Abstract.—Although juvenile fish are studied extensively in estuarine and nearshore environments, surprisingly little is known about the basic habitat requirements of juveniles for offshore settlement and nursery areas. Between June 1996 and July 1997, settlement and nurserv habitats of age-0 (early juvenile) demersal fish on the continental shelf of the New York Bight were investigated by using a two-meter beam trawl. Replicate tows at 21 stations along three cross-shelf transects (20-95 m depth), were sampled on a near monthly basis to determine general ecology (21,309 fish collected in 659 tows). Of the 47 species collected, 33 included age-0 juveniles, and 25 included near-settlement size individuals. The two dominant species, Pleuronectes ferrugineus and Merluccius bilinearis, constituted 88.9% of the total catch of age-0 fish. Of all age-0 fish, 94% were collected during summer and fall. Comparisons of weighted means and the use of canonical correspondence analysis determined that settlement and nursery habitats across the shelf are primarily delineated by depth, temperature, and time of year. Three zones across the shelf (inner, middle, and outer) each had distinct juvenile fish assemblages. Knowledge gained about the distribution and quality of juvenile habitat for commercially important offshore species should facilitate their improved management.

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Settlement and nursery habitats for demersal fishes on the continental shelf of the New York Bight*

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With the decrease in fish abundance in the latter half of the twentieth century, particularly in the Northwest Atlantic (McHugh, 1972; NEFSC, 1992), fisheries managers have been concerned with both overfishing and habitat degradation. Much effort has been put into understanding the abundance, distribution (Colton, 1972; Colvocoresses and Musick, 1984), and environmental preferences (Scott, 1982; Auster et al., 1991; Felley and Vecchione, 1995) of adult groundfishes in the northwestern Atlantic. Although information on adult groundfishes is useful, events during the early life history of fish may be more important in determining recruitment variability (Sissenwine, 1984; Houde, 1987; Peterman et al., 1988; Bradford, 1992; Miller, 1994). Several ichthyoplankton surveys have helped to increase our understanding of egg and larval distributions of groundfishes in the Mid-Atlantic Bight (MAB; Morse

et al., 1987; Cowen et al. 1993). However, less is known about the juvenile stage, which represents a dramatic change in lifestyle for groundfishes: they leave the threedimensional environment of the plankton and settle onto the twodimensional world of the sea floor (Chambers and Leggett, 1992).

Within this two-dimensional environment, the growth, survival, and recruitment of groundfishes are affected by various factors associated with the quality (value for growth) and quantity (area) of their nursery habitat (Gibson, 1994). Research involving the nurseries of groundfishes has been limited to estuaries and nearby coastal habitats where they can readily be studied (Riley et al., 1981; Able et al., 1989; Bolle et al., 1994; Henderson and Seaby, 1994; Nash et al., 1994;

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but see Toole et al., 1997). However, Able et al. (1989) have suggested that there is a lack of studies that examine the continental shelves of the MAB as potential nursery grounds. This is remarkable because the early life history stages of many species of groundfish are believed to inhabit almost the entire shelf as well as the slope (Fahay, 1983; Miller et al., 1991).

A wide assortment of biotic and abiotic variables may have a role in determining the distribution of continental shelf nursery grounds. Variations of abiotic parameters, such as temperature, salinity, and oxygen, can affect the metabolism of marine flatfishes during the juvenile stage (Malloy and Targett, 1991; Pihl et al., 1991; Gibson, 1994; Neill et al., 1994). Changes in temperature, for example, can have a marked effect on feeding rate and growth; thus lower temperatures may slow growth and consequently increase susceptibility to mortality due to size-selective predation (Van der Veer et al., 1994). Salinity seems to have a small influence on the growth rate of fish, but it is often effective in controlling their distribution (Rodgers, 1992). By adjusting their position in relation to local abiotic factors, fish may modify their growth rate and survival with respect to average environmental parameters (Gibson, 1994).

Biotic factors, particularly food resources and shelter related to biological activity, may also be a potent determinant of nursery habitat. Auster et al. (1991) found that several biotic microhabitat types, including amphipod tube mats, shells, and biogenic depressions, significantly affected the abundance of fishes and other megafauna. Other biotic factors that influence the distribution of juvenile fishes include the presence of potential predators (Bailey, 1994) and the availability of potential prey species. Biotic factors may be ephemeral; however their presence or absence at a given time and space may control the distribution of associated fish species. The spatial distribution of amphipod tubes in particular have been shown to have a strong influence on the abundance of age-0 silver hake (Merluccius bilinearis) during fall in the MAB (Auster et al., 1997).

