Settlement and distribution of Age-0 juvenile cod, *Gadus morhua* and *G. ogac*, following a large-scale habitat manipulation

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ABSTRACT: In Bonavista Bay, Newfoundland, we monitored patterns of settlement and distribution of 2 species of gadids, Atlantic cod *Gadus morhua* and Greenland cod *G. ogac*, following a large-scale alteration of nearshore eelgrass *Zostera marina* habitat. Comparisons between control and experimental sites, based on bi-weekly sampling from 1995 to 2001, indicated a significant increase in cod abundance at sites enhanced with simulated eelgrass and a corresponding decrease in cod numbers at sites where eelgrass had been removed. These data supported predictions, demonstrating that: (1) there was a sufficient supply of juvenile cod within the areas that have historically been unoccupied (i.e. sand) and (2) both species preferred to settle in complex habitats. However, *G. ogac* responded significantly to the removal of eelgrass in more comparisons than *G. morhua* (70 and 37 % respectively), suggesting that *G. ogac* has a higher affinity for complex vegetative habitats than *G. morhua* at the scale of manipulation (ca. 800 m^2). Furthermore, despite an overall preference for eelgrass habitat, high within-site catch variation of post-settled juvenile cod indicated that both species were not restricted to a seine site. Such variation was occurring well after the settlement period, suggesting that juvenile cod were moving and occasionally aggregating (i.e. shoaling) throughout the study period. Our results support previously described associations between juvenile cod and eelgrass, but contradict other published accounts of high site-attachment and restricted movement in *G. morhua* following settlement.

KEY WORDS: Eelgrass · Habitat selection · Atlantic cod · Greenland cod · Habitat enhancement · BACI design

INTRODUCTION

The identification of critical nursery habitat has become an important task for the management of commercially important marine fish species (e.g. Schmitten 1996). Although habitat use is known to be species-specific, many studies have demonstrated that nearshore abundance and diversity of juvenile fish is often higher in eelgrass (*Zostera* spp.) habitats relative to simple, unvegetated mineral substrates (Bell & Pollard 1989, Edgar & Shaw 1995a,b, Mattila et al. 1999). Eelgrass has been shown to provide refuge for juvenile fish species in laboratory observations (Gotceitas et al. 1995, 1997), tethering studies (Linehan et al. 2001, Laurel et al. 2003) and predator-exclusion experiments

(Hindell et al. 2000). High food levels (Connolly 1994, Parker et al. 2001), reduced physical exposure (Bell & Pollard 1989) and increased water quality (Orth et al. 1984) are other possible benefits of nearshore eelgrass habitat to juvenile fish.

Regardless of the survival and growth benefits associated with eelgrass, habitat quality may not always predict fish distribution. Competitive interactions may prevent pelagic juveniles from initially settling in areas of preferred habitat (Sweatman 1985). Post-settlement processes (e.g. emigration or mortality) may later reshape distributions of juvenile fish settling in poor-quality habitat (e.g. Tupper & Boutlier 1995a). Fish–habitat relationships can also break down, due to large-scale processes such as differential larval supply

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(Bell & Westoby 1986, Caselle & Warner 1996, Jenkins et al. 1997a, 1998). Jenkins et al. (1996) found that juvenile whiting abundance decreased in eelgrass habitats further from the spawning ground, a result attributed to a diminishing supply of pre-settling juveniles. Differential larval supply may also affect overall community structure in eelgrass, including the abundance and diversity of juvenile fish and their prey species (Bell et al. 1988). Although these patterns may disappear through eventual movement to a habitat of higher quality (Sogard 1989), initial settlement patterns have prolonged effects on the distribution of fish if post-settlement movement is limited (Bell & Westoby 1986, Tupper & Boutlier 1995a). Therefore, evaluating critical nursery habitat for juvenile fish has to be considered from multiple spatial and temporal scales.

Generally, habitat studies for marine fish have been conducted as either laboratory experiments, small-scale field manipulations or large-scale field observations. Laboratory and small-scale field experiments typically investigate how the behaviour of an organism influences habitat use, i.e. habitat selection. In the laboratory, predators or food may be introduced to determine how fish choose habitats when faced with trade-offs between predator risk and opportunities for faster growth (e.g. Schmitt & Holbrook 1985, Holbrook & Schmitt 1988). Such studies are useful in isolating small-scale processes, but may not always reflect patterns of habitat use in the field. Alternatively, small-scale field experiments may be insufficient in area to convey the fitness benefits (e.g. predator refuge) necessary for habitat selection to occur (Laurel et al. 2003). Instead, small habitat manipulations may be best suited to smaller, more sedentary marine organisms such as shellfish (e.g. Irlandi 1997) and certain species of reef fish (e.g. Levin 1991). It is perhaps for these reasons that *in situ* habitat studies of marine fish are most commonly investigated through large-scale field observations. Although these studies examine fish distribution in the context of large-scale phenomena (e.g. physical processes, pelagic larval supply, predator distribution), they lack an experimental framework in which to measure the mechanisms contributing to the observed patterns of distribution. Thus, it has been difficult to resolve the contribution of small (e.g. behavioural) and large (e.g. oceanographic) scale processes of habitat use in many marine fish species.

One solution is to conduct controlled *in situ* experiments with habitat on large scales. Aquatic field experiments are not novel, but seagrass manipulations are typically restricted to less than 4 m^2 (Sogard 1989, Irlandi 1997, Horinouchi & Sano 1999, Lee et al. 2001, Jenkins et al. 2002). Larger-scale habitat manipulations are ideal when investigating fish–habitat relationships, but spatial replication of these studies is logistically difficult. Similarly, removing large areas of potentially critical fish habitat may have long-term detrimental consequences to the species being investigated. However, recent statistical tools using randomized time replicates in conjunction with historical data have reduced statistical requirements for spatial replication (randomized intervention analysis, RIA; Carpenter et al. 1989). With such tools, it is logistically possible to carry out large-scale habitat-manipulation experiments.

We conducted a large-scale habitat-manipulation experiment to determine the effect of eelgrass (*Zostera marina*) on the distribution of juveniles of 2 cod species, Atlantic cod *Gadus morhua* and Greenland cod *G. ogac*. Age-0 juvenile cod associate with a number of highly structured demersal habitats (i.e. reefs, cobble, eelgrass; Lough et al. 1989, Tupper & Boutilier 1995a,b). However, juvenile cod distribution in the waters off Newfoundland is almost exclusively restricted to eelgrass habitat in nearshore areas (Gotceitas et al. 1997), where abundance is highly variable among beds of this plant (Grant & Brown 1998a). In this study, we added and removed large sections of eelgrass to investigate sources of variability of habitat use in juvenile cod. Specifically, we addressed the following questions: (1) Is eelgrass a preferred habitat for juvenile cod? (2) Does the association of juvenile cod with habitat occur during or after settlement? (3) Are patterns of habitat use similar between 2 congeneric species?

