Behavioural consequences of density-dependent habitat use in juvenile cod *Gadus morhua* and *G. ogac*: the role of movement and aggregation

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ABSTRACT: Fish behaviour can change to accommodate a variable environment, but changes in behaviour have not been considered in the context of density-dependent habitat use. In Bonavista Bay, Newfoundland, we measured how fish density movement and schooling behaviour changed with habitat in 2 gadids, Atlantic cod *Gadus morhua* and Greenland cod *Gadus ogac*, using a combination of field-seines, mark–recapture and laboratory experiments. Density estimates from seines (n = 427) over 5 yr (1996, 1998 to 2001) indicated that these species associated with eelgrass but periodically were detected in high abundance over unvegetated habitat (i.e. sand). Within-site catch variation indicated both species aggregated more in sand than eelgrass habitat, and, in Atlantic cod, aggregations over sand increased as density in eelgrass increased. Although such patterns in catch data could be interpreted as due to the effects of differential mortality between habitats, a mark–recapture experiment indicated that both species of cod were not site-attached and moved between seine locations. Furthermore, video-analysis from laboratory experiments demonstrated that cod formed tighter aggregations over sand compared to eelgrass habitats. Our results suggest that juvenile cod modify their behaviour with changing density, possibly as a means of exploiting poor-quality habitats when high-quality habitats are saturated with conspecifics. Consequently, habitat suitability for Atlantic cod may be a dynamic rather than fixed variable in density-dependent habitat models.

KEY WORDS: Density-dependence · Habitat selection · Atlantic cod · Greenland cod · Aggregation · Shoaling

INTRODUCTION

Predation in aquatic systems can have profound effects on the distribution of many species of fish (Sih 1987). Predators can shape prey fish distribution either directly through selective mortality (e.g. Tupper & Boutlier 1995a, Steele 1999) or indirectly through risk-induced behaviour such as schooling or use of protective habitat (see Godin 1997 for review). It is likely both direct and indirect effects of predation on fish distribution are magnified during the early life stages of fish when predation risk is highest (e.g. Houde 1987, Sogard 1997).

Complex habitats (e.g. rock, woody debris, coral, submerged vegetation) are often used by fish as a means of reducing predation risk (Savino & Stein 1982, Gotceitas & Colgan 1989, Gotceitas & Brown 1993). In particular, highly structured aquatic vegetation (e.g. eelgrass) has received much attention as a refuge habitat (Orth et al. 1984, Gotceitas et al. 1997, Linehan et al. 2001, Laurel et al. 2003a), likely due to its wide distribution and high productivity relative to neighbouring unvegetated sites (Orth et al. 1984, Bell & Pollard 1989). The likelihood of encountering and capturing prey is reduced in eelgrass (Gotceitas et al. 1997), and, consequently, predation rates are typically lower despite sometimes higher predator densities in these habitats (Linehan et al. 2001, Laurel et al. 2003b). It is therefore not surprising that structured habitat is often used as nursery habitat by many species of recently

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settled marine fish (Bell & Pollard 1989, Levin 1991, Sogard & Able 1991, Edgar & Shaw 1995, Grant & Brown 1998a, Matilla et al. 1999, Heck et al. 2003).

Despite the benefits of using complex habitats, fish may be forced to use high-risk habitats (e.g. sand, bedrock) when preferential habitats are saturated by conspecifics. The decline in habitat selection with increasing population abundance was first outlined by Fretwell & Lucas (1970) and has subsequently formed the basis for frequency-dependent modeling, i.e. ideal-free distribution. When populations are low, individuals should be restricted to habitats offering the highest fitness benefits, e.g. high survival and growth. As population density increases, individual fitness benefits decrease (via competitive interactions), and, consequently, poorer quality habitats become more attractive. These relationships have been explored and reviewed for many taxa, including fish (MacCall 1990, Kramer et al. 1997).

One shortcoming with density-dependent habitat models is that they assume the organism's behaviour is the same across all habitats. Such an assumption is problematic because changes in behaviour can modify the fitness benefits associated with a particular habitat. Density-dependent habitat models rely on a static measure of habitat suitability, equal to the fitness benefits acquired by an organism at zero density. The fitness benefits of a habitat cannot be static if the organism has a dynamic behavioural strategy. Therefore, density-dependent changes in behaviour should also be considered when modeling habitat suitability and predicting distribution.

Fish adopt different strategies to compensate for the increased predation risk associated with specific habitats. Immediate, short-term responses include freezing (motionless) (e.g. Brown 1984, Radabaugh 1989), reduced activity (Rahel & Stein 1988) and increased flight-initiation distances (Ydenberg & Dill 1986). However, employing these tactics can result in reduced mating success (e.g. Hastings 1991) and lost foraging opportunities (e.g. Williams & Brown 1991). Alternatively, group tactics (e.g. schooling, shoaling) may be more viable long-term solutions when using poorer-quality habitat. Shoaling has been shown to reduce predation risk through increased predator confusion (e.g. Milinski 1979, 1985), dilution (Foster & Treherne 1981, Krebs & Davies 1991) and vigilance (Bertram 1978). The cost of group association (e.g. food competition, increased conspicuousness) may be ameliorated by increased food searching (Pitcher et al. 1982), group defense (Krebs & Davies 1991) and increased hydrodynamic efficiency (Weihs 1975). However, the use of shoaling as an alternative tactic in habitats with low suitability has not been considered in the context of density-dependent habitat selection.

Little is known of mechanisms of variable habitat use of juvenile Atlantic cod. Since the collapse of Atlantic cod populations off Newfoundland, Age 0 juvenile cod have been largely restricted to inshore areas (Dalley & Anderson 1997), where they are commonly associated with complex bottom habitats (Gotceitas et al. 1997, Grant & Brown 1998a). Field experiments have demonstrated that these fish prefer to settle in eelgrass in July/August (Laurel et al. 2003a) and remain there until late November, when they presumably move to deeper waters (Methven & Bajdik 1994). Eelgrass has been shown to reduce predation risk for Age 0 juvenile cod in both laboratory (Gotceitas et al. 1997) and field (Linehan et al. 2001, Laurel et al. 2003b) experiments. Despite their preference for eelgrass, however, juvenile cod are occasionally observed over less-structured habitats such as sand and cobble (Lough et al. 1989, Tupper & Boutlier 1995a,b, Laurel et al. 2003a). Juvenile cod are believed to move little immediately following settlement (Tupper & Boutilier 1995a,b, Grant & Brown 1998a), and, consequently, the occupation of less-structured habitats is taken to be the result of indiscriminate settlement patterns. By implication, temporal variation in distribution following settlement is the result of selective predation across habitats (Tupper & Boutilier 1995a,b). However, Schneider et al. (1999) demonstrated that movement prevails over mortality at the scales studied by Tupper & Boutilier (1995a,b), i.e. ca. <1000 m and <100 d. Furthermore, a recent study by Laurel et al. (2003a) suggested that temporal variation in distribution is the result of post-settlement movement and habitat mediated aggregation. Therefore, the mechanisms of variable habitat use in these fish remains unclear.

