Predators and distance between habitat patches modify gap crossing behaviour of juvenile Atlantic cod (*Gadus morhua*, L. 1758)

Mary R. Ryan [a,*], Shaun S. Killen [b,1], Robert S. Gregory [c], Paul V.R. Snelgrove [b,d]

[a] Cognitive and Behavioural Ecology Programme, Memorial University of Newfoundland, St. John's, NL, Canada A1C 5 S7
[b] Ocean Sciences Centre, Memorial University of Newfoundland, St. John's, NL, Canada A1C 5 S7
[c] Centre of Expertise for Aquatic Habitat Research, Fisheries & Oceans Canada, St. John's, NL, Canada A1C 5X1
[d] Biology Department, Memorial University of Newfoundland, St. John's, NL, Canada A1C 5 S7

ARTICLE INFO

ABSTRACT

When habitat refugia is fragmented and limited, movement of potential prey animals between patches of protective habitat may be driven by biotic factors including foraging opportunities, risk of predation mortality, as well as density effects. However, few studies have examined these factors in marine landscapes. We examined gap crossing behaviour of juvenile Atlantic cod, *Gadus morhua* L. 1758, a species with high mortality throughout its juvenile stage. We examined the effect of inter-patch distance, fish length, group size, and the presence of a predator on gap crossing behaviour by juvenile cod in a 12×3 m experimental arena. Habitat patches consisting of artificial eelgrass were positioned within the arena with inter-patch distances of 3.0 m and 7.5 m. We observed a 37% reduction in frequency of gap crossing movements at larger distances compared to small ones. At the greater inter-patch distance, fish delayed departing a patch, depending on average group size. Juvenile fish released into a patch with a nearby predator moved across gaps 75% less frequently than fish originating in a predator-free patch. We also found that the presence of a predator delayed fish departure from a patch, again depending on group size. Our study demonstrates a suite of complex behavioural mechanisms that juvenile cod may exhibit to reduce predation risk as they navigate a landscape of fragmented habitat patches.

© 2012 Elsevier B.V. All rights reserved.

1. Introduction

Complex habitat provides protection from predators for many animal taxa, increasing the incentive of individuals to associate with complex areas and influencing many aspects of animal behaviour (Lima and Dill, 1990; Pierce et al., 2004). Protection mechanisms include reduction in prey detection probability by the predator (Crowder and Cooper, 1982; Kopp et al., 2006) or forcing the predator to use less effective hunting tactics (Savino and Stein, 1982). Several studies demonstrate advantages of structurally complex habitat use for fishes, especially for small-bodied or juvenile fish prey (Gotceitas and Colgan, 1989; Linehan et al., 2001; Savino and Stein, 1982; Sogard and Olla, 1993).

In aquatic environments, complex physical habitat such as vegetation, rocks, or coral reefs tends to occur as discontinuous patches within a landscape mosaic dominated by simpler, often barren, substrate. In many cases, fishes must move between areas of preferred habitat, often crossing inter-patch gaps. The rich literature on terrestrial gap crossing and the management of species that move between discrete habitat patches (e.g., Baker, 2007; Beier, 1993; Tull and Krausman, 2001) is lacking for aquatic species. The few studies on aquatic systems suggest that several factors mediate departure from habitat patches. Foraging success by bluegill sunfish *Lepomis macrochirus* affects the length of time an individual remains in a given habitat patch before it seeks a new resource patch (DeVries et al., 1989; Gotceitas, 1990). Similarly, the interaction of predator presence and foraging factors affects patch departure decisions in surfperch *Embiotoca jacksoni* (Schmitt and Holbrook, 1985). The willingness and ability to move over open areas between patches may also vary among species (Sogard, 1989; Sorgard, 1997).

Juvenile Atlantic cod *Gadus morhua* L. 1758, are well known to associate with complex habitat such as cobble or eelgrass *Zostera marina* (Gotceitas et al., 1997; Grant and Brown, 1998; Laurel et al., 2003a,b). Age 0 juveniles settle into complex seabed habitats, typically in late summer and autumn months, after pelagic egg, larval, and early juvenile

* Corresponding author at: College of Medical, Veterinary and Life Sciences, Institute of Biodiversity, Animal Health and Comparative Medicine, University of Glasgow, Graham Kerr Building, Glasgow G12 8QQ, United Kingdom. Tel.: +44 077 33166490.
E-mail addresses: f02mrar@mun.ca (M.R. Ryan), s.killen@bio.gla.ac.uk (S.S. Killen), Robert.Gregory@dfo-mpo.gc.ca (R.S. Gregory), psnelgro@mun.ca (P.V.R. Snelgrove).
[1] Present address: College of Medical, Veterinary and Life Sciences, Institute of Biodiversity, Animal Health and Comparative Medicine, University of Glasgow, Glasgow G12 8QQ, United Kingdom.

stages earlier the same year. On the northeast coast of Newfoundland, juvenile Atlantic cod are prey to many piscivorous fishes (e.g., larger Atlantic cod, Greenland cod *Gadus ogac*, cunner *Tautogolabrus adspersus*, and shorthorn sculpin *Myoxocephalus scorpius*; Linehan et al., 2001; Laurel et al., 2003b; Gorman et al., 2009), birds (e.g., eagles, osprey, mergansers, and seabirds), and mammals (e.g., river otter; Cote et al., 2008). Predation on small cod generally decreases with increasing patch size of complex habitats such as eelgrass (Laurel et al., 2003a). However, patch edges can also attract predators (Gorman et al., 2009), resulting in increased predator density compared to smaller patches up to some intermediate patch sizes (~20 m^2 for age 0 Atlantic cod — Laurel et al., 2003a; Gorman et al., 2009). Age 0 Atlantic and Greenland cod outside eelgrass habitat typically aggregate more than individuals within vegetated habitat (Laurel et al., 2004). Aggregation (i.e., grouping or shoaling) is a common response to predation risk in many marine and terrestrial species (Cresswell, 1994; Lingle, 2001; Pitcher, 1986; Wrona and Jamieson Dixon, 1991). Collectively, these studies suggest high risk for juvenile cod venturing into gaps between patches of complex habitat (Gorman et al., 2009; Gotceitas et al., 1995; Laurel et al., 2003a; Linehan et al., 2001; Tupper and Boutilier, 1995), and predict rapid movement across gaps between complex habitat patches whenever they do so. These studies also suggest that movement across such gaps should tend to occur as groups of individuals, rather than singly.