MATERIALS AND METHODS

Study species. Juvenile Age-0 *Gadus morhua* and *G. ogac* are found throughout Newfoundland nearshore coastal waters from August to late December (Methven & Bajdik 1994, Gotceitas et al. 1997, Grant & Brown 1998a). Both species are similar in appearance at early life stages (<100 mm SL) but can be distinguished in the field using lateral line characteristics (Methven & McGowan 1998) and pigment patterns (B. J. Laurel & R. S. Gregory pers. obs.).

The reproductive life histories differ between the 2 species. *Gadus ogac* spawn early (February to March), have demersal eggs and spawn in the nearshore (Scott & Scott 1988). *G. ogac* are considered demersal and non-schooling residents of the nearshore throughout their life (Mikhail & Welch 1989). In contrast, *G. morhua* spawn later (March to April), have pelagic eggs and spawn in deep water both offshore (Templeman 1979) and inshore (Smedbol et al. 1998). Eggs, larvae and pre-settling juveniles of *G. morhua* are transported to the nearshore, where they eventually settle from the pelagial. The 2 species co-occur as demersal juveniles.
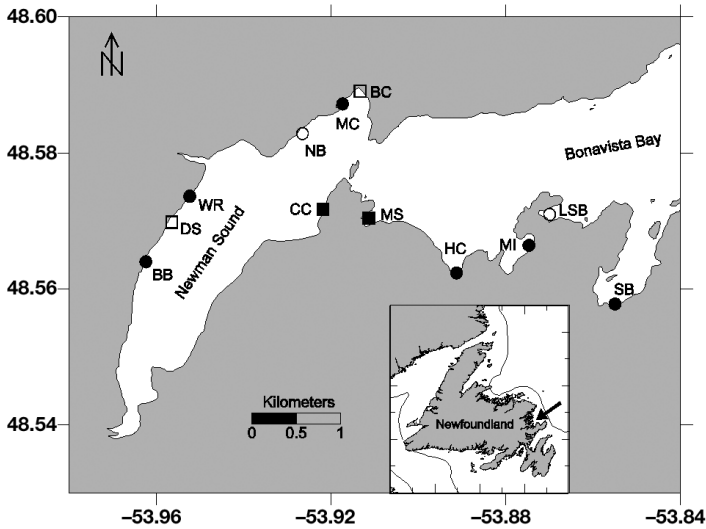
Fig. 1. Study area in Newman Sound, Bonavista Bay, Newfoundland, showing the locations of experimental and reference seine locations. CC: Canning's Cove; MS: Mount Stamford; NB: Newbridge; LSB: Little South Broad Cove; BC: Buckley's Cove; DS: Dockside; BB: Big Brook; HC: Hefferen's Cove; MC: Minchin's Cove; MI: Mistaken Cove; SB: South Broad Cove; WR: White Rock. (●) Eelgrass site, (■) artificial eelgrass site, (○) unvegetated site, (□) removal site

Study area. Newman Sound is a moderately sized (ca. 45 km^2) protected fjord of Bonavista Bay, Newfoundland located adjacent to Terra Nova National Park (TNNP; Fig. 1). Tidal amplitude in the sound is relatively low (1 to 1.5 m) and temperatures vary seasonally from 18.0°C in August to –1.5°C in late December. Eelgrass is the dominant vegetative nearshore habitat, found extensively along the western and southern shores of the sound. Unvegetated mineral substrates are found throughout the sound, comprising the majority of habitat along the northern shore.

Experimental design. We selected 12 sites — 8 'eelgrass' (eelgrass + mud/silt) and 4 'non-eelgrass' (mud/sand) — along southern and eastern sections of Newman Sound (Fig. 1). Eelgrass was removed from 2 eelgrass sites (BC and DS) and artificial eelgrass was added to 2 non-eelgrass sites (CC and MS). Remaining unmanipulated eelgrass and non-eelgrass sites (6 and 2 respectively) were used as controls.

Habitat removal was accomplished by scuba divers in mid-July 1999, approximately 2 wk prior to juvenile cod settlement. Divers marked each site with highly visible transect lines at 1 m intervals over a 500 m^2 area. Eelgrass was harvested between lines by breaking stems away from the rhizome at the base of the substrate. The process was repeated until the entire eelgrass canopy was removed in the 500 m^2 area at each site.

Artificial eelgrass was constructed for 2 sites by attaching green, plastic ribbon (width: 0.8 cm; height: 75.0 cm) to galvanized wire fencing. Ribbon densities fell within the range of eelgrass naturally occurring in Newman Sound, i.e. 600 blades m^2. A total of 80 m^2 of artificial eelgrass was created for each enhancement site, and this was divided into a series of smaller patches to mimic the fragmented characteristics of natural eelgrass. Two replicates of 5 patch sizes (0.3, 1.1, 5.5, 11, 22 m^2) were deployed at both CC and MS, covering a total area of 275 m^2 at each site (Fig. 2). Patches were spaced 2 to 3 m apart and secured to the benthos with 25 cm rebar spikes by divers. Fish were allowed to settle on artificial eelgrass patches for a period of 2 wk before the sampling protocol was initiated. Patches were removed in November 1999 and redeployed in July of 2000 to prevent potential ice-scour damage.

