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Substrate selection by juvenile Atlantic cod (*Gadus morhua*): effects of predation risk

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Abstract. Although predator avoidance has been proposed as one possible factor influencing the distribution of fish among substrate types, no study has addressed this question directly. Groups of juvenile Atlantic cod were offered a choice between pairs of the following three substrates: sand, gravel-pebble and cobble. Their distribution on these substrates was compared prior to, during and following exposure to a predator (i.e. a larger conspecific). With no apparent risk of predation, juvenile cod preferred sand or gravel-pebble. When cobble was present, juveniles hid in the interstitial spaces of this substrate in the presence of a predator. With no cobble present, juveniles showed no preference between sand and gravel-pebble, and did not seek refuge from predation in association with these substrates. Following exposure to a predator (i.e. 2.5 h later) larger juvenile cod again showed a preference for the finer-grained substrates, but smaller individuals continued to associate with the cobble. The presence of cobble resulted in fewer juveniles being captured and a significant increase in the latency until the first juvenile was captured by the predator. Results are discussed with respect to the effects of predation on the distribution and survival of fishes among substrate types.

Key words: Substrate selection – Habitat – Atlantic cod – Predation

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Numerous studies have demonstrated a significant negative relationship between predator foraging success and increasing habitat complexity, and use of these more complex habitats by prey when confronted with the risk of predation (e.g. Lima and Dill 1990). In aquatic systems, such studies have concentrated on the effects of variation in the complexity (i.e. density, composition) of vegetated habitats (e.g. Orth et al. 1984; Gotceitas and Colgan 1989). However, in a variety of freshwater (e.g. higher gradient lotic systems, oligotrophic lentic systems) and marine (e.g. subarctic and arctic regions) systems, habitats characterized by the presence of upright forms of vegetation are rare, and variation in habitat complexity is primarily related to the size and composition of the mineral substrates present.

Substrate type has been shown to influence the distribution of various freshwater and marine invertebrates (Flecker and Allan 1984; Clifford et al. 1989; Henschel et al. 1990) and fishes (Scott 1982; Johnson and Kucera 1985; Becker 1988). Research with invertebrates has shown that substrate selection can be significantly affected by the risk of predation (e.g. Stein and Magnuson 1976). While the observed distribution of various fish species with respect to substrate has been attributed to a response by the fish to reduce their risk of predation (Rankin 1986; Adams et al. 1988; Lough et al. 1989), to our knowledge no study has directly examined the effect of predation risk on distribution and selection among substrate types by fish.

Atlantic cod (*Gadus morhua*) is an economically important groundfish species inhabiting cool-temperate to subarctic waters on both sides of the North Atlantic (Scott and Scott 1988). Juveniles and adults can be found in both inshore and offshore environments extending out to the edge of the continental shelf, environments including habitat with and without vegetative cover (Keats et al. 1987; Lough et al. 1989; pers. obs.). Where present, vegetative cover appears to influence the distribution of juvenile cod, and use of this habitat has, indirectly, been attributed to avoiding predation (Keats et al. 1987). However, substrate type has also been demonstrated to significantly influence the distribution of cod, as well as a number of other groundfish species (Scott 1982; Horne and Campana 1989; Clark and Green 1990). In their study, Lough et al. (1989) attributed the distribution of juvenile cod among substrate types to a response by the juveniles to reduce their risk of predation, but no direct evidence for this interpretation was provided. A number of recent studies have shown that predation risk affects both foraging by juvenile cod (Nordeide and Svasand 1990) and juvenile cod distribution in relation to that of the predator (Gjosaeter 1987). Therefore, in this study we examined substrate selection by juvenile Atlantic cod in the absence

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and presence of a predator in order to investigate factors affecting habitat selection in this species, and to address the more general question of the effects of predation risk on substrate selection by fish.

