

Spatial pattern and patchiness during ontogeny: post-settled *Gadus morhua* from coastal Newfoundland

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We tested the hypothesis that patchiness increases after settlement to the bottom in a marine broadcast spawner, the Atlantic cod *Gadus morhua*. Patchiness $P=1+1/k$ was estimated from the dispersion parameter k of the negative binomial distribution. Estimates were based on length frequency distributions of fish from 18–330 mm that were seined from shallow nursery areas (<10 m depth) during autumn. Patchiness was highest for small cod (<24 mm) in the process of settling to benthic or epibenthic habitats. Settling cod were only collected from coastal sites located in deep fjords where adults overwinter and spawn. Patchiness was lowest for fish newly settled to benthic habitats (c. 50 mm SL) and increased thereafter with length to 200 mm SL. Our analyses suggest that patchiness in *G. morhua* >200 mm depends on a shifting balance between establishment of home ranges (tending to reduce patchiness) and schooling behaviour (tending to increase patchiness). Patchiness generally increased for *G. morhua* between 25–200 mm SL when examined at different spatial (major bays along the northeast coast of Newfoundland) and temporal (years) scales suggesting processes responsible for these patterns may be consistent among the bays and years examined. Our results show that more is learned about the distribution of fish by examining the zeroth, first, and second moments (presence/absence, mean abundance and patchiness) than by examining only one measure. We hypothesize that patchiness continues to increase for larger juvenile and adult *G. morhua* that were not examined in this study. We propose that patchiness may then decrease for the very largest cod, “mother fish” that may not undergo extensive annual spawning migrations.

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Introduction

Most animals and plants in aquatic and terrestrial environments are aggregated. Hence densities are seldom random or uniform. A random sampling of the environment usually results in many empty or nearly empty collections with a small number of samples containing the majority of the organisms. The variance typically exceeds the mean. This property of contagious

distribution has long been regarded as a statistical nuisance with little appreciation given to its importance or necessity in biological systems (Cassie, 1962; Smith, 1981). Patchiness or clumping of animals occurs as individuals aggregate in response to differences in habitat, to temporal changes in environmental factors such as weather and to behavioural requirements of reproduction, feeding, and social interactions (Krebs, 1999). Classic explanations for different distributions of

animals are resource monopolization and/or territoriality in the case of more uniform distributions and environmental heterogeneity in the case of aggregated (i.e., patchy) distributions (Pielou, 1974).

In the marine environment, patchiness of fishes has many origins (Smith, 1981). These include aggregation of adults during spawning and feeding (Harden Jones, 1968; Lawson and Rose, 2000), ocean processes such as upwelling, convergence, gyres (Smith, 1981), and variation in abiotic factors, prey availability, and predation (Swartzmann *et al.*, 1999; Rose and Leggett, 1990). Patchiness has been shown to change in a consistent manner with body size for pelagic larvae and juveniles of several fish species. It often starts high, decreases for slightly larger larvae and then increases once again for the oldest larvae when plotted against length or age (Hewitt, 1981; McGurk, 1987). Patchiness of early stage pelagic eggs is initially high if adults aggregate when spawning. Patchiness decreases as a result of dispersal processes for passive egg and larva stages but then increases as locomotion capacity of larvae and pelagic juveniles develops with increasing length (Matsuura and Hewitt, 1995). Patchiness of larvae may also be related to egg type (Suthers and Frank, 1991). Larvae from demersal eggs spawned in shallow water exhibit a clumped distribution near spawning sites compared to the low patchiness of larvae from pelagic eggs. Pelagic larvae from demersal eggs are said to be spatially persistent given that eggs are non-dispersing and remain aggregated in the vicinity of adult spawning sites (e.g. McGurk, 1987; Suthers and Frank, 1991). Patchiness has been shown to decrease with age for eggs of *Sardinops sagax* Pacific sardine, a pelagic schooling species (Smith, 1973) and increase with age for eggs of *Melanogrammus aeglefinus* haddock, a serial spawning demersal species (Koslow *et al.*, 1985). Patchiness has been described for the egg, larval, and pelagic juvenile stages of several fish species (Hewitt, 1981; McGurk, 1987; Matsuura and Hewitt, 1995). This represents a very small portion of the life of most fishes.

We examined post-pelagic processes in juvenile *G. morhua* Atlantic cod collected in standardized seine hauls from the northeast coast of Newfoundland. Atlantic cod taken in 1996 and 1997 surveys, were among the most abundant species collected, were taken over a wide range of sizes, and were collected throughout the spatial extent of the survey. During the 1990s, recently settled juvenile *G. morhua* occurred in highest densities at 4–7 m depth in a narrow band along the coast of northeast Newfoundland (Methven and Schneider, 1998). Abundance of age-0 cod decreases with depth and distance offshore such that demersal age-0 cod are rarely found outside the major bays along Newfoundland's northeast coast (Dalley and Anderson, 1997; Anderson and Gregory, 2000). Concentration on favourable habitat shortly after settlement (Tupper and

Boutilier, 1995) and shoaling at larger sizes (Rose, 1993) are processes that increase patchiness in the coastal zone. In this paper we test the hypothesis that patchiness of settled juvenile *G. morhua* increases with length.

The main objective of our study is to estimate change in patchiness with increase in length for juvenile *G. morhua* from coastal Newfoundland. We also examine whether size related patterns of patchiness are spatially and temporally consistent. Patterns of patchiness that are spatially and temporally consistent suggest that processes responsible for these patterns may also be consistent (Wiens *et al.*, 1986; Denman, 1992; Horne and Schneider, 1995; Hewitt *et al.*, 1996).

Methods

Data collection

Fish were collected in 1996 and 1997 as part of a survey that was initiated in 1959 by Alistair Fleming, Tom Collier, and other researchers of the Fisheries Research Board of Canada, St. John's, Newfoundland. The survey was conducted in 1959–1964 and 1992–1997. There was no sampling from 1965 to 1991. The survey measured change in abundance (e.g., Ings *et al.*, 1997) of recently settled *G. morhua* along the northeast coast of Newfoundland (Figure 1; Lear *et al.*, 1980; Schneider *et al.*, 1997). In 1996–1997 local fishermen became an integral part of the survey. The survey was well established by 1996–1997 and was organized and conducted by the same person ensuring consistency between years. Forty-five sites were sampled in 1996 (19 September to 22 October) and 38 of the same set of sites were resampled in 1997 (23 September to 27 October). Sampling was done during daylight and was not confined to any particular tide stage. Weather influenced the number of sites sampled each year. A sampling schedule was maintained such that the same sites were sampled on approximately the same dates each year.

