacific Oceans (den Hartog 1971), where it grows in complex structural arrangements, from sparsely scattered patches to continuous monospecific meadows (Robbins & Bell 1994). Metrics used to assess seagrass complexity include patch size (Irlandi 1997), number of patches (Salita et al. 2003), shoot density (Bell & Westoby 1986a,b), biomass (Adams 1976), percent cover (Heck & Orth 1980) and leaf height (Bell & Westoby 1986a,b). These measured components largely quantify abundance and rarely incorporate the co-occurrence of vegetated and non-vegetated substrate, which is considered an important factor influencing many aquatic faunal species (e.g. Heck & Orth 1980, Orth et al. 1984, Irlandi et al. 1995, Barberá-Cebrián et al. 2002, Hyndes et al. 2003).

Quantification of habitat heterogeneity based on spatial patterning is rare. However, scaling exponents known as fractals have been used to describe how habitat changes across a range of scales, and can quantify habitat heterogeneity and shape in order to examine relationships with organism distribution or abundance (Gee & Warwick 1994, Davenport et al. 1996, Beck 1998, Turner et al. 1999, Salita et al. 2003). Furthermore, eelgrass growth reveals a hierarchical arrangement of spatial structure, spanning millimetres to kilometres: from blades in shoot groups, to shoot groups in patches, to patches in meadows (sensu Rob-

bins & Bell 1994). Given the structure and pattern of eelgrass growth, the potential biological importance of barren and vegetated areas, and the ability to assess habitat across multiple spatial scales, the use of fractal geometry to describe eelgrass-site shape complexity is biologically appropriate (Davidson 1998, Gustafson 1998, Bogaert 2003).

Using a fractal metric from Lovejoy (1982), Wells (2002) showed that eelgrass area scales with perimeter at several sites and derived an estimate of spatial heterogeneity (complexity), the scaling exponent,  $\beta_{A=f(P)}$ .  $\beta_{A=f(P)}$  was estimated from the regression of area on perimeter as measured at multiple scales of resolution. Wells (2002) also demonstrated a parabolic relationship between Age-0 Atlantic cod density and eelgrass complexity, with an intermediate maximum, hypothesised to result from a trade-off between food availability and predation risk when cod selected habitat (IOH). While the fractal measure  $\beta_{A=f(P)}$  is appealing, its behaviour with respect to changes in its components (perimeter and area) is not known. Furthermore, its sensitivity to bias attendant on regression against a variable measured with error is unknown.

In the present study, we investigated which spatial characteristics of eelgrass sites account for the variation in Age-0 Atlantic cod catch density. Specifically, we (1) examined the relationship of single-scale measurements of eelgrass perimeter or area to cod distribution; (2) developed a bias-free estimation of Lovejoy's scaling exponent and compared it to alternative scaling exponents; and (3) examined the relationships between these scaling exponents and cod distributions.

To assess these relationships, we tested the IOH at the scale of sites within a single fjord (Newman Sound) and at the scale of locations along ~1500 km of coastline (Fleming survey). We then examined whether the relationship between habitat and Atlantic cod applies to 2 co-occurring species, Greenland cod and white hake *Urophycis tenuis*, which experience similar predation risks and food sources in the nearshore community.

## MATERIALS AND METHODS

**Study areas.** The present study used data from 2 coastal surveys, encompassing different geographical scales. The Newman Sound survey extends over ~25 km of coastline and lies within the range of the larger Fleming survey (Methven et al. 2003), which spans ~1500 km of coastline along the eastern shore of the island of Newfoundland, Canada.

Newman Sound is a fjord that lies adjacent to Terra Nova National Park, within southwestern Bonavista

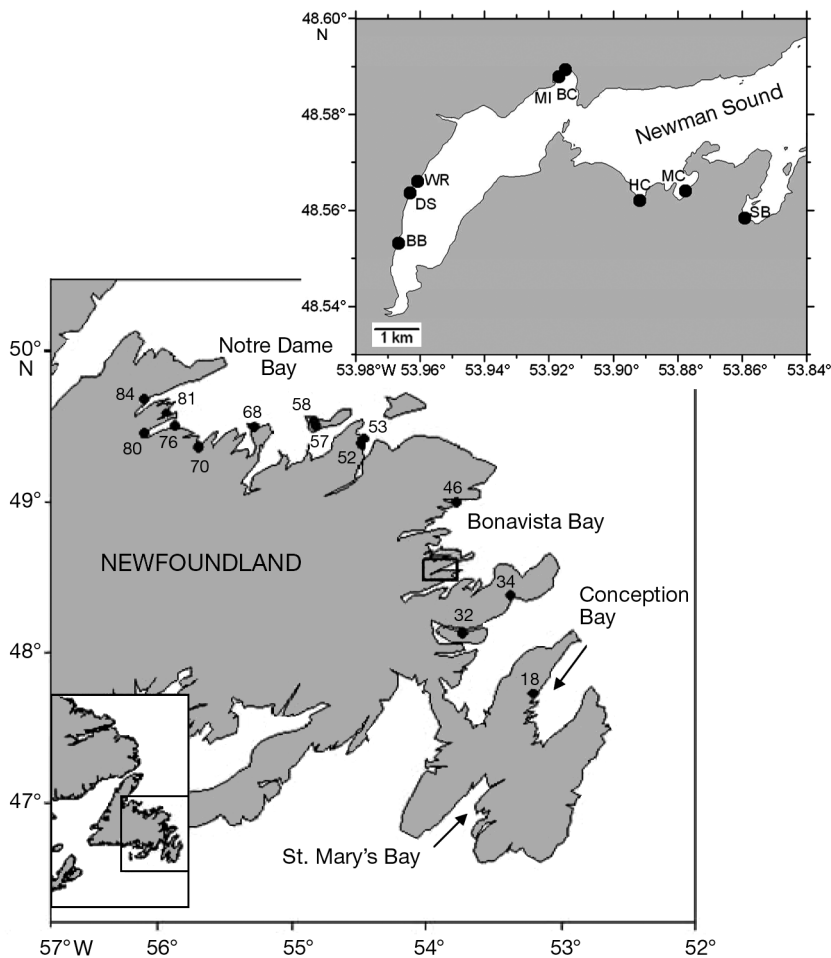


Fig. 1. Study area showing the location of the 8 eelgrass sites used in the Newman Sound survey, Bonavista Bay, Newfoundland (outlined area and inset: BB: Big Brook; BC: Buckley's Cove; DS: Dockside; HC: Heffern's Cove; MC: Minchin's Cove; MI: Mistaken Cove; SB: South Broad Cove; WR: White Rock) and the 14 eelgrass sites used in the Fleming survey, northeast coast of Newfoundland (numbered sites)

Bay (Fig. 1). A sheltered inlet extending 41 km in length and 1.5 to 3.0 km in width, it is divided into 2 basins by a sill located ~7 km from the head of the sound. The substrate and associated vegetative cover in the nearshore environment (0 to 15 m depth) is varied. Eelgrass is the dominant vegetation in waters <6 m deep, occurring in monospecific beds in mud, sand and gravel substrates. Other aquatic vegetation, including various algae species, also occur in these coastal waters, but to a lesser degree. For example, fucoid algae (*Fucus vesiculosus* and *Ascophyllum nodosum*) occur in the intertidal zone, at depths more shallow than those commonly occupied by the 3 fish species we investigated. Irish moss *Chondrus crispus* occurs throughout waters <6 m, and 2 kelp species (*Agarum cribrosum* and *Laminaria digitata*) occur in

waters deeper than our study sites. We selected 8 sites based on the presence of eelgrass and the existence of concurrent juvenile cod and hake data.

The larger scale Fleming survey study area extends from Notre Dame Bay, southeast along Newfoundland's northeast coast to St. Mary's Bay (Fig. 1). Substrate and vegetative cover found at sampling sites along this coast are similar to that in Newman Sound. We identified 14 Fleming sites using the same selection criteria as for the 8 sites in Newman Sound. These sites extend from Notre Dame Bay to Conception Bay (Fig. 1). Among the sites used in the present study, eelgrass landscapes were stable over at least a 3 yr period in Newman Sound (1999 to 2001 in Sheppard 2002). During 2002–2006, eelgrass in Newman Sound expanded into formerly unvegetated areas (Warren 2007); these areas were not part of our study. We have no detailed knowledge of possible changes in eelgrass landscapes for our Fleming survey sites, as suitable aerial photographs were only available in 2001. However, anecdotal records taken during the Fleming survey in 1995 and 1996 suggested that there was no change in eelgrass percent cover during the period 1995 to 2001. Eelgrass in Newfoundland coastal waters had been stable or expanding in spatial distribution during our period of study (Hanson 2004).

**Aerial photography.** Aerial photographs of the 8 Newman Sound sites were taken in August 2000 and July 2001, and at 14 Fleming survey sites in July 2001, in order to assess eelgrass spatial structural

characteristics. Photographs were taken from a single-engine Cessna (2000) or deHavilland Beaver (2001) floatplane at altitudes between 230 and 250 m. Photographs were taken during monthly low-tide periods to allow greater visibility of substrate and vegetative cover. Flights were executed as near midday as possible, when surface glare and winds were at a minimum. Images were taken with a 35 mm Pentax SF10 camera fitted with a 28 to 80 mm Pentax-F zoom lens (set at 50 mm), and with both haze and polarising filters to reduce water-surface glare.

Prior to aerial photography in Newman Sound, 3 fluorescent orange plywood markers (0.6 × 0.6 m) were placed at all 8 sites to indicate the seining area, permit calculation of the area covered by the image, and correct for the camera angle (the maximum error due to

camera angle was determined by Hammond (2003) to be <3%). Two markers were fastened to the shore at the high-tide mark 25 m apart. The third marker was secured 50 m offshore by a length of rope tied to a concrete block. Floating at the water's surface, the offshore marker was placed such that it formed a right angle triangle with the onshore markers (Wells 2002). At all 14 Fleming survey sites, the seining area and landmarks for editing images were identified using physical site characteristics, determined during ground truthing.

Aerial photographs were developed to compact discs with the highest resolution of 2048 × 3072 pixels. Photos were edited and rectified to a square grid with 1 m intervals in Adobe Photoshop 5.5.

#### Estimating eelgrass characteristics by box counting.

A box-counting technique (Sugihara & May 1990) was employed to quantify spatial characteristics of eelgrass (area and perimeter) at several resolutions from the aerial photographs. A grid containing 3600 boxes (1 box = 1 m<sup>2</sup>) was positioned over each digital photograph. We reproduced by hand 2 hard-copy replicas of each image on grids of the same dimension. On these copies, the presence or absence of eelgrass area (area measurement), and the presence or absence of eelgrass perimeter (perimeter measurement) were recorded. Eelgrass perimeter (or eelgrass edge) was defined as the visible presence of a boundary between

eelgrass and non-eelgrass habitat within a box. Grids of lower resolution (i.e. fewer boxes) were placed over the drawings, and the number of boxes containing area and perimeter were counted for resolutions of 1, 4, 9, 16, 25, 36, 100, 225, 400 and 900 m<sup>2</sup>. Eelgrass perimeter was estimated at each resolution by multiplying the number of boxes containing eelgrass perimeter with the length (m) of the side of the box. Eelgrass area was estimated at each resolution by multiplying the number of boxes containing eelgrass area by the area (m<sup>2</sup>) of the box (Table 1). Eelgrass was considered 'present' if it occupied any percentage area of the box (>0).