We examined gap crossing behaviour in juvenile Atlantic cod across two inter-patch distances and in the presence and absence of a predator in a large experimental arena designed to represent potential gap crossing options for juveniles in the wild. We predicted that increasing inter-patch distance would delay departure from patches, increase the speed of gap crossing, and decrease gap crossing frequency. We also predicted that predator presence would delay departure from a patch, increase the speed of gap crossings, and decrease gap crossing frequency. For all experiments, we predicted that larger fish would depart the release patch more readily than smaller fish, complete more gap crosses, and move faster between patches.

2. Methods

2.1. Study species

We captured approximately 500 juvenile Atlantic cod by beach seine in Smith Sound, Trinity Bay, Newfoundland in July 2007, and then transferred them to holding facilities at the Ocean Sciences Centre of Memorial University. Fish were held in flow-through ambient seawater holding tanks (1.0 m × 1.0 m × 0.5 m; approximately 150 fish per tank) and fed chopped herring *Clupea harengus* daily to satiation. We conducted all experiments at temperatures between 7 °C and 8.5 °C. Throughout all experiments, we followed a fixed 16 h light:8 h dark photoperiod schedule. All fish were fasted for 24 h prior to exposure to experimental conditions to standardize gut fullness at zero for all fish tested, similar to fasting periods chosen for other behavioural experiments (e.g., Gotceitas et al., 1995).

For our predator we used a wild-caught age 3+ Atlantic cod (43 cm SL [standard length]). One week prior to experiments, we transferred the predator into a holding tank (1.0 m × 1.0 m × 0.5 m) supplied with ambient seawater. We fed the predator dry food pellets approximately every two days.

Prior to use in experiments, we tagged juvenile cod externally with individually identifiable coloured plastic beads, to increase their visibility in the experimental arena and facilitate differentiation of focal fish from other fish in the experimental groups. We lightly anaesthetized juvenile cod with 2-phenoxyethanol (0.30 mL·L^{-1}) and affixed the plastic beads (2 mm diameter) to each fish in the musculature anterior to the dorsal fin with surgical sutures, and then allowed the fish to recover in a large bucket of aerated seawater. Tags were rarely lost (<1%·d^{-1}) but replaced as necessary (no individual fish required tag replacement more than once). Given the small size of the beads (diameter <2% of fish length), the absence of attacks directed at the beads of other fish, and no noticeable behavioural effects of the beading or the application of beads on both the focal and conspecific fish, we believe any effect of the beads on fish behaviour was negligible.
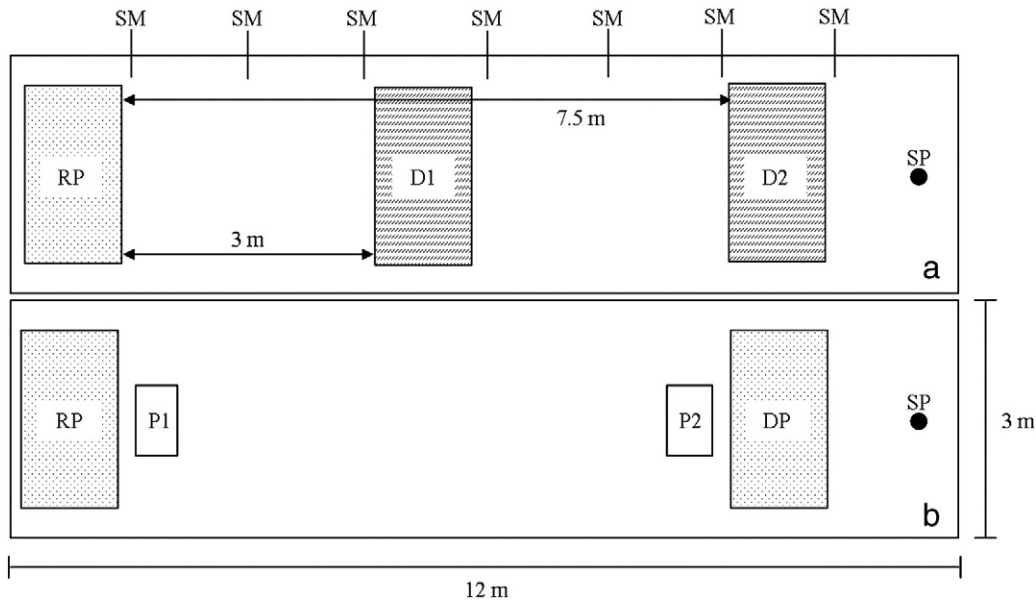
2.2. Experimental arena

For all experiments, the test arena was a large flow-through 12 m × 3 m raceway supplied with ambient seawater and surrounded by a blind to hide the observer from the view of subject fish. This arena provided a large, semi-natural area in which to observe gap crossing behaviour, but its large size precluded the possibility of videotaping trials. We lined the bottom of the tank with small gravel (approximately 0.5 cm diameter), and filled it to a water depth of approximately 1.5 m. We marked one side of the tank with flagging tape to indicate the boundaries of seven numbered, crosswise sections of the experimental arena (see Fig. 1). A series of overhead fluorescent lights created as uniform light coverage as possible and remained constant for all experimental trials. We constructed patches of artificial eelgrass by affixing green polypropylene ribbon (width = 4.7 mm, length = 75 cm) to a wire mesh base at a density of 700 stems·m^{-2}; this density falls within the range of natural eelgrass in the wild (Gotceitas et al., 1997; Orth et al., 1984) and effectively mimics natural eelgrass cover in lab and field habitat studies (e.g. Gotceitas et al., 1997; Laurel et al., 2003a; Sogard and Olla, 1993). We arranged patches 2.5 m^2 in area in configurations within the tank to match the layout requirements of individual experiments and treatments. One patch location served as the release site for all experiments (Fig. 1).