Juvenile cod sampling. A 25 m demersal seine net with 19 mm stretched mesh size was used to collect fish over all sampling sites. The net was deployed from a small boat 50 m from shore and retrieved to shore by 2 individuals standing 16 m apart. The seine sampled 880 m^2 of habitat from the substrate to 2 m into the water column and has been shown to have a capture efficiency of 95% (Gotceitas et al. 1997). We made a series of underwater observations in 1999, using scuba, over all substrates, and confirmed that entire sites were sampled and that fish in the path of the seine did not escape capture. Fish caught in the seine were transferred to holding containers with seawater, identified, measured to the nearest mm (standard length, SL) and then returned alive to the original site of capture. Juveniles were considered 'pre-settled' if SL < 60 mm and 'post-settled' if SL ≥ 60 mm (Templeman 1966, Fahay 1983, Methven & Bajdik 1994, Tupper & Boutlier 1995a,b). We use the term 'pre-settled' to describe a juvenile cod early in the transition from pelagic to demersal life (synonymous terms include 'recently settled'
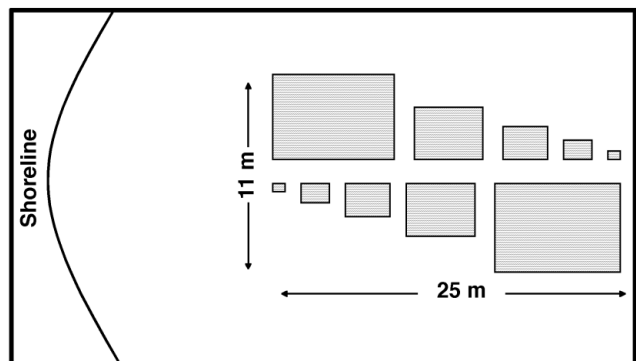

Fig. 2. Experimental layout of artificial eelgrass patches relative to shore at MS and CC

[Grant & Brown 1998a,b] and 'newly settled' [Tupper & Boutilier 1995a]). Our choice of terminology was intentional, since juvenile cod do not have a distinct settlement point and individuals larger than 60 mm SL may continue to forage on semi-pelagic prey such as calanoid copepods (Grant & Brown 1998a, Lomond et al. 1998). However, the seine we used samples the lowermost 2 m of the water column (i.e. near the bottom), and captures only those juvenile cod which are likely associated with the demersal habitat. All sites were sampled within 2 h of low tide during daylight hours on a bi-weekly basis in both pre-   manipulated years

(1995, 1996 and 1998) and post-manipulated years (1999 and 2000). Removal sites were additionally sampled in 2001 to measure long-term effects of habitat removal on juvenile cod distribution.

Additional density estimates of juvenile cod were made visually using the snorkeling methods described by Laurel et al. (2003). This was accomplished by deploying two 15 m transect lines perpendicular to the shore at 2 sites of each treatment (addition, removal, eelgrass, and sand; 2 × 4 = 8 total sites, 2 transects per site). At artificial eelgrass sites, snorkelers surveyed only fish directly over or within 0.5 m of artificial habitat patches. Juvenile cod surveys in other treatment habitats (i.e. removal, eelgrass and sand treatments) were designed to mimic the layout and area of artificial eelgrass at the addition sites (i.e. 10 patches, 80 m² total). This was accomplished by marking the length and spacing of artificial eelgrass patches on each transect line with highly visible tape. The survey width along the transect lines was determined using a delineated plastic pole. Using both the transect line and poles, snorkelers were capable of surveying juvenile cod at the same dimensions as addition sites along each transect line, i.e. 0.3, 1.1, 5.5, 11.0 and 22 m². At all sites, large patches (11 and 22 m²) exceeded the viewing capability of a single snorkeler, so these patches were assessed by 2 snorkelers swimming in parallel. Location and abundance of Age-0 cod were recorded on underwater slates. Surveys were only performed when water clarity exceeded the maximum area censused by a single snorkeler, i.e. 2.8 m. However, we were often unable to distinguish between the smallest *Gadus ogac* and *G. morhua* underwater, even when within 1 m. Therefore, we pooled our juvenile cod observations during snorkel surveys as *Gadus* spp. We surveyed the sites approximately weekly (n = 9) between 10 August and 12 October 2000 (a total of 144 transect surveys).
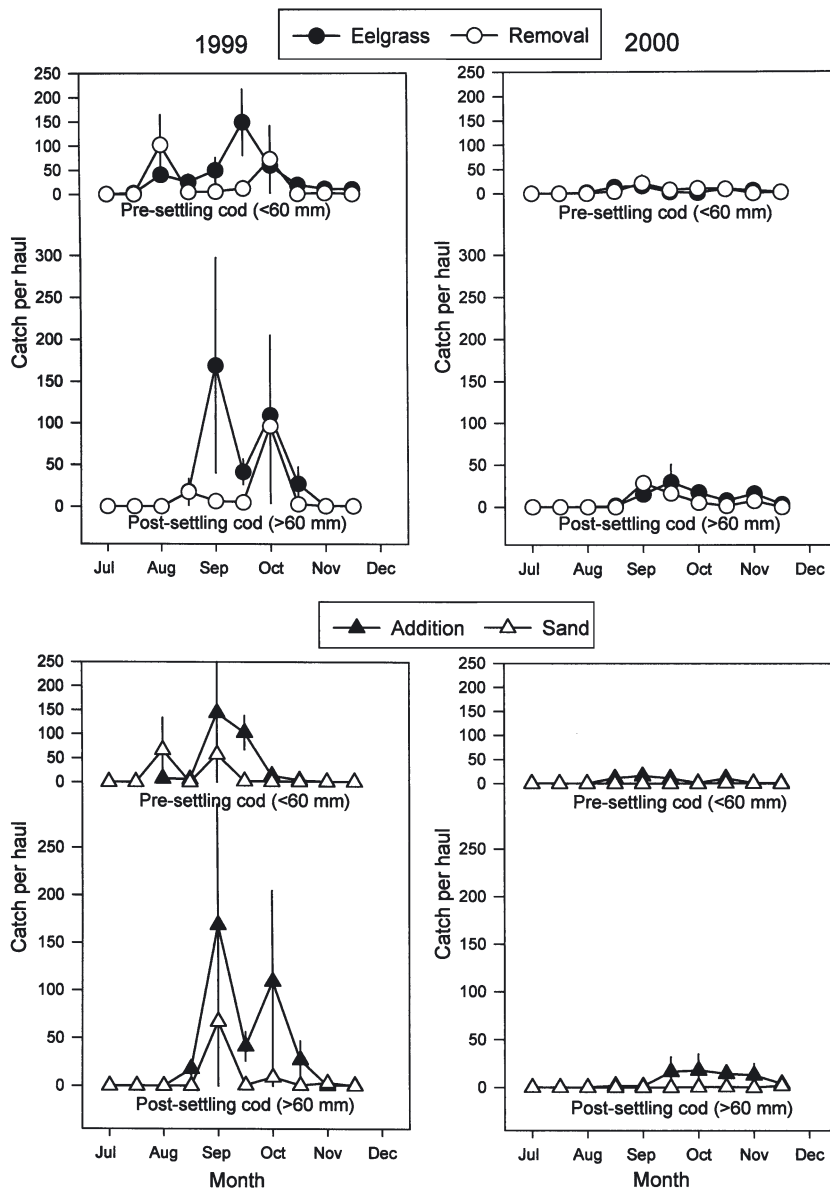
Data analysis. Catch data were analyzed using RIA to test whether a significant change in fish density occurred after the habitat manipulation. A full description of RIA and its utility for detecting treatment effects has been reviewed by Carpenter et al. (1989). RIA is based on a before-after-control-impact (BACI) design model in which experimental and control sites are

