Tidal effects on habitat selection and aggregation by juvenile pollock *Pollachius virens* in the rocky intertidal zone

Robert W. Rangeley*, Donald L. Kramer

Department of Biology, McGill University, 1205 Docteur Penfield Avenue, Montreal, Quebec, Canada H3A 1B1

ABSTRACT: Fucoid macroalgae in the rocky intertidal zone are a potentially important foraging and refuging habitat for juvenile fishes. A dominant feature of this habitat is that its availability changes with the tides. Vegetated habitat availability changes in many other systems as well, yet little is known about the effects of these changes on animal distributions. We addressed this problem by studying young-of-the-year pollock *Pollachius virens* using visual transect surveys in the rocky intertidal zone. We examined tidal effects on pollock distribution, their depth and habitat preferences and the relationship between habitat use and patterns of aggregation. Nearly all the pollock population in our study area moved into the intertidal zone and alternated between aggregation in the open and dispersal in the algae. On rising tides, pollock moved from the subtidal zone to the open intertidal zone in large schools then dispersed among available depths and throughout algal habitats in small schools or as solitary fish. When in algae, pollock preferred the dense algal habitat over the sparse algal habitat. On falling tides, pollock schooled in the open habitat in downshore intertidal and subtidal zones. The main seasonal difference, from early to late summer, was an overall distributional shift towards the downshore open habitat and the subtidal zone and a preference for greater depths in the intertidal zone. These results support the hypothesis that pollock were using both refuging and schooling antipredator tactics during intertidal zone migrations. We suggest that rocky shores are important nurseries for juvenile pollock.

KEY WORDS: Habitat selection · Habitat availability · Refuging · Schooling · Marine fish nursery · Rocky intertidal zone · *Pollachius virens* · Pollock · Macroalgae · Gadidae · Visual transects

INTRODUCTION

Macroalgae in the rocky intertidal zone are thought to be an important habitat for fishes but this has rarely been examined (Wheeler 1980, Rangeley 1994a). The paucity of investigations on fish use of intertidal macroalgae is surprising since use of most other coastal habitats has been well studied. For example, fish move into intertidal sand, mud flat (Raffaelli et al. 1990, Gibson 1993) and vegetated habitats (McIvor & Odum 1988, Sogard et al. 1989), and many coastal habitats are very productive fish nurseries (e.g. Weinstein et al. 1980, Zijlstra 1988, Heck & Crowder 1991).

In the rocky intertidal zone the availability of submerged macroalgae changes almost continually with tidal changes in water level. Tidal effects on juvenile fishes may include changes in prey availability and density-dependent refuge quality (Rangeley 1994b, Rangeley & Kramer 1995, this issue). Little is known about responses to changes in habitat availability despite their widespread occurrence. For example, changes in the area of important fish habitats occur in reservoirs (McDonough & Buchanan 1991), streams (Heggenes et al. 1991), seagrass banks (Sogard et al. 1989), and tidal marshes (Kneib 1987). The short temporal scale and predictability of the tides makes the rocky intertidal zone well-suited for an investigation into fish responses to changes in habitat availability.

We investigated the use of intertidal zone habitats by young-of-the-year pollock *Pollachius virens*. Pollock

*Present address: Huntsman Marine Science Centre, St. Andrews, New Brunswick, Canada E0G 2X0.
E-mail: hunstman@nbnet.nb.ca

are found on both sides of the North Atlantic (Bigelow
& Schroeder 1953). They spawn offshore in winter, and
the developing eggs and larvae drift in surface waters
until spring, when the juveniles (3 to 5 cm in length)
migrate inshore (Steele 1963, Scott & Scott 1988, Clay
et al. 1989). We previously demonstrated that juvenile
pollock make extensive use of the intertidal zone
(Rangeley & Kramer 1995). Pollock were captured in
algae-covered and open patches in similar numbers
but foraged primarily on prey from the algal habitat.
Stomach analyses showed that they fed relatively con-
tinuously suggesting that foraging was not strongly
affected by habitat availability. There was also a high
potential for predation risk in the rocky intertidal zone.
Foraging piscivorous birds were present throughout
the day at all stages of the tide, in all depth zones and
in both algae-covered and open patches (Rangeley
1994b). Because our previous pollock study was lim-
ited to beach seine samples in shallow (<1.2 m) water
we were unable to examine how spatial distribution
over the available area changed with tide level.

The goal of this study was to examine pollock inter-
tidal migration, habitat selection and aggregation in
relation to tidal changes in habitat availability. Pollock
distribution and behaviour were observed visually on
underwater transects. We first examined patterns of
pollock migration by determining how their distribu-
tion in the subtidal and intertidal zones changed over
the tidal cycle. Second, we examined how pollock
preferences for intertidal zone depths and habitats
changed during tidal changes in habitat availability.
Third, we examined the relationship between pollock
habitat use and their patterns of aggregation.

METHODS

Study site. The study site consisted of the intertidal
and subtidal zones along 200 m of shoreline on the north
end of Brandy Cove in Passamaquoddy Bay, New
Brunswick, Canada (45° 05' N, 67° 05' W). It has been
described as a typical, relatively sheltered shore
(Thomas et al. 1983). The site is delimited by rocky points
at the north and south ends and bordered by a mudflat to
the south and an exposed shore with a steep slope to the
north. The total area sampled in the intertidal zone was
approximately 28 000 m² (200 × 140 m). Although the
width of the intertidal zone was 170 m, time constraints
prevented sampling of the highest upshore area. The
subtidal zone sampling area extended horizontally to a
point 20 m out, from low water to depths of 4 to 6 m. This
subtidal sampling area of 4000 m² (200 × 20 m) was
determined during numerous non-census dives to in-
clude the maximum distance young-of-the-year pollock
moved from the intertidal zone during summer.