Fish were collected in shallow water (usually <10 m) using a 25-m seine hauled by two people towards the shore after being deployed from a boat. The seine has a headrope length of 24.4 m and a footrope of 26.2 m. The wings, belly, and codend are made of knotless nylon netting, 19 mm stretch mesh in the wings and belly and 9 mm stretch mesh in the codend. The mesh size of the codend was suitable for retaining fishes as small as 20–30 mm SL. An area of approximately 880 m² was sampled on each haul (16 m along the shore by 55 m offshore). The seine sampled only the bottom two meters of the water column. Three hauls were made at each site if conditions permitted. The first two hauls were done at the same location, i.e., the same 880 m² was sampled twice within about 30–60 min. A third haul was done immediately along side the first two hauls when possible. Fish were sampled by at least two hauls of the seine at

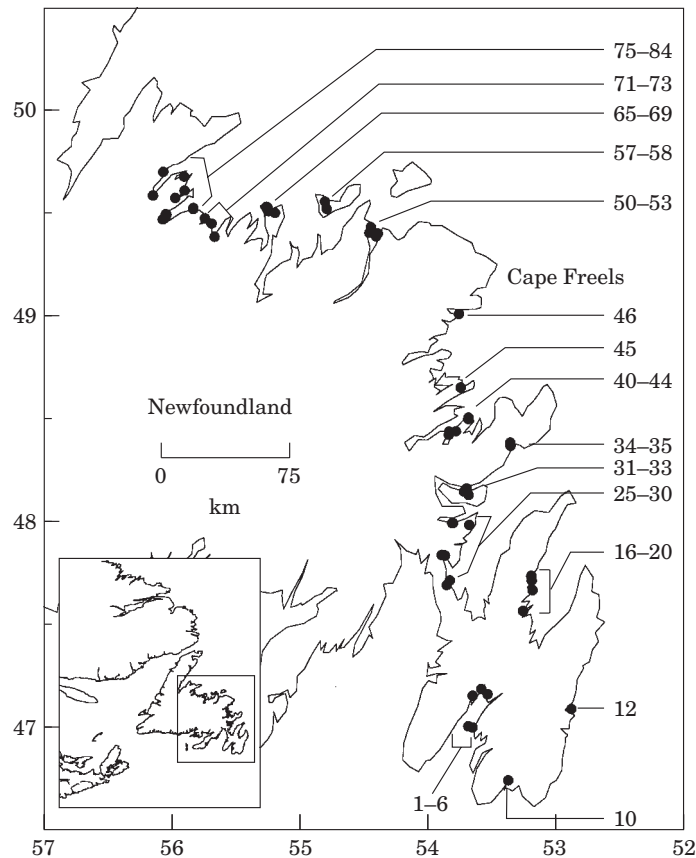


Figure 1. Chart showing the distribution of sites sampled during the 1996 and 1997 surveys for juvenile cod in coastal Newfoundland. Sites 1–6 are in St Mary's Bay, site 10 Trepassey Bay, 16–20 Conception Bay, 25–35 Trinity Bay, 40–46 Bonavista Bay, 50–58 Gander Bay – New World Island, 65–84 Notre Dame Bay. Sites are not numbered consecutively. Sites 31–33 are adjacent to Random Island.

all sites except one (site 18, 1997, $n=1$ haul). A total of 230 standardized seine hauls were made, 128 in 1996 and 102 in 1997. All *G. morhua* ($n=3887$) were between 18–330 mm SL and were taken in a total of 148 seine hauls.

Virtually all surveys of mobile organisms such as juvenile *G. morhua* have counts that contain zeros (Horne and Schneider, 1997). Samples with zero *G. morhua* may be taken by chance from within a patch (if the sampling equipment and the area sampled is small for example), may be taken from between patches (sampling poor habitat for example), or if samples are taken from outside the range where the species usually occurs (Smith, 1973; McGurk, 1987; Gaston and McArdle, 1994). For our study seine hauls where at least one individual of any size was collected were assumed to define the habitat for *G. morhua* in that year. Consequently one site may have been used in one year but not in the next. These samples comprised the data set used in the analyses. To examine what effect excluding the zero samples may have on the calculation of

patchiness we did a subsequent analysis and included all observations zeros as well as positive catches. This increased the sample size from 148 to 230.

Analyses

Random samples from aggregated distributions of fish typically have numerous zero or near zero counts with most specimens being taken in a small number of samples. For example, in 1996 90% all age-0 cod were taken in just 15.6% of the seine hauls (equivalent to 24% of the sites sampled). In 1997, 90% of age-0 cod occurred in 16.6% of the seine hauls, equivalent to 46% of the sites sampled. Aggregation of fish in a small proportion of the samples results in a variance that is greater than the mean. Catch frequencies from such aggregated distributions are often examined using the negative binomial distribution. Comparison of negative binomial distributions to other distributions based on poisson processes have shown that the negative binomial distribution is often the most applicable theoretical distribution to use,

however no single frequency distribution is applicable to all data (Horne and Schneider, 1995).

The negative binomial distribution is defined by two parameters, the mean and a measure of dispersion k . Bliss and Fisher (1953) indicate the dispersion parameter is best estimated using equation [1] below. This equation, which produces the maximum likelihood estimate, is more accurate than equations that estimate k using the first (mean) and second (variance) moments or estimates based on the proportion of zero samples (Bliss and Fisher, 1953). Methods of estimating k are outlined with some examples in Bliss and Fisher (1953); Southwood (1978) and Krebs (1999).

$$N \log_e[1 + (\bar{x}/k)] = \sum [Ax/(k+x)] \quad (1)$$

In equation [1] \bar{x} is the mean catch per standardized tow (density), Ax is the sum of all frequencies of sampling units containing more than x individuals (e.g., $A_5 = \sum f_6 + f_7 + f_8 \dots$ etc. see Bliss and Fisher, 1953; Southwood, 1978) and N is the number of samples with *G. morhua*. The procedure for estimating k in equation [1] is to substitute parameter estimates until the difference between the two sides of the equation is zero, or very close to zero. This is done iteratively and in the case of equation [1] produces the maximum likelihood estimate.

