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Identifying habitat associations of early juvenile cod in nearshore Gulf of Maine waters

by

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Abstract

Recently settled young-of-year (YOY) cod (*Gadus morhua*) are typically found in shallow waters in complex habitats such as seagrass beds and cobble-rocky ledge habitats that provide refuge from predators. As cod mature, they are thought to slowly migrate into deeper water, yet whether these juvenile cod associate with specific habitat types remains unclear. We utilized seafloor mapping information and trawl survey data from 1992-2005 conducted in mid-coast Maine to examine cod habitat associations during early life-history phases. In 2006, we conducted video surveys and hook-and-line sampling to assess how cod relative abundances in these habitats compare to more structured habitats including rocky ledge and cobble bottom. Recently settled YOY (3-9 cm) cod were caught in trawl surveys predominately in < 20 m in sand bottom, which was the only habitat that was prevalent at these shallow depths. Meanwhile, trawl surveys revealed that larger juvenile (10-25 cm) cod were far more abundant on gravel than on mud or sand bottom. Although depth was positively correlated with fish size ($r^2 = 0.35$), examination of tows conducted at similar depths demonstrated that juvenile cod densities on gravel were more abundant than those on either sand (20-35 m) or mud (35-50 m). 89.9% of cod were found in water between 4 and 10 °C. Juvenile cod densities were also consistently higher in gravel than either of the two soft-sediment habitats across this temperature range. Video surveys and hook-and-line sampling suggested that cod are most abundant in complex habitats such as rocky ledge and cobble habitats. Given that these habitats are incapable of being towed because nets are easily entangled on complex bottom, attempts to quantify the abundance of juvenile cod populations using only trawl surveys may be insufficient. Further investigation is merited to determine whether complex nearshore habitats influence juvenile cod survivorship and growth as well as if the availability of these habitats is affecting the recovery of cod populations and their fisheries in the Gulf of Maine.

Key words: Atlantic cod, *Gadus morhua*, density, essential fish habitat, population dynamics, cobble-ledge, gravel, mud, sand

Introduction

Given Atlantic cod's (*Gahdus morhua*) ecological role historically as a key top predator in the northwest Atlantic (Bigelow and Schroeder 1953, Jackson et al. 2001) coupled with its economic importance to northeastern North America over the past 4 centuries (Kurlansky 1997), investigations of the factors that limit cod populations in areas such as the Gulf of Maine will be critical to its recovery. Similar to other demersal fish species, cod endure disproportionately high mortality rates as juveniles. Thus the processes that mediate cod population dynamics during these early life-history phases could limit the overall abundance of cod in the Gulf of Maine. The heightened risk of being consumed by predators probably explains why juvenile cod forge much stronger habitat associations than adult cod. Investigation of the importance of these habitat associations for juvenile cod could illuminate bottlenecks currently limiting the recovery of cod populations in the Gulf of Maine. In a review of factors influencing mortality of early life history phases of cod in Canadian waters, Anderson and Gregory (2000) suggested that adult cod are regulated by juvenile populations, and implied that preferred seabed habitat by juveniles may be limiting cod populations. Similar analyses of long-term cod datasets from Scandinavian waters have also suggested that cod population dynamics are largely influenced by seabed habitat characteristics because they determine both food and refuge availability for juveniles (Bjornstad et al. 1999, Fromentin et al. 2001). Here we utilize trawl surveys over the past 15 years and field sampling efforts to investigate how habitat influences the abundance and size distribution of juvenile cod in the central portions of coastal Maine.

Young-of-year cod (0 age class) typically settle in relatively shallow water and move to deeper depths with age (Swain 1993, Lineham et al. 2001). They are thought to settle indiscriminately and suffer disproportionate mortality in relatively featureless habitats (Gotceitas and Brown 1993). Laboratory investigations of habitat usage by juvenile cod in the northwest Atlantic demonstrated that they prefer structured habitats (i.e., cobble, sea grass, kelp, and sponge habitats) when predators are present (Gotceitas and Brown 1993, Gotceitas et al. 1995, Fraser et al. 1996, Gotceitas et al. 1997, Lindholm et al. 1999). Subsequent field surveys from inshore sites in the Canadian maritime provinces have confirmed that juvenile cod associate with structured habitats such as sea grass beds and cobble/boulder habitat with high relief, suggesting that predation risk is high during early life-history phases (Keats et al. 1987, Tupper and Boutilier 1995, Gotceitas et al. 1997, Gregory and Anderson 1997, Grant and Brown 1998, Cote et al. 2001, Laurel et al. 2003). In most cases, habitats with protective cover promote higher cod recruitment, and coastal cod probably recruit to habitats that are both highly heterogeneous and the same color of recruiting cod (Gregory and Anderson 1997). Cod also survive better at shallower depths, suggesting the mechanism why they typically settle at shallow depths (Lineham et al. 2001).

Wigley and Serchuk (1992) noted that studies of fish distributions should extend beyond describing geographic distributions of fish by examining mechanisms (e.g., temperature, depth, spawning behavior, feeding behavior, habitat) underlying the observed distribution patterns. They found that juvenile cod aggregations on Georges Bank are influenced mostly by water temperature on larger (i.e., 10 minute squares latitude and longitude) spatial scales. While strong habitat associations have been established for young-of-year cod in inshore waters of the northwest Atlantic that are highly vulnerable to predators, understanding of how habitat influences the distribution of larger juveniles (i.e., >15 mm TL, 1+ year-olds) as they begin to migrate further offshore is less clear. Scott (1982) found that cod are generally associated with sand and gravel habitats on the Scotian Shelf, but concluded that cod distributions likely reflect their prey because they were prevalent in all substrate types. Methratta and Link (2006) utilized the Northeast Fisheries Science Center (NEFSC) bottom trawl survey data to examine groundfish distributions throughout the Gulf of Maine-Georges Bank region and found greater overall cod biomass in habitats with larger (> 2 mm) substrate grains. A better understanding of fine-scale habitat associations of older juvenile cod will assists managers rebuild cod populations in the Gulf of Maine.

Here we examine whether nearshore habitats in the Gulf of Maine influence the distribution and abundance of juvenile cod. We also examine how physical factors such as bottom depth and temperature influence size-specific patterns in fish distributions in nearshore habitats. Given that cod experience substantial mortality during early life-history phases, we hypothesized that recently settled YOY and larger juvenile cod are more abundant in more complex (i.e., rocky ledge, cobble, and gravel) habitats in nearshore waters. We also hypothesized that smaller fish are more common in shallower water, whereas older juvenile and young adult fish are more abundant in deeper waters. Our study revealed that the relative importance of habitat type, bottom temperature, and depth varied as cod shift from recently settled YOY to larger juveniles.

Methods

Overlaying trawl survey data on habitat maps to infer fish habitat preferences

The Maine Department of Marine Resources (DMR) has conducted multiple trawl surveys of the inshore waters of the Gulf of Maine over the past two decades. Data from three of these surveys (1992-1994 groundfish/shrimp, 1996-1999 fish habitat, and 2000-2005 ME/NH inshore trawl surveys) and existing information on seafloor habitat (Barnhardt et al. 1996) were utilized to assess juvenile cod use of habitat in the nearshore waters of mid-coast Maine. The latter two survey studies collected data predominately during the spring and the fall, so that all summer tows conducted in any of the three studies were excluded from our analyses. Information on bottom habitat south of Cape Small was used to identify whether trawl sampling efforts were conducted in gravel, mud, or sand (Figure 1). Seafloor maps were created using side-scan sonar to resolve the geophysical characteristics of the nearshore region of mid-coast Maine. Trawls that were conducted on a mixture of different habitats were excluded from our analyses to avoid confounding our results.

All three trawl surveys used roughly comparable net designs and similar methodology (i.e., net width and length, mesh size, towing speed etc.) in the field (see ME/NH inshore trawl survey protocol at http://www.maine.gov/dmr/rm/trawl/reports.htm for more detailed information regarding the net design). Tows were short duration (target time of 20 minutes) at a fixed speed of ~2.4 knots/hr to ensure consistent sampling. Tows shorter than 13 minutes were excluded from analyses, and all tows that were shorter than 20 minutes were standardized. Tows were conducted in gravel, sand, and mud habitats, and all individuals that were captured were identified, sorted by species, and enumerated. Atlantic cod were measured (total length [TL]) and weighed, and the bottom temperature, depth, and salinity were recorded during each tow.

Video and hook-and-line surveys

In the spring of 2006, we conducted video and hook-and-line sampling to examine further juvenile cod use of nearshore habitats in the Gulf of Maine. These 2 methods permitted us to sample more structurally complex habitats such as cobble/ledge bottom that were avoided by the above trawl surveys. Video surveys were conducted in cobble/ledge, gravel, and sand/mud habitats using the habitat map above (Figure 1). Sand and mud habitats were combined because fish visitation rates were extremely low in these habitats. Sony Handycam® Camcorders (DCR-SR100) were deployed individually in PREVCO™ clear Polycarbonate rectangular (9.2 x 11.9 x 19.7 cm) housings. Each camera was equipped with a 30 gigabyte hard drive and a 7.5 hr battery. Cameras were also outfitted with a 0.5X lens in order to ~double the camera's field of view.

Each camera-housing unit was attached to a blank lobster trap (92 x 58 x 42 cm, l x w x h). The unit was mounted just inside the trap 22 cm's from the bottom and along the longer trap axis (Figure 2). The camera was oriented slightly downward to capture the bottom habitat immediately adjacent to the trap. A one-inch PVC pipe was mounted to the lobster trap so that the pipe extended 1 m from the trap directly into the field of view of the camera. At the end of the pipe, an additional 1 m PVC pipe was attached to it forming a T. Holes were drilled in both pipes at 10 cm intervals and black cable ties attached in order to qualitatively gauge the size of fish in the field of view. A buoy line with sinking pot warp was attached to each trap so that each unit was able to be deployed and recovered from a small vessel.