Methods

Experimental animals

Juvenile, 0+ (i.e. < 1 year old, 5–13 cm standard length, SL), and larger, 3+ (25–40 cm SL), cod were collected by beach seine and/or bottom trawl from an inshore area at Bellevue, Newfoundland, Canada (43° 38′ N, 53° 44′ W). Fish were brought to the laboratory at the Ocean Sciences Centre, Logy Bay, Newfoundland, where the two size classes were housed in separate flow-through tanks (1 × 1 × 0.47 m deep). Tanks were supplied with a mixture of ambient and heated seawater to maintain temperature between 5° and 10°C. While in the holding tanks, cod were fed chopped capelin (*Mallotus villosus*).

Experimental apparatus

Substrate selection experiments were conducted in a large flow through tank (2 × 2 × 0.5 m deep) (Fig. 1), housed in a separate room to minimize outside disturbance. A blind (1 m × 2 m high), with a viewing slit (45 cm × 17 cm high), was set up along one edge of the tank. All observations were made from behind the blind, to eliminate any observer disturbance. The experimental tank was maintained at a water temperature of 5–10°C, to match that in the holding tanks. Water depth was 0.4 m. Illumination was provided by four 15-W incandescent light bulbs suspended 1.17 m above the water. Bulbs were centred over the tank, with each bulb located at the corner of a 0.9 × 0.9 m square frame. A 12-h L:12-h D light regime was used.

The four corners of the tank were closed off by an opaque piece of plexiglas (1 m × 0.5 m high), each piece with a sliding door (15 cm × 19 cm high) built into its centre (Fig. 1). The resulting enclosures housed one 3+ cod (= "predator") in each corner of the tank. The sliding door to each enclosure could be opened and closed by the observer from behind the blind.

Substrates, within the size range commonly found in the inshore and offshore (e.g. Georges Bank, Lough et al. 1989) area, were collected at low tide from along the shore line in a local Provincial Park. In the laboratory, the substrate was cleaned by flushing it with hot freshwater and then allowing it to dry. Once dry, the substrate was sorted into size categories (= "substrate types") by sieving it through a series of metal sieves (Tyler Sieves, Canadian Standard Sieve Series). Substrate was divided into three categories based on individual particle size; sand (<1 mm diameter), gravel-pebble (4–16 mm diameter), and cobble (70–200 mm along its longest axis).

Experimental design

Prior to testing substrate selection by 0+ cod (= "juvenile cod"), the predators (i.e. 3+ cod) in the four predator enclosures were trained to leave their enclosure and enter the central area of the experimental tank (= "experimental area") to feed when the sliding door to their enclosure was opened. This was done by repeatedly opening the door and then offering food (i.e. capelin) to the predator in the experimental area. Training was deemed complete once all four predators readily entered the experimental area when the door to their enclosure was opened.

Substrates were tested in pairs, with each substrate type covering half the bottom of the experimental area (Fig. 1). All possible combinations of substrate types (i.e. Sand/Cobble, Gravel-pebble/Cobble, and Sand/Gravel-pebble) were tested. Location of substrate

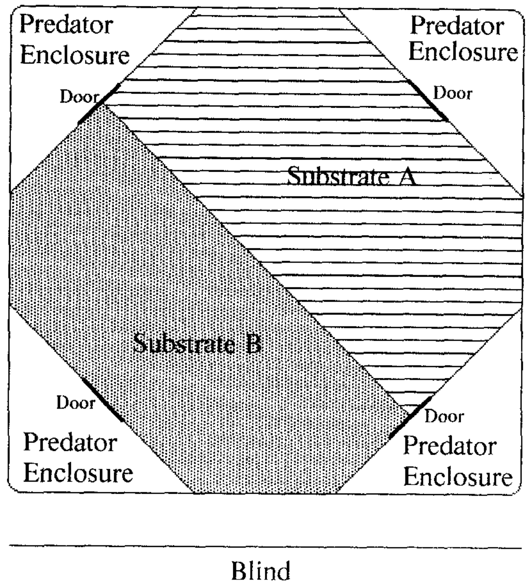

Fig. 1. Top view of the experimental tank

type in the experimental area (i.e. which half of the tank) was assigned randomly. Each pair of substrates was presented to at least five different groups ($n = 5$ fish/group) of juvenile cod, in the absence and presence of a predator.