Lloyd's (1967) index of patchiness P measures intensity of aggregation and is defined by two parameters, the mean (\bar{x}) and variance (s^2).

$$P = 1 + [(s^2 - \bar{x})/\bar{x}^2] \quad (2)$$

This index measures how many times as crowded an individual is on average than it would have to be if the same population had a random (non aggregated) distribution (Lloyd, 1967). The variance of the negative binomial is related to the mean and k as

$$s^2 = \bar{x} + (\bar{x}^2/k) \quad (3)$$

When the formula for variance [3] is substituted into Lloyd's index of patchiness [2], patchiness simplifies to

$$P = 1 + (1/k) \quad (4)$$

where k is estimated using [1]. k has long been known as a measure of dispersion (Waters, 1959; Cassie, 1962). Its use as an index of dispersion in ecology is briefly reviewed by Horne and Schneider (1995).

Patterns of patchiness will change depending on the resolution of data analyses. We initially used 3 mm length groupings (i.e., width of the length bin analysed) in this study and then doubled the width of the length groupings thereafter such that patchiness was estimated at length groupings of 3, 6, 12, and 24 mm. The 3 mm size bin was subsequently judged to be too fine a

resolution for the analyses and was dropped because poor estimates may result from low numbers. Six and 12 mm length groupings showed similar patterns of patchiness to that observed at 24 mm, hence, patchiness at length curves are only shown for 24 mm length groupings in this study.

k was estimated using Microsoft's Excel solver routine (2000). This routine stops at local minima and has to be restarted for calculation of individual k values. We recalculated numerous values of the dispersion parameter k from Bliss and Fisher (1953); Matsuura and Hewitt (1995) and Krebs (1999), to ensure that values reported in this study had reached a global minimum. Recalculated values agreed closely with previously reported values, often to one place after the decimal point. k and the corresponding estimates of patchiness were estimated to four decimal places.

Frequency distributions of catches shown in relation to length (Table 1) form the basis for calculating the dispersion parameter and corresponding indices of patchiness. Similar but larger tables were prepared but are not shown for fish grouped at 3, 6, and 12 mm length bins. Occasionally, methods of estimating the dispersion parameter would yield estimates approaching infinity with the corresponding values of patchiness approaching unity. In these cases the mean was usually slightly greater than or equal to the variance, a statistical distribution more typical of randomness than of aggregation. Values of k for these catch frequencies were assigned an open circle in the accompanying figures. Values of patchiness would approach unity as data become sparse. Values of patchiness approaching unity therefore tend to become more common as the width of length bins becomes smaller (e.g., 3 and 6 mm) or when subsections of the data are examined, for example when examining the two years separately.

Results

A bimodal size distribution of juvenile *G. morhua* was observed in both years (Figure 2). Modes occurred at c. 50 and 150 mm SL when mean data from two years were combined. Few fish were collected at sizes between these two length modes or at sizes >225–250 mm SL. High mean catches at modes of c. 50 and 150 mm were characterized by a corresponding decrease in the proportion of zero catches (Figure 2) and a high variance associated with the long tailed catch frequency distributions at these sizes (Table 1).

Most studies that examine patchiness of ichthyoplankton exclude samples that did not catch larvae, i.e., remove samples when catch equals zero, as we have done here for juvenile *G. morhua*. An analysis of all the data, samples with no catch as well as samples with positive catches increased the sample size from 148 to

Table 1. Size specific catch statistics for juvenile *G. morhua* collected in coastal Newfoundland with a 25-m seine, 1996–1997 combined. A total of 3887 *G. morhua* were collected in 148 seine hauls that contained juvenile *G. morhua*. Values are number of samples with the indicated number of fish. For example, length grouping 0 had 143 samples with no fish ≤ 23.9 mm SL, length bin 24 had 45 samples with no fish and 38 samples with one fish present between 24.0–47.9 mm SL etc. Values at the bottom of this table (last six rows) in italics are calculated based on a sample size of 230 seine hauls. See results.

Length grouping Age (estimated)	0	24	48	72	96	120	144	168	192	216	240	264	288	312
No. of fish per sample														
0	143	45	67	111	128	112	111	126	133	131	136	135	135	143
1	3	38	24	20	16	13	13	9	6	8	7	10	8	4
2	0	16	11	5	3	4	5	3	2	4	1	0	4	1
3 to 4	2	18	5	5	0	10	8	4	3	2	3	1	0	
5 to 8		7	13	4	1	4	5	4	2	3	0	1	1	
9 to 16		8	9	2		4	4	2	2		1			
17 to 32		9	9	1		1	2							
33 to 64		3	3											
65 to 128		3	3											
129 to 256		1	4											
No. of sample with cod	5	103	81	37	20	36	37	22	15	17	12	13	13	5
Total fish	10	1063	2064	112	28	160	186	82	53	42	30	30	21	6
No. of samples	148	148	148	148	148	148	148	148	148	148	148	148	148	148
Mean/sample	0.07	7.18	13.95	0.76	0.19	1.08	1.26	0.55	0.36	0.28	0.20	0.20	0.14	0.04
Variance	0.19	416.12	3646.16	5.49	0.40	11.20	14.07	3.81	2.46	1.14	0.99	1.06	0.31	0.05
Var/mean	2.81	57.94	261.45	7.25	2.11	10.36	11.20	6.88	6.87	4.02	4.88	5.23	2.18	1.23
k	0.03	0.25	0.14	0.15	0.26	0.12	0.11	0.07	0.05	0.08	0.05	0.06	0.11	0.11
P	36.80	4.95	8.24	7.46	4.86	9.68	10.12	14.50	20.64	13.49	19.73	17.12	9.87	10.22
No. of samples	230	230	230	230	230	230	230	230	230	230	230	230	230	230
Mean/sample	0.04	4.62	9.05	0.49	0.12	0.70	0.81	0.36	0.23	0.18	0.13	0.13	0.09	0.03
Variance	0.12	279.00	2405.66	3.66	0.26	7.46	9.40	2.52	1.61	0.75	0.65	0.69	0.21	0.03
Var/mean	3.00	60.39	265.82	7.47	2.17	10.66	11.60	7.00	7.00	4.17	5.00	5.31	2.33	1.00
k	0.15	0.08	0.09	0.09	0.15	0.07	0.07	0.05	0.03	0.05	0.03	0.03	0.07	0.07
P	7.80	13.11	11.68	11.68	7.46	15.33	16.00	22.79	32.40	21.20	30.79	26.52	15.49	16.04