In this study, we gathered data from the field and laboratory to determine how juvenile cod density, movement and schooling behaviour interact to affect habitat use patterns. Specifically, we asked (1) whether juvenile cod aggregate differently between habitats in years of low and high abundance, and (2) whether such aggregations are the result of behaviour (i.e. movement and schooling patterns). For the first question, we used seine data collected over 5 yr (1996, 1998 to 2001) to determine if catch aggregation of juvenile cod is related to habitat type and the density of conspecifics. To address the second question, we used a mark–recapture experiment to determine if juvenile cod moved at scales greater than a seine haul. This experiment was followed by a laboratory study in which we observed whether juveniles school differently between sand and eelgrass habitats. The implications of a changing behavioural strategy between years of high and low abundance are discussed in the context of density-dependent habitat selection.

MATERIALS AND METHODS

Study location. Fieldwork was carried out along shallow coastal areas (≤6 m depth) in Newman Sound, Terra Nova National Park (TNNP), located within Bonavista Bay, Newfoundland (Fig. 1). Newman Sound is a fjord, 41 km long and 1.5 to 3.0 km wide, that is divided into 2 basins by a sill that rises to a depth of 18 m. The inner sound has a maximum depth of 55 m, whereas the outer sound ranges to a depth of 300 m at its seaward end. Coastal substrate ranges from mud to bedrock, often with associated vegetative cover (*Zostera marina* eelgrass, in mud, sand and gravel substrates; the macroalgae *Laminaria digitata* Lamouroux, *Agarum cribrosum* Bory, *Chondrus crispus* Stackhouse, *Fucus oesiculosus* L. and *Ascophyllum nodosum* [L.] Le Jolis, on coarse substrates). However, of these vegetated habitats, eelgrass is the most common and contiguously found in Newman Sound. Seasonal temperatures in the sound range from 20°C in late August to –1.0°C in early December.

Seine surveys. Abundance of Age 0 juvenile cod was determined using demersal beach seines in 1996 and 1998 to 2001. Seines were deployed 55 m from shore from a 6 m boat and pulled toward shore by 2 individuals standing 16 m apart. The seine sampled 880 m² of demersal habitat up to 2 m from the bottom. Seine collections were made only during daylight hours ± 2 h of low tide. Fish collected in the seine were transferred to large containers filled with seawater at ambient temperature. Juvenile cod were counted and identified before being returned alive to their site of capture. SCUBA observations have shown that the seine samples 95% of the fish community within its path (Gotceitas et al. 1997). A full description of the seine, mesh size and deployment method is found in Schneider et al. (1997).

In each year, seines were pulled every 2 wk over 4 unvegetated 'sand' sites (Mt. Stamford, MS; Newbridge, NB; Canning's Cove, CC; Little South Broad Cove, LSB) and 8 'eelgrass' sites (Big Brook, BB; Dockside, DS; White Rock, WR; Mistaken Cove, MS; Buckley's Cove, BC; Heffern's Cove, HC; Minchin's Cove, MC; South Broad Cove, SB) between mid-July and late November (Fig. 1). However, in 1996 sites were characterised by 2 unvegetated sites (NB, CC) and 4 vegetated sites (BB, DS, WR, BC) during the first 3 sampling periods. An additional unvegetated site (MS) and 2 vegetated sites (HC, MC) were added to the survey for the remainder of sampling in that year. Full sampling of sites occurred in the years 1998, 1999, 2000 and 2001. 'Eelgrass' sites consisted of mixed mud/silt bottoms, with small amounts of sand and gravel overlayed with silt and supporting moderate to dense eelgrass. 'Sand' sites were comprised of sand or gravel and contained little to no vegetation in the path or near the vicinity of the seine.

Nearshore studies in Newfoundland have shown that *Gadus morhua* settle in at least 2 distinctive recruitment pulses. The first pulse occurs in August/September, which is then followed by a 2 second pulse occurring approximately 30 d later (Methven & Bajdik 1994, Grant & Brown 1998a). In contrast, *G. ogac* settle in a single recruitment pulse in July/August (Laurel et al. 2003a).

Mark–recapture experiment. A mark–recapture experiment was performed between 16 August and 3 September 1999 on the western shore of inner Newman Sound in Terra Nova National Park (48° 35' N, 53° 55' W) to determine if juvenile cod are highly mobile or strongly site-attached. The site was chosen because it contained a contiguous band of eelgrass and it was conducive to pulling multiple adjacent seines, i.e. few boulders and other obstructions. Fifteen adjacent seine sites (16 m wide) were initially marked with flagging tape along 274 m of unobstructed shoreline; the survey area encompassed 13 504 m². Five of the interior sites of the survey area proved to be difficult to seine, so these were not surveyed during the mark–recapture experiment. The remaining 10 sites representing the survey area are illustrated in Fig. 2.

We collected 1109 *Gadus* spp. (47% *G. morhua*; 53% *G. ogac*) on 18 August from Site 4 (i.e. location 0 m) and mass-marked with fluorescent grit following the procedure described by Phinney et al. (1973). The marking apparatus consisted of a marking gun (commercial sandblast gun) retrofitted with a 5 mm orifice and attached canister holding Saturn yellow fluores-
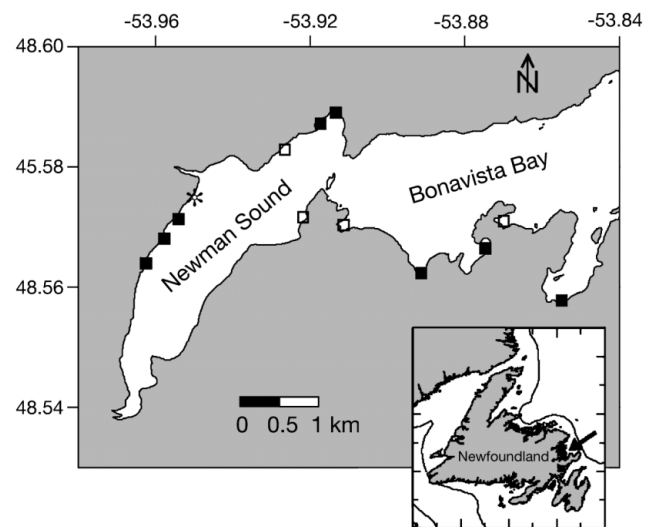