Each presentation of a substrate pair to a group of juveniles (= "experimental trial") lasted 2 days. The evening (5 p.m.) prior to the first day of observations, a group of five naive juvenile cod were introduced into the experimental area of the tank to acclimatize. The following day (Day 1 of the experimental trial), distribution of the juveniles with respect to the two substrates was monitored during three 15-min observation periods, conducted at 9 a.m., 12 noon, and 4 p.m. To test for temporal/experience effects on substrate use, similar observation periods were conducted at 9 a.m. and 12 noon on the second day (Day 2) of the experimental trial. Immediately following the 12 noon observation period on Day 2, one predator, chosen at random, was released into the experimental area and the distribution of both juvenile cod and the predator with respect to the substrates present was recorded for the next 15 min. Following this 15-min observation period (= "predator introduction"), the predator was kept in the experimental area for a subsequent 45 min, at the end of which a second 15-min observation period (= "predator final") was conducted. Following this second observation period with the predator present, the predator was returned to its enclosure. Finally, to investigate for possible lasting effects on substrate use by juvenile cod following exposure to a predator, one last 15-min observation period was conducted at 4 p.m. (i.e. 2.5 h after removal of the predator) on Day 2 of each experimental trial.

The above experiment tested 0+ cod averaging 10.43 cm (SE = ± 0.117) SL. In a second experiment we specifically tested smaller (i.e. $\bar{x} \pm 1$ SE; 7.83 ± 0.164 cm SL) 0+ cod, that is fish closer to the size at which they first become demersal following their pelagic larval and juvenile stages (i.e. 2.5–5 cm SL; Fahay 1983). Fish used in the second experiment were significantly smaller (SL) ($F_{1,117} = 30.16$, $P = 0.0001$) than those used in the first. Mean size (SL ± 1 SE) of the four predators used in the second experiment ($\bar{x} = 33.0 \pm 2.14$) was not significantly different (t-test, $t = 0.174$, $df = 6$, $P = 0.87$) from those used in the first ($\bar{x} = 33.5 \pm 2.11$). The experimental protocol for the second experiment was identical to the first. Its purpose was to examine for possible effects on substrate use due to juvenile cod body size, and to provide some insight into the influence of substrate type on the distribution of 0+ cod closer to the size at which they first become demersal. Based on the results from the first experiment, only the Sand/Cobble substrate combination was tested.

Data collected and analyses

0+ *Juvenile cod.* Because individual juvenile cod could not be followed over the 15-min observation period, an estimate of the time juveniles spent on the smallest-grained substrate present was calculated for each observation period. This was done by recording the number of fish present on the smallest-grained substrate at 1-min intervals (maximum $n=5$ fish) over the course of each 15-min observation period. Counts within each observation period were then summed over the 15 min (maximum = 5 fish × 15 min, for any one substrate), and this sum was then divided by the total time available during that observation period (total time available = the sum of the number of fish present at the end of each 1-min interval over the 15-min observation period, maximum = 5 fish × 15 one-minute intervals). It was necessary to use the proportion of total time available spent on a substrate, in order to correct for reductions in the total number of juveniles present between observation periods within any one trial, as a result of prey captures during exposure to the predator.

These data were used to compare substrate use by juvenile cod prior to, during and following exposure to a predator in relation to the substrate types available (GLM procedure, SAS 1988). Data for the Sand/Cobble combination from the first and second experiment were also used to investigate whether body size of 0+ juvenile cod affects substrate use.

Qualitative observations were also made of juvenile cod behaviour prior to, during and following exposure to a predator.

Predator. During each of the two observation periods with the predator present, its distribution with respect to the substrates available was recorded at 1-min intervals (maximum = 15 min on any one substrate type/observation period). These data were used to compare the predator's use of the smallest-grained substrate present when first introduced to the experimental area and during the 15 min immediately prior to its removal (i.e. 45 min later) (GLM procedure, SAS 1988).

Additional observations were made over the entire period that the predator was present in the experimental area (i.e. both 15-min observation periods and the 45 min between). With the predator present we recorded: (1) latency (min) until the first juvenile cod was captured, and (2) the total number of juveniles captured. These data were compared among the three substrate combinations tested (GLM procedure, SAS 1988). For analysis, these data had to be rank-transformed.