**Multi-scale measures of structural complexity.** We used perimeter and area estimates of eelgrass to produce multi-scale measures of spatial complexity for the 8 Newman Sound and 14 Fleming survey sites. Two of these measures were the fractal dimensions of perimeter ( $D_p$ ) and area ( $D_A$ ), which describe eelgrass perimeter convolution, and area patchiness, respectively (Table 1).  $D_p$  was calculated from the slope (scaling coefficient) of the log-log regression of eelgrass perimeter and box length (resolution).  $D_A$  was determined in a similar fashion from the log-log regression of eelgrass area and box area (resolution). As a third measure of spatial complexity, we calculated the scaling coefficient ( $\beta_{P/A}$ ), from a log-log plot describing how the ratio of perimeter:area (using the perimeter and area esti-

Table 1. Parameters and variables used in multi-scale analysis of eelgrass site structural complexity

Parameters and variables	Symbol	Definition	Mathematical definition
Length	$L$	Extent of 1 side of a box at 1 resolution in the box-counting technique protocol	
	$L_o$	Extent of 1 side of a box at a different resolution in the box-counting technique protocol	
Perimeter	$P$	Length of boundary between eelgrass and non-eelgrass substrate for 1 resolution	$P = (L)(\text{no. of boxes at resolution } L)$
	$P_o$	Length of boundary between eelgrass and non-eelgrass substrate for a different resolution	$P_o = (L_o)(\text{no. of boxes at resolution } L)$
Area	$A$	2-dimensional eelgrass surface included by an eelgrass/non-eelgrass boundary for 1 resolution	$A = (L^2)(\text{no. of boxes at resolution } L)$
	$A_o$	2-dimensional eelgrass surface included by an eelgrass/non-eelgrass boundary for a different resolution	$A_o = (L_o^2)(\text{no. of boxes at resolution } L_o)$
Fractal dimension of perimeter	$D_p$	Equal to 1 minus the scaling coefficient describing how perimeter estimates change with scale. Indicates edge convolution	$\frac{P}{P_o} = \left(\frac{L}{L_o}\right)^{1-D_p}$
Fractal dimension of area	$D_A$	Equal to 1 minus the scaling coefficient describing how area estimates change with scale. Indicates area patchiness	$\frac{A}{A_o} = \left(\frac{L}{L_o}\right)^{1-D_A}$
Scaling coefficient of P:A vs. resolution	$\beta_{P/A}$	Scaling coefficient describing how perimeter:area estimates change with scale. Indicates convolution and patchiness	$\frac{P:A}{P_o:A_o} = \left(\frac{L}{L_o}\right)^{\beta_{P/A}}$

mates calculated at each scale) changes with scale of measurement (Table 1). Note that  $\beta_{P/A}$  does not entail regression against a variable measured with error, a problem that can lead to biased estimates as with  $\beta_{A=f(P)}$ . Also,  $\beta_{P/A}$  does not involve part-whole correlation (e.g. Jackson et al. 1990) because the perimeter:area ratio was regressed against box size, not against either component of the ratio. In the absence of part-whole correlation, the use of a ratio is a legitimate and well-recognised technique for reducing the residual or error variance (Cochran 1977). As  $\beta_{P/A}$  is a negative number, we report absolute values. To further understand the behaviour of this measure, we investigated how it relates to, and can be derived from, known values of  $D_P$  and  $D_A$ .

Landscape features (e.g. perimeter or area) usually display fractal properties across a limited range of resolutions (Johnson et al. 1995). Across the 10 resolutions utilised, a 'scaling region' (Kenkel & Walker 1996) was determined for each site and included the resolutions over which eelgrass area estimates changed linearly with box size on a log-log scale. For each site, the scaling region defined the resolutions used to compute all 3 multi-scale complexity measures.

**Measuring juvenile fish densities.** Age-0 juvenile fish densities at all Newman Sound and Fleming survey sites were estimated via a 25 m demersal beach seine. The seine was deployed 55 m from shore from a 6 m boat that motored out from the shore and back. It was retrieved by 2 individuals on shore standing 16 m apart. Pulled along the seafloor, the seine samples the bottom 2 m of the water column, covering approximately 880 m<sup>2</sup> of demersal habitat. SCUBA divers have observed that the seine catches 95% of the fish in its path when deployed in this manner (Gotceitas et al. 1997) and induces negligible mortality. For a detailed description of the seine specifications and deployment, see Schneider et al. (1997b).

Collected fish were transferred to containers of seawater, counted, measured, and identified to species. Fish were measured to standard length (most anterior point to caudal peduncle; Table 2) then aged by applying previously established age-length relationships for these species (Gregory et al. 2006). Fish were released to their site of capture following sorting.

We collected fish density data from the 8 Newman Sound sites on a bi-weekly basis for the month of September from 1998 to 2002 (Gregory et al. 2006). Fish density data collected during 1999 and 2000 at Buckley's Cove (BC) and Dockside (DS) were not included due to a concurrent habitat manipulation experiment (Laurel et al. 2003b). Fish density data from 14 Fleming survey sites were collected in September and October of 1996 and 1997 (Methven et al. 2003), and in 2001 in conjunction with an aerial survey. Fleming survey sites

Table 2. *Gadus morhua*, *G. ogac*, and *Urophycis tenuis*. Mean standard lengths from the month of September from 1998 to 2002 in 8 Newman Sound (NS) survey sites and 14 Fleming Survey (FS) sites

Species	Survey	Year	Standard length (mm) mean $\pm$ SD	n
<i>G. morhua</i>	NS	1998	48.00 $\pm$ 5.39	5
	NS	1999	60.90 $\pm$ 10.06	129
	NS	2000	61.17 $\pm$ 8.69	393
	NS	2001	63.82 $\pm$ 7.04	207
	NS	2002	54.67 $\pm$ 6.24	384
	FS	2001	59.14 $\pm$ 11.02	504
<i>G. ogac</i>	NS	1998	61.00 $\pm$ 7.21	3
	NS	1999	83.30 $\pm$ 9.70	145
	NS	2000	81.56 $\pm$ 7.90	416
	NS	2001	69.99 $\pm$ 5.80	1322
	NS	2002	76.23 $\pm$ 8.46	757
<i>U. tenuis</i>	NS	1998	98.69 $\pm$ 17.59	195
	NS	1999	97.40 $\pm$ 20.15	196
	NS	2000	94.12 $\pm$ 14.23	532
	NS	2001	93.99 $\pm$ 13.69	797
	NS	2002	90.91 $\pm$ 16.74	422

were sampled via 3 seine hauls site<sup>-1</sup>, once a year. Atlantic cod density data were available for both surveys, whereas Greenland cod and white hake data were only available from the Newman Sound survey.

**Relating juvenile fish density to habitat structural complexity.** We used density (if present) to investigate the relationships between Age-0 juvenile Atlantic cod density and the eelgrass complexity indices  $D_P$ ,  $D_A$  and  $\beta_{P/A}$ . The relationships of Age-0 Greenland cod *Gadus ogac* and Age-0 white hake *Urophycis tenuis* to  $\beta_{P/A}$  (Newman Sound survey) were investigated in the same way. Densities were computed as number of fish per seine haul (number of fish per 880 m<sup>2</sup>). We analysed both surveys separately, as sampling intensity was greater in the Newman Sound survey than the Fleming survey (3 sampling dates yr<sup>-1</sup> for 5 yr in Newman Sound sites versus 1 sampling date yr<sup>-1</sup> for 3 yr at Fleming sites).

We regressed fish density against each complexity measure in a quadratic model, where the explanatory variable appears as  $x + x^2$ , the simplest possible model of a response variable reaching a maximum at some intermediate value of  $x$ , the measure of complexity. Regressions were executed within the framework of the generalised linear model (McCullagh & Nelder 1989). We used a log link, which allows estimation of a logarithmic relation without transformation of the response variable. We began analysis with a normal error, consistent with prevailing practice in ordinary least-squares regression. Residuals were examined to ensure they were homogeneous, independent and normal (Neter et al. 1990). If these assumptions were vio-



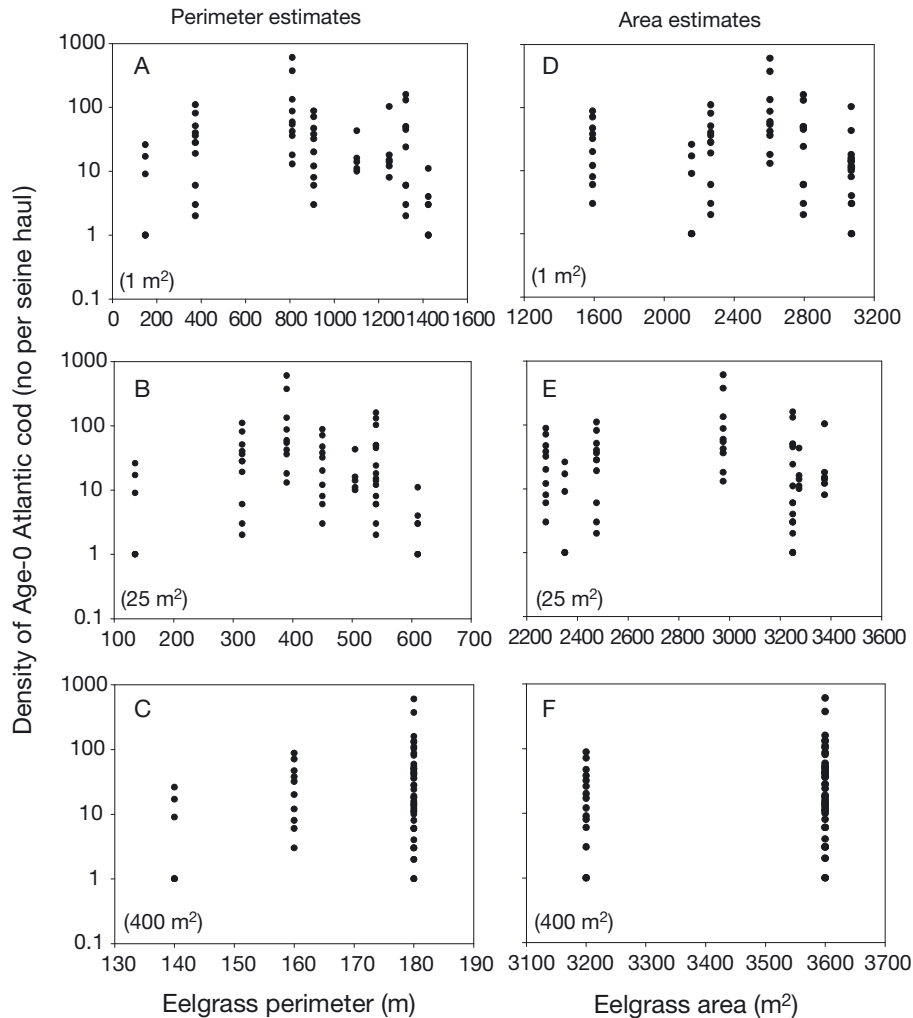


Fig. 2. *Gadus morhua*. Relationships between Age-0 density and (A–C) eelgrass perimeter and (D–F) eelgrass area as estimated at 3 resolutions (1, 25, and 400 m<sup>2</sup>) for 8 Newman Sound sites in September of all years 1998 to 2002

lated, a gamma error structure was then used. In all cases this alternative error structure resolved the violations of assumptions when a normal error was not warranted. Analyses were performed using the Genmod procedure in SAS (Release 6.03). The tolerance of Type I error was  $\alpha = 0.05$ .