Individual camera units were deployed in 3 different types of habitat: cobble/ledge, gravel, and sand/mud bottom type. Camera units were deployed for ~60-90-minute intervals between 8:00AM and 3:00PM to maximize ambient light conditions on the seafloor. Relatively short intervals permitted multiple deployments in order to increase the replicate number of video observations. When multiple deployments were conducted at a particular site, they were spaced by > 50 m apart from each other. All deployments where we were unable to identify fish within 1 m of the video camera because of poor visibility were excluded from our analyses. Camera units were retrieved and returned to the laboratory where video surveys were scored. Fish visitation rates were quantified by species. For each species, we quantified the number of discrete appearances within the field of view.

Hook-and-line surveys were conducted in each habitat during the spring of 2006. Jigging was conducted in each habitat type for ~ 30 minute intervals at multiple sites in mid-coast Maine using the above map (Figure 1). Because we were incapable of fishing each habitat simultaneously, we randomly selected the order in which each habitat type was fished during each sampling date. During each sampling interval, 1-3 rods were utilized to retrieve fish. Each rod was outfitted with a #14 Sabiki mix-flasher leader hook, and frozen soft-shell clam bait (~5 grams per hook) was used to attract fish. Each fish that was captured was measured, identified, and weighed. We then calculated the number of fish landed for each species per hour per rod.

Data Analysis

Cod density data from trawl surveys required either log (total cod density) or fourth root (all other cod density analyses) transformation to remove heterogeneity of variance (Underwood

1981). These data were analyzed with two-way ANOVA to determine the effects of habitat (gravel, mud, and sand) type and season (spring and fall) on cod density. We analyzed the effect of habitat on the density of YOY (i.e., 3-9 cm TL) cod in the spring using ANOVA. We next analyzed the effect of habitat on the density of YOY cod in sites of similar (20-40 m) depth using a one-way ANOVA. We examined the effects of habitat and season on the density of larger juvenile (i.e., 10-25 cm TL) cod using ANOVA. Scheffe's post hoc comparisons were conducted on all significant interaction terms and main effects with more than two treatment levels. The Scheffe test was selected because the number of trawls conducted in each habitat type and each season were unequal (Day and Quinn 1989).

Regression analysis was utilized to examine the relationship between bottom depth and fish length. We also analyzed whether tow bottom depths differed among habitats using a one-way ANOVA. Next we compared whether cod densities differed between gravel and sand habitats at similar (i.e., 20-35 m) bottom depths using an unpaired t-test. We conducted a second unpaired t-test to examine whether cod densities differed between gravel and mud habitats within a depth (i.e., 35-50 m) range where these two habitats were towed frequently. The effects of season and habitat on bottom temperature were analyzed using a two-way ANOVA. The effects of habitat on cod densities within each of three temperature ranges (4-6, 6-8, and 8-10 °C) were analyzed using separate one-way ANOVAs.

Cod visitation and hook-and-line data were non-normal (Shapiro-Wilk test, $p < 0.05$) and violated the assumption of homogeneity (Levine's test, $p < 0.05$). Therefore, the effects of habitat (cobble/ledge, gravel, mud/sand) type on cod visitation and catch rates were analyzed using separate Kruskal-Wallis tests (SAS 2005). The effects of habitat type on pollock (*Pollachius virens*), unidentified gadids, total gadids, cunner (*Tautogolabrus adspersus*), sculpin (*Myoxocephalus* spp.), and flounder (Pleuronectiformes) visitation rates and pollock and sea raven hook-and-line catch rates were analyzed individually using Kruskal-Wallis tests. When the effect of habitat type was significant, we conducted a series of pairwise comparisons of all possible combinations of the three habitat types using the Mann Whitney U test.

Results

Trawl survey results

Although the majority of tows were conducted in the second survey, the relative densities of cod in each habitat were consistent across all three surveys (Table 1). Only habitat influenced the total density of cod caught in trawl surveys in nearshore waters of mid-coast Maine (Table 2). Total cod densities caught in trawls were highest in gravel habitat, and were ~3 and ~27 times more abundant than those in sand and mud, respectively (Scheffe's post hoc tests: $p < 0.05$; Figure 3). Comparison of the size frequency distributions of fish caught in each habitat revealed a bimodal cod distribution at each site (Figure 4). However, the distribution of cod caught in sand was dominated by extremely small cod (3-9 cm, young-of-year [YOY] cod), whereas gravel habitat was dominated by larger (10-25 cm, large juvenile cod that are predominately 1 year-olds) juvenile cod. The total number of cod captured in tows was lowest in the mud habitat (Figure 3).

Separation of the density of cod caught in trawls by life-history stage revealed age-specific patterns in habitat utilization by cod. For instance, the density of YOY cod was highest in sand habitat (Table 3a, Figure 5a). Meanwhile, the density of YOY cod was intermediate in gravel and lowest in mud habitat. However, there was no effect of habitat on the density of YOY cod at depths of 20-40 m (Table 3b, $p = 0.50$). The density of larger juveniles was greatest in gravel habitat, intermediate in sand, and lowest in mud (Table 3c, Figure 5b). Although very few larger cod were caught in this study, 11 of the largest 12 cod caught in trawl surveys were located in the mud habitat. We conducted additional analyses of trawl survey data in order to parse out the influence of bottom depth on juvenile cod habitat use. There was a significant positive relationship between depth and fish length ($p < 0.0001$, $r^2 = 0.35$, Figure 6). In general, smaller cod were predominately captured in shallow water, with 95.7% of YOY cod captured at depths less than 20 m.

Trawls conducted in sand habitat were shallowest (22.1 ± 0.5 m, mean ± 1 SE), those in gravel were intermediate (34. 8 ± 0.4 m), and those in mud were deepest (70.0 ± 0.7 m; Table 4, Figure 7). The interaction between habitat and season on bottom depth was significant largely because tows conducted in the mud were 13.1% deeper in the fall than in the spring. Examination of the frequencies of tows and cod captured at each depth revealed that cod densities were fairly consistent in gravel and mud habitats, whereas cod densities in the sand at 10-15 m were disproportionately higher than those at deeper depths in this habitat (Figures 8 and 9). Next we compared cod densities in gravel vs. sand habitat at relatively shallow depths (i.e., 20-35 m), and we found much higher densities of cod in gravel habitat at this depth range (t-test, $p = 0.0023$, Figure 10a). Trawl surveys conducted at deeper depths (i.e., 35-50 m) in gravel and mud habitat also revealed that cod densities were much higher in gravel habitat (t-test, $p < 0.0001$, Figure 10b).

Bottom temperature varied as a function of both habitat and season (significant interaction term: $p = 0.007$, Table 5, Figure 11). In general, seafloor temperature was colder in the spring than in the fall. In the spring, bottom temperature did not differ among habitats, whereas in the fall temperature differed among the three habitats (Scheffe post hoc tests: $p < 0.05$). Specifically, bottom temperatures in the fall were warmest in the sand, intermediate in gravel, and coldest in mud habitat. Comparison of the distribution of cod caught across the range of bottom temperatures revealed that 89.9% of cod were caught in bottom water between 4 and 10 °C (Figure 12). Greatest cod densities (12.2-14.6 cod/tow) were found on seafloor bottom ranging from 8 to 10 °C. Analysis of each of the three temperature (4-6, 6-8, and 8-10 °C) intervals with greatest cod densities individually determined that cod densities were consistently higher on gravel regardless of bottom temperature (Table 6, Figure 13). However, the magnitude of difference between gravel and the two soft-sediment habitats was much greater at warmer (i.e., 8-10 °C) bottom temperatures. Cod densities were consistently higher in sand than in mud habitat for each of the three temperature intervals. There was no relationship between cod size and bottom temperature (

Video and hook-and-line survey results

Video assays determined that cod visitation rates were significantly higher in cobble/ledge habitat than either gravel or mud/sand bottom (Figure 14a; Kruskal Wallis test: $p = 0.002$; pairwise comparison of treatments with Mann Whitney U tests: $p < 0.05$). Cod visitation rates on both gravel and mud/sand bottom did not differ from each other and were extremely low. Cod observed in video surveys ranged in size from ~15-35 cm TL. Pollock visitation rates did not differ between cobble/ledge and grave habitats, both of which were higher than on mud/sand bottom. A portion of the gadids that were obseverd in cobble/ledge habitat was unable to be identified. These gadids were typically observed in large (up to several hundred gadid fish) schools and were likely pollock. Total gadid visitation rates on cobble/ledge bottom were eight times as high as those on gravel bottom (Figure 14b). Gadids were not observed on mud or sand bottom.

Cunner visitation rates were the highest of any species observed in video surveys (Figure 14c). Cunner were typically observed individually and spent the most time of any fish species directly in front of the camera system, occasionally occluding the view of the bottom. Cunner visitation rates were extremely high on cobble/ledge habitat in comparison to either gravel or mud/sand bottom. Both sculpin and flounder visitation rates were higher in mud/sand than in cobble/ledge (Figure 15d). Flounder visitation rates were also marginally higher in mud/sand than in gravel bottom (Mann Whitney U test: $p = 0.054$). Unidentified fish were more common in both cobble/ledge and gravel bottom and were suspected to be either cunner or gadids (Figure 14e). Finally, redfish (*Sebastes fasciatus*) and crustaceans were observed occasionally, but these data were not analyzed.