We recognized 3 major habitat types at the site. The
open habitat, occurring in both subtidal and intertidal
zones, was defined by the absence of large macro-
algae. The subtidal zone is devoid of macroalgae
throughout the region. In the intertidal zone, the open
habitat consisted of areas with mud, sand and gravel
substrates incapable of providing a sufficient anchor
for the holdfasts of large macroalgae. These sub-
strates can support patches of green and red sea-
weeds which in our study were small (<10 cm high),
often ephemeral and ignored by us as a pollock habi-
tat. The algal habitats, occurring only in the intertidal
zone, were dominated by brown fucoids, especially
rockweed *Ascophyllum nodosum*, attached to rock
boulders and reefs. Rockweed forms a dense canopy
covering up to 80% of sheltered shores with frond
lengths ranging from 1 to 3 m (Keser et al. 1981,
Thomas et al. 1983, Vadas et al. 1990, Briand 1991).
Algal habitats were categorized as sparse or dense by
floating a 1 m² quadrat on the water surface and mea-
suring the percent of surface cover when the algae
was completely submerged and thus vertically
extended. Sparse algal habitat had ≤50% of the
quadrat covered with algae and dense algal habitat
had >50% cover.

Transect sampling. A strip transect sampling pro-
cedure was used to estimate pollock density. Each
strip was essentially a long narrow (1 m wide)
quadrat in which a complete census of all pollock
was assumed (Buckland et al. 1993). A total of 7 tran-
sects were located perpendicular to the shoreline
across the full width of the intertidal and subtidal
study site. Transect positions were selected randomly
from a graduated reference line stretched across the
full width of the shore. In addition, 25 transects,
ranging from 25 to 80 m in length, were located par-
allel to the shore and intersecting on the perpendicu-
lar transects.

The sample units were transect strips marked off
with numbered flagging tape on the larger transects.
Because habitats do not fit neatly into predefined strip
lengths, sampling units were determined by stratifying
the transect strip by both habitat type and water depth
(Buckland et al. 1993). Therefore, strip length de-
pended on the location of a habitat boundary. Contigu-
ous strips were often the same habitat type but a strip
length of approximately 10 m ensured that changes in
depth did not exceed 50 cm within a sample.

Pollock were censused on different transects by 2
SCUBA divers equipped with dive slate and metre
stick, swimming at a rate of approximately 10 m min⁻¹
This was sufficient to ensure a complete census of the
1 m wide strip through the height of the water column
and in the most dense algal habitat, where the algal
fronds were easily parted for the search. To validate

the census technique we conducted a series of preliminary censuses where a second diver either searched the algae for undetected fish or watched along the transect boundaries to determine whether fish were fleeing the diver conducting the census. These preliminary trials also served to ensure that the 2 divers were consistent in their technique and counting accuracy. The divers censused different areas of the site simultaneously. For each transect strip the water depth and pollock count were recorded. An assistant in a rowboat recorded the sea level at 5 min intervals from a tidal marker located in Brandy Cove. In addition to pollock counts, shoal sizes were also recorded. We used Pitcher's (1986) definition of a shoal as a social group of fish and a school as a behaviour of shoals in which fish are travelling in a synchronous and polarized fashion. The whole shoal was counted in the census if the centre of the shoal was within the transect strip.

A total of 55 census trips, ranging in duration from 30 to 60 min, were made from 08:00 to 18:00 h in 1989 and 1990. Sampling effort was equally divided between early summer (May 10 to July 5) and late summer (July 6 to August 17). We divided intertidal habitat availability into 2 levels: low habitat availability when the tide level was ≤307 cm above chart datum and high habitat availability when tide level was >307 cm. Data from the 2 divers were summed. The transect data were divided into four 35 m wide locations in the intertidal zone, from low to high shore, for the purpose of determining the distance of pollock migrations. The submerged area of these locations varied with the state of the tide and with changes in the shape of the cove from the low to high zone.

Data analysis. Two-way analysis of variance was used to test for differences in pollock density among tidal stages and shore locations and among tidal stages and habitats for each seasonal period. Tukey's test was used for multiple comparisons. General linear models (GLM) procedures in SAS (SAS Institute 1988) were used for these analyses. All variables were $\log_e$-transformed to normalize distributions and to reduce the heteroscedascity in variance. All means are presented with their standard errors.

Habitat and depth stratum preferences were examined using the G-test for goodness-of-fit (Sokal & Rohlf 1981) with the null hypothesis that pollock were distributed in proportion to availability of habitats or depths. When the null hypothesis was rejected, we tested for differences between observed and expected proportions of pollock in each individual habitat or depth stratum using the Bonferroni z-statistic (Neu et al. 1974). The effects of tide level on the size of pollock shoals in the open habitat were compared using the Kolmogorov-Smirnov goodness-of-fit test (Siegel & Castellan 1988).

RESULTS

Intertidal zone distribution

The distribution of pollock from the subtidal zone to the high shore locations is presented in Tables 1 & 2 for each of the 4 tidal stages in early summer and late summer In early summer, there were significant differences (p = 0.0156) in pollock densities between the low ($\bar{x}$ = 0.420 ± 0.13 fish m^{-2}) and high ($\bar{x}$ = 0.041 ± 0.01 fish m^{-2}) tidal stages (Tukey's test, p < 0.05) but no difference (p = 0.6345) among the 5 locations from the subtidal zone through the intertidal zone (Tables 1 & 2a). On the low-rising tide, the overall mean density was 0.376 ± 0.077 fish m^{-2}. By the high-rising tide, the mean density of pollock was 0.192 ± 0.090 fish m^{-2} at the highest upshore location, though not statistically different than the overall mean density of 0.029 ± 0.011 fish m^{-2} for the other locations. There were no pollock in the subtidal zone during either high tidal stage. The overall mean pollock density was 0.044 ± 0.024 fish m^{-2} on the high-falling tide and 0.531 ± 0.287 fish m^{-2} on the low-falling tide. There were no observations in the highest location (106 to 140 m) on the high-falling tide due to a sampling error. However, there were no pollock in the next location (71 to 105 m) suggesting that there may not have been pollock in either location.