Fish were randomly selected from holding tanks prior to the start of each trial. We lowered fish into the release patch in a wire cage (50 cm × 40 cm × 15 cm) hinged on one side. After 5 min, we opened the cage from outside the blind using a rope affixed to the hinged side. We made all observations through viewing slits cut in the blind and continually observed one randomly selected "focal fish" for the duration of the trial. Individual trials began when the focal fish left the release cage (up to 6 min after cage opening). We recorded the section occupied by the focal fish continually throughout each of the trials, as well as the number of individuals within any group that this focal fish joined ("conspecifics"). We considered any fish located within three body lengths of each other and moving in the same direction to be part of a group. Any attacks among conspecifics or startle behaviours were also noted. We considered any focal fish within one body length of the outermost edge of the patch to be on the edge of an eelgrass patch.

2.3. Experimental design: inter-patch distance

We positioned the release patch in one end of the arena, and the destination patch either 3.0 m or 7.5 m away from the release patch (Fig. 1). Eelgrass patches bordered the sections in which they were located. We placed the destination patch at the 7.5 m location in order to avoid the standpipe located at that end of the arena. The standpipe did not noticeably affect fish behaviour.

We released five fish at a time to test the effects of varying gap sizes on movement between patches. We used groups of five fish specifically to provide the opportunity for focal fish to associate with conspecifics while still allowing the observer to quickly and easily determine the number of fish in any given group. All age 0 fish used in our study were experimentally naïve to the test conditions. Mean length of age 0 fish used in this experiment was 112 ± 3 mm SL (including both focal and other individuals; mean fish lengths for each of the two distance trials were not significantly different). All trials were 15 min in duration, not including the time taken for the fish to leave the release cage. All observations were made using a PSION™ (Geo Scientific Ltd., Vancouver) observation recorder, a handheld device that allowed continuous recording of fish location and the

Fig. 1. Top view of experimental arena (12 m×3 m×1.5 m) set-up for (a) inter-patch distance and (b) predator experiments, showing the locations of release patches (RP), destination patches (D1, D1, and DP), the predator/enclosure (P1 and P2), section markers used to identify fish location within the tank (SM), and the standpipe (SP).

number of conspecifics. We tested each gap size with 10 separate groups of fish, resulting in 150 min of observation for each distance tested.

2.4. Experimental design: predator presence

We constructed a predator enclosure using a 56 L rectangular plastic storage tote, in which we replaced the side panels with fine wire mesh (mesh opening = 2 mm). This modified enclosure allowed transmission of any visual and chemical cues from the predator to the test fish (i.e., potential prey). The predator was placed in the enclosure which we then placed in the experimental arena prior to fish release. We used the same predator fish in each trial to minimize the likelihood of different predators influencing juvenile cod behaviour differentially (see Gotceitas et al., 1995).

Potential prey were released into the "release" patch at one end of the experimental arena (see description of release protocols above) with the "destination" patch located 7.5 m away (Fig. 1). We tested two predator locations; one approximately 0.5 m from the outermost edge of the release patch (predator location 1) and the other approximately 0.5 m from the edge of the destination patch closest to the release patch (predator location 2; Fig. 1). The arena was marked into 1.5 sections as above.

We simultaneously released five fish into the arena and then observed a randomly-selected focal fish for the duration of each trial. Mean fish length for this experiment was 138 ± 4 mm SL (including both conspecifics and the focal fish), and did not significantly differ among trials. Again, all trials lasted 15 min and were recorded with a PSION observation recorder. We released each group of fish into the experimental arena twice. During the first release, we observed the fish in the presence of an empty predator enclosure. We then removed the fish from the arena and, after approximately 20 min, re-released them into the arena for a second set of observations. Prior to the second release, we placed the predator in the enclosure and positioned the enclosure in the same location as the first release. The focal fish and conspecifics were then re-released and observed following the same protocol as the first release. We recorded the behaviour of the same focal fish during both observational periods. This procedure controlled for any possible effect of the enclosure itself on our observations. We tested each predator location and the corresponding enclosure control

with 10 groups of fish, resulting in 150 min of observation for each predator and control location tested.

2.5. Data analysis

All data were initially tabulated using The Observer Software™ by Noldus. For each focal fish observed, we recorded the time at which the fish left the release patch for the first time ("patch departure time"), the total number of completed gap crosses and the amount of time taken to complete each cross (amount of time between leaving the edge of one patch and arriving at the edge of the other patch). We calculated the average duration of gap crosses for each focal fish and then determined the average "movement speed" by dividing inter-patch distance by the time taken to move between the patches. Similarly, we calculated an average group size for each focal animal by summing the amount of time spent in each possible group size and determining the weighted average. All statistical analyses were performed using SPSS Statistics 17.0. We used generalized linear models to examine the effects of inter-patch distance (categorical variable), predator presence and location (categorical), and both fish length and mean group size (as covariates) on patch departure time, movement speed, and the total number of gap crossings. Initial models included three-way interactions among the treatments in question, fish length, and mean group size; non-significant interactions were sequentially removed and the models were re-run. While we used different sets of fish to test the effects of predator presence at the release patch versus the departure patch, the same fish were used within each predator location to test the effects of the predator and the empty enclosure. Separate analyses were conducted for data collected within each location treatment using generalized estimating equations and fish identity as a subject variable and all other relevant variables as described above, in order to eliminate bias due to repeated measures present in our experimental design. All data residuals were examined for normality, randomness, independence, and homogeneity. Data for patch departure time and movement speed in the predator experiment followed gamma distributions; therefore all analyses of these variables were conducted using log links in our models. The data for total number of completed crosses in both experiments followed a Poisson distribution, and all analyses of this variable utilized an identity (linear) link in our models. All other data were normally distributed and were analyzed using an identity (linear) link in our models. For analyses

that included the total number of gap crosses, or movement speed, some sample sizes were lower than the total number of fish observed because some fish did not complete any crosses. The critical p-value for all analyses was 0.05. Data values presented in the text are means ± SE.