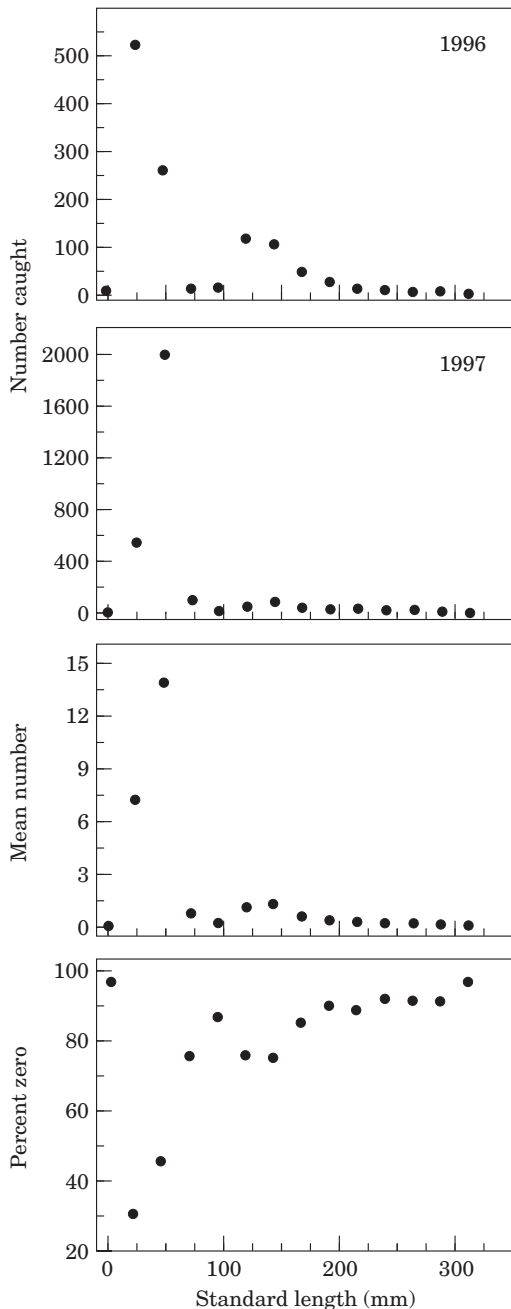


Figure 2. Length frequency distribution of all *G. morhua* caught during the 1996 and 1997 surveys. The bottom two panels show combined data from 1996 and 1997. The lowest panel shows the percentage of samples where no cod were caught for each length interval. Number of cod caught, mean number and percent zero were calculated for length data grouped at an interval of 24 mm SL.

230 (64.3%). The inclusion of the zero samples reduced the mean and also the variance. It also lowered the dispersion parameter k . A reduction in k results in an

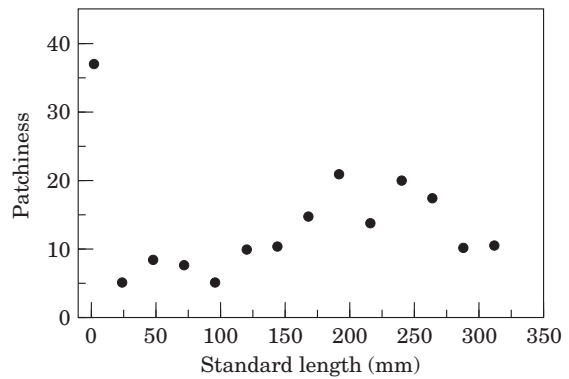


Figure 3. Patchiness of juvenile *G. morhua* calculated for length data grouped at an interval of 24 mm SL from the 1996 and 1997 (combined) surveys.

increase in P . Patchiness between the two sets of data increased by 63–64% for each length grouping however the overall pattern of patchiness with respect to length remained the same (Table 1) an observation reported by McGurk (1986).

Lloyd's index of patchiness was initially high for fish in the process of settling. Patchiness decreased quickly and then increased steadily with length to c. 200 mm (Figure 3). The smallest sizes, <24 mm SL, were patchier in their distribution (high p values) than slightly larger more settled individuals (Table 1). Patchiness was very low for recently settled cod (24–48 mm SL; Figure 3) and remained low for age-0 *G. morhua* in general, the age class that was the most dispersed over the extent of the survey (Figure 4). At increasingly larger sizes, patchiness tended to increase for age-1 cod (c. 100–200 mm) but showed a general decline at lengths greater than 200–250 mm (Figure 3), approximately age-2 fish.

The spatial distribution of juvenile *G. morhua* changed during ontogeny (Figure 4) and was generally related to the values of patchiness shown in Figure 3. The size specific spatial distributions were purposely chosen for illustration in Figure 4 because they represent important stages in the early life of juvenile *G. morhua* in coastal Newfoundland (settlement, early post-settlement, c. ages 1 and 2). The settlement stage is represented by fish less than 24 mm SL. These fish have a high index of patchiness (Figure 3) and are only located in a small portion of the sampling area: Random Island and Bull Arm of Trinity Bay (Figures 1 and 4). The Random Island and Bull Arm areas of Trinity Bay are both characterized by narrow very deep coastal fjord-like projections. Fish between 48–60 mm SL represent the largest size mode evident in Figure 2 and are spatially the most dispersed (Figure 4). High dispersal was associated with a low index of patchiness (Figure 3). *Gadus morhua* between 156–168 mm SL are one year old and are fish from the second size mode evident in Figure 2. The spatial