Hook-and-line results for cod largely reinforced the patterns observed in surveys (Kruskal Wallis test: $p < 0.05$, Figure 15). Cod were more abundant in cobble/ledge than in mud/sand habitat where they were nonexistent (Mann Whitney U test: $p = 0.004$). Cobble/ledge and gravel habitat did not differ from each other even though catch rates in cobble/ledge habitat were 2.5 times greater than those in gravel habitat. A total of 39 cod were caught by hook-and-line and ranged from 17-65 cm TL (mean = 34 cm TL). Although catch rates of cunner did not differ with habitat (Kruskal-Wallis test: $p = 0.25$), there was a slight trend of greater numbers of cunner caught on cobble/ledge habitat than either of the other habitats. A small number of pollock, redfish, sculpins, and sea ravens were caught by hook-and-line. Catch rates for these species were not high enough to merit statistical analysis; however, pollock and sculpin catch rates in each habitat were qualitatively similar to visitation rates of these two species observed in the video surveys.

Discussion

Investigations identifying cod habitat associations during intermediate and later juvenile stages may enhance the ability of managers to rebuild populations of this ecological and economically important species. Here we utilize a variety of sampling methods in an attempt to identify whether age-specific habitat associations exist during the early life-history phases of cod after parsing out the potentially confounding effects of bottom depth and water temperature. Coupling over a decade of trawl survey data with video assays and hook-and-line sampling permitted us to extend our findings to more complex bottom where small-mesh trawl nets are incapable of being towed because of the risk of net entanglement.

Trawl surveys revealed that the density of recently settled YOY cod was greatest in sand habitat less than 20 m deep. However, this finding was largely confounded by depth because gravel and mud habitats in bottom shallower than 20 m were not sampled in this survey because they do not exist in great quantity at shallow depths within the study area. Although YOY cod densities at sites between 20 and 40 m were substantially lower than those at shallower depths, YOY cod densities did not differ among habitats within this intermediate depth range. Therefore, our results largely agree with previous findings that YOY cod settle largely at shallow depths and indiscriminately with regards to habitat (Gotceitas and Brown 1993).

The density of larger juvenile (10-25 cm TL) cod was greatly influenced by benthic habitat. By examining overlapping depth ranges for gravel sites with each of the other two trawled habitats, we found that gravel bottom supported elevated densities of juvenile fish. Furthermore, the relative proportion of cod in gravel vs. the other two habitats in these overlapping depth ranges was consistent with those across the entire depth range sampled in this study. This estimate is likely conservative given that gravel habitat often exists in patches that are not necessarily as large as the tow tracks. Lough et al. (1989) found that YOY cod typically are widespread on Georges Bank in the spring just prior to settling, but by late July these fish are demersal and abundant only in gravel habitat.

Atlantic cod greater than 25 cm rarely were caught in the trawl surveys used in this study, but the few that were captured were typically found on mud at bottom depths greater than 50 m. Because the other habitat types were rarely sampled at these deeper depths, it is difficult to parse whether larger cod captured in our study were located in mud bottom because they prefer mud habitat or this depth range. The rarity of larger cod captured in these trawl surveys is likely a consequence of their ability to evade trawl nets towed at 2.4 knots, but could also be a consequence of either reduced cod abundances in the survey area or the lack of sampling effort in their preferred habitat type and depth range. In general, the majority of cod landed in the ME-

NH inshore trawl survey data from throughout coastal Maine and New Hampshire are juveniles and less than 40 cm TL (Sherman et al. 2005).

Video surveys and hook-and-line sampling provide significant challenges to scientists attempting to quantify the density of fish within particular habitats. However, they can provide important insights regarding the relative abundance of fish in different habitats. These methods are particularly valuable when coupled with other methods such as trawling that provide more rigorous estimates of fish densities because they can be utilized to extrapolate fish densities in more complex habitats that are incapable of being trawled. Our video survey and hook-and-line results suggest that cobble and rocky ledge habitats support even higher abundances of juvenile cod than are found in gravel habitat.

Cod likely utilize complex habitats such as rocky ledge, cobble, and gravel bottom during early life-history phases because these habitats typically provide refuge from juvenile cod predators and contain dense assemblages of prey (Gotceitas and Brown 1993, Gotceitas et al. 1995, Tupper and Boutilier 1995, Gotceitas et al. 1997). Prey abundances are often positively correlated with habitat complexity, yet predator access to prey is typically inversely proportional to habitat complexity levels because characteristics of complex habitats often inhibit the ability of predators to locate prey successfully (Crowder and Cooper 1982). Thus, intermediate predators such as juvenile cod are thought to maximize foraging efficiency at intermediate levels of habitat complexity. However, as the risk of intermediate predators being consumed increases, habitat associations would be expected to shift towards highly complex, refuge habitats. Given that several top predator species such as adult groundfish, elasmobranchs, predatory whales, and pinnipeds consume juvenile cod, it is not surprising that we found that juvenile cod were most prevalent in cobble and rocky ledge habitats when we were able to include them in our analyses of the role of habitat in the distribution of juvenile cod in the nearshore habitats of the Gulf of Maine.

We did not examine in this study whether larger juvenile fish found in structured habitats settled in the same habitats where they were captured or immigrated into them after settling elsewhere. Over 90% of YOY cod were captured in less than 20 m water depth, whereas larger juvenile densities were highest in gravel habitat that was typically located in slightly deeper (i.e., 20-50 m) water. The density of larger juveniles was far greater than the density of YOY cod found in this habitat, further suggesting that a significant proportion of the cod found in gravel habitat could be settling elsewhere. However, net efficiency could also vary with cod size. For instance, smaller cod densities may be underestimated if they pass through the net or are mutilated beyond recognition in the cod end of the net. Yet larger cod densities may also be underestimated because they are more capable of evading capture.

In conclusion, our findings indicate that gravel and more complex hard bottom are important habitat for juvenile cod. Failure to include consideration of cod use of more complex habitats that are incapable of being sampled by trawl surveys could result in largely skewed and unrepresentative estimates of the abundance of juvenile cod populations. Further investigation is necessary to determine the degree to which the availability of these habitats influence juvenile cod growth and survival rates during this early life-history phase and subsequently limit the productivity of cod fisheries. Thus these nearshore habitats could serve as a critical bottleneck that is currently limiting the recovery of cod populations in the Gulf of Maine.

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Table 1. Mean densities of cod in gravel, mud, and sand habitat in mid-coast Maine. Data from each of three trawl surveys are presented separately to examine temporal patterns in cod density.

		Mean Cod Density (per 20 Minute Tow)			Total Number
Study	Time Period	Gravel	Mud	Sand	of Tows
1	1992-1994	8.3	0.0	5.0	9
2	1996-1998	11.1	0.4	3.9	384
3	2000-2005	17.5	1.4	5.9	33
	Total	12.0	0.4	4.1	426

Table 2. Results of ANOVA examining the effects of season, habitat, and their interaction on the total density (#/20 min. tow) of cod captured in trawl surveys conducted in mid-coast Maine. Data were log transformed to remove heterogeneity of variance.

	DF	Sum of Squares	Mean Square	F-Value	P-Value
Season	1	0.01	0.01	0.04	0.84
Habitat	2	25.21	12.60	97.29	<0.0001
Season * Habitat	2	0.44	0.22	1.68	0.19
Residual	420	54.40	0.13		

Table 3. Results of ANOVAs examining the effect of habitat on the density of YOY (i.e., 3-9 cm TL) cod at (a) at all depths and (b) sites that overlap (20-40 m) in depth. Results of ANOVA are also presented below on (c) the effects of season, habitat and their interaction on the density of larger juvenile (i.e., 10-25 cm TL) cod caught in trawl surveys conducted in mid-coast Maine. Data were fourth root transformed to remove heterogeneity of variance.

a) YOY cod – all depths

	DF	Sum of Squares	Mean Square	F-Value	P-Value
Habitat	2	22.3	11.1	48.6	<0.0001
Residual	309	70.8	0.2		

b) YOY cod – 20-40 m

	DF	Sum of Squares	Mean Square	F-Value	P-Value
Habitat	2	11.8	5.9	0.7	0.50
Residual	95	796.7	8.4		

c) Larger juvenile cod – all depths

	DF	Sum of Squares	Mean Square	F-Value	P-Value
Season	1	0.1	0.1	0.2	0.65
Habitat	2	49.2	24.6	76.4	<0.0001
Season * Habitat	2	0.5	0.2	0.7	0.48
Residual	403	129.8	0.3		

Table 4. Results of ANOVA examining the effects of season and habitat on bottom depth at trawl survey sites located in the nearshore waters of mid-coast Maine.

	DF	Sum of Squares	Mean Square	F-Value	P-Value
Season	1	90.0	90.0	1.7	0.20
Habitat	2	49335.2	24667.6	452.7	<.0001
Season * Habitat	2	665.7	332.8	6.1	0.002
Residual	420	22886.6	54.5		

Table 5. Results of ANOVA examining the effects of season and habitat on bottom temperature at trawl survey sites located in the nearshore waters of mid-coast Maine.

	DF	Sum of Squares	Mean Square	F-Value	P-Value
Season	1	1331.0	1331.0	921.0	<0.0001
Habitat	2	86.8	43.4	30.0	<0.0001
Season * Habitat	2	14.5	7.3	5.0	0.007
Residual	342	494.2	1.4		

Table 6. Results of ANOVAs examining the effect of habitat on total cod density at sites with bottom temperatures ranging from (a) 4-6, (b) 6-8, and (c) 8-10 °C

a) 4-6 °C

	DF	Sum of Squares	Mean Square	F-Value	P-Value
Habitat	2	37.9	19.0	54.2	<0.0001
Residual	152	53.2	0.4		

b) 6-8 °C

	DF	Sum of Squares	Mean Square	F-Value	P-Value
Habitat	2	12.4	6.2	19.0	<0.0001
Residual	50	16.3	0.3		

c) 8-10 °C

	DF	Sum of Squares	Mean Square	F-Value	P-Value
Habitat	2	30.6	15.3	35.9	<0.0001
Residual	35	14.9	0.4		

Figure 1. Bottom habitat map of mid-coast Maine region near Cape Small and Seguin Island. Trawl survey data collected from 1992-2005 coupled with video survey and hook-and-line data from2006 in the below geographic region were utilized in this study.