Juvenile cod were measured (SL) at the beginning and end of each experimental trial. These data were used both to compare the size of juvenile cod tested with the different substrate combinations, and to test for any size-selective predation by the predators by comparing the size of juveniles introduced to those remaining at the end of each trial (GLM procedure, SAS 1988).

Results

Juvenile cod

Regardless of the combination of substrate types presented, there was no significant day (i.e. Day 1 or 2 of trial) effect on the pattern of substrate use demonstrated by juvenile cod in the absence of a predator (Sand/Cobble: $F_{1,37}=0.02$, $P=0.89$; Gravel-pebble/Cobble: $F_{1,31}=1.34$, $P=0.26$; Sand/Gravel-pebble: $F_{1,31}=0.13$, $P=0.72$). There was also no significant difference in substrate use among the different groups of juvenile cod tested with the Sand/Cobble ($F_{5,37}=1.84$, $P=0.13$), Gravel-pebble/Cobble ($F_{4,31}=0.96$, $P=0.45$) or Sand/Gravel-pebble ($F_{4,31}=1.63$, $P=0.22$) substrate combinations.

When offered a choice between sand and cobble ($F_{3,37}=33.23$, $P=0.0001$) or gravel-pebble and cobble ($F_{3,31}=22.83$, $P=0.0001$), substrate use by juvenile cod was significantly affected by the presence of a predator. There was, however, no significant difference in the pattern of substrate use by juvenile cod between these two substrate combinations ($F_{1,72}=3.53$, $P=0.07$). In both these combinations, juvenile cod spent significantly more time on the smaller-grained substrate prior to exposure to the predator (Fig. 2). With no threat of predation, juvenile cod, typically, formed loose groups of two to five fish up in the water column. Although most of their time was spent over the smaller grained substrate, fish did move between substrate types. Juveniles did occasionally move down onto both substrate types, but appeared to do so much more often on the smaller-grained substrate. No aggression was noted among individuals.

In contrast, with the predator present, juvenile cod spent significantly more time on the cobble (Fig. 2). Following introduction of the predator, juvenile cod immediately oriented towards it and then moved down out of the water column. Until the initial attack took place, juveniles kept close to the bottom and moved around the tank so as to maintain the maximum distance between themselves and the predator. Following an attack, juveniles, typically, scattered from any loose groupings and sought shelter in the interstitial spaces among the cobbles. Once hidden, juveniles remained under cobbles for the entire time that the predator was present. However, they did occasionally poke their heads out, or even ventured one or two body lengths out from beneath the cobble they were hiding under and then remained motionless down among the cobbles. If at this time the predator swam into the juvenile's field of view, the juvenile cod would immediately withdraw back under cover. If the predator did not pass by, juveniles would slowly move so as to sit on the top of the cobbles, at which time they appeared to notice the predator in the tank and returned to hiding under the cobble. It was during the time prior to seeking shelter in the cobbles, or if caught off guard when venturing out from under the cobbles, that the juveniles were most vulnerable to capture by the predator.

Whereas no aggression was noted among individual juvenile cod prior to exposure to the predator, in its presence, and for a period of 5–15 min after its removal, shelter was not shared among individuals. A number of instances were noted where a juvenile sought shelter under a cobble already occupied by another. In all such cases, the "resident" fish aggressively chased the "intruder" away.

Once the predator was removed, movement up onto the cobbles eventually led to movement over the cobbles and out onto the smaller grained substrate, and finally movement back up into the water column. The appearance of other individuals at any time during this sequence of events led to the formation of loose groups.

In contrast to those substrate combinations including cobble, the presence of a predator had no significant effect on use of the smaller-grained substrate by juvenile cod offered a choice between sand and gravel-pebble ($F_{3,31}=1.68$, $P=0.19$). Juveniles showed a preference for the smaller-grained substrate prior to, and following, exposure to the predator. However, juveniles showed no preference between sand and gravel-pebble when the predator was present (Fig. 2). In this combination of substrates, sand was used equally, both in the absence and presence of the predator.