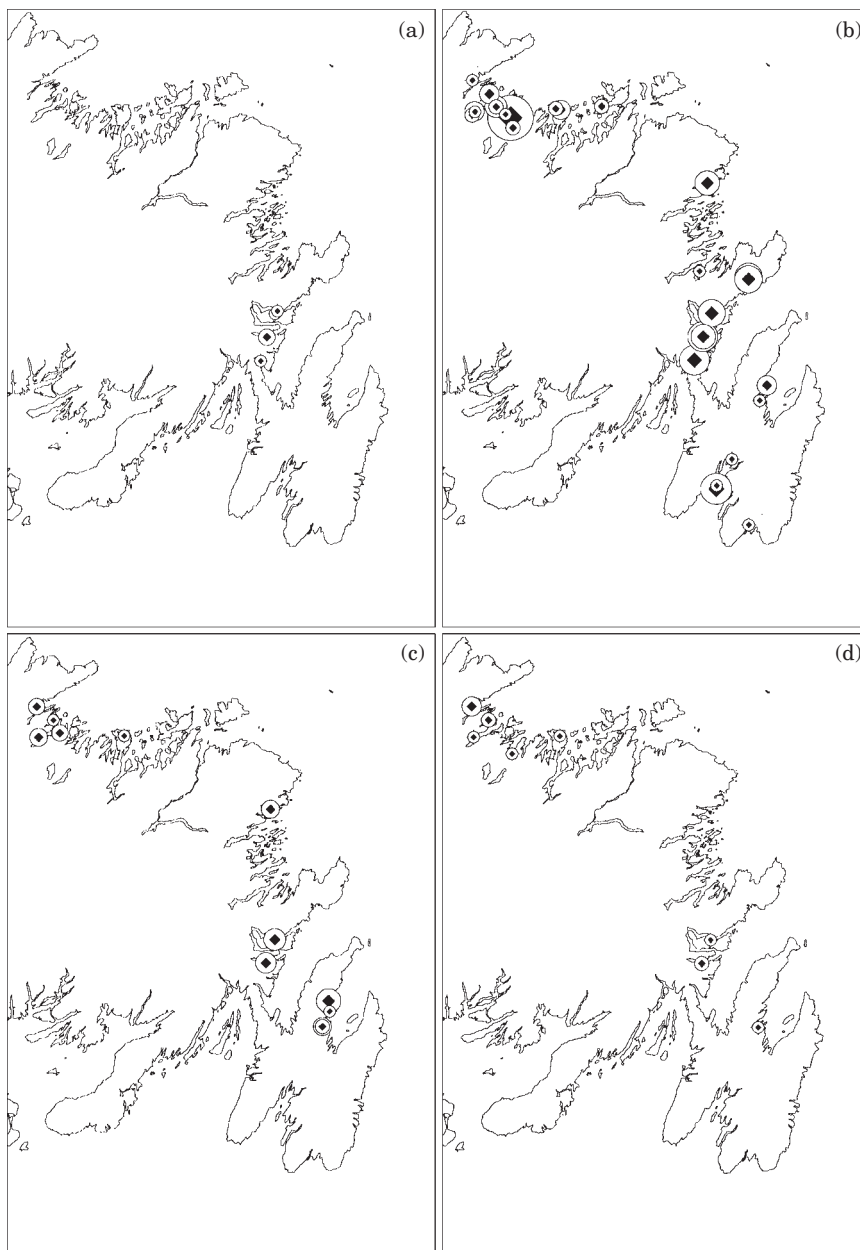


Figure 4. Charts showing the spatial distribution of (a) 12–24 (age-0, settlement), (b) 48–60 (age-0, post-settlement), (c) 156–168 (age-1), and (d) 204–216 mm SL (c. age-2) *G. morhua* from the 1996 and 1997 (combined) surveys.

distribution of age-1 cod is not as extensive as that of 48–60 mm sized (age-0) cod (Figure 4) and this is reflected in the slightly higher index of patchiness (Figure 3). The most patchy distributed post-settled *G. morhua* are c. 200 mm, individuals that were relatively rare in the coastal shallows of northeast Newfoundland. These larger fish showed a more contracted distribution relative to their smaller counterparts, excluding the settlement stage (Figure 4). This was

associated with a higher average index of patchiness (Figure 3).

Patchiness at length plots examined separately for 1996 and 1997 show patchiness to generally increase with increasing length at least for settled fish up to c. 200 mm (Figure 5). Similar patterns of increasing patchiness with increasing length were also observed for juvenile *G. morhua* in two large bays in 1997, Trinity and Notre Dame on the northeast coast of Newfoundland

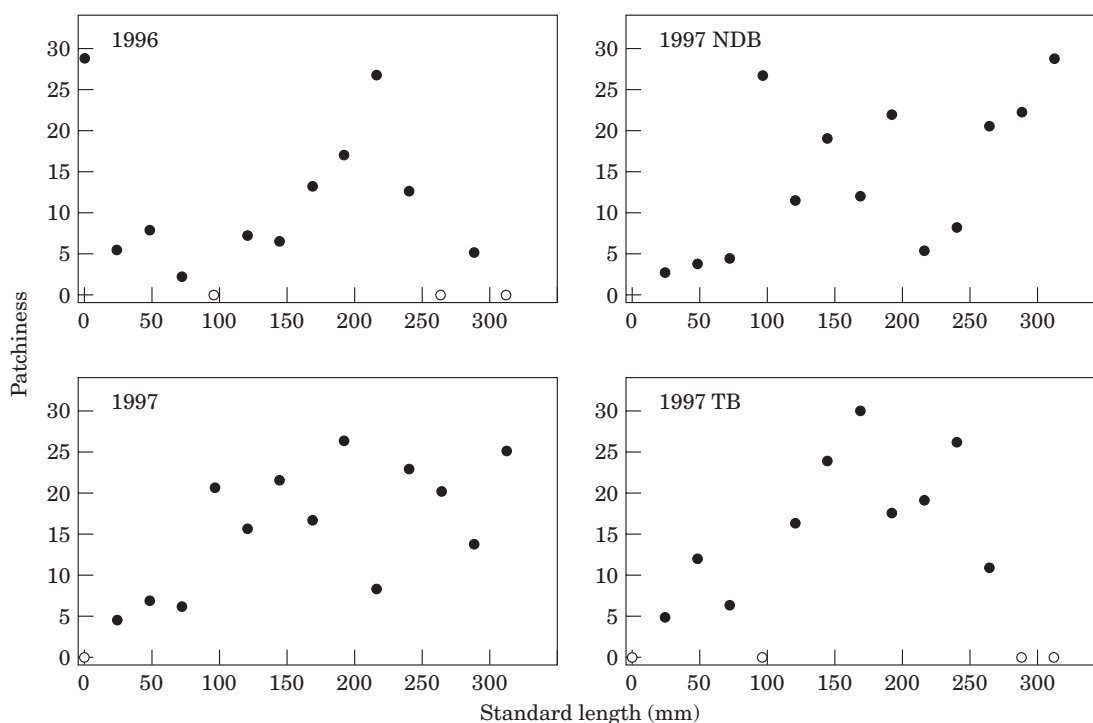


Figure 5. Patchiness–length plots calculated separately for 1996 and 1997 and for two major bays (TB – Trinity Bay; NDB – Notre Dame Bay) on the northeast coast of Newfoundland sampled in 1997. Patchiness was calculated at length groupings of 24 mm SL. Open circles along the x-axis represent instances when the mean exceeded the variance and where the dispersion parameter approached infinity. See Methods.