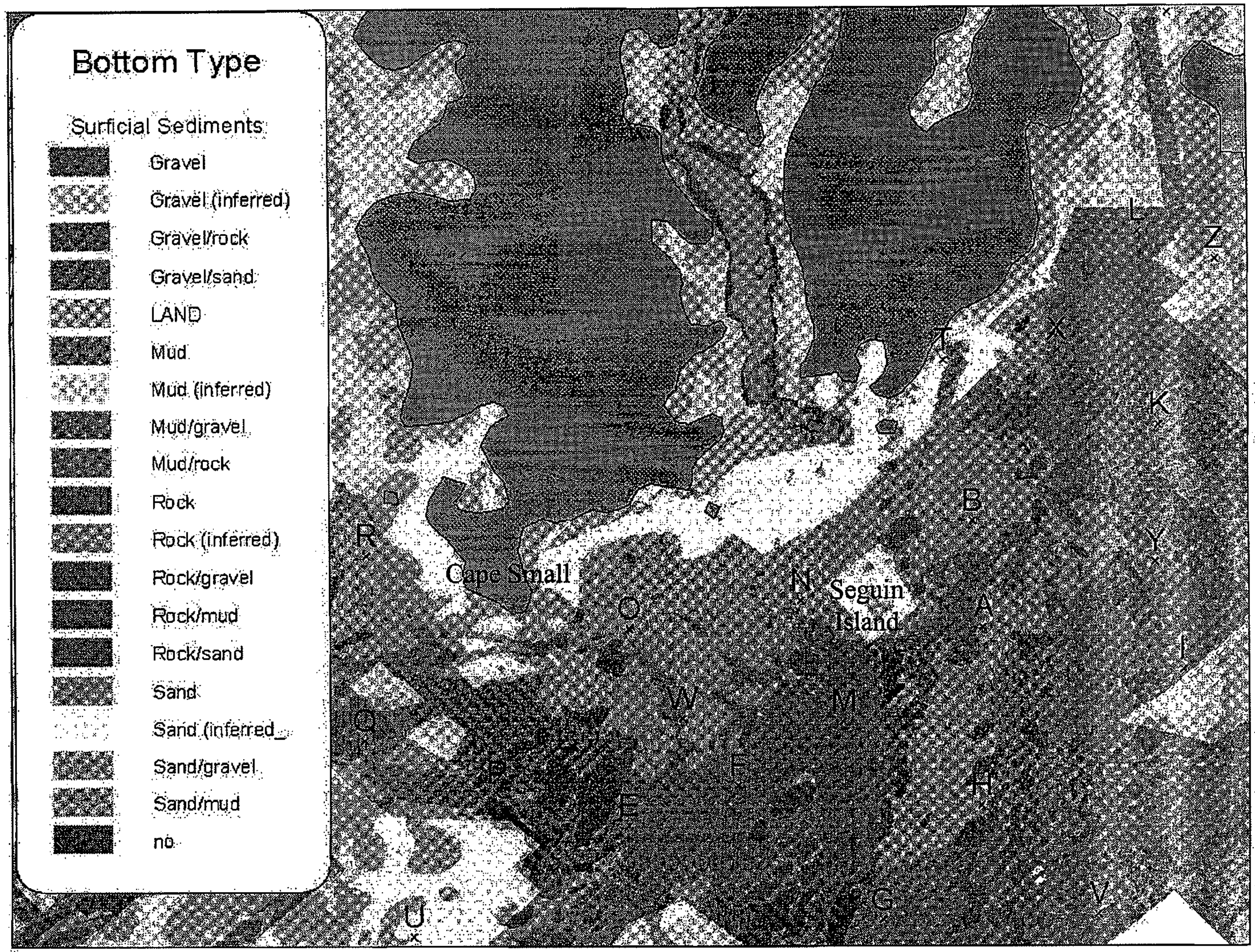


Figure 2. Schematic diagram of the trap-camera system utilized to quantify fish utilization of habitats in nearshore coastal Maine.

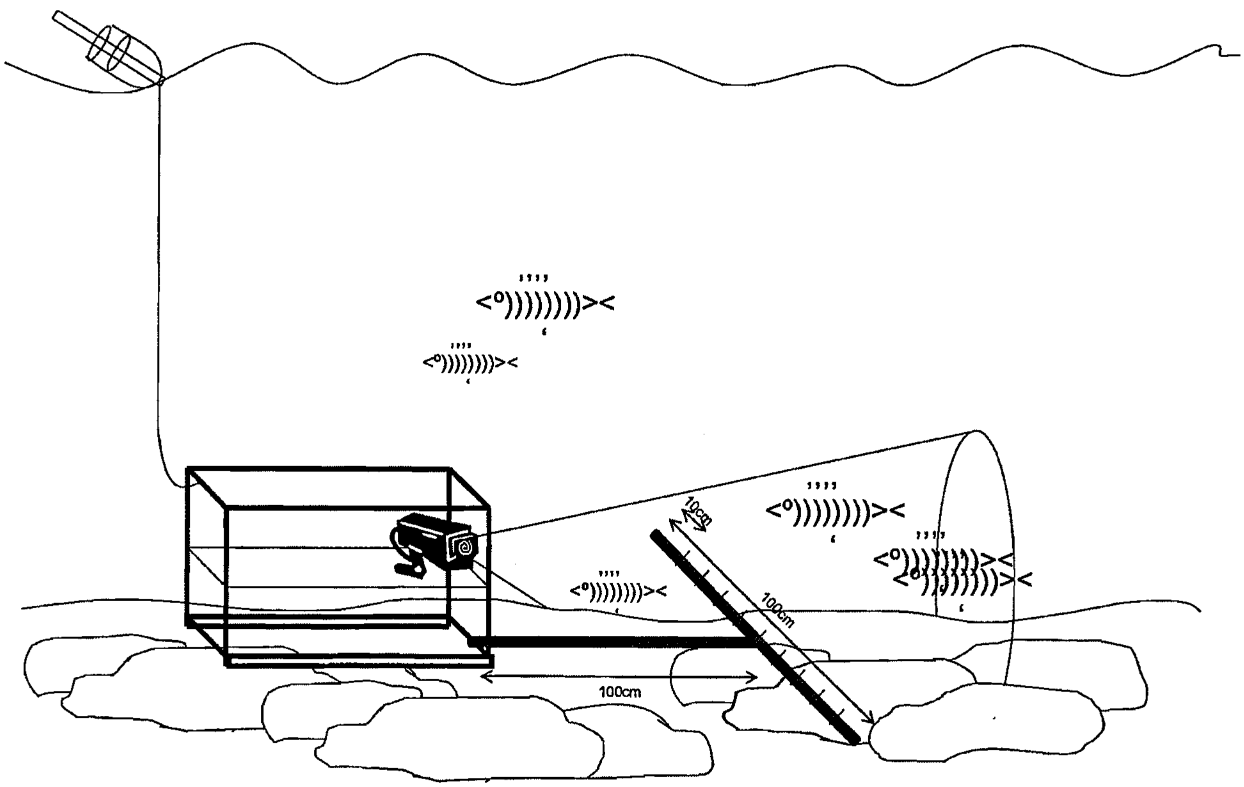


Figure 3. The density of cod caught in inshore trawl surveys around Seguin Island between 1992 and 2005 on gravel, mud, and sand habitat. Scheffe's post hoc tests are represented with letters above the error bars (bars with different letters signify values that were significantly different at $p < 0.05$). Error bars indicate +1 SE.

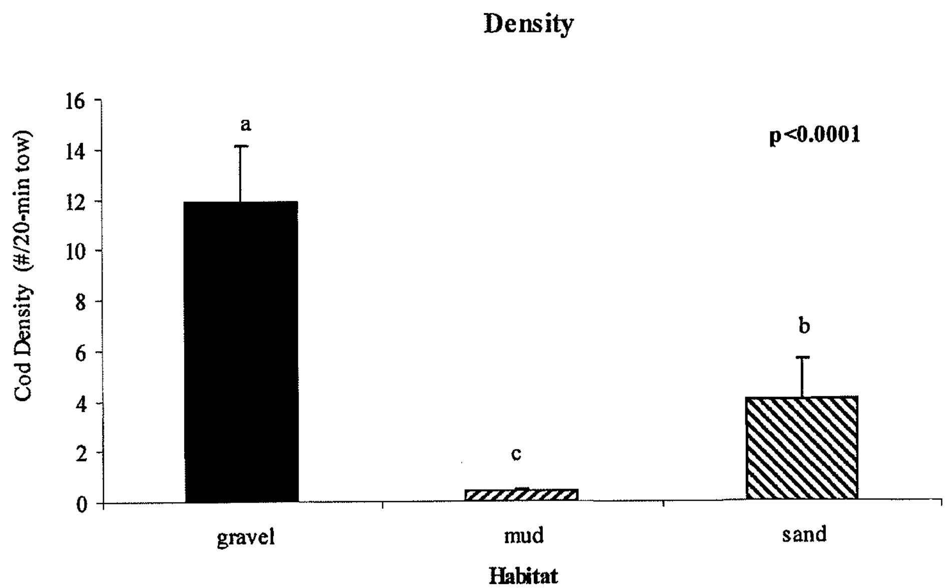


Figure 4. Size-frequency distribution of cod captured on gravel, mud, and sand bottom around Seguin Island, Maine in inshore trawl surveys.