## RESULTS

### Density of Age-0 Atlantic cod vs. single-scale measures of eelgrass structure

The relationships between Age-0 Atlantic cod densities and both eelgrass perimeter and eelgrass area differed depending on the scale of measurement (Fig. 2). Fish density appeared to increase with perimeter and

area at 400 m<sup>2</sup> resolution, but at 1 m<sup>2</sup> resolution appeared to be parabolic with an intermediate optimum or showed no pattern with respect to perimeter and area, respectively. The change in pattern can be attributed to condensation of information as box size increases.

### Multi-scale analysis of eelgrass habitat structure

Log-log regressions of perimeter, area and the perimeter:area ratio versus scale of measurement produced an estimate of  $D_P$ ,  $D_A$  and  $\beta_{P/A}$ , respectively, for each of the 8 Newman Sound and 14 Fleming survey sites. Fig. 3 shows the results for Mistaken Cove (Site MI). The plots from other sites were similar in conformity to a straight line and close fit. Values of  $D_P$  can

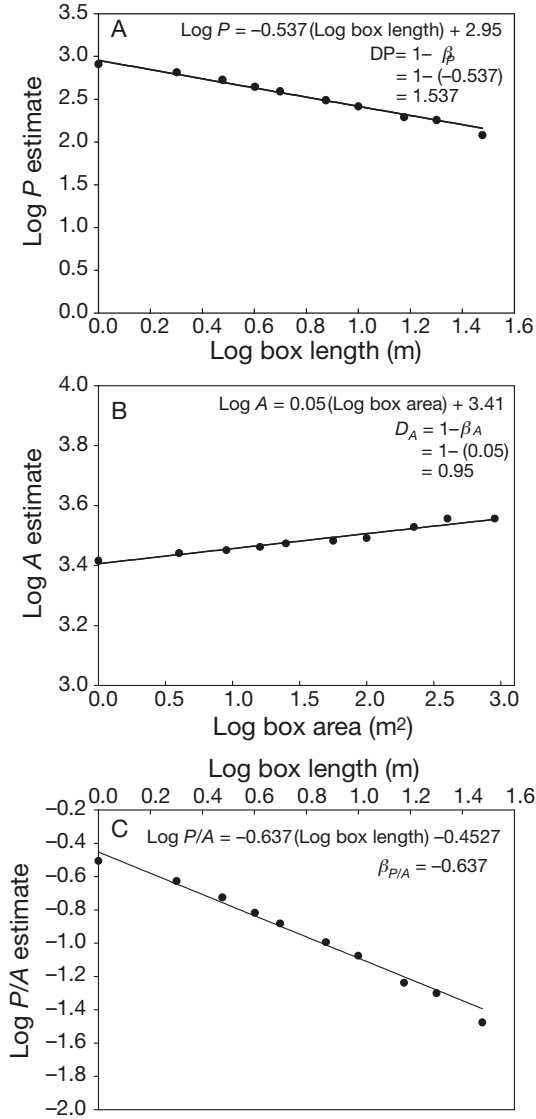


Fig. 3. Example of log-log plots of (A) perimeter vs. resolution, (B) area vs. resolution, and (C) perimeter:area vs. resolution using data taken from Mistaken Cove (Site MI) for illustrative purposes

range from  $1 < D_p < 2$  (Mandelbrot 1983, Barnsley 1988), with increasing values representing sites that have increasingly convoluted eelgrass/non-eelgrass boundaries. Values of  $D_p$  ranged from 1.07 to 1.67 in the Newman Sound survey and from 1.16 to 1.73 in the Fleming survey (Table 3). Values of  $D_A$  can range from  $0 < D_A < 1$  (Mandelbrot 1983, Barnsley 1988). Values approaching zero represent sites with an increasingly sparse, discontinuous eelgrass arrangement. Values approaching 1 represent sites that are increasingly uniform and continuous, while intermediate values represent sites that are patchy. Values of  $D_A$  ranged

Table 3. Values of multi-scale eelgrass structural complexity measures, and maximum scaling region resolution for 8 Newman Sound survey (NS) sites and 14 Fleming survey (FS) sites. BB: Big Brook, BC: Buckley's Cove, DS: Dockside, HC: Heffern's Cove, MC: Minchin's Cove, MI: Mistaken Cove, SB: South Broad Cove, WR: White Rock

Survey	Site	$D_A$	$D_p$	$ \beta_{P/A} $	Maximum scaling region resolution (m <sup>2</sup> )
NS	BB	1.07	0.93	0.22	900
	DS	1.58	0.97	0.61	100
	WR	1.63	0.95	0.72	225
	MI	1.54	0.95	0.64	400
	BC	1.53	0.97	0.59	100
	HC	1.26	0.94	0.39	400
	MC	1.67	0.97	0.74	225
	SB	1.64	0.88	0.87	900
FS	18	1.46	0.86	0.74	400
	32	1.19	0.76	0.67	400
	34	1.49	0.95	0.59	400
	46	1.73	0.94	0.85	400
	52	1.50	0.86	0.78	900
	53	1.24	0.80	0.64	900
	57	1.42	0.91	0.60	400
	58	1.35	0.84	0.67	900
	68	1.62	0.92	0.79	900
	70	1.30	0.97	0.37	36
	76	1.41	0.82	0.77	900
	80	1.57	0.93	0.50	225
	81	1.16	0.74	0.69	400
	84	1.30	0.92	0.46	225

from 0.88 to 0.97 in the Newman Sound survey and from 0.74 to 0.94 in the Fleming survey (Table 3). While sites in the Fleming survey spanned a broader range of values of  $D_A$  than those in the Newman Sound survey, ranges in both surveys suggest sites with limited patchiness.

Absolute values of  $\beta_{P/A}$  ranged from 0.22 to 0.87 in the Newman Sound survey, and from 0.37 to 0.85 in the Fleming survey (Table 3). Larger values of  $|\beta_{P/A}|$  represent sites whose estimate of the perimeter:area ratio changes greatly with scale, and therefore quantify eelgrass arrangements of greater complexity.

### Relationships among scaling exponents

The scaling coefficient  $\beta_{A=f(P)}$ , estimated by log-log regression of area on perimeter (Lovejoy 1982), can result in biased estimates of the attendant statistic  $r^2$  and p-values because perimeter is measured with error. This source of bias can be removed by deriving the relationship of  $\beta_{A=f(P)}$  to  $D_p$  and  $D_A$  (estimated by regression against a fixed variable, box size), then substituting to obtain the estimate of structural complexity  $\beta_{A=f(P)}$ .

Because

$$\frac{A}{A_o} = \left(\frac{P}{P_o}\right)^{\beta_{A=f(P)}} \quad (1)$$

$$\frac{P}{P_o} = \left(\frac{L}{L_o}\right)^{1-D_p} \quad \text{and} \quad \frac{A}{A_o} = \left(\frac{L^2}{L_o^2}\right)^{1-D_A} \quad (2, 3)$$

then

$$\left(\frac{L^2}{L_o^2}\right)^{1-D_A} = \left[\left(\frac{L}{L_o}\right)^{1-D_p}\right]^{\beta_{A=f(P)}} \quad (4)$$

and

$$\left(\frac{L}{L_o}\right)^{2-2D_A} = \left[\left(\frac{L}{L_o}\right)^{1-D_p}\right]^{\beta_{A=f(P)}} \quad (5)$$

The bases of each term being the same, Eq. (5) can be expressed in exponents, yielding the solution for  $\beta_{A=f(P)}$  as

$$\beta_{A=f(P)} = 2\left(\frac{1-D_A}{1-D_p}\right) \quad (6)$$

The relationship of  $\beta_{A=f(P)}$  to  $D_p$  and  $D_A$  is clearly non-linear.

The relationship of the perimeter:area ratio to box size can be shown to have a linear relationship to the scaling exponents for perimeter and area  $D_p$  and  $D_A$ .

Since:

$$\frac{P:A}{P_o:A_o} = \left(\frac{L}{L_o}\right)^{\beta_{P/A}} \quad (7)$$

then

$$\left(\frac{P}{A}\right)\left(\frac{A_o}{P_o}\right) = \left(\frac{L}{L_o}\right)^{\beta_{P/A}} \quad (8)$$

and

$$\left(\frac{P}{P_o}\right)\left(\frac{A_o}{A}\right) = \left(\frac{L}{L_o}\right)^{\beta_{P/A}} \quad (9)$$

Substituting for  $P/P_o$  (Table 1) and reciprocating  $A_o/A$ ,

$$\left(\frac{L}{L_o}\right)^{1-D_p} \left(\frac{A}{A_o}\right)^{-1} = \left(\frac{L}{L_o}\right)^{\beta_{P/A}} \quad (10)$$

Now substituting for  $A/A_o$  (Table 1) gives

$$\left(\frac{L}{L_o}\right)^{1-D_p} \left[\left(\frac{L}{L_o}\right)^{2-2D_A}\right]^{-1} = \left(\frac{L}{L_o}\right)^{\beta_{P/A}} \quad (11)$$

As the bases of each term are the same, the exponents are related as:

$$(1-D_p) + (-2+2D_A) = \beta_{P/A} \quad (12)$$

and

$$2D_A - D_p - 1 = \beta_{P/A} \quad (13)$$

A generalisation of this derivation can be found in Schneider (2009, p. 355). Plots of  $\beta_{P/A}$  and  $\beta_{A=f(P)}$  across various values of  $D_p$  and  $D_A$  (Fig. 4) show that, as expected,  $\beta_{P/A}$  changed monotonically with respect to  $D_p$  and  $D_A$ . Plots of  $\beta_{A=f(P)}$  exhibited non-monotonic behaviour that can result in a single value representing sites of very different structural complexity (Fig. 5).

### Density of Age-0 fish vs. multi-scale measures of eelgrass structural complexity

For both surveys, Age-0 Atlantic cod data were combined for all years and compared to each of the 3 multi-scale structural complexity measures,  $D_p$ ,  $D_A$  and  $|\beta_{P/A}|$ , in the following model:

$$D = e^{\mu} + \varepsilon \quad (14a)$$

$$\mu = \beta_o + \beta_C \cdot C + \beta_{C^2} \cdot C^2 + \beta_Y \cdot Y + \beta_{Y \cdot C} \cdot Y \cdot C + \beta_{Y \cdot C^2} \cdot Y \cdot C^2 \quad (14b)$$

where  $D$  = cod density (no. of cod seine haul<sup>-1</sup>),  $C$  = complexity index ( $D_p$ ,  $D_A$  or  $|\beta_{P/A}|$ ) and  $Y$  = year. Initial analysis with a normal error structure showed that errors were not homogeneous. To address this we used a gamma error structure, which resulted in homogeneous errors. This allowed us to compute Type I error (p-values) from a chi-squared distribution (McCullagh & Nelder 1989). Neither of the interaction terms,  $\beta_{Y \cdot C} \cdot Y \cdot C$  and  $\beta_{Y \cdot C^2} \cdot Y \cdot C^2$ , nor the year term  $\beta_Y \cdot Y$  were significant for each of the 3 analyses in the Newman Sound survey, and therefore were removed from further analysis (Table 4). The same was true of the analyses for  $D_A$  and  $|\beta_{P/A}|$  in the Fleming survey (Table 4). In these cases, we used a gamma distribution and tested the model:

$$D = e^{\mu} + \varepsilon \quad (15a)$$

$$\mu = \beta_o + \beta_C \cdot C + \beta_{C^2} \cdot C^2 \quad (15b)$$

Significant  $\beta_{Y \cdot C} \cdot Y \cdot C$  and  $\beta_{Y \cdot C^2} \cdot Y \cdot C^2$  interactions existed for the Fleming survey data when the complexity measure was  $D_p$ .