(Figures 1 and 5). Patchiness could be either high or low for lengths greater than 200 mm (Figure 5).

Discussion

Repeated sampling with a 25-m seine in coastal nursery areas of Newfoundland during autumn 1996 and 1997 indicated that patchiness increased with increasing length for post-settlement *G. morhua* up to 200 mm SL. This pattern was obtained from pooling data over large spatial (c. 1500 km coastline) and temporal (2 years) scales and as such represents average conditions for the period considered. Increases in patchiness with length were also observed at smaller spatial and temporal scales for two major bays on the northeast coast of Newfoundland and for both years of sampling when analyzed separately. Patchiness was high for small *G. morhua* (<24 mm SL) that were limited to a small portion of the survey area and lowest for slightly larger individuals that were dispersed throughout the survey. Patchiness continued to increase up to approximately 200 mm and on average showed a decline for lengths >200 mm SL. When patchiness was estimated separately for each length class (LG0) c. age-0 (<96 mm SL), LG1 (97–192 mm SL) and all remaining *G. morhua* (mostly age-2, 193–290 mm SL, Methven and Schneider, 1998)

the same pattern was observed. Patchiness was lowest for age-0 *G. morhua* ($P=5.2$), increased for age-1 ($P=7.6$) and showed a slight decrease for age-2 ($P=7.2$).

Data support our initial hypothesis of patchiness generally increasing with length of *G. morhua* up to c. 200 mm. However, patchiness plots were initially high with respect to length for the earliest stages of settling cod and hence were comparable in shape to curves derived for the pelagic stages of several species of teleosts examined by Matsuura and Hewitt (1995). Consequently, patchiness decreased with increasing length for the smallest fish collected in this study. This was an unexpected finding. This result may reflect the highly aggregated nature of pelagic juvenile *G. morhua* during settlement from pelagic to benthic habitats. It is difficult to determine precisely when and at what size *G. morhua* are fully settled to the bottom, especially when the depth of water where the seine samples is shallow (usually <10 m). In this study, fish in the process of settling were small, transparent (almost “see through”, especially the region posterior to the gut), and lacked the encysted metacercaria of the digenean *Cryptocotyle lingua*, that is often observed on larger fishes from nearshore waters (Methven and Bajdik, 1994; Grant and Brown, 1998). This suite of characters applied only to *G. morhua* that were <24 mm SL in this study. The spatial

distribution of *G. morhua* with these characteristics was limited to just four sites in Trinity Bay (site 28, Bald Point Beach; site 29, Long Beach east; site 32, Middle Lance Cove; site 33, Burgoyne Cove; longitude and latitudes are in Schneider *et al.*, 1997) that were located along the coast in deep (200–300 m) fjords where adults are known to overwinter and spawn (Hutchings *et al.*, 1993; Wroblewski *et al.*, 1994; Smedbol and Wroblewski, 1997). Moreover, this area has sustained this overwintering population since at least 1995. Settlement of the smallest stages is however not limited to the western side of Trinity Bay in Newfoundland. Earlier studies have reported small cod settling in late summer, autumn and early winter (Methven and Bajdik, 1994; Grant and Brown, 1998) in shallow coastal regions of southern Trinity Bay.

High patchiness associated with settling *G. morhua* is replaced with low values of patchiness for slightly larger (c. 50 mm, age-0; Anderson *et al.*, 1995; Campana, 1996; Methven and Schneider, 1998) *G. morhua* that were present at many sites throughout the survey. This portion of the patchiness–length plot (c. 50 mm SL) is characterized by a change in slope where the relation between patchiness and length goes from negative to positive. The change in slope suggests different processes may be responsible for the change in patchiness. We hypothesize that lower patchiness occurs when settled juveniles disperse to search for suitable habitat with adequate food and shelter. Dispersal may be a density dependent process if density of new settlers is high and if suitable habitat is limiting. Dispersal of recently settled cod in the 1990s is limited to coastal Newfoundland, only rarely do age-0 *G. morhua* occur offshore (Dalley and Anderson, 1997). At a smaller spatial scale, Methven and Schneider (1998) show highest densities occur at 4–7 m along the coast. The relatively confined coastal distribution and a preference for sheltered eelgrass habitat (Gotceitas *et al.*, 1997) suggests density dependent processes of dispersal for suitable habitat may be important in explaining the longshore distribution of age-0 cod. A second factor that may also contribute to the distribution of settling fish is their proximity to nearby deeper water adult spawning sites as we have observed for settling cod in the Random Island area of Trinity Bay.

Patchiness of one-year-old *G. morhua* (c. 150 mm SL) was generally higher than patchiness observed for age-0 cod. Larger *G. morhua* are more mobile and likely perceive habitat over larger distances. Keats *et al.* (1987) observed larger *G. morhua* were not as closely associated with macroalgae as age-0 cod were, an observation supported by field observations (Gotceitas *et al.*, 1997; Gregory and Anderson, 1997) and by laboratory experiments (Gotceitas and Brown, 1993). The larger size and increased mobility allows age-1 cod to decouple themselves somewhat from habitat (relative to age-0 cod) and

adopt a shoaling behaviour as observed for age-1 cod by Keats *et al.* (1987). Shoals of one-year-old cod have been observed acoustically with size and age verified by Scuba divers on several instances in coastal Newfoundland (Figure 6). We suggest this decoupling of age-1 *G. morhua* from the eelgrass–macroalgae habitat and the initiation of shoaling behaviour are important processes leading to increased patchiness and overall range expansion to deeper offshore waters relative to age-0 *G. morhua*.