In late summer, there were significant differences in pollock densities among tidal stages (p = 0.0053) and shore locations (p = 0.0001) and there was a significant interaction (p = 0.0005) between the 2 factors (Table 1). Out of all tidal stages, the greatest density was on the low-falling tide ($\bar{x}$ = 0.376 ± 0.251 fish m^{-2}), with the densities in the other 3 stages not significantly different (pooled = 0.038 ± 0.007 fish m^{-2}, Tukey's test, α = 0.05; Table 2b). The mean density of 0.447 ± 0.275 fish m^{-2} over all tidal stages in the subtidal location was greater (Tukey's test, p < 0.05) than that for the other

Table 1. *Pollachius virens*. Results of 2-way ANOVA of $\log_e$-transformed number of age 0+ pollock per m^2 among tidal stages and locations on the shore. Comparisons were made for both early and late summer during the day

Source of variation	df	SS	F	p
Early summer				
Tidal stage	3	1.33	3.48	0.0156
Location	4	0.33	0.64	0.6345
Tide × Location	11	1.40	0.99	0.4494
Late summer				
Tidal stage	3	0.36	4.28	0.0053
Location	4	1.27	11.35	0.0001
Tide × Location	11	0.94	3.08	0.0005

Table 2. *Pollachius virens*. Mean number (± SE) of juvenile pollock per m^2 for transect censuses (N) during 4 stages of the tide. Shore locations consisted of the subtidal zone and four 35 m wide bands from low to high shore. The number and percentage abundance of pollock were calculated from the product of location area and mean density for both (a) early summer and (b) late summer

Tide	Location	Area (m^2)	N	Mean	Abundance No.	%
(a) Early summer						
Low-rise	Subtidal	4000	45	0.407 (0.338)	1630	39.9
	0–35 m	3676	128	0.482 (0.122)	1771	43.4
	36–70 m	2810	78	0.193 (0.073)	542	13.3
	71–105 m	239	54	0.378 (0.157)	91	2.2
	106–140 m	206	6	0.250 (0.193)	51	1.3
	Total	10931	311	0.376 (0.077)	4085	100
High-rise	Subtidal	4000	16	0.000	0	0
	0–35 m	6112	50	0.039 (0.031)	240	16.8
	36–70 m	5365	42	0.018 (0.009)	96	6.7
	71–105 m	4835	52	0.038 (0.015)	184	12.9
	106–140 m	4755	16	0.192 (0.090)	914	63.7
	Total	25067	176	0.044 (0.013)	1434	100
High-fall	Subtidal	4000	12	0.000	0	0
	0–35 m	6112	44	0.084 (0.059)	516	69.2
	36–70 m	5365	28	0.043 (0.023)	230	30.8
	71–105 m	4835	29	0.000	0	0
	106–140 m	4755	0	–	–	–
	Total	25067	113	0.044 (0.024)	746	100
Low-fall	Subtidal	4000	44	2.276 (1.754)	9105	87.1
	0–35 m	3676	130	0.324 (0.135)	1190	11.4
	36–70 m	2810	61	0.051 (0.020)	144	1.4
	71–105 m	239	37	0.045 (0.023)	11	0.1
	106–140 m	206	5	0.000	0	0
	Total	10931	277	0.531 (0.287)	10450	100
(b) Late summer						
Low-rise	Subtidal	4000	16	0.256 (0.234)	1025	83.7
	0–35 m	3676	58	0.047 (0.017)	172	14.0
	36–70 m	2810	33	0.008 (0.004)	22	1.8
	71–105 m	239	37	0.027 (0.012)	7	0.5
	106–140 m	206	5	0.000	0	0
	Total	10931	149	0.054 (0.026)	1226	100
High-rise	Subtidal	4000	28	0.098 (0.044)	393	39.2
	0–35 m	6112	106	0.034 (0.010)	209	20.8
	36–70 m	5365	112	0.028 (0.010)	149	14.9
	71–105 m	4835	81	0.030 (0.008)	147	14.7
	106–140 m	4755	18	0.022 (0.022)	106	10.5
	Total	25067	345	0.036 (0.006)	1004	100
High-fall	Subtidal	4000	20	0.083 (0.058)	330	45.7
	0–35 m	6112	65	0.062 (0.024)	381	52.7
	36–70 m	5365	47	0.002 (0.002)	11	1.6
	71–105 m	4835	42	0.000	0	0
	106–140 m	4755	15	0.000	0	0
	Total	25067	189	0.031 (0.010)	722	100
Low-fall	Subtidal	4000	12	2.125 (1.688)	8500	95.1
	0–35 m	3676	48	0.120 (0.066)	440	4.9
	36–70 m	2810	14	0.000	0	0
	71–105 m	239	97	0.000	0	0
	106–140 m	206	0	–	–	–
	Total	10931	171	0.376 (0.251)	8940	100

4 locations (pooled $\bar{x} = 0.034 \pm 0.006$ fish m^{-2}). Further analyses (1-way ANOVA) within each tidal stage showed how pollock densities were distributed among the locations on the shore. There were no differences in densities among shore locations on either the low-rising tide ($\bar{x} = 0.054 \pm 0.026$ fish m^{-2}; 1-way ANOVA, $F_4 = 1.67$, $p = 0.1594$) or high-rising tide ($\bar{x} = 0.036 \pm 0.006$ fish m^{-2}; $F_4 = 2.25$, $p = 0.0632$). By contrast, on the high-falling tide densities did differ ($F_4 = 2.90$, $p = 0.0232$), with the means being greater in the subtidal ($\bar{x} = 0.083 \pm 0.058$ fish m^{-2}) and the lowest intertidal locations ($\bar{x} = 0.062 \pm 0.024$ fish m^{-2}), although Tukey's multiple comparisons test could not distinguish among the 5 locations ($p > 0.05$). On the low-falling tide, the difference in densities among the locations was statistically marginal ($F_3 = 2.79$, $p = 0.0457$). Tukey's test again could not distinguish among locations, but the greatest density ($\bar{x} = 2.125 \pm 1.688$ fish m^{-2}) was in the subtidal zone. The lowest shore location was the only other location where pollock were observed ($\bar{x} = 0.120 \pm 0.066$ fish m^{-2}).