Fig. 1. Study area in Newman Sound, Bonavista Bay, Newfoundland, showing sand (□) and eelgrass (■) seine locations. Mark-recapture effort (✳) was conducted on the western shore of the sound
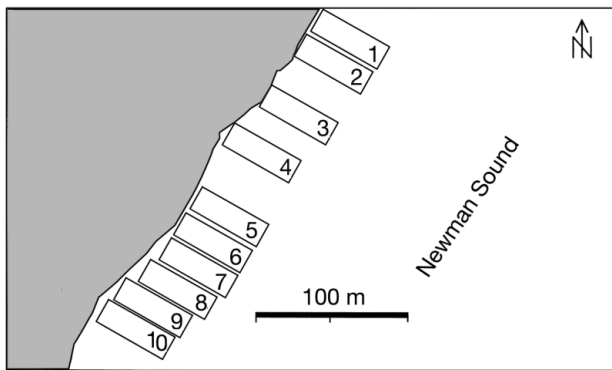
Fig. 2. Illustration of the layout of sites seined to measure movement of *Gadus morhua* and *G. ogac* on a 219 m section of shoreline in Newman Sound, Bonavista Bay, Newfoundland, between 18 August and 3 September 1999. Marine habitat within and beyond the seine sites consists of eelgrass *Zostera marina*

cent grit (DayGLO Color). The marking apparatus was attached to a SCUBA cylinder with a high-pressure hose and regulator that reduced air pressure to 550 kPa during marking. Fish (50 to 250 at a time) were marked in a plastic tub (0.5 m width, 0.5 m height, 1.0 m length) with a screen bottom (1 mm mesh). The plastic tub was nested in a similar-sized tub holding ambient seawater to minimise the time fish spent out of water. The marking gun was held ca. 40 cm from the fish and sprayed for 2 to 3 s. Fish were then transferred to partially submerged, plastic holding pens at the site of capture. Marked individuals were released back into the site of capture (Site 4; Fig. 2) 10 h following the last batch marking. Mark retention is nearly 100% within the first 2 mo of marking juvenile fish (Phinney et al. 1973), and preliminary trials on juvenile cod placed in holding pens demonstrated no mark loss over a 3 wk period.

A recapture seining series was initiated on Day 1 (15 h after release) and repeated on Days 2, 6, 9 and 16. One seine haul was pulled at each site (1 to 10) on each recapture day using 2 seining teams. Team A and Team B sampled simultaneously; Team A started at Site 5 and worked towards Site 1, while Team B started at Site 10 and worked towards Site 6. Captured juvenile cod were transferred to holding containers with seawater and examined in a dark tent under ultraviolet light for presence of fluorescent marks. All fish were transferred to holding containers and released after seining was completed for the day, after which fish were released back into the site of their recapture.

Laboratory experiments. *Fish collection:* Juvenile Age 0 *Gadus morhua* (70 to 90 mm standard length) were caught by beach seine in early October from additional eelgrass sites elsewhere in Newman Sound and transferred to the laboratory. Fish were held in

$1 \times 1 \times 0.5$ m flow-through tanks at ambient water temperature and fed a mixture of chopped herring and commercial pelleted food. Fish were allowed to acclimate to laboratory conditions for a period of 2 wk prior to initiating experiments.

Experimental design: Juvenile cod distribution was digitally videotaped over sand and simulated eelgrass in a large flow-through tank ($2.0 \times 1.5 \times 0.4$ m) maintained at 5 to 10°C. A digital video camera, fixed with a wide-angle lens, was mounted 2.2 m directly above the tank. The field of view and focus of the camera were locked to maintain a clear, perpendicular view of the entire tank and its inhabitants. The camera could be operated remotely from an adjacent room outfitted with a video-screen to start and stop trials. Illumination was provided by 2 light stands (1.8 m high) on opposite sides of the tank; each light stand was fitted with 2 halogen lamps (300 W). Lamps were angled into each side of the tank to highlight fish as well as intentionally create a shadow on the tank bottom.

Bottom habitat was switched repeatedly between trials to either unvegetated sand or simulated eelgrass. Sand (<1 mm) was washed and placed into the tank to cover the entire bottom at a thickness of 10 cm. Eelgrass was manufactured by attaching green, plastic ribbon (0.8 cm width, 20 cm height) to mats of galvanised wire fencing at a density of 400 blades m^2. Field experiments have shown that these blade densities are preferred by juvenile cod during settlement (Laurel et al. 2003a). During placement of eelgrass into the tank, fencing was fully covered by a sand layer so that only the ribbon was visible during trials. Simulated eelgrass emerging from the substrate varied in length between 17 and 19 cm. Field experiments have shown that similarly constructed eelgrass attracts (Laurel et al. 2003a) and reduces (Laurel et al. 2003b) predation of juvenile cod.

Five experimentally naïve Age 0 juvenile cod (*Gadus morhua*; 7.8 ± 0.14 cm) were transferred from holding tanks to the experimental tank using a 2 l transparent glass container with ambient seawater. Fish were allowed to acclimate to the temperature of the experimental tank by placing the holding container in the centre of the tank for 15 min. Fish were then released into the tank and filmed for a 1 h period. All operations to manipulate the camera were conducted in a separate room to minimise disturbances during a trial. Following each trial, fish were collected by dip net and moved to a separate holding tank. A total of 10 trials (1 h each) in each habitat (eelgrass and sand) were recorded over 3 wk.

Video analysis: Digital video recordings were uploaded to a computer with image analysis software (Matrox Inspector) to gather 3-dimensional positioning and orientation data for each juvenile cod. Frame grabs of video were insufficient by themselves because

fish were difficult to distinguish against the heterogeneity of the habitat. Instead, short 10 s clips of video were captured and looped repeatedly from a reference frame. Fish were digitally marked at the reference frame, while the video looped to reveal the position of each fish. Reference frames along with 10 s video clips were captured at 3 min intervals for 57 min during each trial (n = 20 reference frames/trial).

From each reference frame we gathered the orientation and position in space (*x*, *y*, *z* coordinates) of each fish. Orientation was acquired by drawing a digital line from head to tail of each fish from each reference frame (n = 5 angles/frame, n = 100 angles/trial). The software outputs an angle (0° to 360°) based on the counterclockwise difference between digitally marked fish and a 3 o′clock reference line.

The calculation of fish position in 3 dimensions followed the procedure outlined by Laurel (2003). Digital images were calibrated at the far field such that any measurements assumed fish were at the substrate level. Fish positions were measured by placing a digital point at the anterior end of each cod in each reference frame (n = 5 *x*, *y* coordinates/frame, 100 *x*, *y* coordinates/trial). From each digital point, the Cartesian coordinate system of the software output a fish position in a 2-dimensional plane (*x*, *y*). Measurements were also taken of the distance of each fish′s shadow cast on the substrate from 1 of the 2 light sources. The last known shadow distance was used in rare instances when the walls of the tank obstructed both shadows cast by a fish. Using the measurements from image analysis (i.e. shadow distance and *x*, *y* coordinates) as well as the known light and camera positions (*x*, *y*, *z*), we calculated true fish position in 3 dimensions from vector equations described by Laurel (2003).