The relationship between cod density and eelgrass perimeter convolution ( $D_p$ ) was inconsistent between surveys, and therefore across geographical scales. The relationship of cod density to  $D_p$  in the Newman Sound survey yielded a significant negative (downward opening) quadratic ( $\beta_{(D_p)}$ :  $\chi^2 = 16.84$ ,  $p < 0.0001$ ,  $\beta_{(D_p^2)}$ :  $\chi^2 = 16.36$ ,  $p < 0.0001$ ; Table 5, Fig. 6). In the larger-scale Fleming survey, the relationship of cod density to  $D_p$  depended on year. In 2001, the significant relationships produced a positive (upward opening) quadratic ( $\beta_{(D_p)}$ :  $\chi^2 = 9.33$ ,  $p = 0.0023$ ,  $\beta_{(D_p^2)}$ :  $\chi^2 = 8.67$ ,  $p = 0.0032$ ; Table 5); however, no significant quadratic or linear relationship was present in 1996 ( $\beta_{(D_p)}$ :  $\chi^2 = 3.03$ ,  $p = 0.0815$  and  $\beta_{(D_p^2)}$ :  $\chi^2 = 3.53$ ,  $p = 0.0602$ , respectively) or 1997 ( $\beta_{(D_p)}$ :  $\chi^2 = 2.04$ ,  $p = 0.1530$  and  $\beta_{(D_p^2)}$ :  $\chi^2 = 2.27$ ,  $p = 0.1317$ , respectively).

A similar inconsistency between surveys (geographical scales) was evident in the relationship between cod density and  $D_A$ , the measure of eelgrass area patchiness. We observed a significant negative quadratic relationship between cod density and  $D_A$  in the Newman Sound survey ( $\beta_{(D_A)}$ :  $\chi^2 = 5.43$ ,  $p = 0.0197$ ,  $\beta_{(D_A^2)}$ :  $\chi^2 = 5.41$ ,  $p = 0.0201$ ; Table 5, Fig. 6) while the



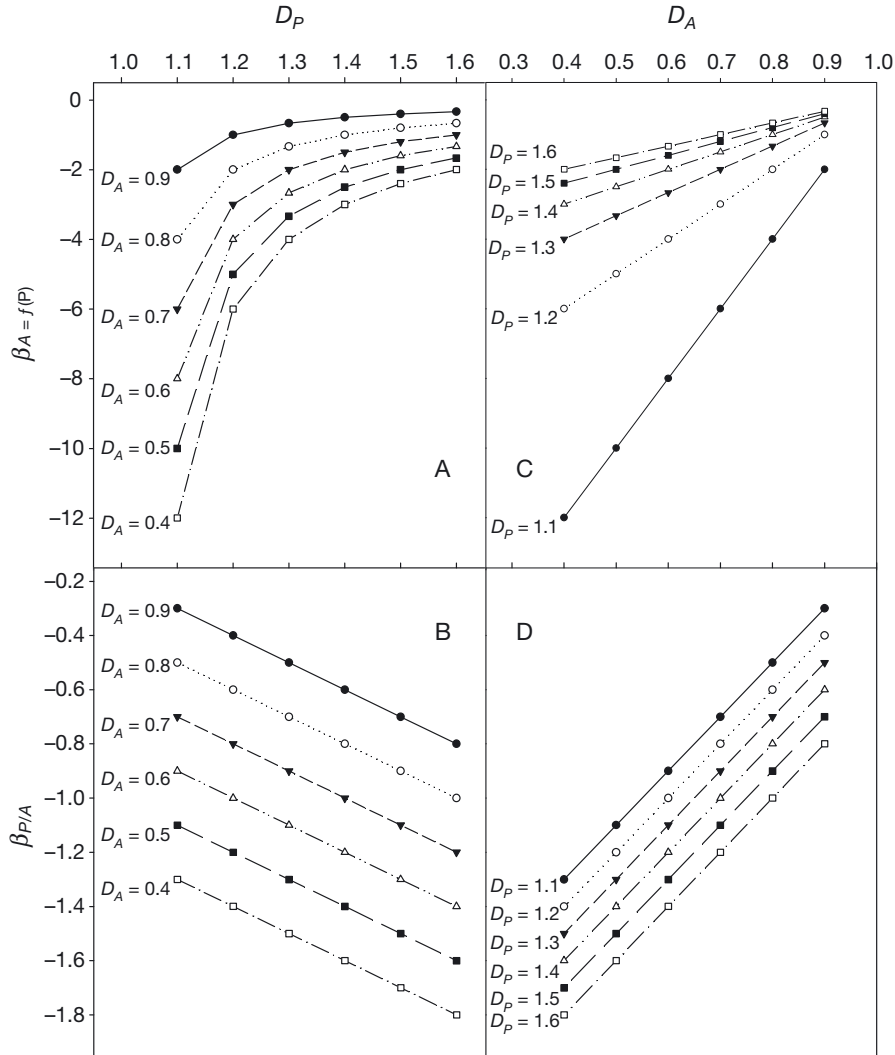


Fig. 4. Behaviour of (A,B)  $\beta_{A=f(P)}$  and (C,D)  $\beta_{P/A}$  for varying values of (A,C)  $D_P$  and (B,D)  $D_A$

Fleming survey data revealed a significant positive quadratic ( $\beta_{(D_A)}$ :  $\chi^2 = 15.77$ ,  $p < 0.0001$ ,  $\beta_{(D_A)^2}$ :  $\chi^2 = 15.30$ ,  $p < 0.0001$ ; Table 5, Fig. 6).

Consistent, significant, negative quadratic relationships were found between cod density and  $|\beta_{P/A}|$  for both surveys (Newman Sound survey:  $\beta_{(|\beta_{P/A}|)}$ :  $\chi^2 = 9.81$ ,  $p = 0.0017$ ,  $\beta_{(|\beta_{P/A}|)^2}$ :  $\chi^2 = 9.02$ ,  $p = 0.0027$ ; Fleming survey:  $\beta_{(|\beta_{P/A}|)}$ :  $\chi^2 = 7.75$ ,  $p = 0.0054$ ,  $\beta_{(|\beta_{P/A}|)^2}$ :  $\chi^2 = 7.67$ ,  $p = 0.0056$ ; Table 5, Fig. 7). These analyses demonstrated an intermediate maximum of Age-0 Atlantic cod density with respect to habitat complexity at 2 spatial scales of sampling, consistent with the IOH.

We extended the test of the IOH by investigating the relationships between  $|\beta_{P/A}|$  and Age-0 densities of 2 sympatric species, Greenland cod *Gadus ogac* and white hake *Urophycis tenuis* using Newman Sound survey data and the same model (Eq. 14). As in the pre-

vious analyses, a normal error distribution was not appropriate and a suitable gamma distribution was employed instead. Again, neither of the interaction terms  $\beta_{Y \cdot C} \cdot Y \cdot C$  and  $\beta_{Y \cdot C^2} \cdot Y \cdot C^2$  nor the year term  $\beta_Y \cdot Y$  were significant (Table 4), and so the reduced model (Eq. 15) with a gamma distribution was used to test for significance. Similar to the Atlantic cod data, the Greenland cod density- $|\beta_{P/A}|$  relationship produced a significant, negative quadratic ( $\beta_{(|\beta_{P/A}|)}$ :  $\chi^2 = 10.73$ ,  $p = 0.0011$ ,  $\beta_{(|\beta_{P/A}|)^2}$ :  $\chi^2 = 13.71$ ,  $p = 0.0002$ ; Table 5, Fig. 7).

The complete model (Eq. 14) with a gamma error distribution was applied to the white hake density- $|\beta_{P/A}|$  relationship. Neither of the interaction terms nor the year term were significant (Table 4), and so the truncated model (Eq. 15) was applied instead, where a normal error distribution was found to be appropriate. Using this model, and like Atlantic cod and Green-

land cod, the white hake density- $|\beta_{P/A}|$  relationship yielded a significant, negative, parabolic result ( $\beta(|\beta_{P/A}|)$ :  $\chi^2 = 11.01$ ,  $p = 0.0009$ ,  $\beta(|\beta_{P/A}|^2)$ :  $\chi^2 = 12.28$ ,  $p = 0.0005$ ; Table 5, Fig. 7).

White hake settled in Newman Sound prior to either cod species in the years of the present study (Ings et al. 2008). Consequently, they were larger than cod by September, and hence, may not be comparable with respect to habitat use. To account for this possibility, we tested whether or not the relationship of white hake

density to  $|\beta_{P/A}|$  was the same in August (when white hake would be a comparable size to cod in September) using a quadratic model based on a log link:

$$D = e^{\mu} + \varepsilon \quad (16a)$$

$$\mu = \beta_o + \beta_C \cdot C + \beta_{C^2} \cdot C^2 + \beta_M \cdot M + \beta_{M \cdot C} \cdot M \cdot C + \beta_{M \cdot C^2} \cdot M \cdot C^2 \quad (16b)$$

where  $C$  = complexity index (in this case,  $|\beta_{P/A}|$ ) and  $M$  = month (August or September). The model was executed with a normal error distribution. The patterns in August and September differed significantly ( $\beta_{M \cdot C^2}$ :  $\chi^2 = 9.38$ ,  $p = 0.0022$ ), and (using Eq. 15) there was no significant linear or quadratic relationship between white hake density and  $|\beta_{P/A}|$  in August ( $\beta(|\beta_{P/A}|)$ :  $\chi^2 = 0.28$ ,  $p = 0.5963$ ,  $\beta(|\beta_{P/A}|^2)$ :  $\chi^2 = 1.68$ ,  $p = 0.1952$ ).

## DISCUSSION

Consistent with the IOH, the density of Age-0 Atlantic cod in Newfoundland waters was parabolically related to eelgrass site complexity, as measured by a scaling exponent  $\beta_{P/A}$  that includes perimeter convolution and degree of patchiness. This relationship held at 2 different geographical scales, thus addressing a key research need: verification of models at more than 1 scale (Boström et al. 2006). The relationship applied to juveniles of 2 co-occurring species, Greenland cod and white hake, during the month of September. The density of juvenile Atlantic cod was not related to single-scale estimates of eelgrass perimeter or area, a multi-scale measure of eelgrass perimeter convolution ( $D_p$ ), or a multiscale measure of eelgrass area patchiness ( $D_A$ ).