Abundance (number of fish present) was estimated for each shore location and tidal stage from the product of the average area and the mean density of pollock (Table 2a, b). The sum of these values for each tidal stage provides an estimate of the number of fish in the sampled population. These estimates fluctuated widely. In early summer, the total abundance estimates from the low-rising to low-falling tidal stages were 4085, 1434, 746 and 10450 pollock, respectively (Table 2a). On the low-rising tide, the large area in the down-shore locations relative to the small sub-merged area of the upshore locations resulted in an estimated 97% of the pollock occupying the area from the subtidal to 70 m upshore. In contrast, on the low-falling tide, 87% of the pollock were in the subtidal zone. A similar contrast in pollock location occurred between rising and falling high tides except that no fish were in the subtidal zone. In late summer, the abundance estimates over the 4 tidal stages were

1226, 1004, 722 and 8940 pollock (Table 2b). On the low-rising and low-falling tides, 84% and 95%, respectively, were estimated to be in the subtidal zone. On the high tides about 40% were in the subtidal zone. On the high-rising tide the remaining 60% were distributed among the 4 intertidal locations while on the high-falling tide over 50% were in the 0 to 35 m shore location.

Depth distribution

Pollock distribution in relation to water depth for each tidal stage is presented in Table 3. Pollock had significant depth preferences during each tidal stage in early summer (p < 0.001) and late summer (p < 0.001 to p < 0.025). Pollock were in deeper water at high-rising than at low-rising tidal stages and were deeper in late than in early summer on the rising tides (Table 3a & b).

In early summer, 89% of the observed pollock were in water 0 to 100 cm on the low-rising tide (Table 3a). By the high-rising tide, 90% were in depths between 50 and 200 cm with the remaining 10% in water deeper than 200 cm. On the high-falling tide 97% were in 51 to 150 cm depths. On the low-falling tide,

pollock were divided into a shallow and a deep group. The 51 to 100 cm depth stratum was used by 45% and the 151 to 200 cm stratum was used by 42% of the observed pollock. In late summer, at each tidal stage pollock were usually about 1 depth stratum deeper than they had been in early summer. On the low-rising tide, 80% were in depths from 51 to 150 cm (Table 3b). By the high-rising tide, 84% were in depths greater than 150 cm. There was a shift to shallower water on the high-falling tide, with 95% in 51 to 150 cm depths. This became more extreme on the low-falling tide with 98% in the 51 to 100 cm depth strata.

Habitat distribution

Pollock densities in the 3 intertidal zone habitat types during the 4 tidal stages are presented in Fig. 1. There were significant effects of tidal stage (p = 0.0001) and habitat type (p = 0.0017) on pollock density in early summer but only a habitat effect (p = 0.0055) in late summer (Table 4). The interaction between the 2 factors was also significant (p < 0.02) in both seasonal periods (Table 4).

In early summer, pollock density was highest in the open habitat ($\bar{x} = 0.46 \pm 0.09$ fish m^{-2}) and there was no
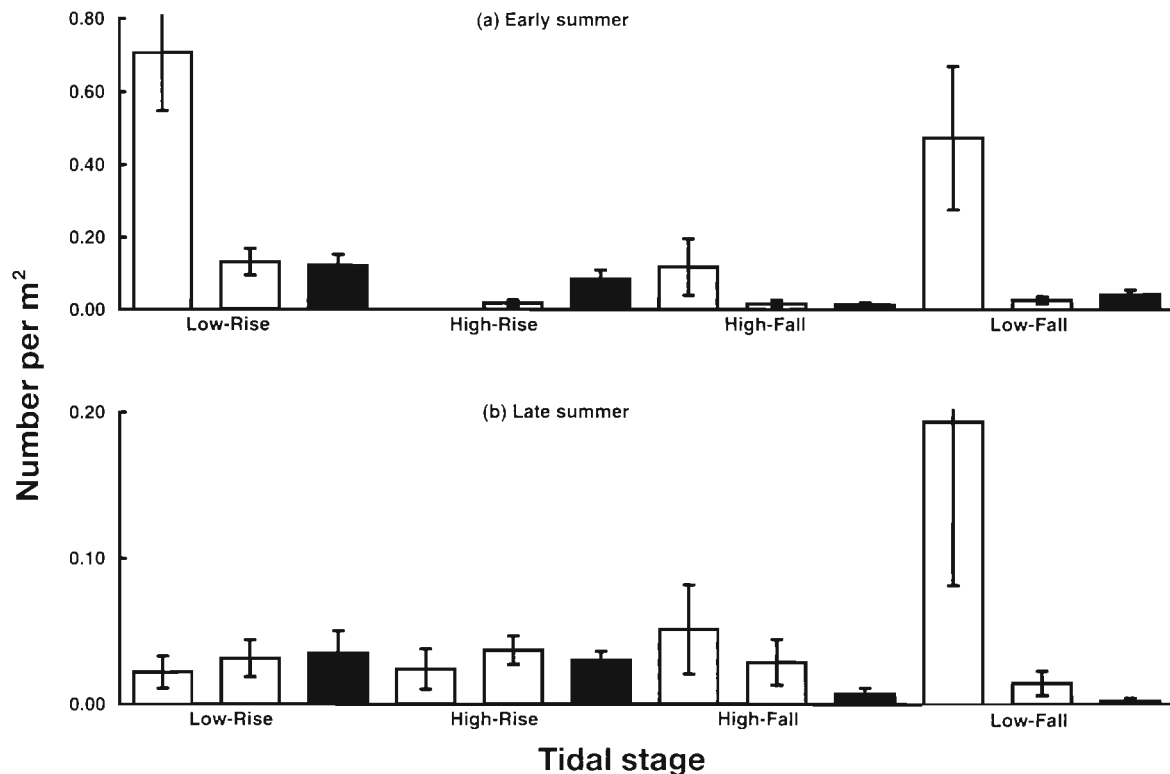