When provided with a choice between sand and gravel-pebble, juvenile cod behaviour prior to exposure to a predator was similar to that described above for the other two substrate combinations. In the presence of the predator, juveniles again immediately oriented toward the predator and moved down in the water column closer to the substrates. Prior to the initial attack, fish moved closer together forming a single tight group which then moved around the tank so as to maintain the maximum distance between themselves and the predator. Once attacked, juveniles scattered and came to rest in the water/air interface along the tank walls, where they remained motionless unless again attacked. While motionless in the water/air interface, juveniles were generally ignored by the predator; however, movement by the juveniles typically initiated an attack. Juveniles were most vulnerable to capture when in the water column or down near the substrates. Few juveniles were captured in the water/air interface.

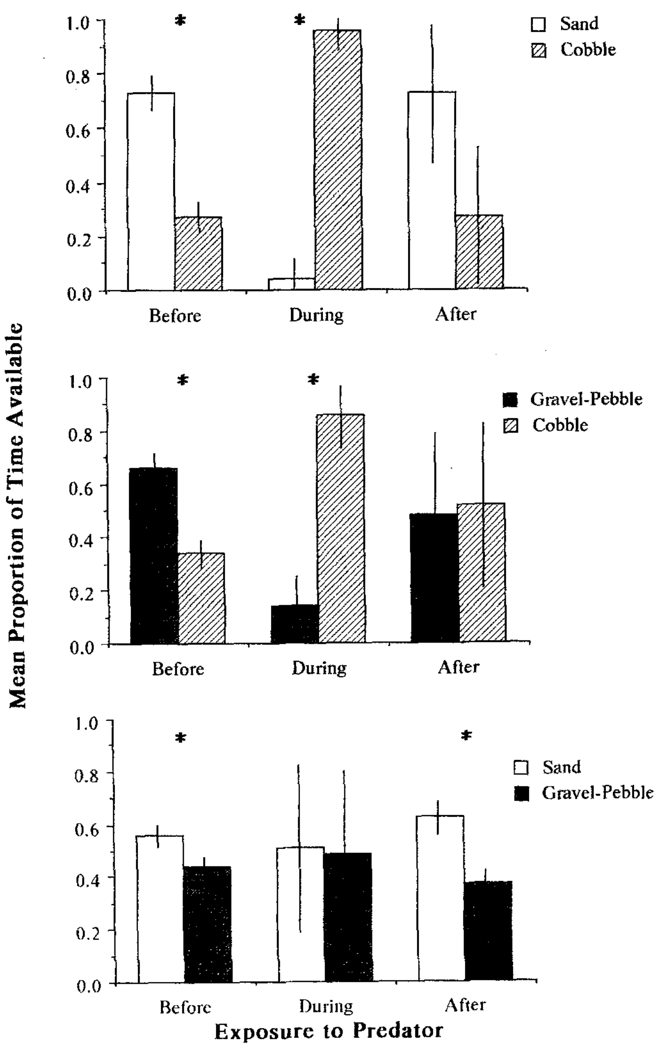

Fig. 2. Mean proportion of time juvenile cod spent on different substrates before, during and after exposure to a predator. *Vertical bars* represent 95% confidence intervals. (* indicates a significant difference in the proportion of time spent on the two substrates)

Concentration of the juvenile cod in the water/air interface while in the presence of the predator was most likely an artifact of experimental constraints on juvenile movement. In the absence of any suitable sized substrate, or other form of cover, in which to hide, it would appear that the escape response of juvenile cod is simply to flee from the predator. In this experiment, such a response would be artificially curtailed by the presence of the tank walls, resulting in the juveniles fleeing as far as possible only to end up in the water/air interface. Regardless, these results demonstrate that neither sand nor gravel-pebble were viewed by the juvenile cod as offering safety from predation.