Recent recruitment research has emphasized factors that affect survival of the early life history stages of fishes. Identification of the habitats preferred by juvenile fishes in offshore waters will allow for a more complete understanding of recruitment variation. Although shelf habitat is magnitudes larger in area than the nearshore habitat traditionally studied, there is currently little knowledge of its role as a nursery. For many flatfish species, the size of nursery habitat and year-class strength have been correlated (Rijnsdorp et al., 1992; Gibson, 1994). Our objectives were to provide a first-order analysis of the species that use the shelf as settlement and nursery habitat during the course of a year and to address the relation of these distributions to environmental correlates.

Description of the study area

The New York Bight (NYB), a central portion of the MAB, encompasses an area of 39,000 km² on the East Coast of the United States. Its boundary extends out to the 200-m isobath between Montauk Point, New York, and Cape May at the southern end of New Jersey. The bathymetry of the NYB varies on several geographical scales. Although the continental shelf in this area is, to the most extent, gently sloping, large-scale features do exist. The Hudson River Canyon, which almost bisects the NYB, is the most obvious of these. Imposed on this bathymetry are the convoluted isobaths of the ridge and the swale topography that dominates the NYB (Freeland and Swift, 1978). Surficial sediments range from fine sand along the southern shore of Long Island to pebbly gravel off the coast of New Jersey (Schlee, 1964). On a somewhat smaller scale, the sediments vary in color from yellow ochre to greenish gray and in composition from biogenic calcium carbonate to quartz and feldspar (Freeland and Swift, 1978).

The hydrography of the NYB changes seasonally. During the winter months, the entire water column is well mixed, but the coldest waters are found nearshore (Bowman and Wunderlich, 1977). Stratification begins in the spring and peaks in the summer. During stratification, a body of cold dense water, known as the cold pool, remains trapped on the bottom under the pycnocline on the midshelf. This cold pool forms a distinct band of midshelf temperature minima (about 4-5°C in midsummer) from Georges Bank to Cape Hatteras, persisting from late spring to early autumn (Houghton et al., 1982). Outside the cold pool, bottom temperatures in the NYB range inshore from less than 1°C in the winter to above 21°C in the summer. Deeper bottom water, near the 100-m isobath, is less variable, ranging from 7° to 12°C (Ketchum and Corwin, 1964). Salinity in the NYB varies less, with only a mild seasonal cycle. The lowest salinities (<31 psu) are found near the apex of the NYB, southeast of the Hudson River. However, salinities as high as 35 psu are found at the 200-m isobath. As with temperature, the largest seasonal fluctuations in salinity are found nearshore (Bowman and Wunderlich, 1977). Overall, nearshore habitats are less stable than those offshore in terms of both salinity and temperature.

Materials and methods

Sample collection

Ten sampling cruises were conducted between June 1996 and July 1997 on board an 85-foot commercial fishing vessel, the Illusion. Summer and fall cruises were conducted monthly, and winter and spring cruises were conducted every other month (Table 1). The 21 stations sampled during each cruise were arranged in three transects (west, central, and east), each with seven stations ranging in depth from about 20 meters to 90 meters (Fig. 1). Stations on each transect were located according to bathymetry so that six stations were distributed evenly across the range of depths (one approximately every 15 m of depth). The seventh station was placed to fill any large distance between stations that was due to variability in the slope. The distance from shore of stations at a particular depth varied between transects.

Not all stations were sampled during every cruise (Table 1). Owing to weather, only five stations were sampled during cruise 6 (December 1996) and only two of the three transects were sampled during the February 1997 and April 1997 cruises. Because less than 25% of the stations were sampled during cruise 6, we did not include these data in some of the analyses. However, cruises 7 and 8 were included because of their broader range of coverage (between the two cruises all three transects were covered at least once).

Temperature and salinity data were collected after trawling at each station by using an internally recording conductivity-temperature-depth (CTD) probe (Applied Microsystems Inc. model AMS-STD 12). Care was taken to collect data from as close to the bottom as possible without risking damage to the CTD. Because a backup CTD was unavailable and the CTD used was not always reliable, gaps in the physical data exist. Expendable bathythermograph (XBT) data collected nearby in early August by the MV *Oleander* as part of the NOAA Ship of Opportunity Program (SOOP) were substituted for missing temperature data for the central transect in that month.

Juvenile groundfishes were collected with a modified 2-m beam trawl with 4-mm stretch mesh net (and 5-cm stretch mesh outer net for chaffing), towed at about 2–2.5 knots. The addition of a meter wheel allowed us to measure the area swept as the distance trawled, multiplied by the width of the trawl (as in Carney and Carey, 1980). At each station, three 5-min tows were made; a fouled trawl was discounted and another trawl was repeated. The mean area swept during a 5-min tow was 698 m² ±35.1 m² (95% CI).



Figure 1

Twenty-one stations (numbers) on the continental shelf of the New York Bight were sampled with a two-meter beam trawl.

Table 1

Dates and sampling stations in the New York Bight for each of the ten cruises in this study. For each of the three transects, numbers indicate the stations sampled on a given cruise (sample locations are depicted in Figure 1).