Fig. 3. *Gadus morhua.* Interannual pre- and post-settlement distribution of Age-0 juveniles in experimental and reference sites. Values are means of seine hauls at replicate sites (n = 2–6) ± SE

compared against each other both before and after any experimental intervention. Removal sites (n = 2) were compared against natural eelgrass sites (n = 6); artificial eelgrass sites (n = 2) were compared against naturally unvegetated sites (n = 2). RIA tests were performed on data from individual and combined years in all possible experiment–control site comparisons. However, combined years (1999 to 2001) were not included in the analysis of removal sites, because annual regrowth at each site effectively changed the treatment over time. Catch data were transformed [$y = \log_{10}(x + 1)$] prior to analysis to control for interannual variation in cod abundance. Each RIA calculated differences between fish abundance at control and manipulated sites during each survey period. The mean of these differences both before ($\bar{E}_{PRE}$) and after the experimental manipulation ($\bar{E}_{POST}$) was used to generate the test statistic [$\bar{E}_{(PRE)} - \bar{E}_{(POST)}$]. The test statistic was then compared against 5000 random permutations of [$\bar{E}_{(PRE)} - \bar{E}_{(POST)}$] using the data of each experiment–control site comparison. The error distribution was self-derived from the randomization, and therefore data did not have to meet the assumptions of normality.

RESULTS

Juvenile Age-0 *Gadus morhua* settled in 2 pulses: the first pulse in late August, the second approximately 30 d later (Fig. 3). *G. ogac* settled in a single pulse at the beginning of August (Fig. 4). Interannual variation in abundance of *G. morhua* was high between 1999 and 2000 (Fig. 3), almost an order of magnitude higher in 1999 (n = 6405) than in 2000 (n = 845). *G. ogac* abundance varied little between 1999 (n = 8985) and 2000 (n = 6614), but was higher than *G. morhua* in all years.

The distribution of pre- and post-settled cod differed between habitat, species and year. Pre- and post-settled cod (<60 mm SL) of both species were present in all habitats in 1999, but were not present at sand sites in 2000 (Figs. 3 & 4). Differences in the abundance of post-settled *Gadus morhua* caught in natural eel-

grass and removal sites were more apparent in the first year of the removal (1999) than in later years. However, post-settled *G. ogac* were seldom caught in the removal sites during both years.

Snorkelers observed juvenile cod settling within the artificial eelgrass in early August, approximately 2 wk after patches were deployed. *Gadus* spp. were detected only in natural and artificial eelgrass sites at the time of settlement for both the first pulse (August 10 to 30) and second pulse (October 1 to 12; Fig. 5). Lower numbers of cod were observed in the removal sites, and these fish were often seen along the edge area of
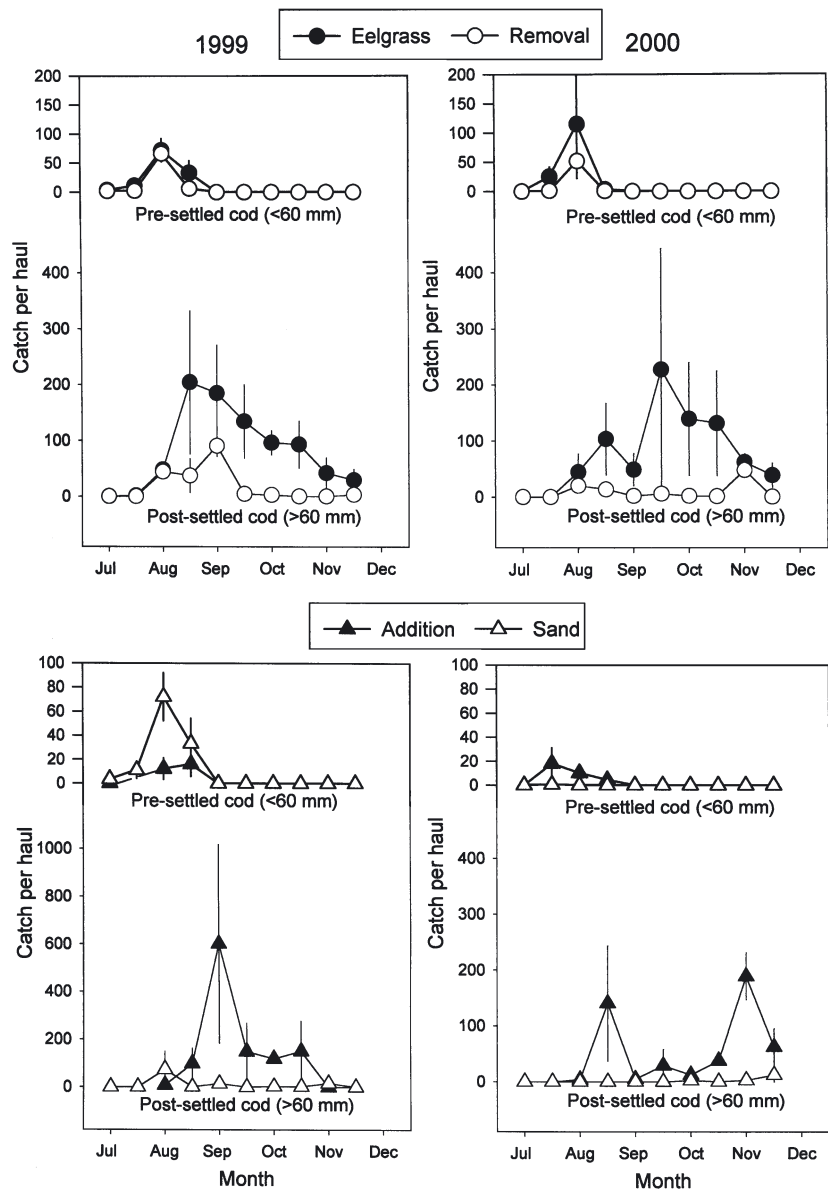