Our results are restricted to a single month (September) when all 3 fish species are abundant as juveniles and eelgrass is present in abundance. In this area, which is subject to ice scour and strong wave action in the winter, eelgrass is an annually consistent structural feature of the seafloor only in summer and through the autumn. We restricted our analysis to seagrass beds, which at this latitude consist of a single species. Our results should apply to other vegetated habitats with which cod associate at this latitude, notably kelp (Schneider et al. 2008). Our results are from the northern edge of the range of white hake. Accounts of this species occur from more southerly latitudes (e.g. Macdonald et al. 1984) where it is a common member of the inshore fish community.

### Measuring habitat configuration

Our study demonstrates that density of marine fish, such as Atlantic cod, cannot consistently be related to single-scale measurements of seagrass configuration.

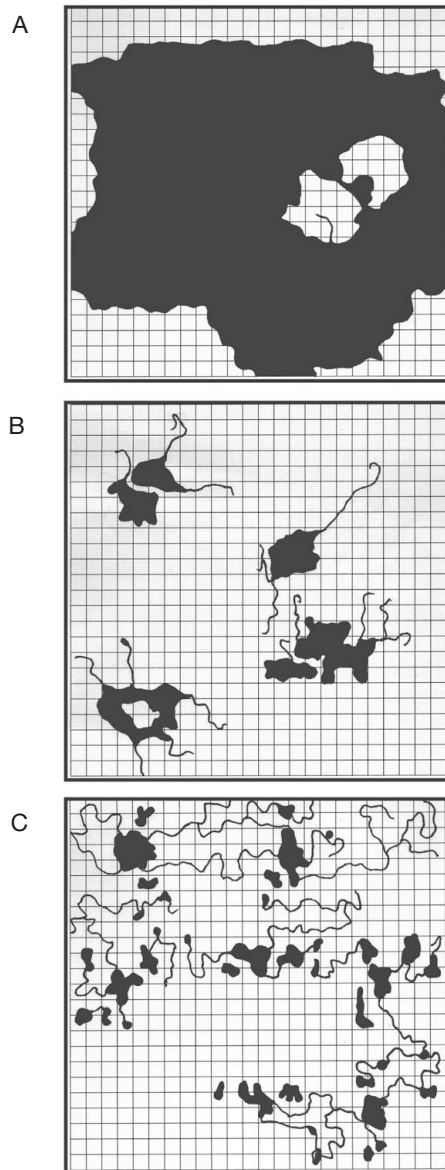


Fig. 5. Illustration of single  $|\beta_{A=f(P)}|$  representing sites of different structural complexity, drawn at the same spatial scale (box size same in all panels). Shaded areas and lines represent eelgrass presence. Eelgrass site structural complexity differs dramatically in panels A, B and C, however each panel is represented by the same value of  $|\beta_{A=f(P)}|$ .  $|\beta_{P/A}|$  values are different for each panel

Table 4. *Gadus morhua*, *G. ogac*, and *Urophycis tenuis*. p-values and  $\chi^2$  values for analyses investigating the relationship between Age 0 fish density ( $D$ ) and 1 of 3 eelgrass complexity measures ( $C$ ) using the model:

$$D = e^{\beta_0 + \beta_C \cdot C + \beta_{C^2} \cdot C^2 + \beta_Y \cdot Y + \beta_{Y \cdot C} \cdot Y \cdot C + \beta_{Y \cdot C^2} \cdot Y \cdot C^2} + \epsilon$$

where  $Y$  = year. Residuals were homogenous in all executions. Results in **bold** are statistically significant. NS: Newman Sound survey, FS: Fleming survey

Species Survey	C	df	$Y \cdot C^2$		$Y \cdot C$		Y		
			$\chi^2$	p	$\chi^2$	p	$\chi^2$	p	
<i>G. morhua</i>	NS	$D_P$	64	2.11	0.715	2.26	0.6882	2.47	0.6499
		$D_A$	64	1.87	0.7594	1.84	0.7656	1.81	0.7708
		$\beta_{P/A}$	64	7.87	0.0964	7.97	0.0926	6.49	0.1656
	FS	$D_P$	28	<b>7.33</b>	<b>0.0256</b>	<b>8.31</b>	<b>0.0157</b>	<b>9.32</b>	<b>0.0095</b>
		$D_A$	28	2.17	0.3383	2.41	0.3001	2.65	0.266
		$\beta_{P/A}$	28	0.67	0.7145	1.16	0.5602	1.77	0.4137
<i>G. ogac</i>	NS	$\beta_{P/A}$	73	1.91	0.7526	3.04	0.5506	4.09	0.3938
		$\beta_{P/A}$	74	1.47	0.8313	0.99	0.912	0.63	0.9599

Our results may thus explain the inconsistent findings from several studies on the relationship of marine animal density and/or survival to single-scale measures of seagrass habitat configuration (Boström et al. 2006). For example, Bell et al. (2001) found no relationship between fish density and patch size, amphipods and patch size, or infaunal polychaetes and interior/edge habitat (where a seagrass edge is defined as the interface between a seagrass and non-vegetated habitat). Contrary to Bell et al. (2001), Bologna & Heck (2002) reported that amphipod and polychaete densities were significantly greater at seagrass edges than interiors. In a study concerning juvenile blue crab survival and abundance, Hovel & Lipcius (2002) found that densities were greater in patch interiors than edges, and increased with shoot density, but that there was no relationship to patch size. They also found that survival of crab was reduced in isolated

patches and decreased with shoot density; the latter result was attributed to high incidence of predation by older conspecifics. Patch size, however, was found to affect tethered juvenile cod survival, as Laurel et al. (2003a) found that predation rates were negatively correlated with the size of artificial eelgrass patches. The inconsistent findings of these single-scale studies make comparisons to and interpretation of the literature difficult. The present study found that relating fish density to a multi-scale estimate of eelgrass configuration yielded consistent results for 3 species.

Remarkably few studies use multi-scale metrics of patchiness or edge convolution, such as  $D_P$ ,  $D_A$  or  $\beta_{P/A}$ , despite the call to move from individual patch studies (such as those listed in the previous paragraph) to patches in landscapes (Frost et al. 1999, Hokit et al. 1999, Bell et al. 2001, Boström et al. 2006, Jackson et al. 2006). We identified only 2 studies that examined the effect of a fractal measure of seagrass complexity on its associated faunal community (Turner et al. 1999, Salita et al. 2003). Turner et al. (1999) showed that a fractal measure of seagrass perimeter contributed to an overall canonical correlate of invertebrate community structure with environmental factors. However, the same study did not directly measure the relationship of faunal abundance or community structure to a fractal measure. Salita et al. (2003), in an investigation concerning the effects of seagrass configuration on fish communities, reported a statistically significant, positive parabolic relationship between fish abundance (% fish caught relative to control site) and a composite measure of

Table 5. *Gadus morhua*, *G. ogac*, and *Urophycis tenuis*. Parameter estimates and standard errors (SE) for statistically significant analyses investigating the relationship between Age-0 fish density ( $D$ ) and 1 of 3 eelgrass complexity measures ( $C$ ) using the model  $D = e^{(\beta_0 + \beta_C \cdot C + \beta_{C^2} \cdot C^2)} + \epsilon$ . All analyses were executed with a gamma error distribution, except for *U. tenuis*, which used a normal error distribution. NS: Newman Sound survey, FS: Fleming survey

Species	Survey	C	df	Year	C		C <sup>2</sup>		y-axis intercept	
					$\beta_C$	SE	$\beta_{C^2}$	SE		SE
<i>G. morhua</i>	NS	$D_P$	64	2001	69.48	15.59	-24.7	5.71	-44.18	10.39
		$D_A$	64		1004.98	403.45	-543.62	218.62	-460.12	185.92
		$\beta_{P/A}$	64		15.25	4.30	-12.56	3.75	-0.47	1.16
	FS	$D_P$	9		-93.32	27.41	31.13	9.88	71.08	18.84
		$D_A$	28		-414.02	87.35	238.58	51.13	180.63	37.06
		$\beta_{P/A}$	28		54.78	14.91	-43.12	12.06	-13.94	4.55
<i>G. ogac</i>	NS	$\beta_{P/A}$	73	13.95	3.83	-13.78	3.31	1.66	1.03	
<i>U. tenuis</i>	NS	$\beta_{P/A}$	74	21.44	6.32	-26.88	7.47	0.07	1.3	

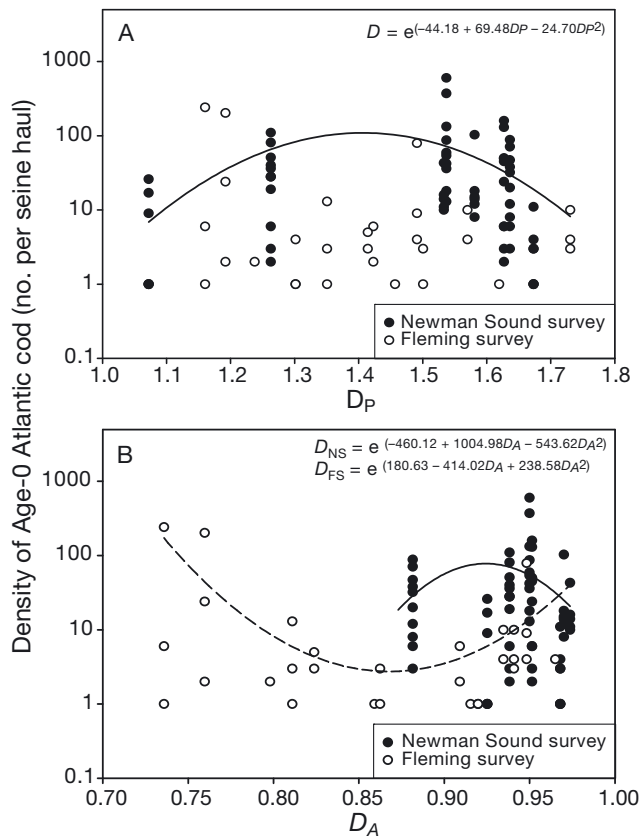


Fig. 6. *Gadus morhua*. Relationship between Age-0 density ( $D$ ) and (A)  $D_P$  or (B)  $D_A$  for both the Newman Sound survey (●) and the Fleming survey (○). In (A), a significant negative quadratic relationship exists for Newman Sound data only. In (B), a significant negative quadratic relationship exists for Newman Sound data (solid line), while a significant positive quadratic relationship exists for Fleming survey data (broken line)

patch configuration ('continuity of vegetation') extracted by principal component analysis of 6 variables. However, of the 6, 'percent cover' had the largest factor weight (0.93) on the first principle component, thus making it difficult to differentiate between the effects of percent cover and configuration in their analysis. Not surprisingly, the relationship of fish abundance to percent cover estimated from their data ( $r^2 = 0.66$  in February and  $r^2 = 0.67$  in June) approaches that for the relationship of abundance to PC1 ( $r^2 = 0.71$  in February and  $r^2 = 0.94$  in June). A reanalysis of their data shows that when the relationship of fish abundance to percent cover is controlled by regression, there was no relationship of fish abundance to the other 5 measures of patch configuration ( $F_{5,4} = 0.81$ ,  $p = 0.599$  in February,  $F_{5,4} = 3.73$ ,  $p = 0.113$  in June). Further analysis showed that there was no relationship of fish density to a principal component based on 5 measures of config-