3. Results

3.1. Inter-patch distance

There was no effect of inter-patch distance on average group size ($\chi^2 = 0.48$; df = 1, n = 20, p = 0.49), nor was there any effect of fish length on average group size ($\chi^2 = 1.53$; df = 1, n = 20, p = 0.22). Average group size was therefore included as an explanatory variable in all subsequent analyses.

3.1.1. Patch departure time

The length of time before focal fish initially departed the release patch was affected by the three-way interaction among inter-patch distance, fish length, and group size ($\chi^2 = 7.443$; df = 1, n = 20, p = 0.006). To investigate the nature of this interaction we examined the effects of fish length and group size within each inter-patch distance treatment (i.e., 3 m and 7.5 m). At 3 m there was a significant interaction between fish length and group size, with smaller fish leaving patches later, especially when moving in smaller groups ($\chi^2 = 18.372$; df = 1, p < 0.0001). At 7.5 m there was no effect of fish length but a significant effect of group size; fish in smaller groups left the release patch later ($\chi^2 = 3.941$, df = 1, n = 20, p = 0.047) than fish in larger ones (Fig. 2). Fish exposed to a 7.5 m inter-patch distance stayed in the release patch approximately 18% longer than fish exposed to the 3 m inter-patch distance (patch departure times were 125 ± 46 s at 7.5 m and 106 ± 27 s at 3 m).

3.1.2. Movement speed

Fish movement was faster between patches at the 7.5 m gap size (0.16 m·s^{-1} ± 0.02) as compared to 3 m gap size (0.12 m·s^{-1} ± 0.06; $\chi^2 = 7.666$, df = 1, n = 20, p = 0.006; Fig. 2). There was also a significant effect of fish length on movement speed between patches ($\chi^2 = 13.619$, df = 1, n = 20, p < 0.0001), with larger fish crossing gaps faster than smaller fish regardless of the distance treatment (Fig. 3).

3.1.3. Total gap crossings

Overall, fish crossed inter-patch distance gaps of 3 m (4.6 crosses ± 0.60) more frequently than at 7.5 m (2.9 crosses ± 0.73), but this difference was not significant (unpaired t-test: t = 1.789; df = 18; n = 20; p = 0.091). However, this decrease in gap-crossing frequency at 7.5 m, compared to 3 m inter-patch distance is significantly less than the 2.5-fold decrease we expected based solely on the difference in inter-patch distance (i.e. all else being equal, fish should be able to cross the 3 m gap 2.5 times more often than the 7.5 m gap; one-sample t-test: t = 3.805; df = 19; n = 20; p = 0.001). The total number of gap crosses was affected by an interaction between inter-patch distance and group size ($\chi^2 = 8.034$; df = 1; n = 20; p = 0.005). At the 7.5 m inter-patch distance fish moved more frequently across gaps when in larger groups ($\chi^2 = 12.23$; df = 1; n = 20; p < 0.0001), while at the 3 m inter-patch distance there was no effect of group size on the number of gap crossings (Fig. 2).

3.2. Predator presence

There was no difference in average group size for fish exposed to different predator conditions (different predator locations, or presence/absence at a given location; $\chi^2 = 7.00$; df = 3, n = 40, p = 0.07), nor did fish length affect average group size ($\chi^2 = 2.38$; df = 1, n = 38, p = 0.12). Average group size was therefore included as an explanatory variable in all subsequent analyses.
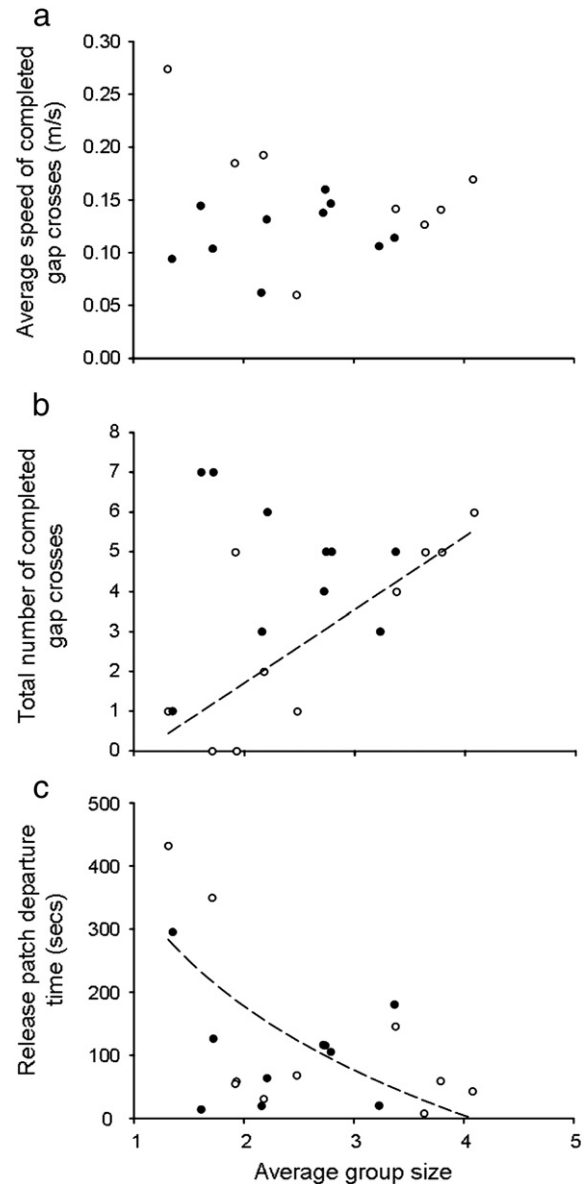