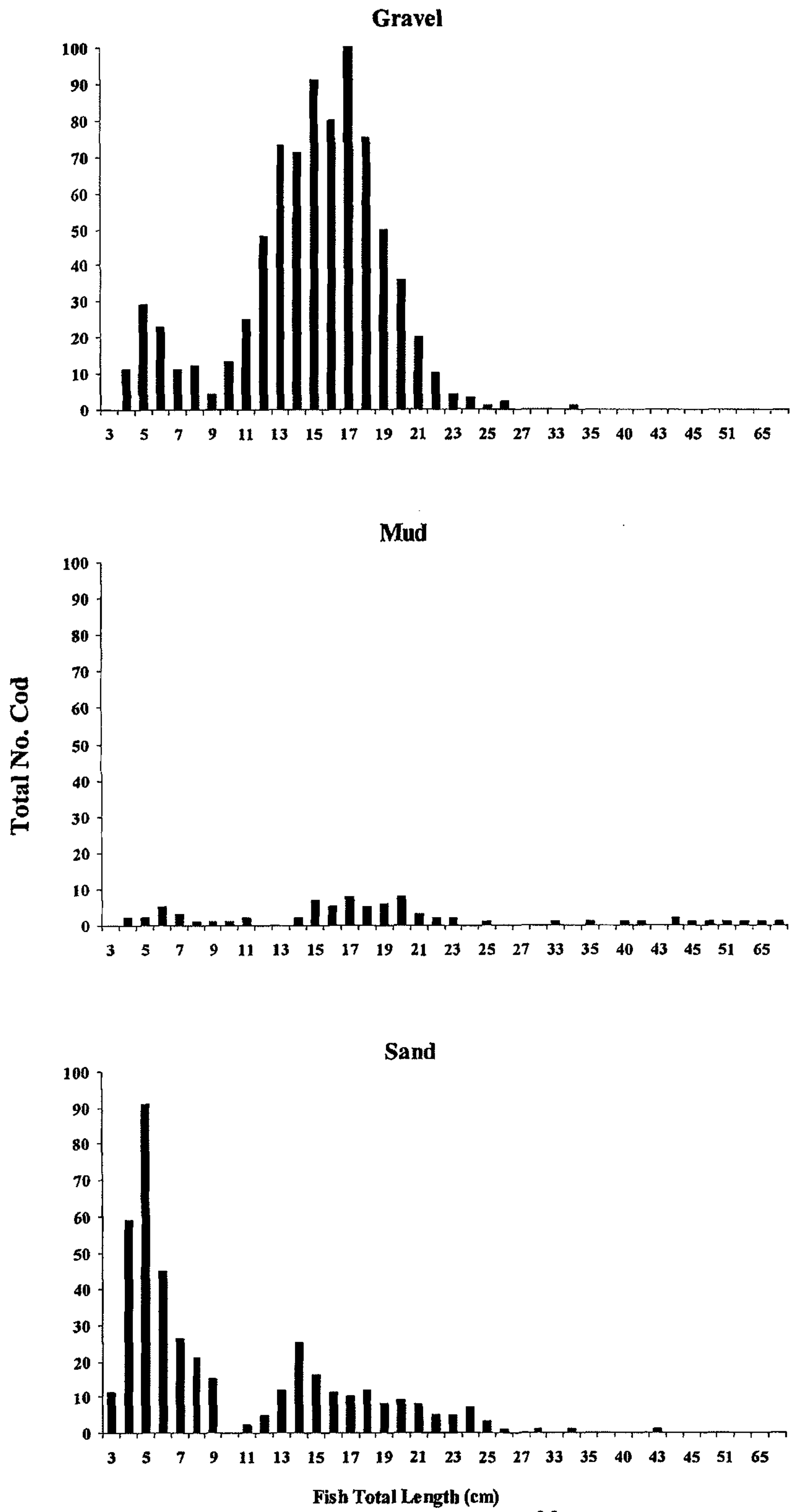
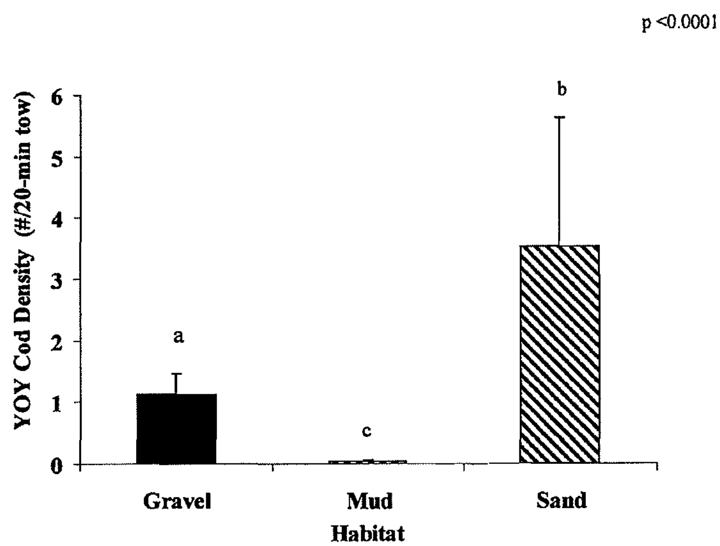


Figure 5. The density of (a) YOY and (b) larger juvenile cod caught in inshore trawl surveys around Seguin Island between 1992 and 2005 on gravel, mud, and sand habitat. Scheffe's post hoc tests are represented with letters above the error bars (bars with different letters signify values that were significantly different at $p < 0.05$). Error bars indicate +1 SE.

a) YOY (3-9 mm TL) cod



b) Larger juvenile (10-25 mm TL) cod

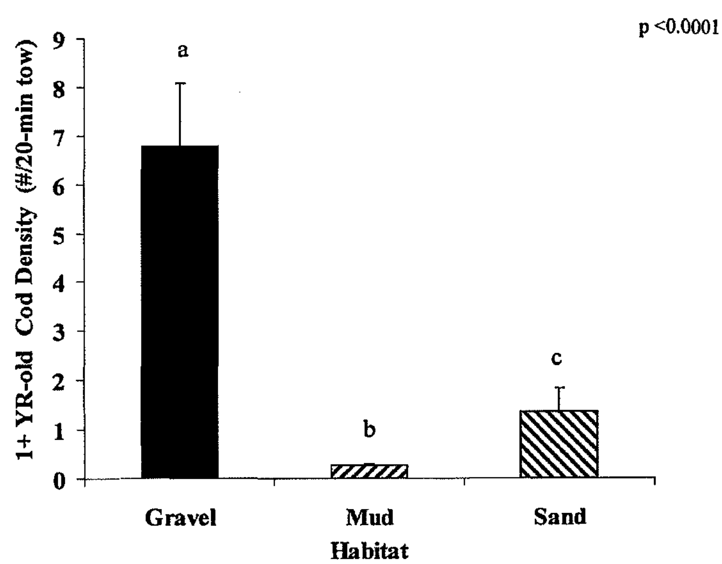


Figure 6. Simple regression defining the relationship between bottom depth and cod TL for cod captured in trawl surveys conducted in mid-coast Maine.

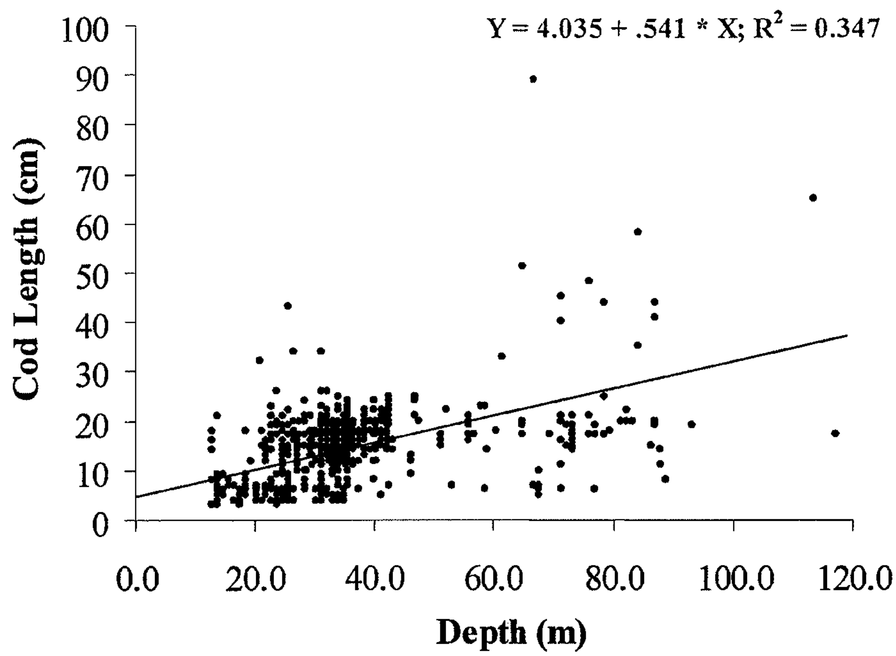


Figure 7. The effects of habitat and season on the bottom depth of trawl tows conducted around Seguin Island between 1992 and 2005. Scheffe's post hoc tests were conducted to determine whether the bottom depth of trawls conducted in the spring differed from those in the fall in each habitat type (bar pairs with an asterisk signify values that were significantly different at $p < 0.05$). Error bars indicate -1 SE.