Fig. 4. *Gadus ogac*. Interannual pre- and post-settlement distribution of Age-0 juveniles in experimental and reference sites. Values are means of seine hauls at replicate sites (n = 2–6) ± SE
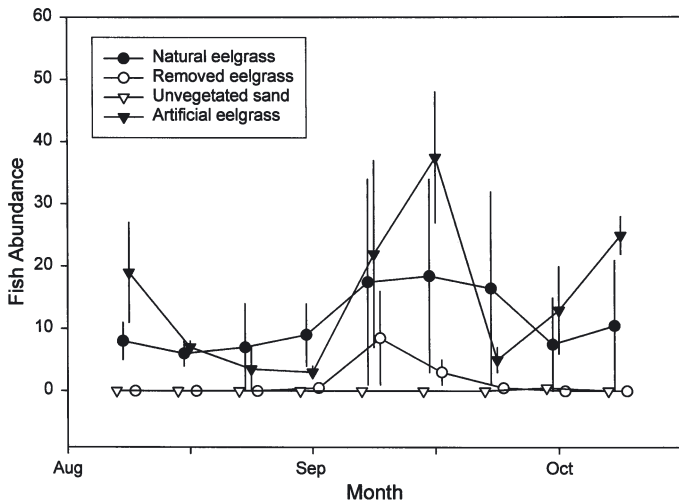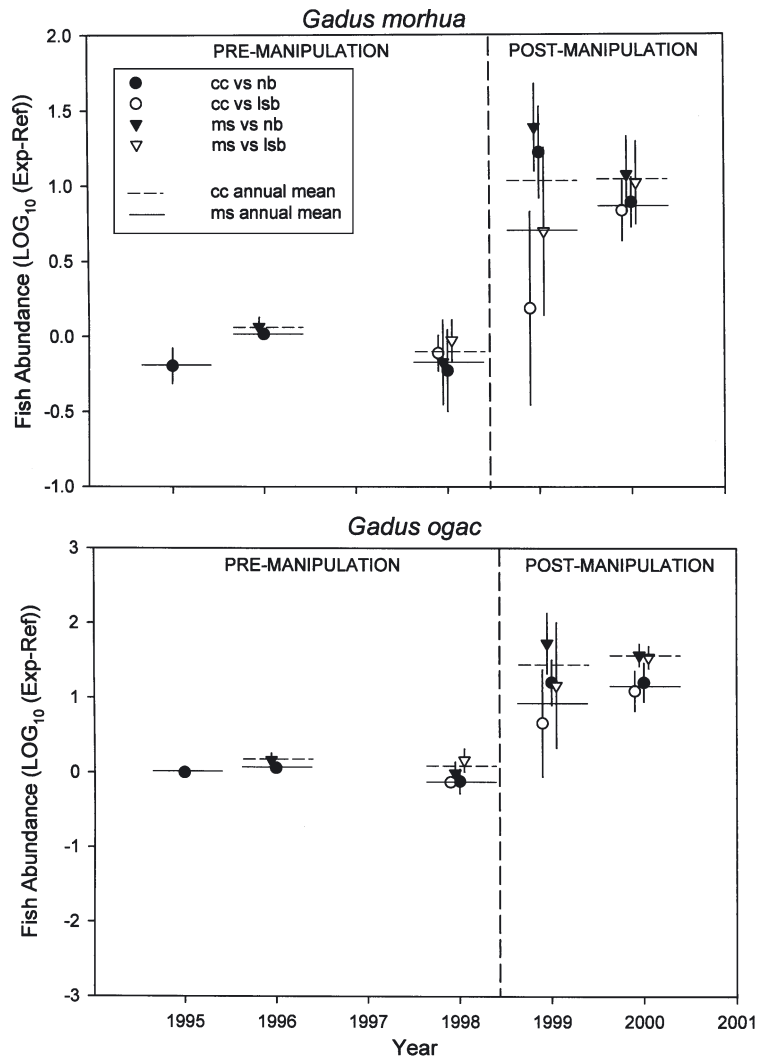
Fig. 5. Visual observations of Age-0 juvenile cod *Gadus* spp. abundance over a 9 wk period (August 12 to October 12) at eelgrass, removal, unvegetated sand and artificial eelgrass sites. Values are means of replicate transect lines (n = 4) ± SE. Points at each week are staggered (0.1 wk) for visual purposes

species showed signs of recovery towards the end of the experiment. Mean abundance of cod was lower in nearly all control site comparisons in all years following the removal of eelgrass (Table 2). In the first year of removal (1999), 50 and 75% of comparisons indicated a significant decline in abundance of *G. morhua* and *G. ogac* respectively (Table 2, Figs. 7 & 8). In 2000, 16.7% of *G. morhua* and 50% of *G. ogac* comparisons were significantly lower than historic levels. However, in the final year (2001), with the exception of one *G. morhua* comparison, fish abundance generally recovered to historic levels (1995 to 1998).

DISCUSSION

Eelgrass benefits juvenile fish by reducing predator risk (Linehan et al. 2001, Laurel et al. 2003), increasing food availability (Connolly 1994), improving water quality and reducing physical exposure (Orth et al. 1984). However, juvenile fish may be distributed inde-

the removal. Almost no cod were sighted over open sand areas (<0.1% of all observations).

The RIA of catch data indicated a positive change in cod abundance in response to the artificial eelgrass, but the magnitude of the response differed between species and years. Differences were attributed to high catch variability at one unvegetated control site (LSB) rather than an absence of cod at the artificial eelgrass sites (Figs. 3 & 6). In combined years (1999 and 2000), there was a significant increase in *Gadus ogac* abundance at artificial eelgrass sites in all comparisons. In contrast, increases in *G. morhua* at the artificial eelgrass sites were significant in comparisons with the unvegetated control site NB (Table 1, Fig. 6). However, the trends were similar between species in individually analyzed years. Seine catches of *G. ogac* and *G. morhua* were higher at artificial eelgrass sites relative to unvegetated control sites in 50% of comparisons in 1999 and 100% in 2000 (Table 1).

Gadus ogac and *G. morhua* also responded differently to eelgrass removal, although both

Fig. 6. *Gadus morhua* and *Gadus ogac.* Relative differences of juvenile abundance at artificial eelgrass sites (CC and MS) and unvegetated reference sites (NB and LSB) during pre- and post-manipulation years. Values represent annual mean bi-weekly seine catches (n = 14–20) ± SE. Points at each year are staggered (0.05 yr) for visual purposes

pendent of habitat quality. Differential planktonic supply (Bell & Westoby 1986, Caselle & Warner 1996, Jenkins et al. 1997a, 1998), competitive interactions (e.g. Sweatman 1985) or indiscriminate settlement patterns (Tupper & Boutlier 1995a) are known to influence spatial distribution. Therefore, proposed mechanisms of habitat use in juvenile cod have been equivocal, despite frequent observations of associations between cod and eelgrass in the field (Morin et al. 1991, Gotceitas et al. 1997, Grant & Brown 1998a). Our study experimentally demonstrates that differential habitat-use in Age-0 juvenile cod is, in part, behaviourally mediated. Juvenile cod appeared to differentiate between habitats of varying quality and preferentially occupied eelgrass areas where growth and survival were potentially highest.