Fig. 2. Effect of average group size for fish exposed to inter-patch distances of 3 m (filled circles) and 7.5 m (open circles and dashed lines) on (a) average movement speed during gap crossing. p-Values for 3 m distance = 0.51, for 7.5 m distance = 0.19 and (b) total number of completed gap crosses. p-Values for 3 m distance = 0.91, for 7.5 m distance < 0.01 and (c) patch departure time. p-Values for 3 m distance = 0.45, for 7.5 m distance = 0.04.
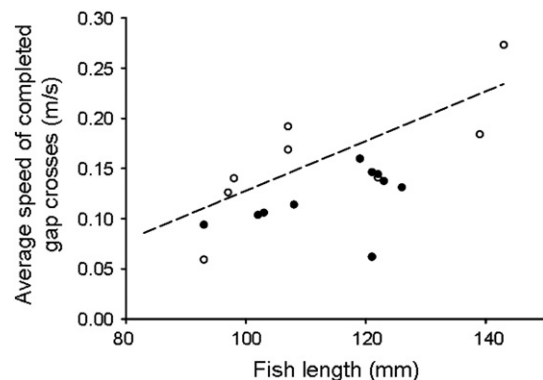

Fig. 3. Effect of focal fish length on average movement speed for fish exposed to inter-patch distances of 3 m (filled circles) and 7.5 m (open circles and dashed line). p-Values for 3 m distance = 0.17, for 7.5 m distance = 0.02.

3.2.1. Patch departure time

At both the release and departure patches, the presence of a predator tended to delay the time until departure from the release patch compared to an empty enclosure alone, though these differences were not statistically significant (release patch: empty enclosure = 59.9 ± 21.5 s; predator = 177.90 ± 98.2; paired t-test: t = −1.22; df = 7; n = 8; p = 0.260; destination patch: empty enclosure = 134.8 ± 76.2 s; predator = 222.51 ± 72.59 s; paired t-test: t = −0.75; df = 9; n = 10; p = 0.470). There was also no effect of predator location on patch departure time. When the predator was near the release patch, however, the patch departure time for the focal fish was influenced by an interaction between fish length and group size (χ^2 = 8.912; df = 1; n = 8; p = 0.003). This initial analysis was strongly influenced by the presence of an outlier, which when excluded, indicated only a significant main effect of group size on departure time with fish that spent time in larger groups leaving the patch earlier (χ^2 = 8.46; df = 1; n = 7; p = 0.004; Fig. 4). There was an effect of group size when the enclosure near the release patch was empty, though in this case fish that spent more time in smaller groups left the release patch earliest (χ^2 = 5.072; df = 1; n = 10; p = 0.024; Fig. 4). Similar trends were observed when the predator or empty enclosure was placed near the destination patch. When the predator was present, fish that associated with larger groups left the release patch earlier than those in smaller groups (χ^2 = 18.4; df = 1; n = 9; p < 0.0001; Fig. 4). When the enclosure was empty, fish with smaller mean group sizes left the release patch earlier than those in larger groups (χ^2 = 13.43; df = 1; n = 8; p < 0.0001; Fig. 4).

3.2.2. Movement speed

When the enclosure was placed near the destination patch, there was no difference in mean movement speed whether the enclosure was empty (0.19 ± 0.03 m·s^{-1}) or contained a predator (0.16 ± 0.04 m·s^{-1}; paired t-test: t = 0.86; df = 5; n = 6; p = 0.43). However, there was a significant effect of fish length on movement speed, in that smaller fish moved faster when there was a predator near the release patch (χ^2 = 7.918; df = 1; n = 6; p = 0.005). There was never an effect of group size on movement speed regardless of enclosure location or contents (predator versus empty). When directly comparing the two predator treatments (predator at the release patch or the destination patch), there was no effect of predator location on movement speed, though there was a significant interaction between fish length and predator location (χ^2 = 4.450; df = 1; n = 12; p = 0.035), again indicating that when the predator was at the destination patch smaller fish moved across the gap faster.

3.2.3. Total gap crossings

Fish completed more crossings when the predator was near the destination patch (2.60 ± 1.19 crossings) compared to when the predator was near the release patch (0.60 ± 0.16 crossings; χ^2 = 6.885; df = 1;

n = 19; p = 0.009; Fig. 5), with no effect of either fish length or group size. The number of crossings when the predator was near the release patch was also much lower than with an empty enclosure near the release patch (2.4 ± 0.8 versus 0.6 ± 0.2 crossings; paired t-test: t = 2.71; df = 19; n = 20; p = 0.024; Fig. 5). At the destination patch, total crossings were unaffected by whether the enclosure contained a predator or was empty (2.1 ± 0.7 versus 2.6 ± 0.8 crossings; paired t-test: t = −0.70; df = 19; n = 20; p = 0.504; Fig. 5).

4. Discussion

4.1. Inter-patch distance

Our findings suggest that marine and terrestrial fauna respond similarly to habitat fragmentation. With large gaps between similar habitat patches fish delayed their departure from patches, moved faster through gaps, and completed fewer gap crosses compared to patches separated by small gaps. These observations suggest that spatially complex habitat may affect movement patterns of small fish, such that movements within highly fragmented landscapes may be more tentative and sporadic than those with smaller gaps. Several species display similar responses to gaps in complex terrestrial habitat. Numerous bird species choose routes through protective cover, even if those routes increase total travel distance compared to a direct but open route, presumably to minimize exposure to predators (Bélisle and Desrochers, 2002; Creegan and Osborne, 2005; Desrochers and Hannon, 1997). Similarity in movement patterns between terrestrial and aquatic species perhaps should be expected given the ubiquity of fragmented habitat landscapes in marine ecosystems, even at small spatial scales (metres).