Given that there was no significant difference in the use of either sand or gravel-pebble when paired with cobble, and that both these substrates were avoided in the presence of a predator, the smaller 0+ juvenile cod tested in the second experiment were only exposed to the Sand/Cobble combination. As in the earlier experiment, while there was no significant day ($F_{1,38}=0.06, P=0.81$) or group of fish ($F_{5,38}=1.03, P=0.41$) affects, the presence of a predator did significantly affect the pattern of substrate use by these smaller 0+ juveniles. Again, juveniles spent significantly more time ($\bar{x}$ proportion of total time available spent on the smaller-grained substrate; 95% confidence interval) on the sand prior to exposure to the predator (0.65; 0.59–0.71), and hid under the cobbles (0.12; 0.08–0.32) when the predator was present. In both these cases, there was no significant difference in the pattern of substrate use between the larger (experiment 1) and smaller (experiment 2) 0+ juveniles (Prior to predator: $F_{1,57}=3.20, P=0.08$; Predator introduction: $F_{1,10}=0.65, P=0.44$; Predator final: $F_{1,10}=0.90, P=0.36$). However, in contrast to the larger 0+ cod, the smaller juveniles spent significantly ($F_{1,10}=8.27, P=0.02$) more time on cobble following exposure to the predator (i.e. 2.5 h after removal of the predator). Qualitative observations indicate that the smaller juveniles behaved in a similar manner as the larger 0+ cod in relation to each other, the two substrates and the predator.

Predator

Regardless of the combination of substrates present, there was no significant difference among trials (i.e. predators) (Sand/Cobble: $F_{5,5}=1.54, P=0.32$; Gravel-pebble/Cobble: $F_{4,4}=0.50, P=0.74$; Sand/Gravel-pebble: $F_{4,4}=0.44, P=0.78$), or between the two observation periods (i.e. Predator introduction and Predator final) (Sand/Cobble: $F_{1,5}=2.29, P=0.19$; Gravel-pebble/Cobble: $F_{1,4}=0.77, P=0.43$; Sand/Gravel-pebble: $F_{1,4}=1.71, P=0.26$) with respect to substrate use by the predator. The predator(s) showed no preference between substrate types regardless of the combination present.

There was no significant difference in the size of juvenile cod tested with the three different combinations of substrate ($F_{2,117}=1.88, P=0.16$), except for that already mentioned for the experiment looking at possible effects of body size on substrate use by juvenile cod (i.e. experiment 1 vs. 2). In all cases, there was no significant difference between the size of juveniles introduced at the beginning of a trial and those remaining following exposure to the predator ($F_{1,117}=0.33$, $P=0.57$). Therefore, there was no size-selective predation by the 3+ cod within the size range of 0+ juveniles tested.

The combination of substrates present had a significant effect on latency (min) until the first juvenile cod was captured by a predator ($F_{2,19}=6.14$, $P=0.009$). It took the predator significantly longer to capture a juvenile cod with cobble present (Fig. 3A). Although not significant ($F_{2,19}=3.18$, $P=0.06$), an average of 2.5–3 times as many juvenile cod were captured in the absence of cobble (Fig. 3B). Both these results indicate that the presence of cobble reduced the risk of predation to juvenile cod, and, therefore, provide an explanation for the use of cobble by the juveniles in the presence of a predator.

There was no significant difference in either the latency until the first juvenile was captured ($F_{1,10}=0.19$, $P=0.67$) or the number of juveniles captured ($F_{1,10}=0.04$, $P=0.84$) between trials with the smaller 0+ juveniles versus the larger ones used in trials with the Sand/Cobble combination.