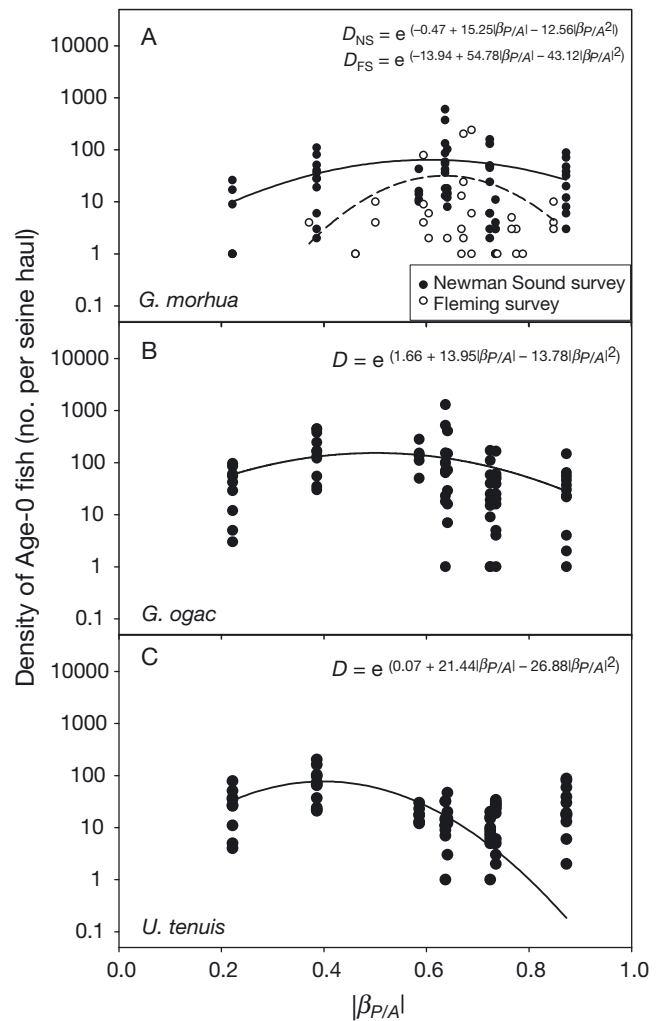


Fig. 7. (A) *Gadus morhua*, (B) *G. ogac*, and (C) *Urophycis tenuis*. Relationship between Age-0 fish densities ( $D$ ) and  $|\beta_{P/A}|$  for both the Newman Sound (●, solid line) and Fleming surveys (○, dashed line). Density data for *G. ogac* and *U. tenuis* were not available from the Fleming surveys

uration, omitting percent cover from the ordination ( $F_{2,7} = 2.2$ ,  $p = 0.181$  in February,  $F_{2,7} = 3.66$ ,  $p = 0.082$  in June).

In other systems, studies that have used fractal analysis to describe habitat have primarily used a measure analogous to  $D_P$  and have found differing effects on the density of the associated fauna. The density of freshwater invertebrate species increased with fractal dimension of stream bottoms (Taniguchi & Tokeshi 2004) but no relationship between resident fauna and fractal dimension of habitat was found in a study on spider diversity in shrub patches (Whitehouse et al. 2002), or a study of barnacle larvae settlement to benthic substrates (Hills et al. 1999). Gastropod density

increased with fractal dimension on rocky intertidal shores, but not in mangrove habitat (Beck 1998).

In the present study, we showed that the scaling exponent  $\beta_{P/A}$  is more informative than estimates of perimeter convolution or area patchiness alone, is statistically sound, and yielded consistent results in 3 different species at 2 geographical scales (in the species where this could be tested).  $D_p$  accurately describes the boundary between both habitat types in these systems (e.g. eelgrass and unvegetated substrate), but provides no information on which side of this boundary the eelgrass lies. Therefore, sites with the same  $D_p$  value can have dramatically different conformations and biological implications. In a mixed-habitat system, interpreting  $D_p$  can best be accomplished in concert with an area measurement of the habitat of interest.  $\beta_{P/A}$  combines both of these elements in a way that is appropriate in terms of the mathematical definitions of perimeter and area, and the biological implications of perimeter:area ratios. Unlike Lovejoy's (1982) measure,  $\beta_{P/A}$  avoids the statistical problem of regression against a variable measured with error, as it quantifies a change in the perimeter:area ratio with respect to a fixed measure (resolution, in m). In so doing,  $\beta_{P/A}$  provides a less ambiguous estimate of habitat complexity than  $\beta_{A=f(P)}$ . In these ways, we argue that  $\beta_{P/A}$  transcends the suggestion that fractal measures used to assess habitat complexity are statistical and lack biological content (e.g. as in Beck 1998, Imre & Bogaert 2004).

### Comparing patterns and interpretations for all 3 species

Previous studies of Age-0 Greenland cod have suggested that this species is more dependent on eelgrass habitat than Atlantic cod (Laurel et al. 2003b, 2004). Our results were consistent with these studies. We identified a stronger relationship of Greenland cod to eelgrass complexity than Atlantic cod ( $\chi^2 = 13.71$  vs. 9.02 for parabolic term, indicating a larger 'improvement of fit' upon addition of  $\beta_{P/A}^2$  to the model for Greenland cod). Greenland cod, like their congener, have the ability to differentiate habitat types (Laurel et al. 2003b), and are capable of moving between eelgrass sites (Laurel et al. 2004). However, during years of high conspecific density, juvenile Greenland cod were less likely to utilise suboptimal barren habitat than their congeners (Laurel et al. 2004). Greenland cod densities decreased more than Atlantic cod densities in response to eelgrass removal (Laurel et al. 2003b), which suggests that the increased use of barren habitat by Atlantic cod observed by Laurel et al. (2004) was not caused by com-

petitive displacement by Greenland cod. Rather, as for Atlantic cod, the parabolic relationship of Greenland cod density to  $|\beta_{P/A}|$  might result from a habitat-mediated trade-off between feeding and protection from predators.

Potential predators in our study area were numerous, taxonomically diverse, and have been the subject of several studies. Piscivorous fishes in the nearshore include several cruising predators such as larger Atlantic and Greenland cod, cunner *Tautoglabrus adspersus* and at least 2 epibenthic ambush predators (large Age-0 white hake and shorthorned sculpin *Myoxocephalus scorpius*) (Linehan et al. 2001, Laurel et al. 2003a, Gorman et al. 2009). River otter *Lontra canadensis* (Cote et al. 2008) and piscivorous birds occur in the area and may have affected the behaviour of fishes in the present study.

Patterns of juvenile hake distribution in eelgrass habitat in nearshore Newfoundland waters have not been described. The strength of the relationship of hake to eelgrass habitat complexity was significant but the form of the relationship was not the same (Fig. 7). Like both cod species, hake densities were highest at an intermediate value of  $|\beta_{P/A}|$ , but remained elevated at high values of  $|\beta_{P/A}|$ , in contrast to *Gadus morhua* and *G. ogac*. There are a number of factors that might allow white hake to exploit the barren substrates afforded at sites of high  $|\beta_{P/A}|$ . With growth rates close to  $1.0 \text{ mm d}^{-1}$  (Lang et al. 1996), size-selective foraging (Coates et al. 1982), and a relatively large-gape, Age-0 hake may 'outgrow' the predator field located in these relatively shallow nearshore sites, and therefore, more easily exploit patchy eelgrass sites. Relief from predation over open substrates might also result from the more sedentary demersal lifestyle employed by white hake, as compared to the more mobile cod species (Lewis 2007). As an ambush predator, white hake remain stationary to avoid detection by prey. Similarly, white hake may exploit this tactic in barren areas, evading dangerous predator encounters. Additionally, the ability for juvenile white hake to exploit shallow (~1 m deep) areas (Macdonald et al. 1984) may permit the use of barren areas within high- $|\beta_{P/A}|$  sites in warmer, shallow waters. In this way, juveniles may avoid predation from larger fish or competitors with lower thermal tolerances, which are unlikely to occupy warm shallow waters.

### What generates the parabolic relationship of fish to eelgrass complexity?

Could a parabolic relationship of density to complexity be an artefact of a parabolic relationship of perimeter to area? Using the equation for  $P/A$  from Fig. 3C,



we obtain  $p = A \exp(-0.637 \ln L - 0.45)$ . At any box length  $L$  this is not a parabola. This of course only applies within the limited range of our data. We conclude that within the limited range of our data, the parabolic relationship of density of complexity is not an artefact of a parabolic relationship of Euclidean perimeter to Euclidean area.

The results of the present study support the IOH, that sites of intermediate structural complexity support highest fish densities due to a habitat-mediated trade-off in access to food and predators. Specifically, intermediate sites provide adequate opportunity for juvenile cod to forage on zooplankton and benthic invertebrates over sandy, unvegetated areas, while providing enough structural refuge in which to evade predators or effectively camouflage. Several lines of evidence support this hypothesis. First, Age-0 Atlantic cod can discriminate and selectively recruit to preferred habitat (Gregory & Anderson 1997, Laurel et al. 2003b). Structural refuge has been shown to be important to juvenile Atlantic cod in a number of laboratory studies (cobble: Gotceitas & Brown 1993, Fraser et al. 1996; sponges: Lindholm et al. 1999) and field-based studies (kelp: Gotceitas et al. 1995; eelgrass: Gotceitas et al. 1997, Linehan et al. 2001, Laurel et al. 2003a). In these investigations, cod used structure in the presence of a predator, and effectively reduced predation rates. The use of structured habitat to offset predation is well documented in the animal kingdom (reviewed by Lima & Dill 1990). Habitats with an intricate morphology have been shown to provide protection from predation to juvenile fish in a number of species, including bluegill sunfish *Lepomis macrochirus* (Crowder & Cooper 1982, Savino & Stein 1982, Werner et al. 1983, Gotceitas & Colgan 1987, 1989), cunner *Tautoglabrus adspersus* (Tupper & Boutilier 1997) and red drum *Sciaenops ocellatus* (Rooker et al. 1998). Protection for prey results from impaired swimming and searching abilities of predators (Crowder & Cooper 1982, Savino & Stein 1982, Orth et al. 1984, Mattila 1992), as well as increased crypsis and anti-predatory behaviours (Savino & Stein 1982, 1989). In addition, several studies investigating the effects of physical structure on predation have been conducted between fish and their planktonic/invertebrate prey (e.g. Heck & Thorman 1981, Crowder & Cooper 1982, Mattila 1992, James & Heck 1994) and provide support for reduced foraging ability in highly structured habitat. Borg et al. (1997) suggested that juvenile cod utilise protective cover to offset predation during the day, and forage over barren areas under the cover of darkness at night. As these studies demonstrate a requirement for both open substrate and protective cover, they support the IOH.

The requirement for fish to have access to both vegetated and unvegetated habitat has been noted by several authors (e.g. Holt et al. 1983, Orth et al. 1984, Jackson et al. 2006). Mittelbach (1981) suggested that the reason why juvenile sunfish were not found in open areas, despite the potential for rapid growth, was the lack of protective cover there. This requirement to forage in open areas adjacent to protective sites is common to many species, including invertebrates such as web-building spiders (Bilde et al. 2002) and the American lobster (Spanier et al. 1998), small birds such as tits (*Parus* spp.; Walther & Gosler 2001) and black-capped chickadees (Lima 1985), as well as mammalian species including grey squirrels (Lima et al. 1985), guinea pigs (Cassini & Galante 1992) and mule deer (Pierce et al. 2004).