Data analysis. *Field seines:* Juvenile cod densities estimated from seine catches were examined using quantile–quantile plots of percent abundance versus percent area to determine the degree of aggregation of fish in the field, i.e. Lorenz curves (Dagum 1985). Plots were constructed for eelgrass and sand separately for each year by first calculating the percentage of the total population within a year associated with a single seine haul *i* from either eelgrass or sand sites:

$$n_i = 100(w_i + 1)/\bar{E} \qquad (1)$$

where w_i is the number of fish caught in a seine haul *i* and $\bar{E}$ indicates the mean catch per haul. These data were compared against the percentage area associated with each tow ($A_i = 100\, c_i$), where c_i was the proportion of the annual catch in a single seine haul *i*. Seine hauls were sorted by n_i and plotted as cumulative percent area against cumulative percent abundance for each year, species and habitat. A highly concave curve indicates high aggregation (i.e. shoaling or high mortality), whereas increased linearity with a slope approaching 1 indicates an even distribution (i.e. territoriality or low mortality) of fish among seine hauls. The range in concavity is related to the statistical distribution (e.g. normal, Poisson, negative binomial) of the catch data (Fig. 3). The total area underneath each curve was integrated (*k*) to determine the discrepancy from a perfectly even distribution i.e. 1:1 line. Then, *k* was plotted against the corresponding yearly mean catch to determine if density was related to aggregation as measured by *k*. Data were then log-transformed and regressed to determine if *k* increased with annual abundance. Such a relationship would indicate a density-dependent effect on aggregation.

We also examined within-site aggregation over the course of a season (July to November). Within-site catch variability for each year and each species was determined using coefficients of variation (CV) of bi-weekly catch data (w_i +1). These data were regressed against the log-transformed total catch within each site for each species within a year [log ($W_{tot} + N_{tot}$)]. Residuals from regression met the assumptions of normality and homogeneity.

Mark–recapture: Movement rate was calculated by regressing the number of recaptures against time:

$$\ln (N + 1) = \alpha + \beta (T) \qquad (2)$$

where *N* was the number of recaptures of juvenile cod and *T* was the time in days. A constant ($N+1$) was added to the equation to include possible days when
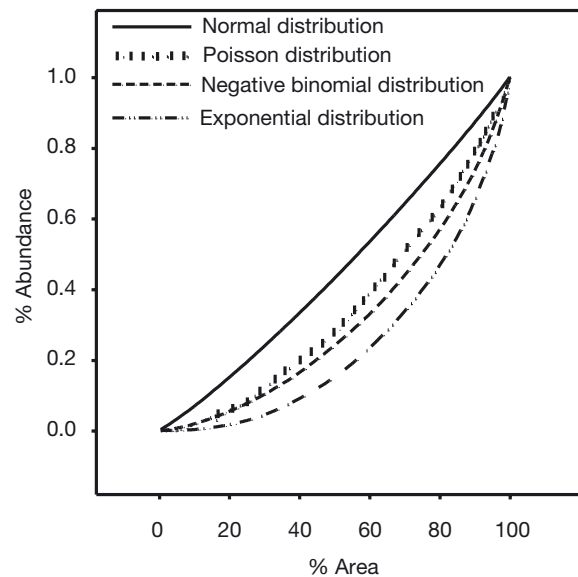

Fig. 3. Quantile-quantile plots for randomly generated data from normal, Poisson and negative binomial distributions (*k* < 1). High concavity suggests high aggregation of an organism in time or space

0 fish would be recaptured. We determined movement rate from the slope ($100 \times \beta$) and expressed it as the percent of fish per day leaving the survey area.

We also examined whether movement patterns resembled a simple diffusive process. A simple diffusion model predicts fish move indiscriminately in or among habitats. Alternatively, fish not corresponding with a simple diffusion model would indicate some degree of habitat or site selection. To test the simple diffusion model, we examined the standard deviations of the mean distribution along the beach on each day. The standard deviation on each day was logarithmically transformed and regressed against time in days:

$$\ln(S) = \alpha + \beta \ln(T) \tag{3}$$

where S is the standard deviation of the mean location of captures in a day (metres away from release point) and T is the time (d). We then used the mathematical definition of diffusion:

$$2D = \frac{\Delta v}{\Delta t} \tag{4}$$

where v is variance and t is time, to derive the regression model that describes simple diffusion:

$$\ln(S) = 0.5 \ln(2D) + 0.5 \ln(T) \tag{5}$$

We used the resulting slope ($\beta = 0.5$) as a benchmark for comparing model and field recapture data. A linear relationship where $\beta = 0.5$ indicates fish movement occurs by simple diffusion. Alternatively, a linear relationship where $\beta \neq 0.5$ suggests a process other than simple diffusion.

Video data: We determined the degree of aggregation in tank trials by calculating distances between all fish in each reference frame. The distances between one fish in space (Ax, Ay, Az) and a second fish (Bx, By, Bz) was calculated using the following equation:

$$\text{Dist} = \sqrt{(dx^2 + dy^2 + dz^2)} \tag{6}$$

where $dx = Ax - Bx$, $dy = Ay - By$ and $dz = Az - Bz$. The total sum of all possible distances between fish in each reference frame (n = 10 distances/frame) was then used to calculate an aggregation coefficient (n = 1/frame, n = 20/trial). We used 1-way ANOVA with repeated measures to determine if mean aggregation coefficients within each trial (n = 10 eelgrass, n = 10 sand) differed between habitats. Habitat (eelgrass or sand) formed the between-group factor in the model. Time (min) of observation (e.g. 0, 3, 6, 9, …, 57) within the trial was examined as a within-group factor.