Individuals appear to base decisions to leave patches on information other than immediate predator presence or food availability. Factors such as individual body size, the presence of conspecifics, and the distance until the next patch of suitable habitat also affect patch departures and gap-crossing behaviour. Body size and spatial association with conspecifics (i.e. aggregating or shoaling) are both known to affect predation risk in fish (reviewed by Lima and Dill, 1990). In our study, larger fish crossed gaps faster, while those in larger groups departed to release patch sooner and completed more gap crosses. It is important to note, however, that these effects were only observed when the patches were furthest apart, suggesting that these factors are most important for crossing gaps when risk to predators is high. For juvenile Atlantic cod, several studies show lower predation risk in areas of complex habitat (Gorman et al., 2009; Laurel et al., 2003b; Linehan et al., 2001; Tupper and Boutilier, 1995) and individuals appear capable of assessing their vulnerability to predators, utilizing complex habitat to reduce this risk (Fraser et al., 1996; Gotceitas et al., 1997; Gregory and Anderson, 1997). Spatial analysis suggests that juvenile cod forage outside eelgrass habitat (Thistle et al., 2010), indicating that juvenile
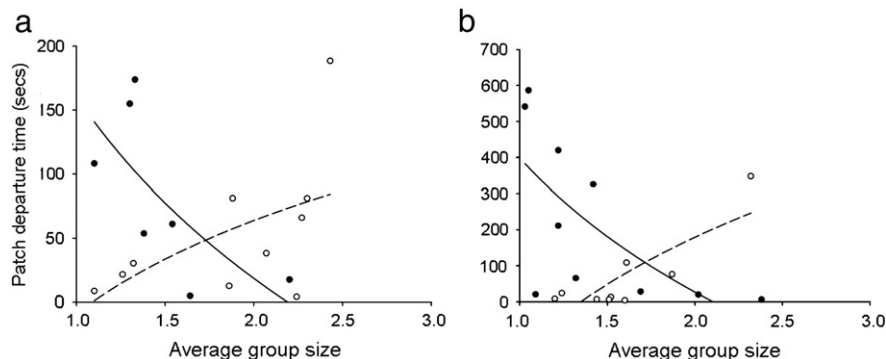
Fig. 4. Effect of average group size on release patch departure time for fish exposed to an empty enclosure (open circles and dashed lines) or a predator (solid circles and solid lines) at the (a) release end (p-values for the empty enclosure = 0.02, predator = 0.004) or (b) destination end (p-values for empty enclosure < 0.0001, predator < 0.0001) of the experimental arena.
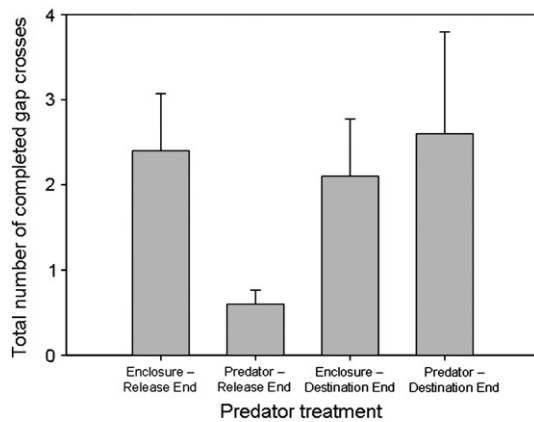
Fig. 5. Total number of completed gap crosses for each predator treatment. Bars denote means and lines denote 95% confidence intervals.

cod associate with eelgrass primarily to escape predators rather than to find food. Given differential predation risk inside and outside eelgrass patches (Laurel et al., 2003b), juvenile Atlantic cod may assess the danger of moving outside a patch in the context of distance to the next area of protective cover, an assessment modified by their body size, swim speed, and numbers of conspecifics present.

The fact that larger fish moved faster than smaller fish between habitat patches may simply reflect the fact that larger fish can swim faster than smaller fish. However, we observed that smaller fish often exhibited saltatory swimming behaviour, moving with frequent pauses in the exposed area between patches. In the wild, small fish generally face more potential predators than larger fish (see Sogard, 1997). Therefore, these small individuals may have paused to scan for predators before advancing further, consistent with many studies describing this type of behaviour (reviewed by Lima and Dill, 1990).

Juvenile Atlantic cod in our study reduced the frequency of gap crossings with increased inter-patch distance. Given that juvenile Atlantic cod predation risk increases over open areas relative to structurally complex seabeds (Linehan et al., 2001), even when close to complex habitat (~5 m away from eelgrass, Laurel et al., 2003a; Gorman et al., 2009), crossing larger distances over bare substrate likely increases predation risk compared to shorter distances. By reducing the number of between-patch movements when gaps between them are large, fish behaviourally reduce risk within a patchy marine landscape. These results support those of Gotceitas et al. (1995), demonstrating that juvenile cod assess predation risk, and also show that risk assessment involves more than simply observing the presence of a predatory threat.

Fish presented with large gaps to cross were more likely to move between patches in large groups than small groups of 1–3 individuals. This behaviour suggests that increasing shoal size may mediate the risk posed by moving over bare substrate (Laurel et al., 2004).

4.2. Predator

The results of this study suggest that the presence of a predator can affect the motivation of juvenile cod to leave a habitat patch, and that the presence of other similar-sized conspecifics can modify these effects. When the predator was present near either the release or destination patch, fish in larger groups departed from the release patch earlier than those in smaller groups. This trend was reversed when the enclosure was empty either at the release or departure patches — in these cases fish in smaller groups tended to leave the release patch earlier. Individual fish in shoals can experience decreased risk of predation (Pitcher, 1986), and so fish in larger and more cohesive groups were likely more willing to depart the release patch in the presence of an immediate threat. However, being in a

group can also carry a number of costs (Krause and Ruxton, 2008). For example, individuals in groups will often need to share resources such as food, and large groups may actually be more conspicuous to predators. It is therefore possible that in the absence of an obvious threat, juvenile cod minimize such costs by departing a habitat patch alone or in small groups.