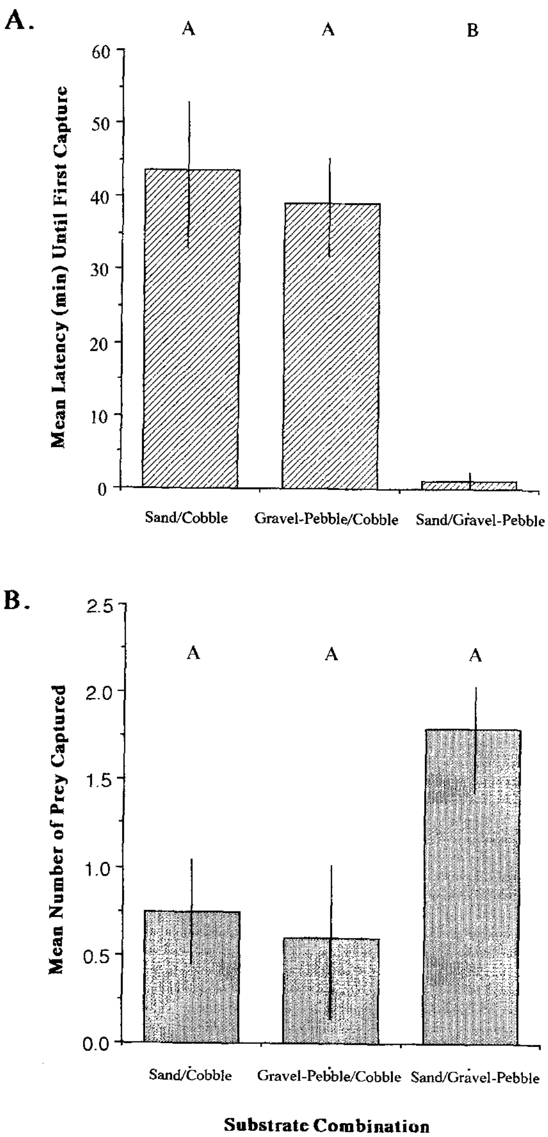

Fig. 3.A Mean (±1 SE) latency (min) until the predator captured its first prey, and **B** mean (±1 SE) number of prey captured by the predator during the 75 min that it had access to the prey, with respect to the combination of substrates present. Means with the same *letter* above them are not significantly different

Discussion

In this study, when there was no apparent risk of predation, juvenile cod demonstrated a preference for finer-grained substrates (i.e. sand and gravel-pebble). In contrast, juveniles sought refuge in the interstitial spaces available in a cobble substrate in the presence of a predator. Selection for cobble significantly reduced the risk of predation to juvenile cod. With no cobble present, juvenile cod showed no preference between sand and gravel-pebble when confronted by the risk of predation, and, instead of seeking shelter in association with one of these substrates, juveniles tried to escape from the vicinity of the predator. Although escape was restricted by the walls of the experimental tank, it is probable that in nature such an escape response would continue until shelter was found or the predator was eluded in some other manner, as suggested by Johns and Mann (1987) in their study with juvenile lobster (*Homarus americanus*).

A number of studies have concluded that substrate size significantly affects habitat selection by a variety of marine (Scott 1982; Becker 1988) and freshwater (Johnson and Kucera 1985; Rankin 1986) fishes. In turn, various factors (e.g. protection from current, distribution of food), including predator avoidance, have been suggested as being responsible for the observed association between fish and specific substrate types. However, our results appear to be the first to demonstrate a direct effect of predation risk on substrate selection by fish. In their study with the crayfish, *Orconectes propinquus*, Stein and Magnuson (1976) also found that in the presence of a predator, crayfish showed a preference for the coarser substrate and sought shelter from predation in the interstitial spaces within this substrate. Given that variation in sediment composition can be the primary source of habitat complexity in a number of different natural systems, our results, and those of Stein and Magnuson (1976), indicate that predator avoidance could significantly influence the distribution of organisms vulnerable to predation in such systems.