We determined how groups of fish oriented over different habitats (n = 10 angle differences/frame, n = 200 angle differences/trial) by examining the similarity between angles within a reference frame. The minimal sum of the angle difference (A_D) between each fish and its neighbours for each reference frame was calculated using the following equation:

$$A_D = \min \left| \sum_{i=1}^{n} \text{Ang}_i - \text{Ang}_{i+1} \right| \tag{7}$$

Angle differences were transformed so that $\text{Ang}_i - \text{Ang}_{i+1} < 180$. If $\text{Ang}_i - \text{Ang}_{i+1} > 180$, angles were adjusted using the equation:

$$360 - [\text{Ang}_i - \text{Ang}_{i+1}] \tag{8}$$

We used the minimal sum, which consisted of 1 reference fish relative to its 4 other neighbours (n = 5 angle differences/sum), as the test statistic from which to measure group orientation. Lower sum values indicated that fish were oriented in the same direction, whereas high sums suggested that fish were moving in separate directions. Mean minimal angle sums (n = 20/trial) were compared between habitat treatments using 1-way ANOVA with repeated measures (n = 10 eelgrass, n = 10 sand). The assumptions for computing p-values were checked by examining residuals for normality and homogeneity. Habitat (eelgrass or sand)
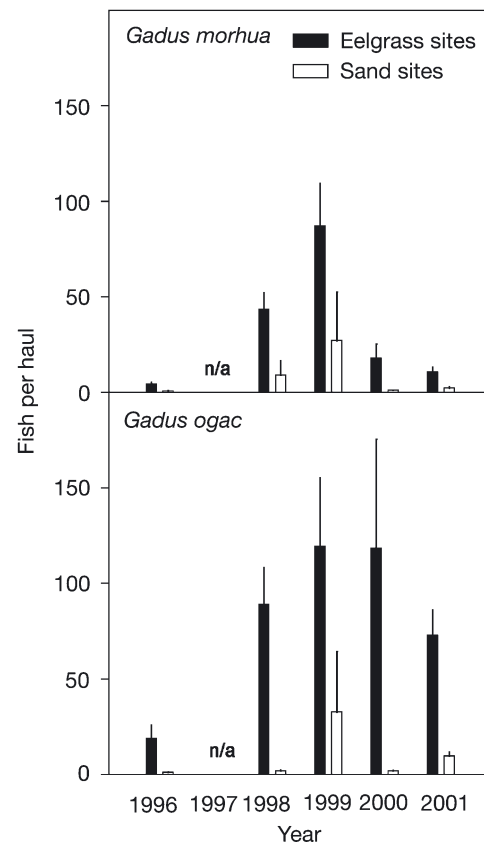

Fig. 4. *Gadus morhua* and *G. ogac.* Mean seasonal (July to November) catch at sand and eelgrass sites from 1996 and 1998 to 2001. Values between 1998 and 2001 are based on 70 to 80 seine hauls ± 1 SE. 1996 values are based on 10 to 20 seine hauls ± 1 SE
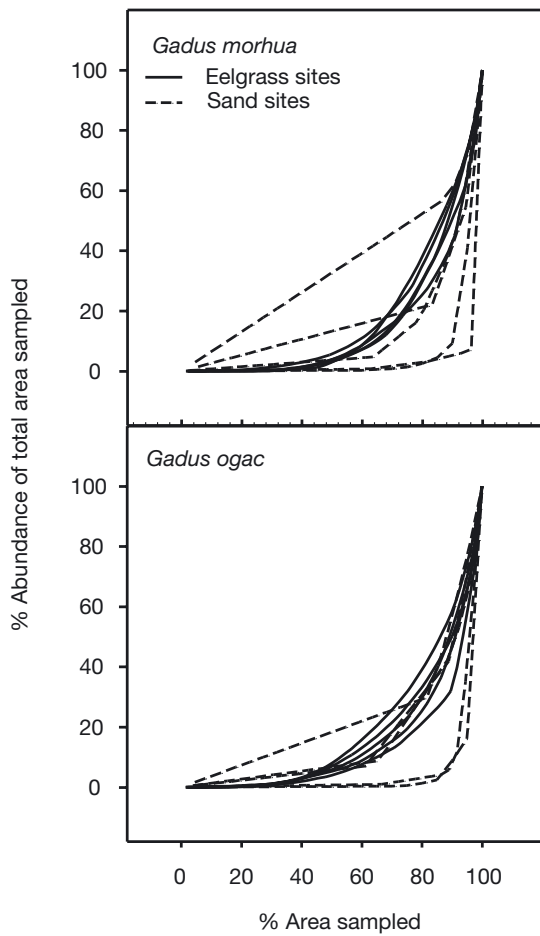
Fig. 5. *Gadus morhua* and *G. ogac.* Quantile-quantile plots of interannual seine catches (1996, 1998 to 2001). Each curve comprises the seasonal catch (July to November) of fish in a single year. A highly concave curve indicates high aggregation (i.e. shoaling or high mortality), whereas increased linearity, with a slope approaching 1, indicates an even distribution (i.e. territoriality or low mortality) of fish among seine hauls

formed the between-group factor in the model and time (min) of observation within the trial was examined as a within-group factor.

RESULTS

Field catch data

There was high interannual variability in late summer and autumnal catches of both *Gadus morhua* and *G. ogac* (Fig. 4). This was most pronounced in *G. morhua*, with more than an order of magnitude difference in mean catch, ranging from a high catch in 1999 (87.3 ± 22.3 fish haul^{-1}; mean ± SE) to a low catch in 2001 (4.6 ± 0.9 fish haul^{-1}). In contrast, *G. ogac* ranged

from a high catch in 1999 (118.5 ± 56.9 fish haul^{-1}) to a low catch in 1996 (19.1 ± 7.0 fish haul^{-1}).

Both *Gadus morhua* and *G. ogac* aggregated more when in sand habitats than eelgrass habitats in most years (Fig. 5), but the degree of aggregation was highly variable in sand habitats between years for both species. The interannual variability in the degree of *G. morhua* aggregations (k) over sand was significantly related to interannual fluctuations in density (n = 5, r^2 = 0.93, p = 0.004; Fig. 6). However, no relationship was found for *G. morhua* at eelgrass sites (n = 5, r^2 = 0.11, p = 0.636) or for *G. ogac* in either sand (n = 5, r^2 = 0.28, p = 0.103) or eelgrass (n = 5, r^2 = 0.01, p = 0.979). Therefore, only *G. morhua* became more aggregated over sand habitats when abundance in eelgrass habitats was higher.

Within-site temporal variability was correlated with abundance in sand for both *Gadus morhua* (n = 17, r^2 = 0.79, p < 0.001) and *G. ogac* (n = 17, r^2 = 0.83, p < 0.001), but not in eelgrass (*G. morhua:* n = 39, r^2 = 0.02, p = 0.444; *G. ogac:* n = 39, r^2 = 0.01, p = 0.829; Fig. 7). These data suggest that, for both cod species, high abundance within a sand site is due to a few large aggregations of fish. In contrast, individual eelgrass sites were much less variable at high abundance, indicating consistent catches over time in this habitat.
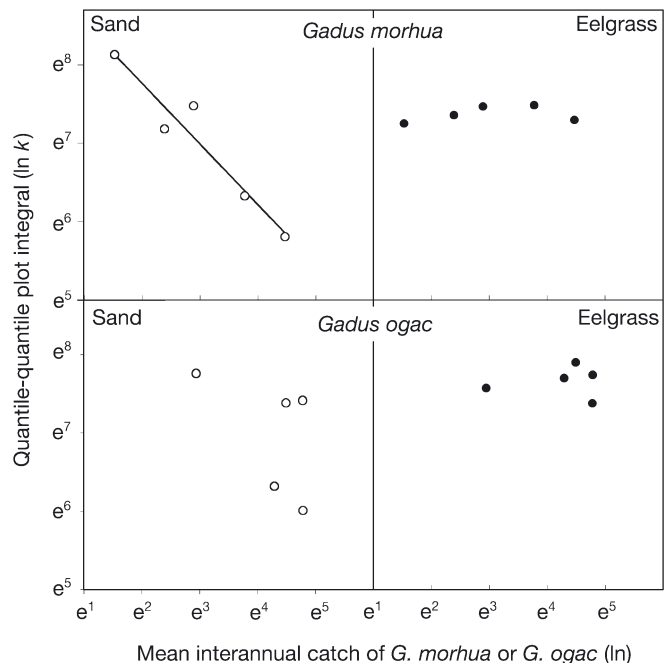