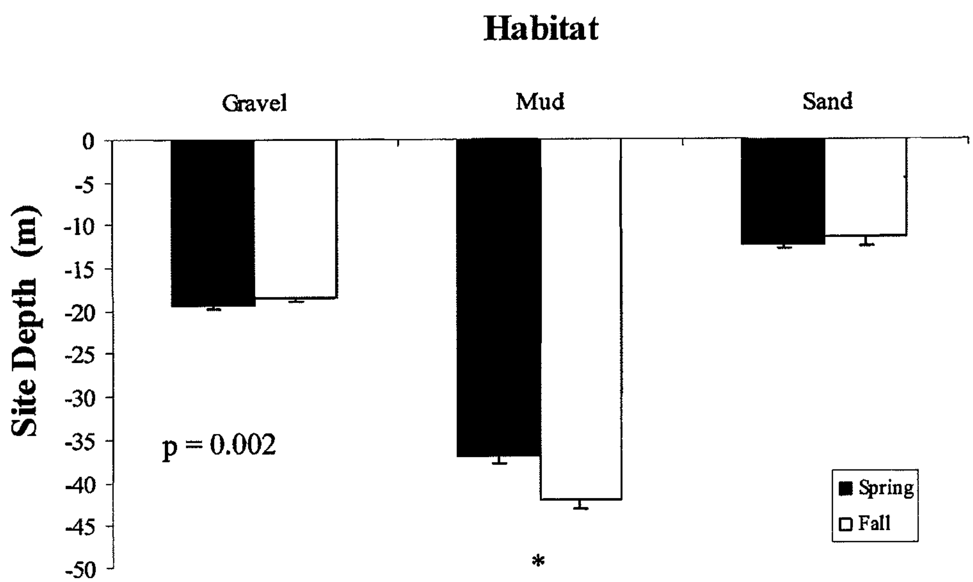


Figure 8. The number of trawl tows conducted at each bottom depth on gravel, mud, and sand bottom around Seguin Island, Maine in inshore trawl surveys.

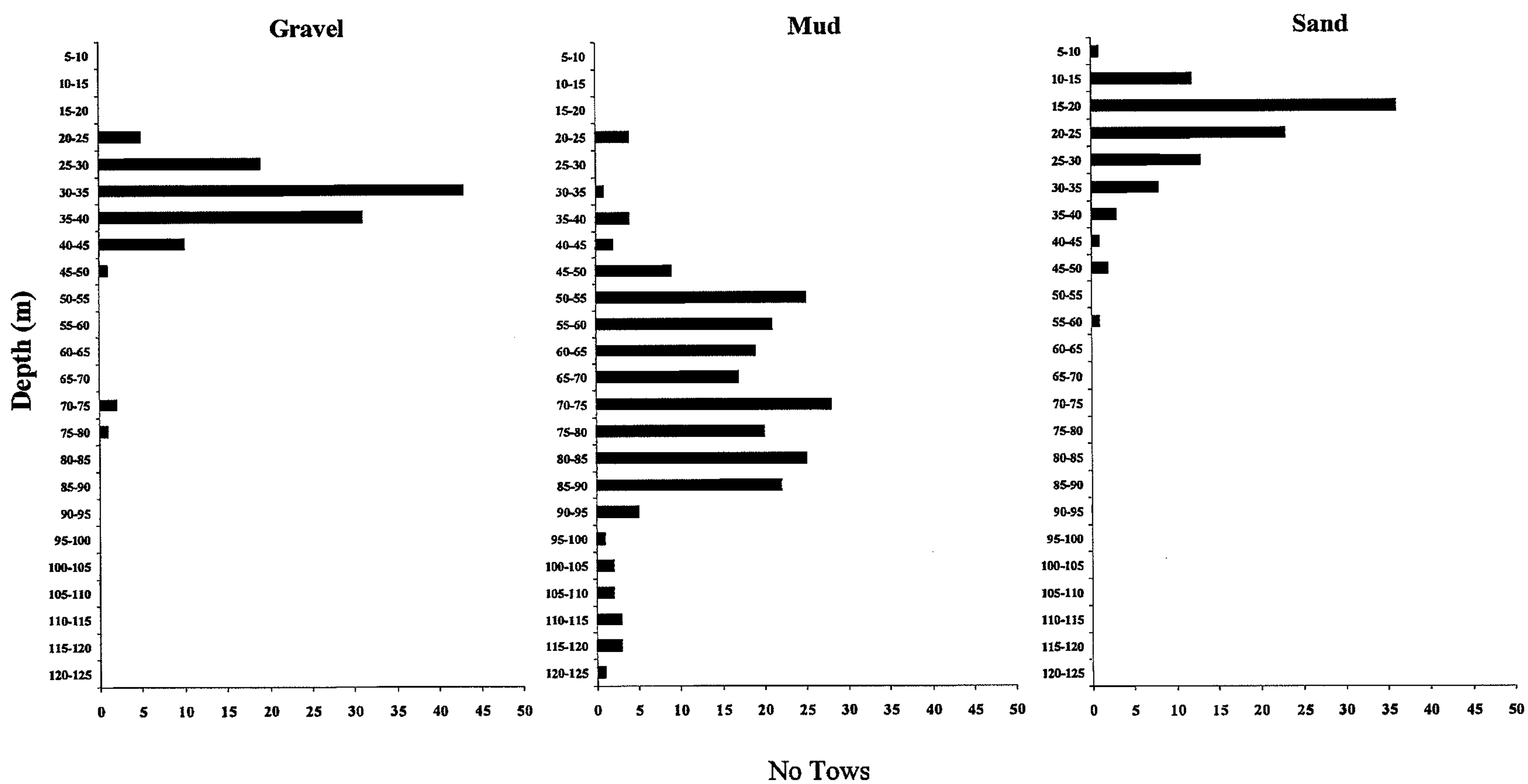


Figure 9. The number of cod captured at each bottom depth on gravel, mud, and sand bottom around Seguin Island, Maine in inshore trawl surveys.

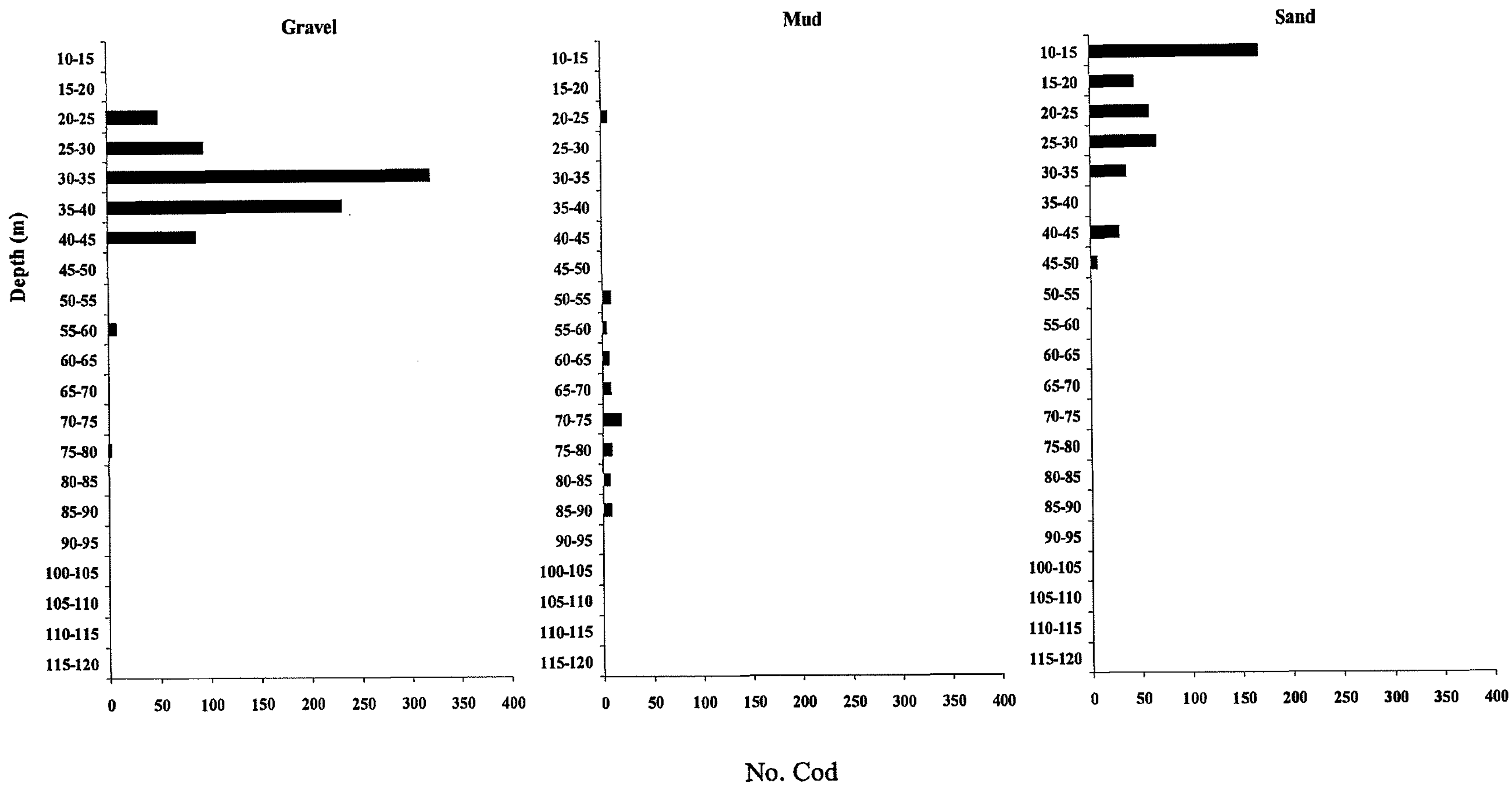


Figure 10. The density of cod in (a) gravel vs. sand habitat at bottom depths between 20-35 m and (b) gravel vs. mud habitat at bottom depths between 35-50 m caught in inshore trawl surveys around Seguin Island between 1992 and 2005. Error bars indicate +1 SE.