Other possible explanations of a parabolic relationship of juvenile Atlantic cod to eelgrass complexity do not entail a trade-off, but rather derive from the influence of either predators or food availability alone. In a predator-driven scenario, predation risk is elevated at highly patchy/convoluted sites due to increased edge effects (Gorman et al. 2009) and exposure to predators (Laurel et al. 2003a). Likewise, predation may also be high in continuous meadows due to high densities of predators. High predation rates at both continuous and highly patchy sites would reduce the density of Age-0 cod in these sites, relative to intermediate ones, resulting in a parabolic distribution. Laurel et al. (2003a) detected these 2 mechanisms influencing predation risk in a study of eelgrass patch size and predation of juvenile cod. They found that predation rates were negatively correlated with patch size; however, in large eelgrass patches (22 m<sup>2</sup>), predation of cod was higher than expected due to high predator densities. However, these 'large' patches are much smaller than the low- $\beta_{P/A}$  eelgrass sites used in the present study (22 vs. 3600 m<sup>2</sup>). Therefore, the mechanism observed by Laurel et al. (2003a) may not be applicable. In a food-driven scenario, cod densities respond to densities of food resources, which could be higher at eelgrass sites of intermediate complexities (e.g. mysid assemblages: Barberá-Cebrián et al. 2002). Alternatively, accessibility might be greatest at sites of intermediate eelgrass complexity due to high densities of prey in vegetated areas (e.g. harpacticoid copepods: Jenkins et al. 2002). The preponderance of evidence favours a risk-reward trade-off over a parabolic relation of either risk or reward to eelgrass habitat structure, but measurement of risk and reward across a range of habitat complexity will be needed to distinguish among alternatives.

The fractal perimeter area metric (as  $\beta_{A=f(P)}$ ) has a long history of application to the study of fragmented landscapes. Hargis et al. (1998) found that this mea-

sure, like many others, was related in a linear fashion to increasing fragmentation, up to 40% disturbance of a landscape. Sleeman et al. (2005) extended the analysis of fragmentation from simulated to more realistic patterns of fragmentation in eelgrass, but did not evaluate a fractal metric. Like Hargis et al. (1998), these authors found that measures are highly correlated over a range of fragmentation, with no single preferred measure. The metric we employed can be expected to perform at least as well in measuring fragmentation through time as in spatial comparisons.

## CONCLUSIONS AND IMPLICATIONS

We showed that juvenile Atlantic cod density depends on structural complexity of eelgrass, not simply the amount of eelgrass, consistent with a hypothesis developed from a limited number of sites (6). We found that this relationship holds at the scale of a single bay scale (25 km coastline) and an entire coastline (on the order of 1000 km). We demonstrate that combining 2 measures based on a defined measurement protocol are preferable to regression against a variable measured with error, when estimating habitat complexity.

We have demonstrated that the density of 2 other gadid species, Greenland cod and white hake, are also related to the spatial arrangement of eelgrass. In other benthic habitats, species utilising or affected by ecotones may be similarly related to the spatial configuration of habitat that provides both shelter and food. In these cases,  $\beta_{P/A}$  provides a useful measure of 2-dimensional configuration. Where a trade-off in feeding and predator avoidance drives distribution of individuals in structurally complex environments, a parabolic relationship is expected.

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## LITERATURE CITED

- Adams SM (1976) The ecology of eelgrass, *Zostera marina* (L.), fish communities. I. Structural analysis. *J Exp Mar Biol Ecol* 22:269–291
- Bailey KM (2000) Shifting control of recruitment of walleye pollock *Theragra chalcogramma* after a major climatic and ecosystem change. *Mar Ecol Prog Ser* 198:215–224
- Barberá-Cebrián C, Sánchez-Jerez P, Ramos-Esplá AA (2002) Fragmented seagrass habitats on the Mediterranean coast, and distribution and abundance of mysid assemblages. *Mar Biol* 141:405–413
- Barnsley MF (1988) *Fractals everywhere*. Academic Press, Boston, MA
- Beck MW (1998) Comparison of the measurement and effects of habitat structure on gastropods in rocky intertidal and mangrove habitats. *Mar Ecol Prog Ser* 169:165–178
- Bell JD, Westoby M (1986a) Importance of local changes in leaf height and density to fish and decapods associated with seagrasses. *J Exp Mar Biol Ecol* 104:249–274
- Bell JD, Westoby M (1986b) Variation in seagrass height and density over a wide spatial scale: effects on common fish and decapods. *J Exp Mar Biol Ecol* 104:275–295
- Bell SS, Brooks RA, Robbins BD, Fonseca MS, Hall MO (2001) Faunal response to fragmentation in seagrass habitats: implications for seagrass conservation. *Biol Conserv* 100:115–123
- Bilde T, Maklakov AA, Taylor PW, Lubin Y (2002) State-dependent decisions in nest site selection by a web-building spider. *Anim Behav* 64:447–452
- Bogaert J (2003) Lack of agreement on fragmentation metric blurs correspondence between fragmentation experiments and predicted effects. *Conserv Ecol* 7(1):r6 Available at: [www.consecol.org/vol7/iss1/resp6/](http://www.consecol.org/vol7/iss1/resp6/)
- Bologna PAX, Heck KL Jr (2002) Impact of habitat edges on density and secondary production of seagrass-associated fauna. *Estuaries* 25:1033–1044
- Borg Å, Pihl L, Wennhage H (1997) Habitat choice by juvenile cod (*Gadus morhua* L.) on sandy soft bottoms with different vegetation types. *Helgol Meeresunters* 51:197–212
- Boström C, Jackson EL, Simenstad CA (2006) Seagrass landscapes and their effects on associated fauna: a review. *Estuar Coast Shelf Sci* 68:383–403
- Cassini MH, Galante ML (1992) Foraging under predation risk in the wild guinea pig: the effect of predation height on habitat utilization. *Ann Zool Fenn* 29:285–290
- Ciannelli L, Bailey KM, Chan KS, Belgrano A, Stenseth NC (2005) Climate change causing phase transitions of walleye pollock (*Theragra chalcogramma*) recruitment dynamics. *Proc Biol Sci* 272:1735–1743
- Coates LJ, Roff JC, Markle DF (1982) Freshwater components in the diet of the marine neustonic fish, *Urophycis tenuis* (Mitchill). *Environ Biol Fishes* 7:69–72
- Cochran WG (1977) *Sampling techniques*, 3rd edn. John Wiley & Sons, New York, NY
- Cote D, Gregory RS, Stewart HMJ (2008) Size-selective predation by river otter (*Lontra canadensis*) improve refuge properties of shallow coastal marine nursery habitats. *Can J Zool* 86:1324–1328
- Crowder LB, Cooper WE (1982) Habitat structural complexity and the interaction between bluegills and their prey. *Ecology* 63:1802–1813
- Davenport J, Pugh PJA, McKechnie J (1996) Mixed fractal and anisotropy in subantarctic macroalgae from South Georgia: implications for epifaunal biomass and abundance. *Mar Ecol Prog Ser* 136:245–255
- Davidson C (1998) Issues in measuring landscape fragmentation. *Wildl Soc Bull* 26:32–37

- den Hartog C (1971) The dynamic aspect in the ecology of seagrass communities. *Thalassia Jugosl* 7:101–112
- Fonseca MS (1992) Restoring seagrass systems in the United States. In: Thayer GW (ed) Restoring the nation's marine environment. Maryland Sea Grant Publication, College Park, MD, p 79–110
- Fraser S, Gotceitas V, Brown JA (1996) Interactions between age-classes of Atlantic cod and their distribution among bottom substrates. *Can J Fish Aquat Sci* 53:305–314
- Frost MT, Rowden AA, Attrill MJ (1999) Effect of habitat fragmentation on the macroinvertebrate infaunal communities associated with the seagrass *Zostera marina* L. *Aquat Conserv Mar Freshw Ecosys* 9:255–263
- Gee JM, Warwick RM (1994) Metazoan community structure in relation to the fractal dimensions of marine macroalgae. *Mar Ecol Prog Ser* 103:141–150
- Gorman AM, Gregory RS, Schneider DC (2009) Eelgrass patch size and proximity to the patch edge affect predation risk of recently settled age 0 cod (*Gadus*). *J Exp Mar Biol Ecol* 371:1–9
- Gotceitas V, Brown JA (1993) Substrate selection by juvenile Atlantic cod (*Gadus morhua*): effects of predation risk. *Oecologia* 93:31–37
- Gotceitas V, Colgan P (1987) Selection between densities of artificial vegetation of young bluegills avoiding predation. *Trans Am Fish Soc* 116:40–49
- Gotceitas V, Colgan P (1989) Predator foraging success and habitat complexity: quantitative test of the threshold hypothesis. *Oecologia* 80:158–166
- Gotceitas V, Fraser S, Brown JA (1995) Habitat use by juvenile Atlantic cod (*Gadus morhua*) in the presence of an actively foraging and non-foraging predator. *Mar Biol* 123: 421–430
- Gotceitas V, Fraser S, Brown JA (1997) Use of eelgrass beds (*Zostera marina*) by juvenile Atlantic cod (*Gadus morhua*). *Can J Fish Aquat Sci* 54:1306–1319
- Gregory RS, Anderson JT (1997) Substrate selection and use of protective cover by juvenile Atlantic cod (*Gadus morhua*) in inshore waters of Newfoundland. *Mar Ecol Prog Ser* 146:9–20
- Gregory RS, Morris C, Sheppard GL, Thistle ME, Linehan JE, Schneider DC (2006) Relative strength of the 2003 and 2004 year classes, from nearshore surveys of demersal age 0 & 1 Atlantic cod in Newman Sound, Bonavista Bay. *Can Sci Advis Sec Res Doc* 2006/038
- Gustafson EJ (1998) Quantifying landscape spatial pattern: What is the state of the art? *Ecosystems* 1:143–156
- Hammond BM (2003) Influence of eelgrass (*Zostera marina*) complexity and area on age-0 Atlantic cod (*Gadus morhua*) abundance in Newfoundland. MES major paper, Memorial University of Newfoundland, St. John's
- Hanson AR (2004) Status and conservation of eelgrass (*Zostera marina*) in eastern Canada. *Can Wildl Serv Tech Rep* 412
- Hargis CD, Bissonette JA, David JL (1998) The behavior of landscape metrics commonly used in the study of habitat fragmentation. *Landscape Ecol* 13:167–186
- Heck KL Jr, Orth RJ (1980) Seagrass habitats: the roles of habitat complexity, competition and predation in structuring associated fish and motile macroinvertebrate assemblages. In: Kennedy VS (ed) Estuarine perspectives. Academic Press, New York, NY
- Heck KL Jr, Thorman TA (1981) Experiments on predator-prey interactions in vegetated aquatic habitats. *J Exp Mar Biol Ecol* 53:125–134
- Hills JM, Thomason JC, Muhl J (1999) Settlement of barnacle larvae is governed by Euclidean and not fractal surface characteristics. *Funct Ecol* 13:868–875
- Hjort J (1914) Fluctuations in the great fisheries of northern Europe viewed in the light of biological research. *Rapp P-V Reun Cons Int Explor Mer* 20:1–228
- Hokit DG, Stith BM, Branch LC (1999) Effects of landscape structure in Florida scrub: a population perspective. *Ecol Appl* 9:124–134
- Holt SA, Kitting CL, Arnold CR (1983) Distribution of young red drums among different sea-grass meadows. *Trans Am Fish Soc* 112:267–271
- Hovel KA, Lipcius RN (2002) Effects of seagrass habitat fragmentation on juvenile blue crab survival and abundance. *J Exp Mar Biol Ecol* 271:75–98
- Hutchings JA (2000) Collapse and recovery of marine fishes. *Nature* 406:882–885
- Hutchings JA, Myers RA (1994) What can be learned from the collapse of a renewable resource: Atlantic cod, *Gadus morhua*, of Newfoundland and Labrador. *Can J Fish Aquat Sci* 51:2126–2146
- Hyndes GA, Kendrick AJ, MacArthur LD, Stewart E (2003) Differences in the species- and size-composition of fish assemblages in three distinct seagrass habitats with differing plant and meadow structure. *Mar Biol* 142:1195–1206
- Imre AR, Bogaert J (2004) The fractal dimension as a measure of the quality of habitats. *Acta Biotheor* 52:41–56
- Ings DW, Schneider DC, Methven DA (1997) Detection of a recruitment signal in juvenile Atlantic cod (*Gadus morhua*) in coastal nursery areas. *Can J Fish Aquat Sci* 54(Suppl 1):25–29
- Ings DW, Gregory RS, Schneider DC (2008) Episodic downwelling predicts recruitment of Atlantic cod, Greenland cod and white hake to Newfoundland coastal waters. *J Mar Res* 66:529–561
- Irlandi EA (1997) Seagrass patch size and survivorship of an infaunal bivalve. *Oikos* 78:511–518
- Irlandi EA, Ambrose WG Jr, Orlando BA (1995) Landscape ecology and the marine environment: how spatial configuration of seagrass habitat influences growth and survival of the bay scallop. *Oikos* 72:307–313
- Jackson DA, Harvey HH, Sorners KM (1990) Ratios in aquatic sciences: statistical shortcomings with mean depth and the morphoedaphic index. *Can J Fish Aquat Sci* 47:1788–1795
- Jackson EL, Attrill MJ, Rowden AA, Jones MB (2006) Seagrass complexity hierarchies: influence on fish groups around the coast of Jersey (English Channel). *J Exp Mar Biol Ecol* 330:38–54
- James PL, Heck KL Jr (1994) The effects of habitat complexity and light intensity on ambush predation within a simulated seagrass habitat. *J Exp Mar Biol Ecol* 176: 187–200
- Jenkins GP, Walker-Smith GK, Hamer PA (2002) Elements of habitat complexity that influence harpacticoid copepods associated with seagrass beds in a temperate bay. *Oecologia* 131:598–605
- Johnson GD, Templeman A, Patil GP (1995) Fractal based methods in ecology: a review for analysis at multiple spatial scales. *Coenoses* 10:123–131
- Kenkel NC, Walker DJ (1996) Fractals in the biological sciences. *Coenoses* 11:77–100
- Lang KL, Almeida FP, Boltz GR, Fahey MP (1996) The use of otolith microstructure in resolving issues of first year growth and spawning seasonality of white hake, *Urophycis tenuis*, in the Gulf of Maine-Georges Bank region. *Fish Bull (US)* 94:170–175
- Laurel BJ, Gregory RS, Brown JA (2003a) Predator distribution and habitat patch area determine predation rates on Age-0 juvenile cod *Gadus* spp. *Mar Ecol Prog Ser* 251: 245–254