Fig. 6. *Gadus morhua* and *G. ogac.* Relationship of yearly aggregation (quantile-quantile plot integration k) and yearly abundance in either sand (○) or eelgrass (●). High values on the *y*-axis indicate low levels of spatio-temporal aggregation
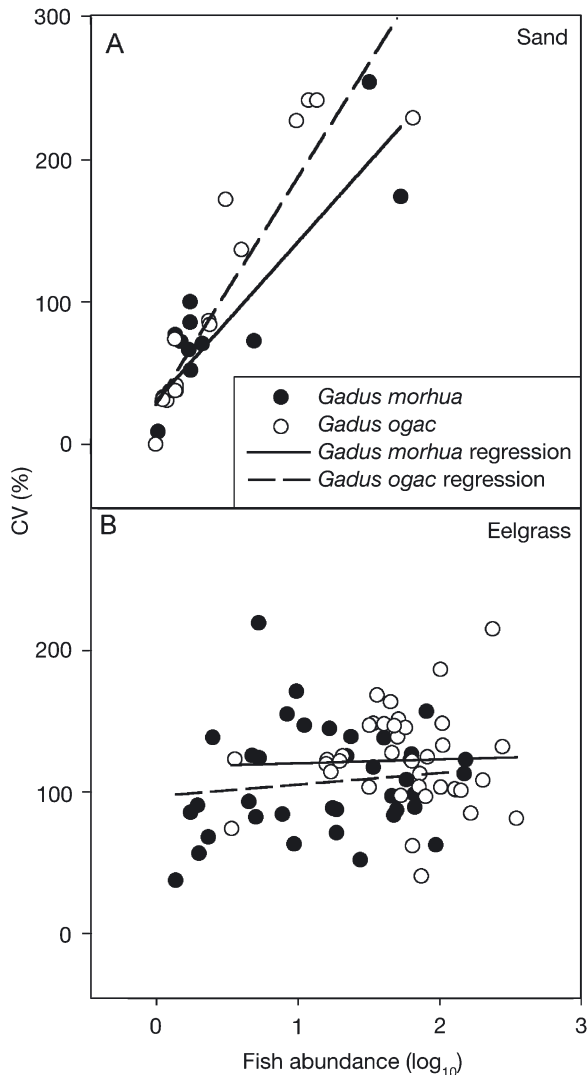
Fig. 7. *Gadus morhua* and *G. ogac.* Coefficients of variation against seasonal abundance at seine sites comprised of either (A) sand or (B) eelgrass. Plotted values represent the coefficient of variation (CV) calculated from 8 to 10 seine hauls within a year (1996, 1998 to 2001) at a single location

Mark–recapture experiment

There was a significant negative relationship ($r^2 = 0.84$, p = 0.0181) between the number of daily recaptures and time (Fig. 8). We interpret this as resulting from cod movement rather than mortality, since marked individuals were caught progressively further from the area of release on successive days (Table 1). The species composition of recaptures was 63% *Gadus morhua* and 37% *G. ogac* over the entire experiment. From the regression equation:

$$\ln (N+1) = 2.70 - 0.167 \times T$$

we calculated the mixed-species movement rate of juvenile cod as 16.7% d^{-1} from an area of 13 035 m^2 (237×55 m).

Significantly fewer fish were caught on Day 6 compared to other days ($F_{1,49} = 11.81$, p = 0.0012). Recapture effort on Day 6 occurred during heavy rainfall, and fish may have moved into deeper water to avoid contact with freshwater run-off. We therefore ran movement models (standard deviation with time) with Day 6 included and excluded. Including Day 6 into the regression produced a non-significant result ($F_{1,3} = 0.1028$, p = 0.779):

$$\ln (S) = 3.306 - 0.112 \ln (T)$$

In contrast, the regression with Day 6 excluded was significant ($F_{1,2} = 173.8$, p = 0.0482):

$$\ln (S) = 3.317 + 0.111 \ln (T)$$

The slope from the latter equation ($\beta = 0.1$) deviated substantially from the slope calculate for simple diffusion ($\beta = 0.5$). Therefore, the pattern of dispersal for Age 0 cod in the study area was not simple diffusion.

Video trials

Video analysis indicated that juvenile cod were more aggregated over sand habitat than eelgrass habitat (ANOVA with repeated measures; $F_{1,18} = 21.716$, p < 0.001, Fig. 9). Within-subject analysis indicated a measurable effect of aggregation over time in sand ($F_{19,179} = 4.165$, p = 0.028) or eelgrass ($F_{19,179} = 8.025$, p = 0.011). Fish were highly aggregated in both habitats early in the trial as a result of being released from a common starting position in
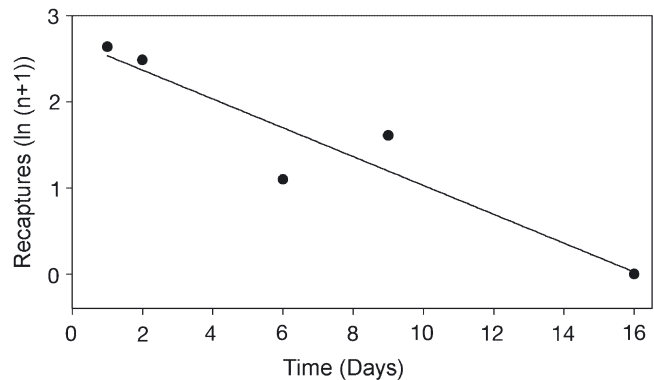

Fig. 8. *Gadus morhua* and *G. ogac.* Recaptures of juvenile cod (fish haul^{-1}) along a 219 m section of shoreline in Newman Sound. Total recaptures consisted of 63% *G. morhua* and 37% *G. ogac*

Fig. 9. *Gadus morhua.* Degree of shoaling (inter-individual distance) over time (min) in experimental tanks with eelgrass (n = 10 trials) or sand (n = 10 trials). Plotted values represent the cumulative distance of each fish to its neighbour from 10 trials ±1 SE

Fig. 10. *Gadus morhua.* Degree of orientation (angle separation between individuals) in experimental tanks outfitted with eelgrass (n = 10 trials) or sand (n = 10 trials). Low values along the *y*-axis indicate fish are orienting in the same direction. Plotted values calculated from angle sums of 5 individuals from 10 trials ±1 SE

the tank. Increases in juvenile cod dispersal in both eelgrass and sand appeared to level after 20 min into the trial, but fish in eelgrass treatments were clearly more dispersed at this point (Fig. 9). No aggressive behaviour was noted between individuals in either treatment.