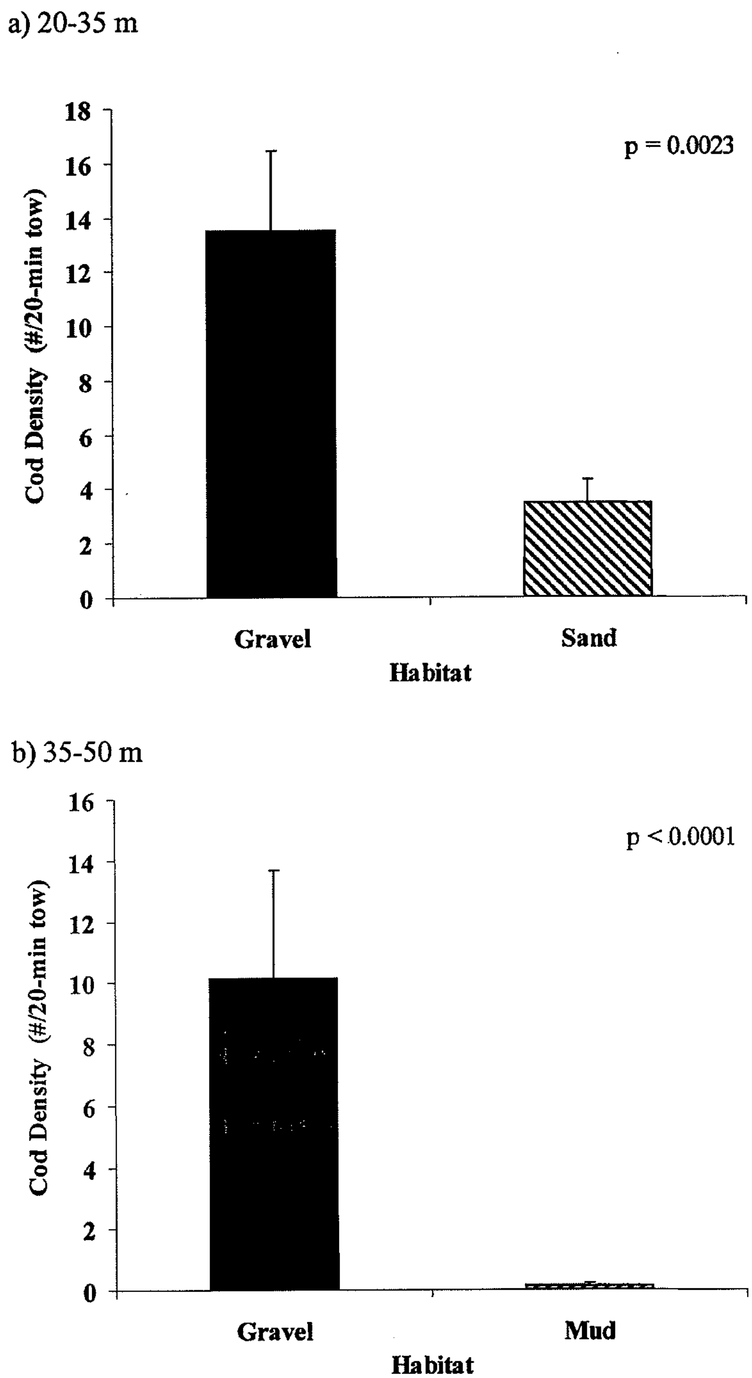


Figure 11. The effects of habitat and season on the bottom temperature at sites around Seguin Island between 1992 and 2005 where trawl surveys were conducted. Scheffe's post hoc tests were conducted to determine whether the bottom temperature of trawl tows in the spring differed from those in the fall in each habitat type (bar pairs with an asterisk signify values that were significantly different at $p < 0.05$). Error bars indicate +1 SE.

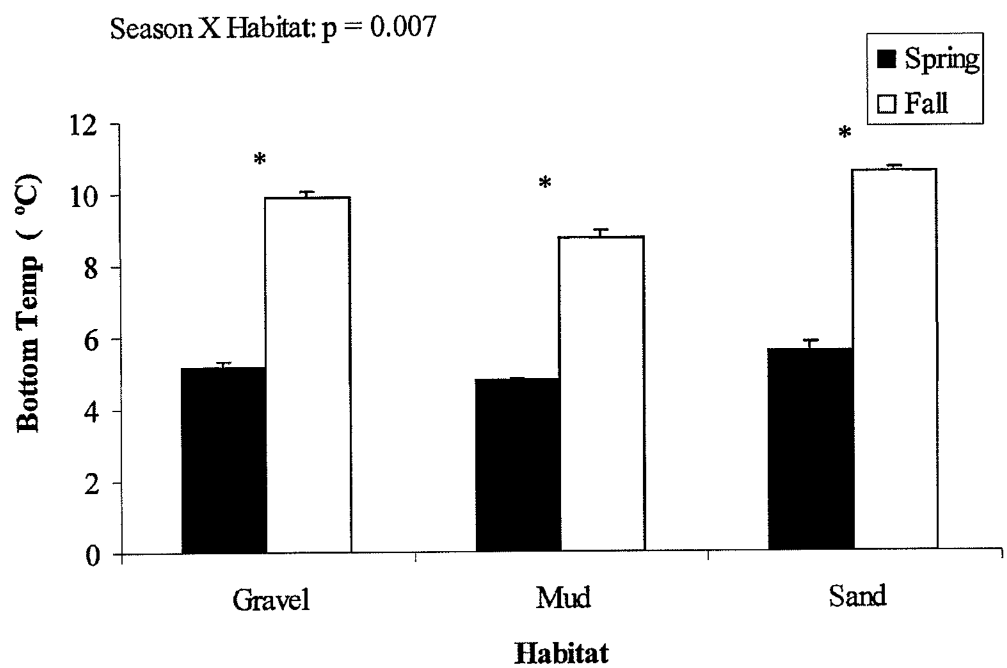


Figure 12. The numbers of cod, trawl tows, and cod per tow within each bottom temperature increment at sites around Seguin Island in mid-coast Maine.

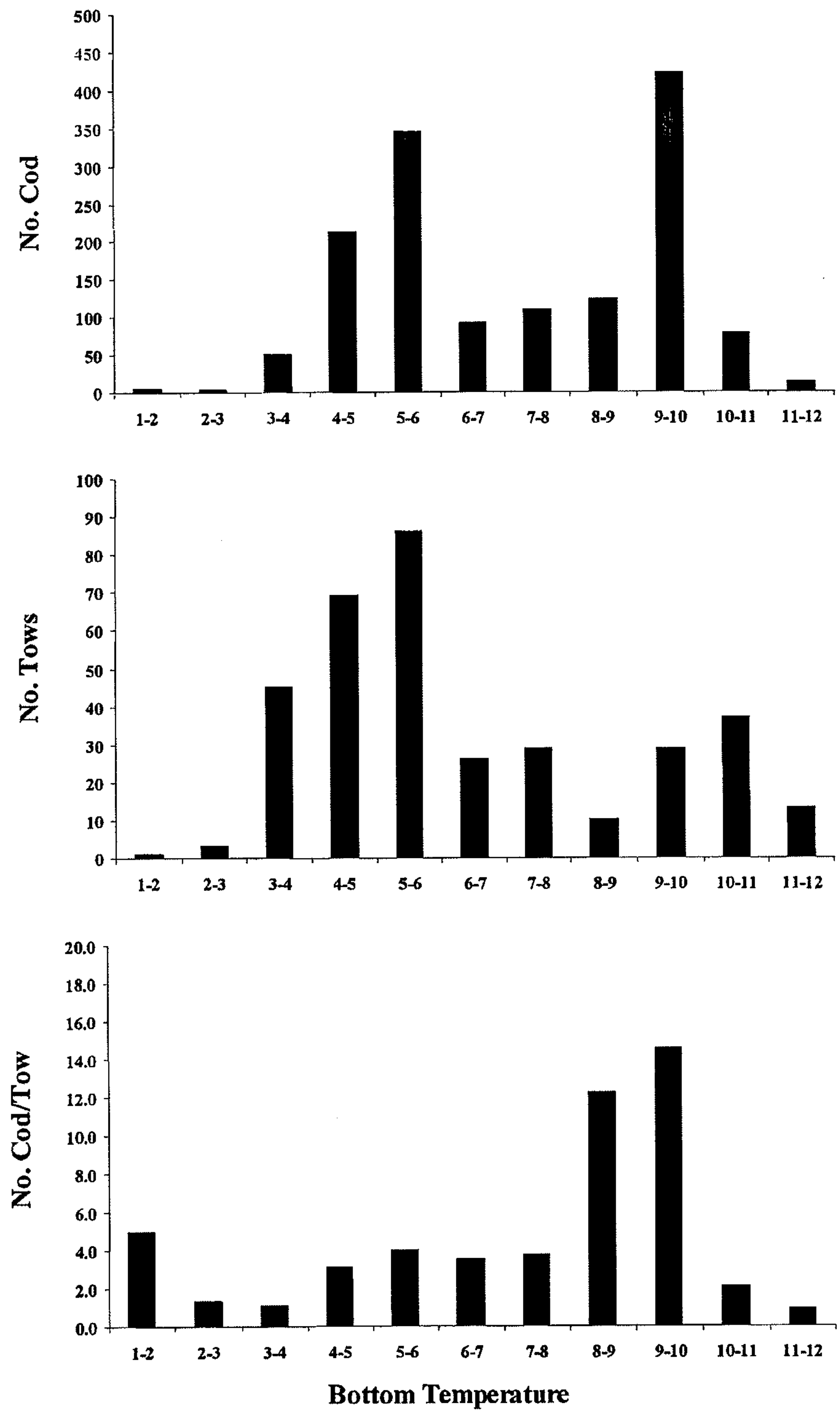
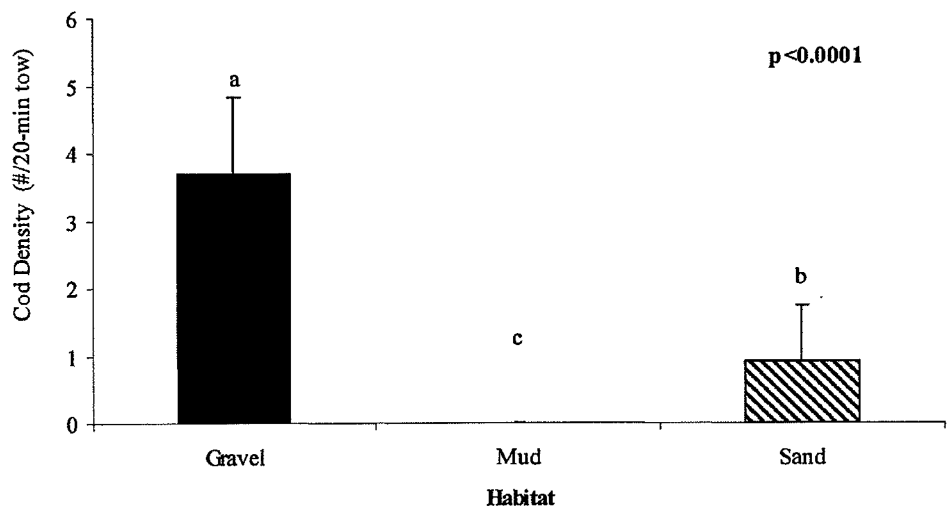
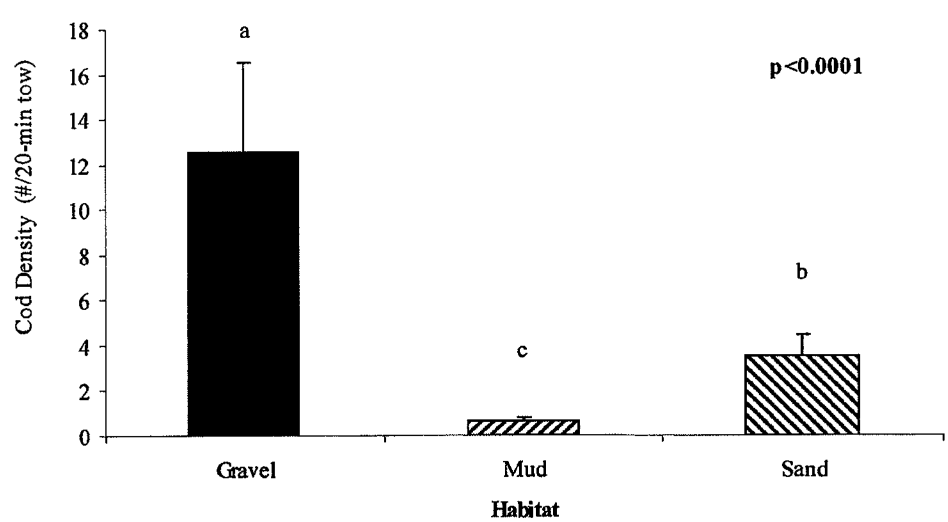