The final phase of our patchiness–length plots occurs at lengths >200 mm SL where the slope of the curve changes, and where patchiness was observed to level off at c. 200–250 m and decrease at >250 m. At least three processes, in addition to the cumulative effect of total mortality, can influence density of larger c. age-2 *G. morhua* in coastal Newfoundland. One process that reduces density is an ontogenetic movement to deeper water (Riley and Parnell, 1984; Dalley and Anderson, 1997). A second process that results in an apparent reduction in density is avoidance of the haul seine (Methven and Schneider, 1998). An additional process consistent with a reduction in patchiness is the establishment of individual home ranges. Establishment of home ranges would reduce spatial variance and patchiness of *G. morhua* if individuals remain within home ranges during the day (when our sampling was done) and if home ranges do not substantially overlap. This spacing and distribution of *G. morhua* results in uniform and random distributions (i.e., low patchiness) where dense aggregations (i.e., high patchiness) are not observed at small scales. Establishment of home ranges was first reported by Hawkins *et al.* (1974, 1980, 1985) for *G. morhua* (>30 cm) at depths between 10–20 m where movements were restricted to relatively small areas in a Scottish Loch during the day. This behaviour has also been observed for cod (260–330 mm) in two coastal Newfoundland locations within the bounds of our survey during autumn when our sampling was done (Clark and Green, 1990; Cote *et al.*, 1998). In autumn, *G. morhua* were active within home ranges during the day at depths <20 m (Clark and Green, 1990). Observations by Cote *et al.* (1998) show *G. morhua* to be active during the day, also within small-restricted areas usually at depths <8 m. The size of mean daily home ranges varies among cod (244–12 549 m²) with the average being 7100 m² for *G. morhua* between 28–33 cm (Clark and Green, 1990). This average is generally consistent with other studies (Hawkins *et al.*, 1980) and is much larger than the area sampled by our haul seine, 16 m × 55 m = 880 m². Consequently we would expect catches of age-2 cod from a single seine haul to be small, usually 1 or 2 fish per haul. This is based on reported average home range sizes and assumes that home ranges do not overlap. This is in fact what was observed. The modal catch of age-2 *G. morhua* was one per haul

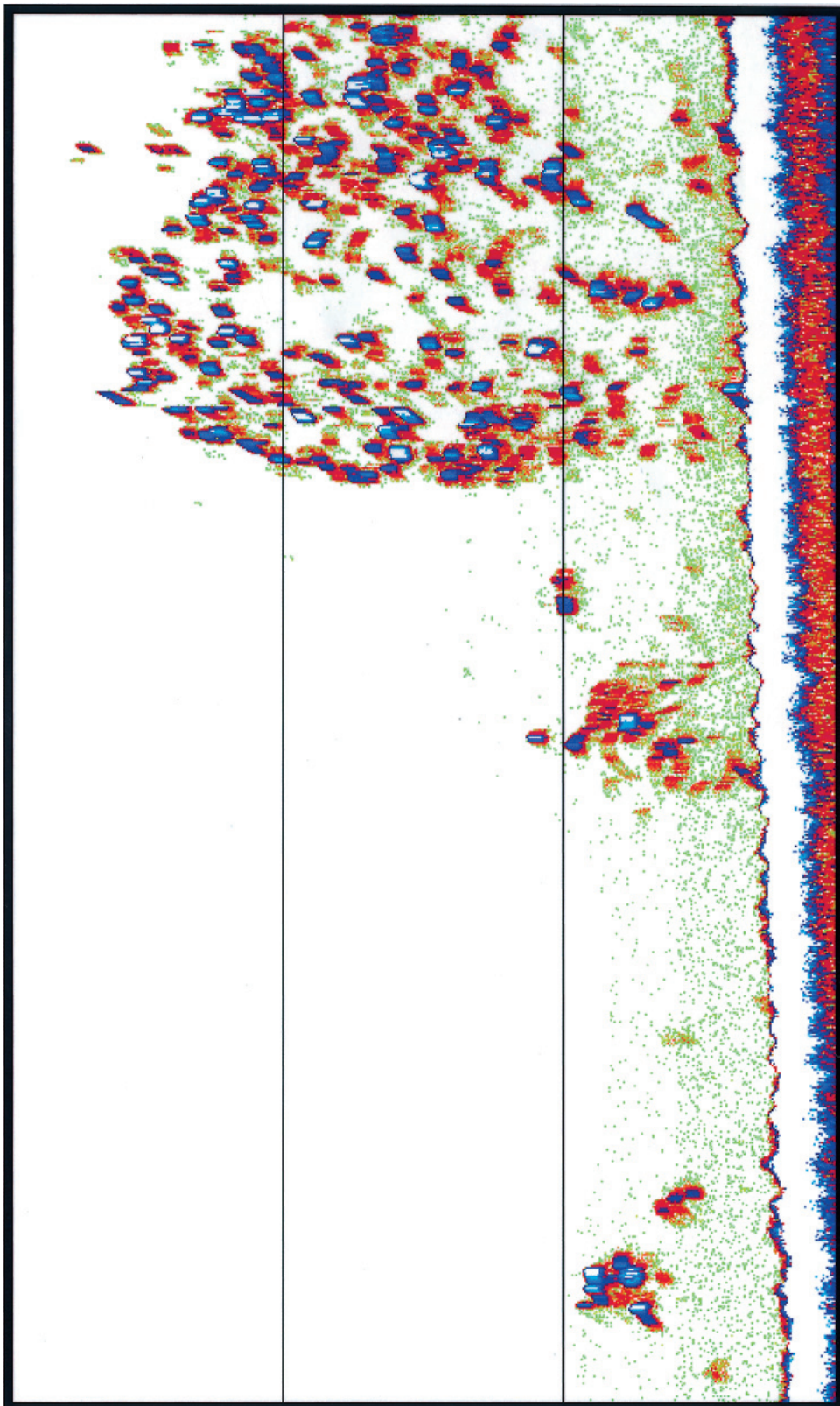


Figure 6. Echogram of age-1 *G. morhua* from coastal Newfoundland. Echogram shows two small and one much larger aggregations. Individual fish can be identified in each aggregation. The two horizontal black lines are at 7 and 13 m with the bottom at approximately 20 m depth. The horizontal view of the echogram is approximately 30 m.