There was weak evidence that propensity to swim in parallel differs between habitats. Fish over sand habitat were oriented in a common direction more so than fish in eelgrass habitat. However, the analysis showed this to be just outside the statistical alpha (ANOVA with repeated measures; $F_{1,18}$ = 3.36, p = 0.087; Fig. 10). Within-subject analysis also indicated no measurable change in orientation over time in sand ($F_{19,179}$ = 0.165, p = 0.828) or eelgrass ($F_{19,179}$ = 0.122, p = 0.751).

DISCUSSION

The relationship of juvenile cod and habitat has been explored from field observations (e.g. Tupper & Boutilier 1995a,b, Gotceitas et al. 1997), laboratory experiments (Fraser et al. 1995, Gotceitas et al. 1995, Lindholm et al. 1999) and field experiments Linehan et al. 2001, Laurel et al. 2003a,b). However, this study provides the first evidence that observed variation in catch of Age 0 juvenile cod is the result of habitat-induced changes in aggregative behaviour, e.g. shoaling or schooling. Juvenile cod use of low-complexity habitats (i.e. sand) was ephemeral and aggregative in nature. More significantly, however, these aggregation patterns for *Gadus morhua* were magnified over sites with low habitat complexity in high-abundance years.

Table 1. *Gadus morhua* and *G. ogac.* Number of Age 0 juvenile cod recaptured by beach seine over 10 seine sites along a 219 m section of shoreline in Newman Sound. Juvenile cod (n = 1109) were captured, marked and released on Day 0 at Site 4 (0 m) and recaptured on Days 1, 2, 6 and 9. *: no recaptures; also, none were recaptured at Site 1 (95 m) or on Day 16

Day	Species	10 (–124 m)	9 (–100 m)	8 (–83 m)	7 (–70 m)	6 (–51 m)	5 (–35 m)	4 (0 m)	3 (29 m)	2 (78 m)
1	*G. morhua*	*	*	*	1	1	2	6	*	*
	G. ogac	*	*	*	1	*	1	1	*	*
2	*G. morhua*	1	*	*	1	*	*	2	2	*
	G. ogac	*	2	*	*	*	*	*	3	*
6	*G. morhua*	*	*	*	*	*	*	*	*	*
	G. ogac	*	*	1	1	*	*	*	*	*
9	*G. morhua*	*	*	*	1	*	1	1	*	*
	G. ogac	*	*	*	*	*	*	*	*	1

Therefore, our study provides a clear example of a density-dependent, induced change of behaviour in a marine fish. Consequently, habitat suitability for Atlantic cod may be a dynamic rather than static function if aggregative behaviour modifies fitness in these habitats.

The effects of space limitation have been widely explored in marine fish. Organisms may use poorer-quality habitat (e.g. low food, high risk) when high-quality habitat (e.g. high food, low risk) becomes saturated (e.g. MacCall 1990, Kramer et al. 1997). Fish settling in poor-quality habitat may either die (e.g. Connell & Jones 1991, Tupper & Boutilier 1995a) or face poor growth (Sogard 1992). Our data from field sampling, mark–recapture and video observations all demonstrated that fish settling in poor habitat can also switch to another behaviour. This 'behaviour switching' hypothesis is supported in several lines of evidence. First, *Gadus morhua* and *G. ogac* were caught in sand habitats infrequently, and, when present, they generally occurred at high densities. Second, video observations confirmed that *G. morhua* aggregated more over sand. Finally, mark–recapture data demonstrated that both cod species move extensively following settlement. We suggest that this aggregation behaviour in open habitats either reduced predator risk or was in response to the possibly unique foraging opportunities available there (Savino & Stein 1982, Pitcher 1986).

Living in groups has a number of antipredator and foraging advantages. Increased shoal cohesion has been shown to occur in fish when exposed to increased predation risk (Andorfer 1980, Magurran & Pitcher 1987). Possible antipredator benefits include increased predator detection (Bertram 1978), confusion (Milinski 1979, 1985) and dilution (Foster & Treherne 1981, Krebs & Davies 1991, but see Pitcher 1986 for alternative view). These mechanisms may offset the cost of increased conspicuousness of group living by reducing predation rates for aggregative species (Calvert et al. 1979, Foster & Treherne 1981), including fish (e.g. Neill & Cullen 1974, Tremblay & Fitzgerald 1979). Foraging benefits include increased search rates and information gathering and sharing (Pitcher et al. 1982). Studies have shown that fish in large groups can allocate more time to foraging in open substrates since less time need be spent refuging in complex habitats (Magurran & Pitcher 1983). However, under certain conditions, habitat-specific behaviour can lead to increased mortality. For example, gobies increase their activity levels in open habitats, which ultimately leads to increased predation rates (Tallmark & Evans 1986). It is therefore difficult to speculate on the advantage of juvenile cod shoaling in sand in years of high abundance since we did not measure the fitness conse-

quences of such behaviour. Based on the mixed evidence of benefits stemming from habitat-specific behaviour, it may be that shoaling over poor-quality habitat is the result of juvenile cod 'making the best of a bad situation' rather than a fitness strategy suitable in all years.

High densities of juvenile cod were found associated with eelgrass in all years, suggesting this is a preferred nursery habitat for these 2 species. Complex habitats such as eelgrass generally support a higher number of species and density of fish than habitats of low complexity (Orth et al. 1984, Bell & Pollard 1989). Eelgrass often supports higher densities of food, namely in the form of pelagic and epiphytic zooplankton. Macrophytes also reduce the risk of predation for young fish from larger piscivores (e.g. Werner & Gilliam 1984, Mittelbach 1986), including juvenile cod from known predators such as older conspecifics (Bogstad et al. 1994) as well as red hake *Urophycis tenuis* and sculpin *Myoxocephalus* spp. (Linehan et al. 2001, Laurel et al. 2003b). Juvenile cod have also been shown to use the interstitial spaces of less complex mineral substrates such as cobble and gravel for predator avoidance (e.g. Lough et al. 1989, Gregory & Anderson 1997). However, the substrate particle size at the sand sites was ca. <1 mm, and therefore, unsuitable for cover. Predation risk is higher over substrates with particle sizes <4 mm (i.e. sand; Gotceitas & Brown 1993), and, consequently, Age 0 cod are seldom observed over small particulate substrates either inshore (Laurel et al. 2003a) or offshore (Lough et al. 1989).