Habitat decision-making occurred at the time of settlement (<60 mm SL), when fish were not fully demersal. Prior to the habitat manipulation, settling cod were restricted to areas with natural eelgrass. However, following the deployment of artificial eelgrass, pre-settling *Gadus ogac* and *G. morhua* were caught at sites historically unoccupied. These data suggest that planktonic supply over non-eelgrass areas was not limiting prior to the deployment of artificial eelgrass, but rather that cod were delaying settlement until preferential habitat was encountered. Although active habitat selection from the pelagial has been reported in other fish species (e.g. Marliave 1977, Sale 1984, Levin 1991), these data contradict other published accounts of settlement in cod. In a one year study, Tupper & Boutilier (1995a) described an indiscriminate settlement pattern in *G. morhua* across habitats of varying complexity. In their study, differences in

Table 1. Probability values from randomized intervention analysis (RIA) of *Gadus morhua* and *Gadus ogac* from 2 artificial eelgrass sites (CC and MS) and 2 unvegetated reference sites (NB and LSB). (+) indicates a positive effect from the enhancement (*p < 0.05, **p < 0.01)

Year	Site	NB	LSB
G. morhua			
1999–2000	CC	(+) 0.001**	(+) 0.251
	MS	(+) 0.001**	(+) 0.063
1999 only	CC	(+) 0.001**	(+) 0.670
	MS	(+) 0.001**	(+) 0.190
2000 only	CC	(+) 0.001**	(+) 0.002**
	MS	(+) 0.001**	(+) 0.006**
G. ogac			
1999–2000	CC	(+) 0.001**	(+) 0.041*
	MS	(+) 0.001**	(+) 0.034*
1999 only	CC	(+) 0.002**	(+) 0.276
	MS	(+) 0.001**	(+) 0.200
2000 only	CC	(+) 0.001**	(+) 0.001**
	MS	(+) 0.001**	(+) 0.001**

abundance of cod between habitats occurred after settlement. They suggested that this was a result of differential predator-induced mortality rather than habitat selection. Our observations did not suggest indiscriminate settlement in 5 of the 6 years of our catch data (1995, 1996, 1998, 2000 or 2001). However, in the year of highest overall juvenile cod abundance (1999), pre-settled cod were caught at all sites, supporting the observations of Tupper & Boutlier (1995a). Their study also indicated high densities of 'newly settling' *G. morhua* (i.e. >0.5 m^{-2}) at many of their sites. Only in

Table 2. Probability values from randomized intervention analysis (RIA) of *Gadus morhua* and *Gadus ogac* from 2 experimental removal sites (DS and BC) and 5 natural eelgrass reference sites (BB, HC, MC, MI, SB and WR). (–) or (+) indicates a negative or positive effect from the removal (*p < 0.05, **p < 0.01)

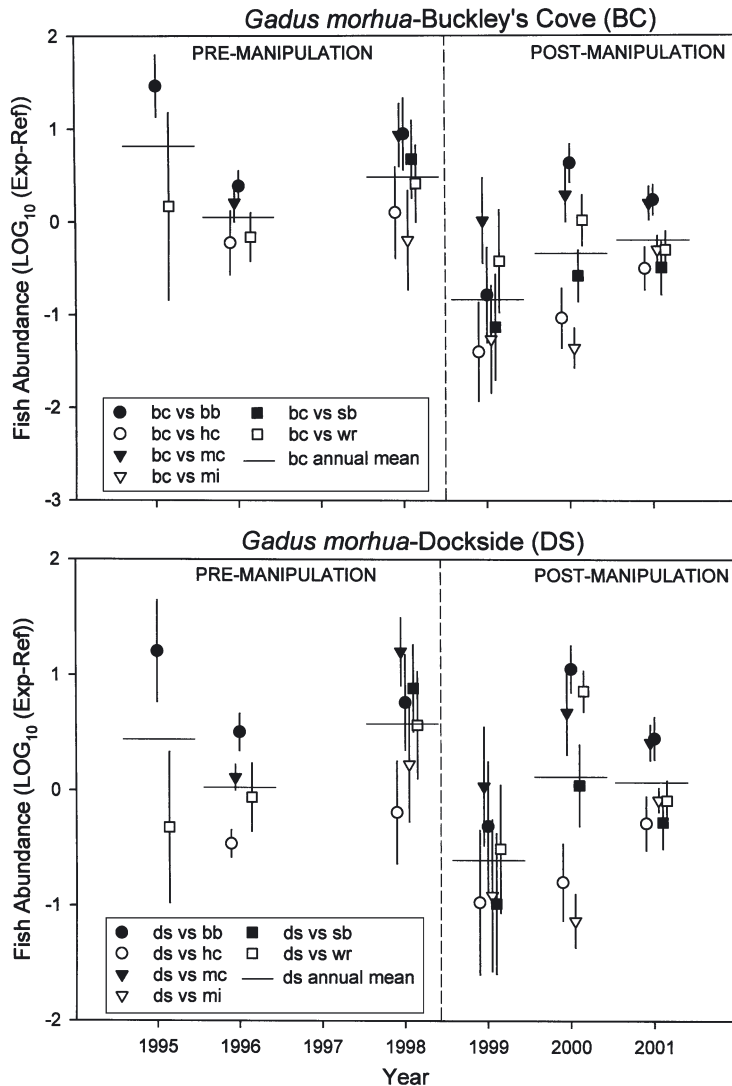| Year	Site	MC	MI	SB	WR	BB	HC
G. morhua							
1999	DS	(–) 0.146	(–) 0.153	(–) 0.029*	(–) 0.217	(–) 0.025*	(–) 0.278
	BC	(–) 0.158	(–) 0.027*	(–) 0.017*	(–) 0.308	(–) 0.001*	(–) 0.026*
2000	DS	(–) 0.484	(–) 0.022*	(–) 0.153	(+) 0.079	(–) 0.650	(–) 0.252
	BC	(–) 0.220	(–) 0.060	(–) 0.035*	(–) 0.794	(–) 0.373	(–) 0.058
2001	DS	(–) 0.277	(–) 0.667	(–) 0.031*	(–) 0.560	(–) 0.462	(–) 0.964
	BC	(–) 0.175	(–) 0.852	(–) 0.055	(–) 0.296	(–) 0.099	(–) 0.304
G. ogac							
1999	DS	(–) 0.024*	(–) 0.212	(–) 0.012*	(–) 0.234	(–) 0.033*	(–) 0.010*
	BC	(–) 0.032*	(–) 0.032*	(–) 0.005*	(–) 0.056	(–) 0.001*	(–) 0.033*
2000	DS	(–) 0.022*	(–) 0.158	(–) 0.002*	(–) 0.655	(–) 0.425	(–) 0.005*
	BC	(–) 0.036*	(–) 0.115	(–) 0.015*	(–) 0.681	(–) 0.110	(–) 0.002*
2001	DS	(–) 0.186	(–) 0.900	(–) 0.289	(–) 0.662	(–) 0.777	(–) 0.675
	BC	(–) 0.293	(–) 0.424	(–) 0.473	(–) 0.741	(–) 0.4116	(–) 0.796