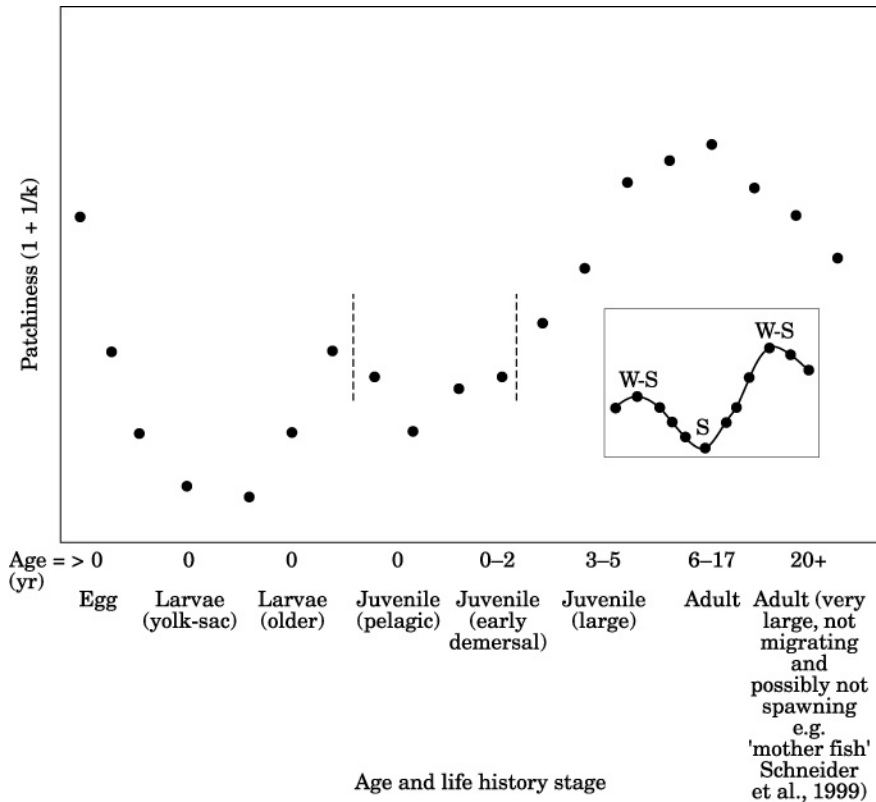


Figure 7. Hypothesized pattern of patchiness for all life history stages of *G. morhua* based on data from Matsuura and Hewitt (1995, eggs and larvae of *Scomber japonicus*) and this study (pelagic and early demersal juveniles, between dotted vertical lines). The insert applies to large juveniles–adults and indicates patchiness has a seasonal component within a given year. Patchiness is proposed to be high in winter–spring (W–S) when *G. morhua* aggregate to spawn and lower during post-spawning when fish disperse to feed in summer (S).

(observed in 16 of 32 positive seine hauls) with 26 of 32 hauls catching 5 or less. A total of 6 hauls however each took >11 cod which is considerably above the density of age-2 cod expected within the 880 m² sampled on each seine haul if cod had established individual home ranges. High densities (>11) of large fish within a small area are more consistent with shoaling. If cod are displaying two types of behaviour (establishing home ranges, and shoaling) during autumn then this could explain the densities of age-2 cod that we were catching and the reduction in patchiness at lengths >200 mm SL. Shoaling serves to increase patchiness (variance>mean) while non-overlapping home ranges and territories tend toward even or random distributions (variance≤mean) and decreased patchiness at the spatial scale sampled by our sampling equipment (880 m²). We believe these four processes: ontogenetic movement offshore, sampler avoidance, shoaling behaviour and occupation of home ranges during the day are important processes influencing patchiness of age-2 cod in coastal Newfoundland.

We propose that patchiness continues to increase for larger and older *G. morhua* and that this is due in large

part to fish becoming increasingly more aggregated with age (Figure 7). Superimposed on this ontogenetic increase in patchiness are within year seasonal changes (Figure 7, insert) that are due to changes in the spatial distribution of fish during annual spawning and feeding migrations. Barents Sea *G. morhua*, for example are found in a smaller area in winter when spawning than in summer when fish disperse to search for food (Harden Jones, 1968, see also Swain *et al.*, 1998). Differences in patchiness might therefore be expected to show most contrast in winter-spring (spawning) and summer-early autumn (feeding) for adult *G. morhua*. We propose that annual measures of patchiness continue to increase until *G. morhua* become very large mother fish (Schneider *et al.*, 1999). Mother fish are scarce due to mortality and have likely reduced the spatial extent of their annual spawning and feeding migrations (Lagler *et al.*, 1962; Templeman, 1974) during the period of senescence. This suggests to us that Lloyds Index of patchiness may decrease somewhat for mother fish.

There is no published information that we are aware of on ontogenetic changes in patchiness for the pelagic

stages of *G. morhua*, however we propose that the egg and larval stages will show patchiness–length plots similar to those for other teleosts, (e.g. Matsuura and Hewitt, 1995). Available evidence suggests that patchiness peaks briefly during the pelagic juvenile stage–settlement stage, when juveniles of demersal fish change habitat and settle to the bottom. Pelagic juvenile *G. morhua* are aggregated when they undergo extensive diel vertical migrations (Koeller *et al.*, 1986; Perry and Neilson, 1988) and this is shown as a small bump in Figure 7. This peak in patchiness occurs at the ends of two length frequency distributions and is due to the limits of pelagic and demersal sampling equipment when catches are small. Hence the small peak in patchiness at the pelagic juvenile stage–settlement stage is based on small sample sizes of both pelagic juveniles and settling juveniles.

We did not observe a simple monotonic increase in patchiness of large *G. morhua*. We propose that patchiness fluctuated at lengths greater than c. 200 mm SL due to the shifting balance between establishing ever larger home ranges (tending to reduce patchiness) and forming shoals (tending to increase patchiness) as *G. morhua* grow in size in shallow coastal habitats. The studies of Hawkins *et al.* (1974, 1980, 1985) and Clark and Green (1990) show cod greater than ages 2–3 can establish home ranges of variable size in coastal habitats. Tupper and Boutilier (1995) have observed that home range area increased with fish length over the range 5–20 cm for *G. morhua* off Nova Scotia. Our findings for this size cod (5–20 cm) are not consistent with the establishment of home ranges. If all *G. morhua* of this size established non-overlapping home ranges and if home range increases with length then fish would be distributed evenly along the coast resulting in patchiness–length plots that would decrease or at best be unchanging with increasing size. This is not consistent with our findings of higher patchiness with increasing size over the range 5–20 cm. The shifting balance concept that we propose for age-2–3 cod in coastal Newfoundland goes beyond home ranges and suggests tradeoffs may occur between establishing home ranges and shoaling behaviour in autumn when *G. morhua* move into deeper water. These findings contribute towards a general and testable model of patchiness increasing with length for north temperate demersal fishes.

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