Fig. 1. *Pollachius virens*. Mean number of age 0+ pollock per m^2 in open (open bars), sparse algal (shaded bars) and dense algal (solid bars) habitats at 4 stages of the tide in (a) early summer and (b) late summer. Vertical lines are standard errors

Table 3. *Pollachius virens*. Depth distribution of juvenile pollock in the intertidal zone during 4 stages of the tide. Expected and observed frequency distributions of pollock in each of the 50 cm depth strata and the results of the *G*-test for goodness-of-fit for the 2 distributions are shown. Expected and observed proportions of pollock and the results of the Bonferroni *z*-statistic, which tests whether each observation occurred more or less frequently than the expectation based on habitat availability, are also given. Comparisons were made for both (a) early and (b) late summer during the day. $^*p < 0.05$; $^{**}p < 0.001$

Tide	Depth (cm)	Pollock frequency		$G_{adj}{}^a$	Pollock proportion			Bonferroni 95%
		Expected	Observed		Expected		Observed	confidence limits
(a) Early summer								
Low-rise	0–50	193	422	2267**	0.152	<	0.331*	0.301–0.362
	51–100	193	715		0.152	<	0.561*	0.529–0.593
	101–150	261	125		0.205	>	0.098*	0.079–0.117
	151–200	338	12		0.265	>	0.009*	0.003–0.016
	200–250	290	0		0.227	>	0.000*	0.000–0.000
High-rise	0–50	10	0	162**	0.095	>	0.000*	0.000–0.000
	51–100	10	26		0.095	<	0.248*	0.145–0.350
	101–150	10	36		0.095	<	0.343*	0.230–0.456
	151–200	15	32		0.143	<	0.305*	0.195–0.414
	200–250	20	8		0.190	>	0.076*	0.013–0.139
	251–300	20	3		0.190	>	0.029*	−0.011–0.068
	301–350+	20	0		0.190	>	0.000*	0.000–0.000
High-fall	0–50	6	2	210**	0.095	>	0.029*	−0.021–0.079
	51–100	6	41		0.095	<	0.603*	0.458–0.748
	101–150	6	25		0.095	<	0.368*	0.225–0.510
	151–200	10	0		0.143	>	0.000*	0.000–0.000
	200–250	13	0		0.190	>	0.000*	0.000–0.000
	251–300	13	0		0.190	>	0.000*	0.000–0.000
	301–350+	13	0		0.190	>	0.000*	0.000–0.000
Low-fall	0–50	145	100	1139**	0.152	>	0.105*	0.082–0.127
	51–100	145	433		0.152	<	0.453*	0.416–0.490
	101–150	196	23		0.205	>	0.024*	0.013–0.036
	151–200	253	400		0.265	<	0.418*	0.382–0.455
	200–250	217	0		0.227	>	0.000*	0.000–0.000
(b) Late summer								
Low-rise	0–50	10	0	80**	0.152	>	0.000*	0.000–0.000
	51–100	10	24		0.152	<	0.348*	0.215–0.480
	101–150	14	31		0.205	<	0.449*	0.311–0.588
	151–200	18	14		0.265	>	0.203	0.091–0.315
	200–250	16	0		0.227	>	0.000*	0.000–0.000
High-rise	0–50	16	2	77**	0.095	>	0.012*	−0.009–0.033
	51–100	16	5		0.095	>	0.030*	−0.002–0.063
	101–150	16	19		0.095	<	0.115	0.055–0.176
	151–200	24	51		0.143	<	0.309*	0.221–0.397
	200–250	31	51		0.190	<	0.309*	0.221–0.397
	251–300	31	22		0.190	>	0.133	0.069–0.198
	301–350+	31	15		0.190	>	0.091*	0.036–0.146
High-fall	0–50	9	0	299**	0.095	>	0.000*	0.000–0.000
	51–100	9	24		0.095	<	0.250*	0.142–0.358
	101–150	9	67		0.095	<	0.698*	0.584–0.812
	151–200	14	5		0.143	>	0.052*	−0.003–0.107
	200–250	18	0		0.190	>	0.000*	0.000–0.000
	251–300	18	0		0.190	>	0.000*	0.000–0.000
	301–350+	18	0		0.190	>	0.000*	0.000–0.000
Low-fall	0–50	18	1	418**	0.152	>	0.008*	−0.011–0.028
	51–100	18	116		0.152	<	0.983*	0.956–1.011
	101–150	24	1		0.205	>	0.008*	−0.011–0.028
	151–200	31	0		0.265	>	0.000*	0.000–0.000
	200–250	27	0		0.227	>	0.000*	0.000–0.000

$^a G_{adj} > \chi^2{}_{0.001\,(1)} = 10.83$

Table 4. *Pollachius virens*. Results of 2-way ANOVA of $\log_e$-transformed number of age 0+ pollock per m^2 among tidal stages and intertidal zone habitats. Comparisons were made for both early and late summer during the day