- Laurel BJ, Gregory RS, Brown JA (2003b) Settlement and distribution of Age-0 juvenile cod, *Gadus morhua* and *G. ogac*, following a large-scale habitat manipulation. *Mar Ecol Prog Ser* 262:241–252
- Laurel BJ, Gregory RS, Brown JA, Hancock JK, Schneider DC (2004) Behavioural consequences of density-dependent habitat use in juvenile cod *Gadus morhua* and *G. ogac*: the role of movement and aggregation. *Mar Ecol Prog Ser* 272:257–270
- Lewis CW (2007) Predator-mediated habitat use by juvenile white hake (*Urophycis tenuis*) and Greenland cod (*Gadus ogac*). MSc thesis, Memorial University of Newfoundland, St. John's
- Lima SL (1985) Maximizing feeding efficiency and minimizing time exposed to predators: a trade-off in the black-capped chickadee. *Oecologia* 66:60–67
- Lima SL, Dill LM (1990) Behavioral decisions made under the risk of predation: a review and prospectus. *Can J Zool* 68:619–640
- Lima SL, Valone TJ, Caraco T (1985) Foraging efficiency–predation risk trade-off in the grey squirrel. *Anim Behav* 33:155–165
- Lindholm JB, Auster PJ, Kaufman LS (1999) Habitat-mediated survivorship of juvenile (0-year) Atlantic cod *Gadus morhua*. *Mar Ecol Prog Ser* 180:247–255
- Linehan JE, Gregory RS, Schneider DC (2001) Predation risk of age 0 cod (*Gadus morhua*) relative to depth and substrate in coastal waters. *J Exp Mar Biol Ecol* 263: 25–44
- Lovejoy S (1982) Area-perimeter relation for rain and cloud areas. *Science* 216:185–187
- Macdonald JS, Dadswell MJ, Appy RG, Melvin GD, Methven DA (1984) Fishes, fish assemblages, and their seasonal movements in lower Bay of Fundy and Passamaquoddy Bay, Canada. *Fish Bull* 82:121–139
- Mandelbrot BB (1983) *The fractal geometry of nature*. WH Freeman, New York, NY
- Mattila J (1992) The effect of habitat complexity on predation efficiency of perch *Perca fluviatilis* L. and ruff *Gymnocephalus cernuus* (L.). *J Exp Mar Biol Ecol* 157:55–67
- McCullagh P, Nelder JA (1989) *Generalized linear models*, 2nd edn. Chapman & Hall, London
- Methven DA, Schneider DC, Rose GA (2003) Spatial pattern and patchiness during ontogeny: post-settled *Gadus morhua* from coastal Newfoundland. *ICES J Mar Sci* 60:38–51
- Mittelbach GG (1981) Foraging efficiency and body size: a study of optimal diet and habitat use by bluegills. *Ecology* 62:1370–1386
- Myers RA, Worm B (2003) Rapid worldwide depletion of predatory fish communities. *Nature* 423:280–283
- Neter J, Wasserman W, Kutner MH (1990) *Applied linear statistical models: regression, analysis of variance, and experimental designs*. Richard D. Irwin Inc., Homewood, IL
- Orth RJ, Heck KL Jr, van Montfrans J (1984) Faunal communities in seagrass beds: a review of the influence of plant structure and prey characteristics on predator-prey relationships. *Estuaries* 7(4A):339–350
- Pierce BM, Bowyer RT, Bleich VC (2004) Habitat selection by mule deer: foraging benefits or risk of predation? *J Wildl Manag* 68:533–541
- Robbins BD, Bell SS (1994) Seagrass landscapes: a terrestrial approach to the marine subtidal environment. *Trends Ecol Evol* 9:301–304
- Rooker JR, Holt GJ, Holt SA (1998) Vulnerability of newly settled red drum *Sciaenops ocellatus* to predatory fish: Is early life survival enhanced by seagrass meadows? *Mar Biol* 131:145–151
- Salita JT, Ekau W, Saint-Paul U (2003) Field evidence on the influence of seagrass landscapes on fish abundance in Bolinao, northern Philippines. *Mar Ecol Prog Ser* 247: 183–195
- Savino JF, Stein RA (1982) Predator-prey interactions between largemouth bass and bluegills as influenced by simulated submersed vegetation. *Trans Am Fish Soc* 111: 255–266
- Savino JF, Stein RA (1989) Behavioral interactions between fish predators and their prey: effects of plant density. *Anim Behav* 37:311–321
- Schneider DC (2009) *Quantitative ecology: measurement, models, and scaling*. Academic Press, San Diego, CA
- Schneider DC, Hennebury P, Methven D, Ings D, Pinsent D (1997a) Fleming survey of demersal juvenile cod in coastal areas of eastern Newfoundland. *NAFO Sci Counc Stud* 29: 13–21
- Schneider DC, Methven DA, Dalley EL (1997b) Geographic contraction in juvenile fish: a test with northern cod (*Gadus morhua*) at low abundances. *Can J Fish Aquat Sci* 54:187–199
- Schneider DC, Norris MJ, Gregory RS (2008) Predictive analysis of scale-dependent habitat association: juvenile cod (*Gadus* spp.) in eastern Newfoundland. *Estuar Coast Shelf Sci* 79:71–78
- Sheppard GL (2002) Annual variation in eelgrass (*Zostera marina* L.) area and complexity within Newman Sound, Newfoundland. Honours thesis, Memorial University of Newfoundland, St. John's
- Sissenwine MP (1984) Why do fish populations vary? In: May RM (ed) *Exploitation of marine communities*. Springer Verlag, Berlin, p 59–94
- Sleeman JC, Kendrick GA, Boggs GS, Hegge BJ (2005) Measuring fragmentation of seagrass landscapes: Which indices are most appropriate for detecting change? *Mar Freshw Res* 56:851–864
- Spanier E, McKenzie TP, Cobb JS, Clancy M (1998) Behavior of juvenile American lobsters, *Homarus americanus*, under predation risk. *Mar Biol* 130:397–406
- Sugihara G, May RM (1990) Applications of fractals in ecology. *Trends Ecol Evol* 5:79–86
- Swain DP, Sinclair AF (2000) Pelagic fishes and the cod recruitment dilemma in the Northwest Atlantic. *Can J Fish Aquat Sci* 57:1321–1325
- Taniguchi H, Tokeshi M (2004) Effects of habitat complexity on benthic assemblages in a variable environment. *Freshw Biol* 49:1164–1178
- Tegner MJ, Dayton PK (1999) Ecosystem effects of fishing. *Trends Ecol Evol* 14:261–262
- Tupper M, Boutillier RG (1997) Effects of habitat on settlement, growth, predation risk and survival of a temperate reef fish. *Mar Ecol Prog Ser* 151:225–236
- Turner SJ, Hewitt JE, Wilkinson MR, Morrisey DJ, Thrush SF, Cummings VJ, Funnell G (1999) Seagrass patches and landscapes: the influence of wind-wave dynamics and hierarchical arrangements of spatial structure on macrofaunal seagrass communities. *Estuaries* 22:1016–1032
- Walther BA, Gosler AG (2001) The effects of food availability and the distance to protective cover on the winter foraging behaviour of tits (*Aves: Parus*). *Oecologia* 129:312–320
- Warren MA (2007) Density of juvenile Atlantic cod (*Gadus morhua*) and Greenland cod (*G. ogac*) with spatial expansion and recovery of eelgrass (*Zostera marina*). BSc honours thesis, Memorial University of Newfoundland, St. John's

Wells NJ (2002) Scaling eelgrass complexity in Newman Sound, Newfoundland, and applications to fish ecology. MSc thesis, Memorial University of Newfoundland, St. John's  
Werner EE, Gilliam JF, Hall DJ, Mittelbach GG (1983) An

experimental test of the effects of predation risk on habitat use in fish. *Ecology* 64:1540–1548  
Whitehouse MEA, Shochat E, Shachak M, Lubin Y (2002) The influence of scales and patchiness on spider diversity in a semi-arid environment. *Ecography* 25:395–404

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