Fig. 7. *Gadus morhua*. Relative differences of juvenile abundance at experimental removal sites (BC and DS) and natural eelgrass reference sites (BB, HC, MC, MI, SB and WR) during pre- and post-habitat manipulation years. Values represent annual mean biweekly seine catches (n = 14–20) ± SE. Points at each year are staggered (0.05 yr) for visual purposes

1999 were comparable densities of *G. morhua* (0.3 m^{-2}) observed in our study. Although comparing densities between studies can be problematic, it is possible that settlement patterns in cod were density dependent. That is, in high abundance years, apparent habitat quality may have decreased through saturation effects (e.g. competition for space, prey, or resources), leading to settlement in suboptimal habitats (i.e. ideal free distribution; MacCall 1990, Kramer et al. 1997). The proximal cause of the disappearance of pre-settling fish from unstructured and removal sites in our study is unknown. However, in a recent study (Laurel et al. in press), we have demonstrated that juvenile cod exhibit increased aggregation behaviour and increased ten-

dency to move under conditions of high density when they occupy unstructured habitat, compared to low density, when they did not occupy such habitat. Such behaviour may be a means of compensating for increased predator risk associated with life in unstructured habitats.

An alternative explanation is that settling cod (<60 mm) initially settled in natural eelgrass sites and shortly afterwards moved to artificial eelgrass sites. However, we suggest that this was unlikely for a number of reasons. First, at our sites, a migration of >1 km across deep or unvegetated habitats would be required to relocate to artificial eelgrass sites from natural eelgrass sites. Such a migration would be improbable because risk of predation in juvenile cod increases with water depth (Linehan et al. 2001) and with declining structural complexity (Gotceitas et al. 1997, Laurel et al. 2003). In addition, the susceptibility of juvenile fish to predators is known to be size-dependent (Sogard 1997). Therefore, the risk of movement among safe habitats at small body sizes would likely be prohibitive. Finally, a recent study analyzing patchiness of demersal *Gadus morhua* within nearshore areas suggests that movement of small pre-settling cod (25 to 40 mm) is less than that in larger, post-settled fish (Methven et al. 2003). Therefore, in our study, the distribution of small cod (<60 mm SL) was likely the result of settlement from the pelagial rather than movements between demersal habitats.

Substantial movement more likely occurred in larger, post-settled juvenile cod. High within-site variation suggests that post-settled cod were not restricted to the area in which they settled. In contrast, Tupper & Boutilier (1995a,b) have argued that juvenile cod are strongly site-attached and shifts in the observed abundance of settled fish is exclusively due to mortality. In these 2 studies, juvenile *Gadus morhua* (60 to 100 mm SL) were observed defending small territories and having limited, size-dependent home ranges (<100 m^2) for 2 to 3 mo following settlement. Our survey methods encompassed these reported home ranges, yet snorkel observations and seine catches were highly variable between sampling periods. We do not attribute observed variation to mortality alone, since density of post-settled individuals often increased within a site through the season. Therefore, it would appear that both cod species were mobile at scales greater than ca. 1000 m^2.

Both cod species altered their distribution following the habitat manipulation, but their habitat use patterns were not identical. *Gadus ogac* abundance decreased in more removed–eelgrass–control comparisons than *G. morhua*, suggesting that *G. ogac* is more sensitive to
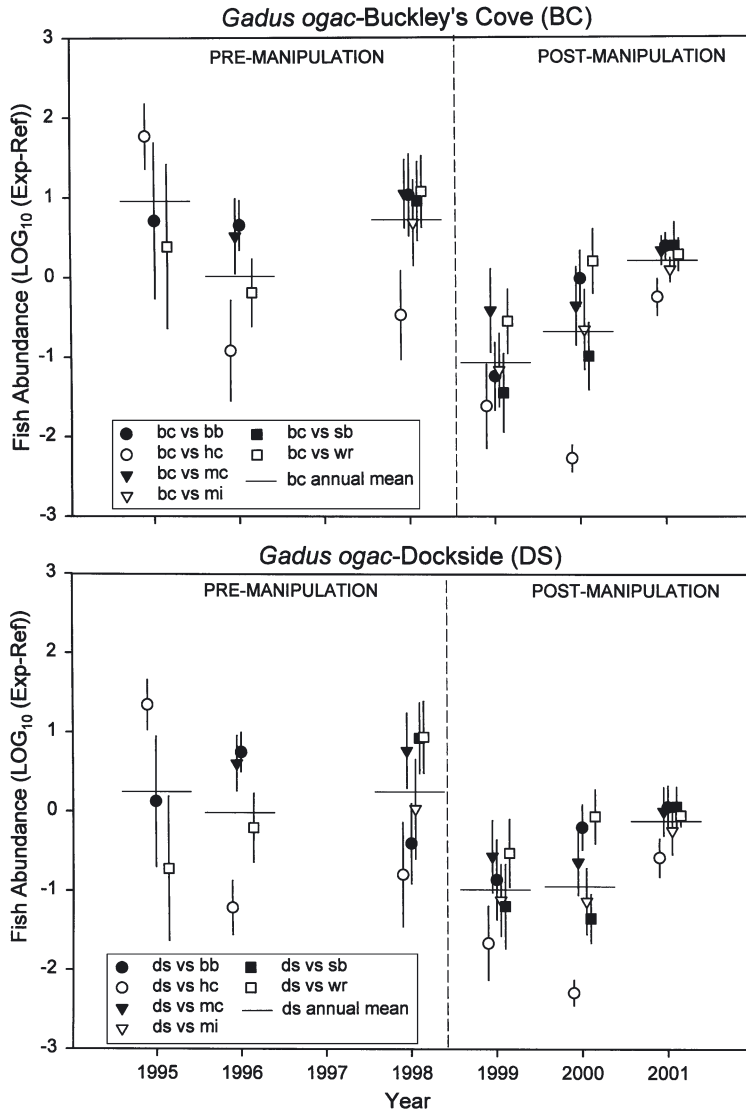
Fig. 8. *Gadus ogac.* Relative differences of juvenile abundance at experimental removal sites (BC and DS) and natural eelgrass reference sites (BB, HC, MC, MI, SB and WR) during pre- and post-habitat manipulation years. Values represent annual mean biweekly seine catches (n = 14–20) ± SE. Points at each year are staggered (0.05 yr) for visual purposes