Source of variation	df	SS	F	p
Early summer				
Tidal stage	3	2.35	8.61	0.0001
Habitat	2	1.18	6.46	0.0017
Tide × Habitat	6	1.39	2.54	0.0193
Late summer				
Tidal stage	3	0.02	0.85	0.4676
Habitat	2	0.10	5.24	0.0055
Tide × Habitat	6	0.22	3.90	0.0008

difference between pollock density in the sparse ($\bar{x} = 0.064 \pm 0.015$ fish m^{-2}) and dense ($\bar{x} = 0.071 \pm 0.012$ fish m^{-2}) algal habitats (Tukey's test, $\alpha = 0.05$). The relatively high densities of pollock in the open habitat on the low-rising ($\bar{x} = 0.71 \pm 0.16$ fish m^{-2}) and low-falling ($\bar{x} = 0.44 \pm 0.20$ fish m^{-2}) tides, compared with the low densities on the high-rising ($\bar{x} = 0.0005 \pm 0.0005$ fish m^{-2}) and high-falling ($\bar{x} = 0.12 \pm 0.08$ fish m^{-2}) tides, were responsible for a significant (p = 0.0193) interaction between the 2 main factors (Table 4). Although large mean differences were apparent in open habitat densities among tidal stages, only the low-rising and high-rising tides differed significantly (1-way ANOVA, $F = 4.94$, p = 0.024; Tukey's test, p < 0.05). Pollock densities in the sparse algal habitat also differed among tidal stages ($F = 5.57$, p = 0.0011). Density in the sparse algal habitat was highest ($\bar{x} = 0.13 \pm 0.04$ fish m^{-2}) on the low-rising tide and the densities ($\bar{x} = 0.022 \pm 0.006$ fish m^{-2}) of the other 3 stages did not differ significantly (Tukey's test, $\alpha = 0.05$). In the dense algal habitat, there was only a significant difference (Tukey's test, p < 0.05) in densities between low-rising ($\bar{x} = 0.12 \pm 0.03$ fish m^{-2}) and high-falling ($\bar{x} = 0.010 \pm 0.006$ fish m^{-2}) tides ($F = 3.73$, p = 0.0118). In late summer, there were significant habitat differences (p = 0.0055) in pollock density, although Tukey's test could not distinguish among mean densities in the open ($\bar{x} = 0.054 \pm 0.019$ fish m^{-2}) habitat or either sparse ($\bar{x} = 0.031 \pm 0.006$ fish m^{-2}) or dense ($\bar{x} = 0.023 \pm 0.004$ fish m^{-2}) algal habitats.

Pollock habitat use compared with habitat availability in the intertidal zone for each tidal stage is presented in Table 5. In early summer, on all but the high-rising tidal stage, pollock preference for the open habitat (82 to 92%) was significantly greater than for algal habitats (Table 5a). On the high-rising tide, 87% of the pollock occupied the dense algal habitat compared with only 1% in the open habitat. Overall in early summer, 1981 of the 2403 (82%) individual pollock observed were in the open habitat.

In late summer, pollock habitat use was not significantly different from habitat availability on the low-rising tide (Table 5b). On the high-rising tide, 75% of the pollock were in the 2 algal habitats, and there was a significant preference for the dense algal habitat. Use of open habitat was 75% on the high-falling tide and 84% on the low-falling tide. The open habitat use was greater than its availability and algal habitat use was significantly less than its availability during both falling tide levels. Overall, in late summer, 242 of the 448 (54%) individual pollock observed were in the open habitat, 28% less than in early summer.

Pollock aggregations

In the open habitat pollock were rarely solitary (Table 6). Only 0.1 to 9.5% of the pollock observed in the open were solitary at all tidal stages, except the high-rising tide in early summer when only 1 pollock was observed in the open. Overall in early summer, only 6 of 1981 (0.3%) pollock observed in the open habitat were solitary and in late summer 10 of 242 (4%) were solitary. Pollock in shoals of less than 10 were also rare in the open (Fig. 2). In early summer, the median shoal size of 63 (range = 2 to 400) during the low tidal stages and 21 (range = 4 to 25) during the high tidal stages [Kolmogorov-Smirnov test (K-S), $D_{58, 1923} = 0.77$, p < 0.001]. In late summer, the median was 10 (range = 2 to 30) during the low tidal stages and 21 (range = 2 to 30) during the higher tidal stages (K-S test, $D_{114, 128} = 0.30$, p < 0.001). Schooling pollock accounted for 93% of the shoals in the open. When non-schooling shoals were observed they were also very cohesive and switched rapidly to schooling when disturbed. Schooling pollock swam slowly, well off the bottom, and were thus easily counted. In contrast, solitary pollock in open habitat swam in a rapid, zig-zag fashion close to the bottom.

In algal habitats pollock were frequently solitary (sparse algae: 38.5 to 100%) and (dense algae: 65.9 to 100%) (Table 6) and shoals were small. Median shoal sizes were 1 in both early summer (range = 1 to 40) and late summer (range = 1 to 12). Of the shoals observed in the algal habitats, 67% were between 2 and 5 pollock and 14% were between 6 and 10. Additional details on shoal size distributions are in Rangeley (1994b).

DISCUSSION

Intertidal zone migration

The patterns of distribution in relation to tidal stage suggest that pollock disperse throughout the intertidal zone on the rising tide. In early summer on the low-

Table 5. *Pollachius virens*. Habitat distribution of juvenile pollock in the intertidal zone during 4 stages of the tide. Expected and observed frequency distributions of pollock in open, sparse algal and dense algal habitats and the results of the G-test for goodness-of-fit for the 2 distributions are shown. Expected and observed proportions of pollock and the results of the Bonferroni z-statistic, which tests whether each observation occurred more or less frequently than the expectation based on habitat availability, are also given. Comparisons were made for both (a) early and (b) late summer during the day. $p < 0.05$; $p < 0.001$