Cruise number	Dates	West transect	Center transect	East transect
1	14–17 Jun 1996	8–13	16-21	1–7
2	9–11 Jul 1996	8-14	15 - 21	1-7
3	9–11 Aug 1996	$8 - 14^{1}$	$15 - 21^2$	$1 - 7^{1}$
4	20–22 Sep 1996	8-14	15 - 21	1 - 7
5	25–27 Oct 1996	8-14	15 - 21	1 - 7
6	10 Dec 1996	_	_	1-5
7	26–27 Feb 1997	8-14	_	1 - 7
8	16–17 Apr 1997	8-14	15 - 21	_
9	11–13 Jun 1997	8-14	15 - 21	1 - 7
10	15–17 Jul 1997	8-14	15 - 21	1 - 7
9 10 ¹ During	11–13 Jun 1997 15–17 Jul 1997 the August cruise, no	8–14 8–14 temperatur	15–21 15–21 e or salinity	1–7 1–7 data were

 $^{\it 2}$ The center transect was supplemented by XBT data.

A 2-m beam trawl is the recommended standard trawl for juvenile groundfish research because its fixed width allows for ready quantification of the area trawled (Kuipers et al., 1992). Our trawl had skids that were heavier than those on most standard 2-m beam trawls in order to reduce the amount of time the trawl took to reach the bottom and to ensure that it was heavy enough to remain there. To accommodate the increased weight (about 38 kg) and prevent the trawl from digging into the sediment, the skids were also longer (0.85 m) and wider (0.1 m). Typically, 2-m beam trawls are not used in depths greater than seven meters (Rodgers, 1992; Gibson, 1994; but see Pearcy, 1978); however, these modifications enabled us to trawl easily in waters as deep as 100 m.

Fish samples were sorted on deck and all recently settled juvenile fishes (age-0) were preserved in 95% denatured ethanol. These fish were measured in the laboratory to the nearest tenth of a millimeter standard length (SL) with digital calipers. Older fish were measured on deck to the nearest millimeter and returned to the water. With the exception of *Sebastes* and *Urophycis* spp., all age-0 fishes were identified to species. Fish stages were identified according to morphological changes such as squamation and, for flatfish, eye migration, as well as analysis of length frequencies of cohorts. The relative abundance and composition of the remaining sample (shell hash, sand dollars, and shrimp) were estimated from subsamples.

Length-frequency distributions of each species collected were calculated for each cruise. To account for differences in sampling effort among cruises, abundance data were standardized to the average cruise, which had 63 tows (21 stations \times 3 tows each) lasting five minutes each. Length frequencies were then used to estimate the size range of the age-0 fishes collected during each cruise, as well as to infer some growth rates of the age-0 cohort between cruises.

Distribution analysis

Abundance data were standardized to the average number of fish per 1000 m². Because we were specifically interested in early juveniles, and adults were not efficiently collected, we limited our analysis to age-0 fishes. All species of age-0 fishes collected were included in the analyses. The distribution of age-0 fishes was evaluated with respect to a suite of environmental data (bottom temperature, bottom salinity, and depth) by comparing weighted means for each species (Scott, 1982). For a given species, an environmental variable such as temperature was weighted by the abundance of that species at each sampling station. The sums of each weighted variable were then divided by the total abundance of that species collected to yield a mean value for that species on that environmental parameter.

Cross-shelf migrations with ontogeny are a common feature of demersal fishes, particularly flatfish (Riley et al., 1981; Toole et al., 1997). To determine changes in cross-shelf distribution with size, weighted mean depths by size class were calculated for the more abundant species collected. In particular, distinct differences between the location of near-settlement size fishes and larger age-0 fishes might indicate migration between settlement and nursery habitats.

Environmental correlates

Distribution and abundance of fishes in relation to underlying multivariate environmental gradients were analyzed by canonical correspondence analysis (CCA) by using the software program CANOCO (ter Braak, 1992). This analysis has been widely applied in the field of community ecology (ter Braak, 1995; ter Braak and Verdonshot, 1995; Rakocinski et al., 1996); it entails reciprocal averaging of species and environmental data based on the assumption of a unimodal response of species abundance to the environment (Palmer, 1993; ter Braak, 1995). In a comparison of ordination techniques, Palmer (1993) found that CCA was robust, being less susceptible to spurious results such as the "arch effect" often common to principal components analysis (PCA). Furthermore, Palmer's (1993) simulations of CCA illustrated that noisy or skewed species data could be compensated for, and a variety of data types and sampling design were possible.