spawned eggs are more likely to be retained in the area spawned relative to pelagic eggs (Bradbury et al. 2003). It is therefore possible that *G. morhua* evolved a greater tolerance for the use of alternative habitats, such as gravel-cobble (Lough et al. 1989) and rocky reefs (Tupper & Boutilier 1995a). However, such explanations are tenuous without data on spatial and temporal distributions of eggs, larvae and pelagic juveniles of each species in our study area.

Our analysis measured a relative effect on fish abundance rather than a shift in absolute abundance. Largely, this was done to control for individual site differences (e.g. eelgrass biomass, patchiness, planktonic supply) that could contribute to differential abundance of cod within a habitat treatment. In addition, the artificial eelgrass may not completely mimic natural eelgrass (e.g. additional structure from wire base, lack of natural die-off). However, the logistical constraints of carrying out a large-scale habitat manipulation did not permit us to manipulate habitat of an area equivalent to natural eelgrass control sites. Therefore, absolute comparisons would be inappropriate regardless of possible inherent site differences. Therefore, the high abundance of juvenile cod, namely *Gadus morhua*, at removal sites was not unexpected; 35% of each removal site still contained undisturbed eelgrass, although this was only in the shallow intertidal zone where few juvenile fish are found regardless (Jenkins et al. 1997b), including *Gadus* spp. (M. Norris unpubl.). Another source of juvenile cod in the removal sites were the edges along the subtidal boundary of the removal. We observed schools of juvenile cod along the deeper edge of our removal sites where the manipulated area adjoined undisturbed eelgrass, but we rarely observed cod over the interior of the removal. Edge areas in eelgrass are known to be profitable foraging areas for fish (Graham et al. 1998), and it is possible that edge-associated fish contributed substantially to our seine catches. In addition, removal sites may have had higher prey levels than sand sites. Although the response of macroinvertebrates to alterations in seagrass is species- and site-specific (e.g. Edgar & Robertson 1992, Connolly & Butler 1996, Lee et al. 2001), Connolly (1994) found higher overall invertebrate abundance in small removal areas (25 m²) compared to naturally unvegetated areas. In our study, we removed the canopy of eelgrass and left the rhizomes intact in the benthos. Potentially, our procedure left a rich benthic invertebrate community relative to naturally unvegetated sites.

alterations in habitat complexity. Conversely, despite an overall preference for eelgrass, *G. morhua* was periodically caught over sand and removal sites, suggesting that habitat use in this species is more flexible at early life stages. Such differences may reflect differences in predation risk outside eelgrass habitat between the 2 species. Alternatively, these differences may reflect different spawning characteristics between the 2 species. *G. ogac* spawn demersal eggs (Scott & Scott 1988) in close proximity to nursery areas, whereas *G. morhua* spawn pelagic eggs, often further offshore (Templeman 1979). Larvae from demersally

In a few instances, highest numbers of juvenile cod were caught in artificial eelgrass sites. This was interesting considering that the eelgrass coverage at artificial sites was substantially less than natural sites. The visual transect data, which controls for habitat area, also confirmed that overall cod abundance was higher in our artificial eelgrass. These results may demonstrate an 'oasis effect', since artificial eelgrass sites were further removed from natural eelgrass patches than natural eelgrass sites. Assuming fish seek the most proximate refuge, patches of suitable habitat may be colonized at high rates when surrounded by large areas of unsuitable habitat (Virnstein & Curran 1986). Other studies have shown that higher densities of fish are found in isolated patches of eelgrass (Sogard 1989) and reef habitat (Schroeder 1987) when compared to continuous sections of the same type of habitat. Similar findings have also been reported for cod. Eelgrass sites with slight fragmentation supported higher densities of Age-0 juvenile cod than eelgrass meadows of equivalent area (Wells 2002). Our results were consistent with these findings.

Appreciable regrowth of eelgrass at the removal sites occurred 2 yr following its initial removal. This regrowth was reflected in the number of significant RIA removal–control site comparisons. In the first year of removal (1999), nearly 50% of the RIA comparisons indicated a significantly lower juvenile cod abundance in removal sites compared to years prior to the removal. By 2001, differences between removal and vegetated sites were no longer significant. Eelgrass reproduces both sexually and asexually (Orth et al. 1994). The close proximity of undisturbed eelgrass to the removal areas also likely facilitated the quick recovery. A larger, more geographically isolated removal location or a complete removal of canopy, including rhizomes (which we left largely intact) may have had longer-term effects on juvenile cod distribution.

CONCLUSIONS

Both *Gadus ogac* and *G. morhua* abundance increased at sites enhanced with artificial eelgrass and decreased at sites where eelgrass was removed, relative to years before we manipulated habitat. Therefore, we reject the hypothesis that broad-scale processes (e.g. larval supply and oceanographic hydrodynamics) were responsible for the differential use of vegetated and unvegetated habitats. The presence of settling cod over sites with artificial eelgrass in years of high and low abundance suggests that these species are capable of selecting habitat while still in the pelagial.

Both species exhibited an overall preference for eelgrass habitat. However, high within-site variability of both species indicated that both species are not strongly site attached. High catch variability was especially evident in *Gadus morhua*. Significant RIA comparisons were fewer in *G. morhua* relative to *G. ogac*, suggesting that *G. morhua* was less site attached or less dependent on habitat complexity than its sibling species. These data contradict Tupper & Boutlier's (1995a,b) accounts of cod (1) settling indiscriminately across a range of habitats and (2) having high site fidelity following settlement.

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