Tide	Habitat	Pollock frequency		G_{adj} [a]	Pollock proportion			Bonferroni 95%
		Expected	Observed		Expected		Observed	confidence limits
(a) Early summer								
Low-rise	Open	593	1045	689**	0.47	<	0.82*	0.79–0.85
	Sparse	415	153		0.33	>	0.12*	0.10–0.14
	Dense	267	76		0.21	>	0.06*	0.04–0.08
High-rise	Open	34	1	165**	0.33	>	0.01*	−0.01–0.03
	Sparse	41	13		0.39	>	0.12*	0.05–0.20
	Dense	30	91		0.28	<	0.87*	0.79–0.95
High-fall	Open	22	57	79**	0.33	<	0.84*	0.73–0.94
	Sparse	27	3		0.39	>	0.04*	−0.02–0.10
	Dense	19	8		0.28	>	0.12*	0.02–0.21
Low-fall	Open	445	878	905**	0.47	<	0.92*	0.90–0.94
	Sparse	311	38		0.33	>	0.04*	0.02–0.05
	Dense	200	40		0.21	>	0.04*	0.03–0.06
(b) Late summer								
Low-rise	Open	32	29	1	0.47	>	0.43	0.28–0.57
	Sparse	22	21		0.33	>	0.31	0.18–0.44
	Dense	14	18		0.21	<	0.26	0.14–0.39
High-rise	Open	54	42	17**	0.33	>	0.25	0.17–0.33
	Sparse	65	52		0.39	>	0.31	0.23–0.40
	Dense	47	72		0.28	<	0.44*	0.34–0.53
High-fall	Open	31	72	72**	0.33	<	0.75*	0.64–0.86
	Sparse	38	15		0.39	>	0.16*	0.07–0.24
	Dense	27	9		0.28	>	0.09*	0.02–0.16
Low-fall	Open	55	99	113**	0.47	<	0.84*	0.76–0.92
	Sparse	38	18		0.33	>	0.15*	0.07–0.23
	Dense	25	1		0.21	>	0.01*	−0.01–0.03

[a] $G_{adj.} > \chi^2_{0.001\,(1)} = 10.83$

rising tide, pollock were either in the subtidal zone or in the lowest downshore location in depths less than 100 cm. By the high-rising tide, pollock were no longer in the subtidal zone and were dispersed among the 4 intertidal zone locations in depths from 51 to 200 cm, with an estimated 77% in the 2 upshore locations. A similar dispersal pattern occurred in late summer on the rising tide. The main seasonal difference was an overall distributional shift towards the subtidal and downshore locations and a preference for greater depths in the intertidal zone. These patterns are consistent with our interpretation of pollock migration when sampled by beach seine (Rangeley & Kramer 1995). In that study, pollock were present in the shallow intertidal zone day and night throughout the summer. Densities were higher at the low than the high tidal stages, especially in early summer, and at least part of the population migrated the full width of the intertidal zone each tide. In the present study, there

was a virtual absence of pollock in the upshore locations on the falling tide in both seasonal periods, suggesting a rapid ebb tide migration out of areas where there might be risk of stranding. This has been observed in other species. Flounder *Platichthys flesus* tracked using ultrasonic telemetry on an intertidal mudflat avoided stranding by increasing movement rates on the falling tide (Wirjoatmodjo & Pitcher 1984). Similarly, juvenile plaice *Pleuronectes platessa* on intertidal sandy beaches increased their frequency of swimming and exhibited more directed downshore movements on the ebb tide (Gibson 1980).

Estimates of total pollock abundance in the intertidal and near subtidal zones fluctuated widely among tidal stages. During both early and late summer, estimates were highest on the low-falling tide, with numbers decreasing through low-rising, high-rising and high-falling tides. One scenario that could explain this pattern is that some pollock aggregating in the study

Table 6. *Pollachius virens*. The number and percentage of pollock that were solitary in each intertidal zone habitat among tidal stages for both early and late summer

Habitat	Early summer			Late summer		
	Total	Solitary	%	Total	Solitary	%
Low-rise						
Open	1045	3	0.3	29	2	6.9
Sparse	153	93	60.8	21	21	100.0
Dense	76	72	94.7	18	18	100.0
High-rise						
Open	1	1	100.0	42	4	9.5
Sparse	13	5	38.5	52	34	65.4
Dense	91	60	65.9	72	72	100.0
High-fall						
Open	57	1	1.8	72	1	1.4
Sparse	3	3	100.0	15	7	46.7
Dense	8	6	75.0	9	9	100.0
Low-fall						
Open	878	1	0.1	99	3	3.0
Sparse	38	38	100.0	18	18	100.0
Dense	40	37	92.5	1	1	100.0

site during the low tide levels migrate to other areas on the higher tide levels. This raises the possibility that the pollock observed at our site did not come from a closed population during the study period. We attempted to assess this by numerous diving surveys around the periphery of the site and found no evidence that pollock moved laterally to either the steep shore on the north side or to the mud flat on the south side of the study site.

Intertidal migration could be accomplished by fish selecting the same depth throughout the tidal cycle

(Gibson 1973). However, pollock did not demonstrate a constant depth preference among tidal stages and in most cases used greater depths at higher tide levels. Pollock therefore appear to lag behind the advancing flood tide. It is unlikely that this is due to limited swimming capability, as they evidently were able to keep ahead of the ebb tide flow. Rather, the physical obstruction of moving through algae or the intensive use of the algal habitat (e.g. for food or refuge) at high tide levels may have slowed pollock movements on the rising tide. Fish, especially juvenile stages, use vegetation as a refuge and foraging habitat (Heck & Crowder 1991). There is evidence that these uses of the rocky intertidal algae also apply to juvenile pollock. Pollock feed on invertebrates associated with fucoid algae but tidal effects may be unimportant as they appeared to forage relatively continuously (Rangeley & Kramer 1995). There is a high potential for predation by piscivorous birds (Rangeley 1994b), and pollock showed a strong refuging response to an experimental presentation of a predator model and to increasing algal habitat availability (Rangeley & Kramer unpubl.). The strong tidal effect on pollock movements suggests that habitat use may be affected by tidal changes in availability, at least on rising tides. On the falling tides, the risk of stranding may have dictated movement patterns.