There are conflicting reports on the range and degree of Age 0 juvenile cod movement following settlement. Age 0 juvenile cod have been observed defending areas of habitat in the field (Tupper & Boutlier 1995a,b) and the laboratory (Gotceitas & Brown 1993). Tupper & Boutlier (1995a,b) also document high site fidelity and limited within-habitat movement for juvenile cod. However, our data stand in contrast to previous discussions of territorial behaviour and limited movement. In both of the above studies, variable use of habitat was attributed to differential, predator-induced mortality between habitats rather than movement. Grant & Brown (1998a) observed some movement in *Gadus morhua* in nearshore areas of Newfoundland, but they suggested these movements were infrequent and restricted to a few hundred metres over an entire season. A subsequent study (Grant & Brown 1998b) showed a diel inshore–offshore movement of juvenile cod, possibly in response to temporal changes in prey availability and predator risk.

Mark–recapture data from the present study suggest juvenile cod movements are spatially and temporally greater than previously reported. Furthermore, juvenile cod movement patterns did not resemble simple

diffusion, suggesting that juvenile cod were making habitat decisions among eelgrass sites. However, movement patterns should be interpreted with caution due to the low number of overall recaptures of juvenile cod. Differences in reported movements between studies may be the result of local habitat characteristics. Our study was conducted in a contiguous eelgrass bed, whereas previous work has been conducted along obstructed shorelines (e.g. Grant & Brown 1998a,b). Other differences in reported movement rates may be linked to unique genetic or phenotypic aspects of the cod populations studied (e.g. Ruzzante et al. 1998). Species of fish can have static and resident components even at small spatial scales (Stott 1967, Taylor 1990, Heggenes et al. 1991, Freeman 1995). Therefore, variable movement within genetically discrete populations should be expected. Moreover, growth rates of cod between populations are highly variable. Growth of juvenile cod in St. Mary's Bay can reach 2.27 mm d^{-1} (Tupper & Boutilier 1994b) relative to ca. 1.5 mm d^{-1} by the cod collected in our study (R.S.G. & B.J.L. unpubl. data). Phenotypic variability (e.g. growth, body size, etc.) often corresponds with a change in behaviour, including strategies of feeding (e.g. Lavin & McPhail 1987), predator defense (e.g. Bronmark & Miner 1992) and territoriality (e.g. Taylor 1990). These differing strategies may ultimately contribute to differing patterns of movement in and among habitats.

Movement rates in fish can also be influenced by the degree of habitat heterogeneity. Fish movement may decrease in preferred habitats if those habitats are isolated or surrounded by unfavourable habitat, i.e. 'oasis effects' (Virnstein & Curran 1986, Schroeder 1987, Sogard 1989). Grant & Brown (1998a) report limited movement of juvenile cod between sites following settlement in nearshore areas, suggesting there were large sections of unfavourable habitat between sampling sites. Age 0 juvenile cod are restricted to shallow, nearshore habitat such as eelgrass, possibly due to increased predation with depth (Linehan et al. 2001) and reduced habitat complexity beyond the littoral zone (Gregory & Anderson 1997). Mark–recapture studies conducted between areas of varying habitat and depth may therefore misrepresent the capacity of movement in juvenile cod. In our study, juvenile cod movement was measured in an unobstructed eelgrass meadow, possibly explaining the higher movement rates compared to those reported in other studies on juvenile cod.

It is interesting that only *Gadus morhua* aggregated over sand in high-abundance years. Juvenile *G. morhua* experienced as much as a 20-fold fluctuation in density between years, whereas juvenile *G. ogac* demonstrated only a 6-fold change. Therefore, *G. ogac* may not have experienced the same pressure as

G. morhua to use alternative tactics in high-abundance years. Such a difference in the interannual variability in abundance between the 2 species may stem from life-history differences. Atlantic cod spawn both inshore (Hutchings et al. 1994) and offshore (Templeman 1979), have pelagic eggs (Scott & Scott 1988) and often rely on local hydrography (i.e. retention areas) for survival (de Young & Rose 1993, Bradbury et al. 1999, Page et al. 1999). Consequently, the recruitment of juvenile Atlantic cod to inshore areas should be expected to be highly variable. In contrast, *G. ogac* spawn inshore with demersal eggs (Scott & Scott 1989) and may therefore be less prone to hydrographic effects associated with recruitment variability (Bradbury et al. 2003).

Gadus morhua expand their range during years of higher abundance (Rose & Leggett 1991, Swain & Wade 1993, Anderson & Gregory 2000). Although we did not measure range expansion directly, it is interesting to note that substantive catches of juvenile cod in sand habitat were restricted to high-abundance years. Such an observation is consistent with the density-dependent spillover effect, but inconsistent with a carefully executed study in Newfoundland where no effect of density was found on range contraction in juvenile cod (Schneider et al. 1997). Differences between the observations in the present study and the analysis by Schneider et al. (1997) may be an issue of scale. Schneider et al. (1997) analysed catch data over a 1500 km range of coastline, and therefore results could have been affected by larval supply due to localised spawning success of several populations (Hutchings et al. 1994). Our study was restricted to a bay scale (i.e. <30 km), and previous work within this bay had shown that differential habitat use patterns by juvenile cod were not the result of larval supply (Laurel et al. 2003a). However, based on our results, a more likely explanation is that the increased schooling and aggregation of juvenile cod in high-abundance years masks the effects of geographic expansion. That is, the high variance associated with schooling may outweigh the lower variance indicative of range expansion. However, it remains to be determined whether the patterns of distribution observed in this study are relevant at larger scales.

In summary, field sampling and laboratory observations demonstrated that juvenile cod aggregate more over unstructured habitats (i.e. unvegetated sand) compared to overstructured habitats, i.e. eelgrass. In every year examined, higher densities of both species of juvenile cod were found in eelgrass, suggesting unvegetated sand is an unfavourable habitat. It is possible that aggregating over sand is a means of offsetting the costs (i.e. high risk and low food) associated with using these habitats. Aggregation of *Gadus*

morhua also increased over sand sites in years when abundance in eelgrass habitats was high, indicating this behaviour is density-dependent. Mark–recapture experiments suggested that juvenile cod are not as site-attached as previously reported, and that aggregations are likely the result of movement in and out of sites rather than mortality over time. Video analysis also demonstrated that juvenile cod form more cohesive shoals over sand, consistent with the interpretation of field catch data. Together, these data underscore the importance of considering density along with behavioural flexibility when evaluating habitat suitability in fish.

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