Both smaller (6–9.1 cm SL) and larger (8.4–12.1 cm SL) 0+ juvenile cod responded to a predation threat in a similar fashion, by hiding in among cobbles. However, this response appeared to be more pronounced in the smaller fish, as even 2.5 h after exposure to a predator the smaller fish were still associated with the cobble substrate. These results suggest that the availability of substrate suitable for providing a refuge from predation could be an important factor affecting subsequent survival of 0+ cod as they settle out of the water column following their pelagic stage and become demersal (i.e. 2.5–5 cm SL, Fahay 1983). The importance of "suitable" substrate for settlement, and subsequent survival, has been well documented for a variety of marine invertebrate larvae (e.g. Doyle 1975; Henschel et al. 1990; Petraitis 1990; Michener and Kenny 1991). The same has been suggested for some fish (e.g. Gibson and Batty 1990). For example, in their study on the distribution of juvenile cod and haddock (*Melanogrammus aeglefinus*) on Georges Bank (42° 05.0′N, 66° 20.0′W), Lough et al. (1989) found that while pelagic juveniles of both species were widespread over the bank, demersal juveniles were only abundant on a pebble-gravel deposit located on the northeastern edge of the bank. Based on their observations, Lough et al. (1989) felt that this localized distribution was most probably a response to reduced predation risk on the pebble-gravel deposit, as compared to that on the sandy bottom found over the rest of the bank. Further, because the pebble-gravel deposit supported the largest number of juveniles, these authors concluded that this area of substrate may be essential to the recruitment success of cod and haddock on Georges Bank. Given that the pebble-gravel deposit on Georges Bank was composed of substrate in the 4–64 mm size range, with areas of larger substrate also present (Lough, pers. com.), results from our study would support the contention that the association of juvenile cod and haddock with this substrate deposit may be to reduce their risk of predation. Taken together, our results and those of Lough et al. (1989), suggest that if predation is an important factor affecting the survival of juvenile cod and other groundfish species, survival following the widely dispersed pelagic stages could be significantly affected by the substrate types available to the newly demersal juveniles.

A number of studies with a variety of freshwater fishes have found that selection among substrate types or structural cover with respect to protection from current (Rankin 1986; Sechnick et al. 1986), predation (Adams et al. 1988; Johnson et al. 1988) or overwintering (Rimmer et al. 1983; Johnson and Kucera 1985) was highly dependent on the presence of "suitable" interstitial spaces. "Suitable" here refers to interstitial spaces of an appropriate size to provide the fish with the protection sought. For example, in their study on the use of artificial habitat structural units, Johnson et al. (1988) found that while juvenile bluegills, *Lepomis macrochirus*, used both small- and medium-interstice structures in the absence of predators, under the risk of predation bluegills showed a significant preference for the small-interstice structures. They attributed this switch to the refuge from predation provided the bluegills by the small-interstice structures, as the predators were too large to enter these structures. However, although use of the medium-interstice structures by bluegill was significantly reduced in the presence of the predators, only a small, or no, increase in the number of bluegills in the small-interstice structures was noted. Based on these results, Johnson et al. (1988) concluded that available structure suitable as a refuge from predation could have a carrying capacity and, therefore, be a limited resource. If suitable habitat does have a carrying capacity, beside available space, the carrying capacity of such habitat could also be influenced by the interactions among the individuals using this space. Helfman (1981) found that juvenile bluegills became highly aggressive towards conspecifics in relation to nocturnal resting sites. Therefore, it is possible that those bluegills which occupied the small-interstice structures in the study of Johnson et al. (1988) in the absence of predation risk, may have aggressively limited the number of additional fish entering these structures when predators were present. In their work with juvenile Atlantic salmon (*Salmo salar*), Rimmer et al. (1983) found that juveniles moved to occupy natural chambers beneath the streambed substrate to overwinter, and that suitable spaces were always occupied by only one fish. Although no direct evidence was provided, given the aggressive nature of juvenile salmonids towards each other with respect to space (Cunjak and Green 1984; Fausch 1984) it is possible that the solitary occupancy of suitable overwintering sites noted by Rimmer et al. (1983) was the result of aggressive exclusion of others. Regardless of the reason(s), solitary occupancy of overwintering sites could limit the carrying capacity of a lotic system with respect to overwintering survival of juvenile salmonids (Glova and Mason 1977). In our study, suitable interstitial spaces in the cobble were always occupied by a single individual, and conspecifics attempting to seek refuge from the predator in an occupied space were always evicted by the resident. Therefore, in conjunction with the studies discussed above, our observations would further support the idea that suitable cover could be a limited resource. As such, the availability of substrate suitable as cover from predation, or protection from other factors affecting survival, could represent one factor affecting the recruitment of juvenile cod and other fish species into the adult population (e.g. Steiner et al. 1982).

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