Dispersing and schooling behaviour

Pollock were aggregated in the open habitat and dispersed when in the algal habitat. These patterns of spatial distribution are not uncommon (Christensen & Persson 1993, Aboul Hosn & Downing 1994). For
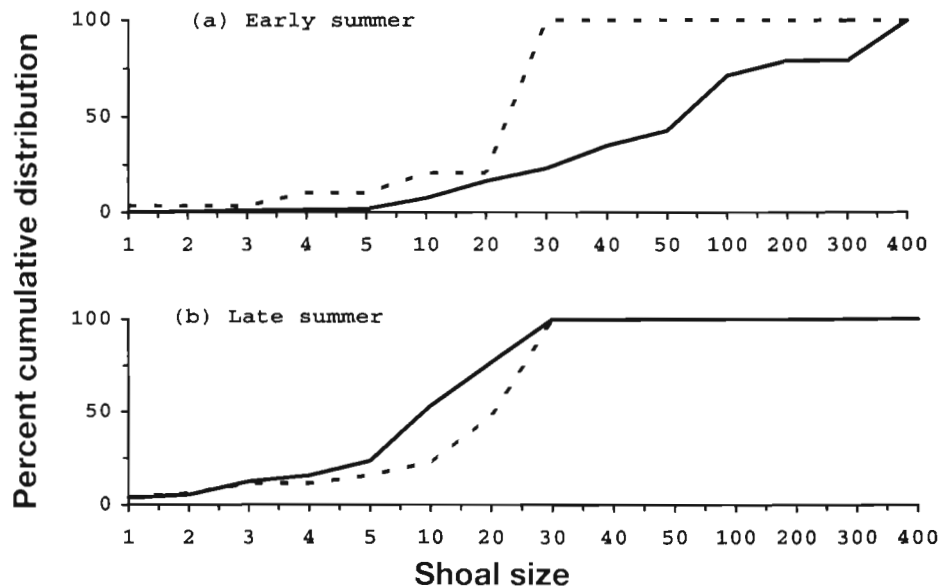

Fig. 2. *Pollachius virens*. Cumulative percentage of pollock in shoal sizes from 1 to 400 in the intertidal zone open habitat. Distributions are presented for low (——) and high (- - - -) tidal stages in (a) early summer and (b) late summer

example, littoral zone lake fish were most aggregated in open habitats but were nearly randomly distributed when in macrophyte habitats (Aboul Hosn & Downing 1994). What is unique about our study is the demonstration that pollock alternated between aggregation in the open and dispersal in the algae in response to changes in tidal stage. Pollock preferred the open habitat on the low-rising tides (though not significantly so in late summer) and on both high- and low-falling tides. In contrast, they preferred the dense algal habitat on the high-rising tide. Use of the sparse algal habitat was less than its availability on all tidal stages. When in the algal habitats, pollock were solitary or in small shoals, and the proportion of solitary pollock appeared to be greater in dense algal habitat (87%) than in sparse algal habitat (70%). However, when in the open habitat pollock were rarely (<1%) solitary, generally in shoals larger than 10 and nearly always in school formation. These patterns of aggregation and habitat use suggest that pollock moved in school formation in the open habitat on their intertidal zone migrations. On the rising-tide migration the shift of pollock from the open to the algal habitats appeared to be accompanied by dispersal and fission of shoals. A mechanistic explanation for these patterns of aggregation is that vegetation hinders, whereas open habitat permits, the formation and maintenance of animal groups (Barrette 1991).

School formation is beneficial to small fishes in open habitats because it reduces predator induced mortality (Pitcher 1986, Booth 1995). Predation risk decreases with increasing shoal size (e.g. Magurran & Pitcher 1987), thus open habitat quality should depend on the number and proximity of conspecifics. Escaping predators is further enhanced when schooling fish have the option of fleeing to refuges when the open water column becomes too risky (Parrish 1992). In the rocky intertidal zone, pollock were rarely solitary and most often in school formation when in the open habitat, suggesting an antipredator function of their aggregations. In contrast, pollock were dispersed when in algae and most dispersed when in the dense algal habitat, which is consistent with the use of algae as a refuge habitat (Sih 1987, Lima & Dill 1990). In addition, there were strong tidal effects on daytime patterns of habitat selection and schooling in juvenile pollock. An interpretation of these results is that pollock were responding to tidal changes in habitat availability. These responses were most pronounced on the rising tide, when it appeared that pollock switched from schooling in the open habitat to dispersing in the algal habitats on an intertidal zone migration. On the falling tide, when habitat availability was decreasing, pollock appeared to school rapidly downshore in the open habitat, possibly to avoid the risk of stranding. The

high potential for predation risk from birds in the intertidal zone and the refuging and schooling responses of pollock to a simulated bird predator (Rangeley 1994b) support the hypothesis that pollock were using both refuging and schooling antipredator tactics during intertidal zone migrations.

Coastal management strategies should acknowledge the potential importance of the rocky intertidal zone as a fish nursery. At our study site, nearly the whole pollock population occupied the intertidal and near subtidal zones for the entire summer. The evidence from this and our other studies strongly suggests an important role of foraging and antipredator tactics in pollock intertidal zone migrations. These findings have important implications for future fisheries and conservation studies; however, obtaining accurate abundance estimates of mobile fishes in the rocky intertidal zone will not be easy. In this study pollock abundance estimates fluctuated widely and were an order of magnitude higher than our beach seine estimates (Rangeley & Kramer 1995) for comparable depths. Despite these difficulties, this study highlights the importance of inferring distribution patterns using more than one method. Using visual transect data we conclude that tidal changes in habitat availability had strong effects on patterns of pollock habitat selection and aggregation, possibly in response to avian predation risk.

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