When the predator was at the release patch, smaller fish moved faster across the gap. This effect was not present when the enclosure was empty (at either the release or destination patches) or if the predator was located at the destination patch. In fact, under all other conditions larger fish moved faster, including in the gap-size study component. It is possible that smaller fish are more vulnerable to potential predators (see Sogard, 1997), and under "routine" conditions move more slowly to improve vigilance and reduce conspicuousness. When there is an obvious threat, however, smaller fish apparently increase their rate of movement, perhaps to avoid the dangerous location.

When the predator was at the release patch, fish completed many fewer crossings compared to trials where the enclosure was empty or located at the destination patch (with or without a predator). Taken together with the effects on patch departure time and movement speed between patches, these results further illustrate that small juvenile Atlantic cod modify patch departure behaviour in fragmented habitats and movement frequency in the presence of a piscivorous fish. These findings complement previous work on predator-mediated habitat associations of small fishes (Fraser et al., 1996; Gorman et al., 2009; Gotceitas and Colgan, 1989). Studies of resource patch selection in aquatic organisms have mainly focused on the tradeoff between foraging and predator avoidance (Werner and Gilliam, 1984; Schmitt and Holbrook, 1985; Lima and Dill, 1990; Gotceitas, 1990). However, no studies in aquatic environments have tested the effects of predation risk on between-patch movement. Our results show that the effects of predation threat, fish size, and average group size affect gap-crossing behaviour between habitat patches. Broadly speaking, in the presence of a predator, the number of conspecifics modifies this response in that individuals decrease the time taken to depart a patch with an immediate predatory threat.

The observation that predator presence affects gap-crossing behaviour of juvenile Atlantic cod agrees with previous work demonstrating that juvenile cod are able to assess the level of predation risk present and adjust their behaviour accordingly. When presented with a predator and various substrate types, for example, juvenile cod select more complex habitat in the presence of a predator and can even distinguish between actively foraging and non-actively foraging predators (Gotceitas et al., 1995). Juvenile Atlantic cod assess risk based not only on the foraging behaviour of the predator, but also based on their location relative to the predator (Gotceitas et al., 1995). The results of this study corroborate these findings, but also suggest that the exact response to a predator threat is highly variable, in that some individuals modify their movement patterns drastically in response to the presence of a predator and the number of conspecifics, whereas others do not. The analysis of patch departure time, for example, was greatly influenced by an outlier, further suggesting variation in individual juvenile cod behaviour toward predators. Reduction in the total number of gap crosses also shows a flexible response to predation risk, further demonstrating the potential for predators to reduce connectivity between isolated patches of habitat. Such variability may reflect differences in the effectiveness of different predator avoidance strategies for fish in large or small groups of similarly-sized conspecifics. Recent work also indicates that individual fish vary widely in risk-taking tendency (Conrad et al., 2011; Killen et al., 2011). It is possible that bolder or more active individuals are more willing to cross gaps in habitat as compared to those that are shyer or less mobile. The role of personality traits in gap-crossing behaviour and connectivity in aquatic environments could be an avenue for further research.

Our results demonstrate that juvenile Atlantic cod actively avoid a perceived predation threat (Gotceitas et al., 1995) by moving away from predators, however a predator may impede movement by juvenile Atlantic cod in highly fragmented habitat. Therefore, factors other than foraging affect the movement decisions of juvenile fish in fragmented landscapes. While foraging may determine small-scale fish movements among individual habitat patches, factors such as group size, fish size, and predation risk must all be considered as possible mediators of movement behaviour. Many terrestrial species minimize predation risk by avoiding open areas between patches of complex habitat. Our results suggest similar risk-averse responses in marine species.

Acknowledgements

References

Baker, L., 2007. Effects of corridors on the movement behaviour of the jumping spider *Phidippus princeps* (Araneae Salticidae). Can. J. Zool. 85, 802–808.

Beier, P., 1993. Determining minimum habitat areas and habitat corridors for cougars. Conserv. Biol. 7, 94–108.

Bélisle, M., Desrochers, A., 2002. Gap-crossing decisions by forest birds: an empirical basis for parameterizing spatially-explicit, individual-based models. Landscape Ecol. 17, 219–231.

Conrad, J.L., Weinersmith, K.L., Brodin, T., Saltz, J.B., Sih, A., 2011. Behavioural syndromes in fishes: a review with implications for ecology and fisheries management. J. Fish Biol. 78, 395–435.

Cote, D., Gregory, R.S., Stewart, H.M.J., 2008. Size-selective predation by river otter (*Lontra canadensis*) improve refuge properties of shallow coastal marine nursery habitats. Can. J. Zool. 86, 1324–1328.

Creegan, H.P., Osborne, P.E., 2005. Gap-crossing decisions of woodland songbirds in Scotland: an experimental approach. J. Appl. Ecol. 42, 678–687.

Cresswell, W., 1994. Flocking is an effective anti-predation strategy in redshanks, *Tringa tetanus*. Anim. Behav. 47, 433–442.

Crowder, L.B., Cooper, W.E., 1982. Habitat structural complexity and the interaction between bluegills and their prey. Ecology 63, 1802–1813.

Desrochers, A., Hannon, S.J., 1997. Gap crossing decisions by forest songbirds during the post-fledgling period. Conserv. Biol. 11, 1204–1210.

DeVries, D.R., Stein, R.A., Chesson, P.L., 1989. Sunfish foraging among patches: the patch-departure decision. Anim. Behav. 37, 455–464.

Fraser, S., Gotceitas, V., Brown, J.A., 1996. Interactions between age-classes of Atlantic cod and their distribution among bottom substrates. Can. J. Fish. Aquat. Sci. 53, 305–314.

Gotceitas, V., 1990. Foraging and predator avoidance: a test of a patch choice model with juvenile bluegill sunfish. Oecologia 83, 346–351.