Figure 13. The density of cod caught in inshore trawl surveys around Seguin Island between 1992 and 2005 on bottom with temperatures ranging from (a) 4-6, (b) 6-8, and 8-10 °C. Scheffe's post hoc tests are represented with letters above the error bars (bars with different letters signify values that were significantly different at $p < 0.05$). Error bars indicate +1 SE.

a. Temperature range: 4-6 °C



b. Temperature range: 6-8 °C



c) Temperature range: 8-10 °C

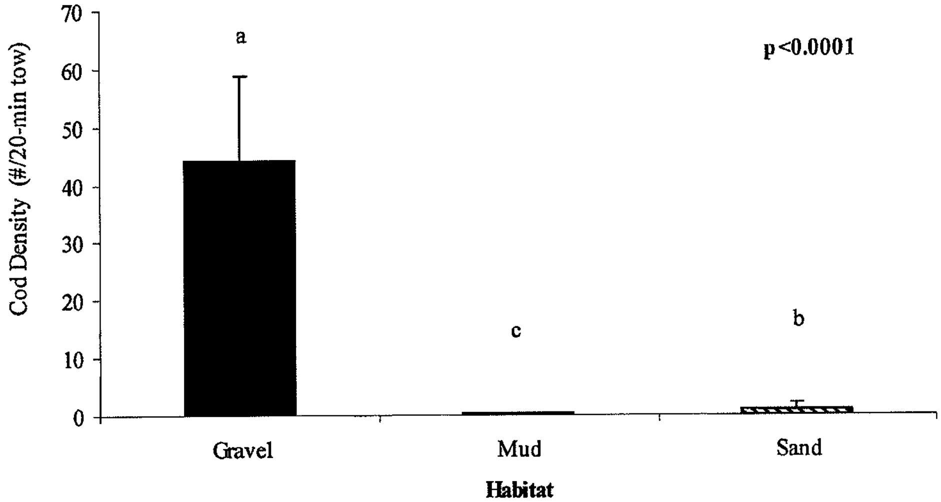


Figure 14. Visiting rates of (a) cod and pollock, (b) unidentified and total gadids, (c) cunner, (d) redfish, sculpin and flounder, and (e) unidentified fish captured in video surveys conducted on cobble/ledge gravel, and mud/sand habitats in mid-coast Maine. Mann Whitney U tests are represented with letters above the error bars (bars with different letters signify values that were significantly different at $p < 0.05$). Error bars indicate +1 SE.

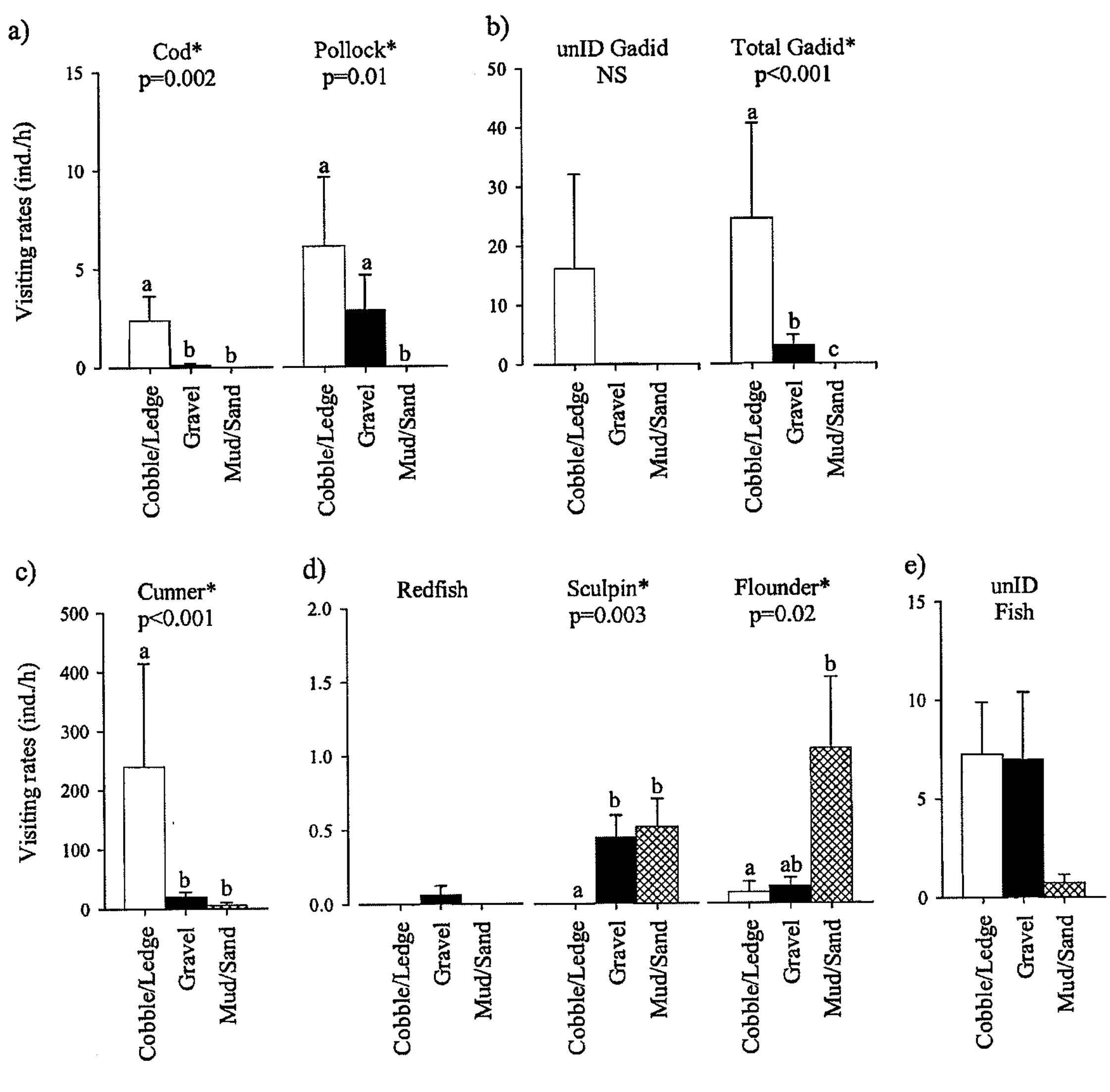


Figure 15. Catch rates of (a) cod and pollock and (b) cunner, redfish, sculpin, and sea ravens. Fish were captured in hook-and-line surveys conducted on cobble/ledge gravel, and mud/sand habitats in mid-coast Maine. Mann Whitney U tests are represented with letters above the error bars (bars with different letters signify values that were significantly different at $p < 0.05$). Error bars indicate +1 SE.