Gorman, A.M., Gregory, R.S., Schneider, D.C., 2009. Eelgrass patch size and proximity to the patch edge affect predation risk of recently settled age 0 cod (*Gadus*). J. Exp. Mar. Biol. Ecol. 371, 1–9.

Gotceitas, V., Colgan, P., 1989. Selection between densities of artificial vegetation by young bluegills avoiding predation. Trans. Am. Fish. Soc. 116, 40–49.

Gotceitas, V., Fraser, S., Brown, J.A., 1995. Habitat use by juvenile Atlantic cod (*Gadus morhua*) in the presence of an actively foraging and non-foraging predator. Mar. Biol. 123, 421–430.

Gotceitas, V., Fraser, S., Brown, J.A., 1997. Use of eelgrass beds (*Zostera marina*) by juvenile Atlantic cod (*Gadus morhua*). Can. J. Fish. Aquat. Sci. 54, 1306–1319.

Grant, S.M., Brown, J.A., 1998. Nearshore settlement and localized populations of age-0 Atlantic cod (*Gadus morhua*) in shallow coastal waters of Newfoundland. Can. J. Fish. Aquat. Sci. 55, 1317–1327.

Gregory, R.S., Anderson, J.T., 1997. Substrate selection and use of protective cover by juvenile Atlantic cod (*Gadus morhua*) in inshore waters of Newfoundland. Mar. Ecol. Prog. Ser. 146, 9–20.

Killen, S.S., Marras, S., McKenzie, D.J., 2012. Fuel, fasting, fear: routine metabolic rate and food deprivation exert synergistic effects on risk-taking in individual juvenile European sea bass. J. Anim. Ecol. 80, 1024–1033.

Kopp, K., Wachlevski, M., Eterovick, P.C., 2006. Environmental complexity reduces tadpole predation by water bugs. Can. J. Zool. 84, 136–140.

Krause, J., Ruxton, G.D., 2008. Living in Groups. Oxford University Press, Oxford.

Laurel, B.J., Gregory, R.S., Brown, J.A., 2003a. Settlement and distribution of Age-0 juvenile cod, *Gadus morhua* and *G. ogac*, following a large-scale habitat manipulation. Mar. Ecol. Prog. Ser. 262, 241–252.

Laurel, B.J., Gregory, R.S., Brown, J.A., 2003b. Predator distribution and habitat patch area determine predation rates on age-0 Atlantic cod, *Gadus* spp. Mar. Ecol. Prog. Ser. 251, 245–254.

Laurel, B.J., Gregory, R.S., Brown, J.A., Hancock, J.K., Schneider, D.C., 2004. Behavioural consequences of density-dependent habitat use in juvenile cod *Gadus morhua* and *G. ogac*: the role of movement and aggregation. Mar. Ecol. Prog. Ser. 272, 257–270.

Lima, S.L., Dill, L.M., 1990. Behavioural decisions made under the risk of predation: a review and prospectus. Can. J. Zool. 68, 619–640.

Linehan, J.E., Gregory, R.S., Schneider, D.C., 2001. Predation risk of age-0 cod (*Gadus*) relative to depth and substrate in coastal waters. J. Exp. Mar. Biol. Ecol. 263, 25–44.

Lingle, S., 2001. Anti-predator strategies and grouping patterns in white-tailed deer and mule deer. Ethology 107, 295–314.

Orth, R.J., Heck, K.L., van Montfrans, J., 1984. Faunal communities in seagrass beds: a review of the influence of plant structure and prey characteristics on predator: prey relationships. Estuaries 7, 339–350.

Pierce, B.M., Bowyer, R.T., Bleich, V.C., 2004. Habitat selection by mule deer: foraging benefits or risk of predation. J. Wildl. Manage. 68, 533–541.

Pitcher, T.J., 1986. Functions of shoaling behaviour in teleosts. In: Pitcher, T.J. (Ed.), Behaviour of Teleost Fishes. Johns Hopkins University Press, Boston, pp. 294–337.

Savino, J.F., Stein, R.A., 1982. Predator–prey interaction between large-mouth bass and bluegills as influenced by simulated, submerged vegetation. Trans. Am. Fish. Soc. 111, 255–266.

Schmitt, R.J., Holbrook, S.J., 1985. Patch selection by juvenile black surfperch (*Embiotocidae*) under variable risk: interactive influence of food quality and structural complexity. J. Exp. Mar. Biol. Ecol. 85, 269–285.

Sogard, S.M., 1989. Colonization of artificial seagrass by fishes and decapod crustaceans: importance of proximity to natural eelgrass. J. Exp. Mar. Biol. Ecol. 133, 15–37.

Sogard, S.M., 1997. Size-selective mortality in the juvenile stage of teleost fishes: a review. Bull. Mar. Sci. 60, 1129–1157.

Sogard, S.M., Olla, B.L., 1993. The influence of predator presence on utilization of artificial seagrass habitats by juvenile walleye pollock, *Theragra chalcogramma*. Environ. Biol. Fishes 37, 57–65.

Thistle, M.E., Schneider, D.C., Gregory, R.S., Wells, N.J., 2010. Fractal measures of habitat structure: maximum densities of juvenile cod occur at intermediate eelgrass complexity. Mar. Ecol. Prog. Ser. 405, 39–56.

Tull, J.C., Krausman, P.R., 2001. Use of a wildlife corridor by desert mule deer. Southwest. Nat. 46, 81–86.

Tupper, M., Boutilier, R.G., 1995. Effects of habitat on settlement, growth, and postsettlement survival of Atlantic cod (*Gadus morhua*). Can. J. Fish. Aquat. Sci. 52, 1834–1841.

Werner, E.E., Gilliam, J.F., 1984. The ontogenetic niche and species interactions in size-structured populations. Ann. Rev. Ecol. Syst. 15, 393–425.

Wrona, F.J., Jamieson Dixon, R.W., 1991. Group size and predation risk: a field analysis of encounter and dilution effects. Am. Nat. 137, 186–201.