In total, 25 environmental variables (Table 2) were sampled during the cruises and included in the CCA analysis. Bottom temperature and salinity (from CTD casts), station depth (from an onboard depth sounder), latitude and longitude (global positioning system [GPS]), and distance from shore (nautical charts) were employed as continuous measures during the analysis. The relative abundances of nonfish constituents collected by the trawl were also considered to be environmental variables. Information on surficial sediment character at each station, another environmental variable we employed, was obtained from published data from the Marine EcoSystems Atlas (MESA) program's New York Bight Project (Freeland and Swift, 1978). Although these data are independent of this study, the MESA sampling area was the same and the spatial resolution of its sediment sampling was fine enough to obtain general information suitable for our analysis. The data on nonfish trawl constituents and surficial sediments were entered into the analysis as scaled values (i.e. as a number describing relative abundance among stations and tows). Because collections of both species and environmental data were made year-round, seasonal variables were also included and coded in the analysis as a set of nominal variables: spring (March–May), summer (June-August), fall (September-November),

Environmental variable	Code	Туре	Units	
Spring	Spr	seasonal	true-false	
Summer	Sum	seasonal	true-false	
Fall	Fall	seasonal	true-false	
Winter	Win	seasonal	true-false	
Latitude	Lat	physical	^o latitude	
Longitude	Long	physical	^o longitude	
Bottom temperature	Т	physical	^o Celsius	
Bottom salinity	Sal	physical	psu	
Distance from shore	D	physical	km	
Depth	Z	physical	m	
Median grain size	MePhi	physical	Φ -scale	
% organics in sediment	%Org	physical	percent	
% calcium carbonate in sediment	%CaCO3	physical	percent	
Northern sea stars, Asterias forbesi	noss	biological	relative volume of sample	
Sand dollars, Echinarchnius parma	snd	biological	relative volume of sample	
Margined sea stars, Pontaster tenuispinus	marg	biological	relative volume of sample	
Small shell fragments	hash	biological	relative volume of sample	
Large mollusk shells and shell pieces	shell	biological	relative volume of sample	
Sea scallops, Placopecten magellanicus	scall	biological	relative volume of sample	
Sand shrimp, Crangon septemspinosa	crang	biological	relative volume of sample	
Boreal shrimp, Pandalus montagui	borsh	biological	relative volume of sample	
Rock crabs, Cancer spp.	crab	biological	relative volume of sample	
Amphipods	amph	biological	relative volume of sample	
Fig sponges, Suberites ficus	spon	biological	relative volume of sample	
Large biogenic tubes	tube	biological	relative volume of sample	

Table 2

and winter (December–February). Each environmental variable was standardized to have a mean of zero and a standard unit of variance so that all variables had equal weight despite differences in the scales of their usual units.

Although seasonal patterns are likely to be important in juvenile fishes, these patterns are likely to be influenced by the spawning patterns of adult fishes rather than by habitat selection of settling fishes. These seasonal effects may dilute the variation explained as due to other factors. Some environmental factors such as temperature, salinity, and the presence of ephemeral biota that vary with season are possibly of more interest than simply accounting for settlement timing. To this end, a partial CCA was conducted using season as a covariable. Partial CCA allows environmental variables to be treated as covariables, thus removing their influence from the rest of the data set (ter Braak and Verdonschot, 1995).

A forward selection of environmental variables was used to select a minimum set of environmental variables that best explained the distribution and abundance of age-0 fishes (ter Braak, 1992). Forward selection begins by the selection of the variable that explains the most variation in the data set. This variable is then treated as a covariable, the data set is then reevaluated, and the next most important variable is selected. This procedure continues until the desired subset of variables has been selected. To test the advisability of adding variables, Monte Carlo permutation simulations are conducted. Variables are added as long as their addition continues to contribute significantly to the explained variance (P<0.05). Forward selection was performed on the data set, with season treated as a covariable. The combination of partial CCA and forward selection is not considered problematic with regard to the assumptions of the analysis (ter Braak, 1992).

Results

Faunal composition and distribution

A total of 21,309 fish representing 47 species and 32 families were collected over the course of the ten cruises and the 659 tows. Of these 47 species, 33 were collected as age-0 juveniles, including 25 spe-

Table 3

Minimum, mean, and maximum standard length (mm) of the 32 species of age-0 demersal fish collected. Maximum larval size (Fahay, 1983) and sample size (n) are also indicated. Maximum sizes estimated from size-frequency distributions are included (see Figs. 4–6). Species are ordered by decreasing total abundance. An asterisk next to minimum standard length indicates that the species was collected at near-settlement size.

Species	Species code	Max larval size (mm)	Min. SL (mm)	Avg. SL (mm)	Max. SL (mm)	n
Pleuronectes ferrugineus	PLEFER	11–16	5.7*	17.4	34.9	10,452
Merluccius bilinearis	MERBIL	17-20	12.6^{*}	28.2	145.0	3,195
Liparis inquilinus	LIPINQ	12-13	9.6*	20.4	49.0	595
Raja erinacea	RAJERI	80-90	87.2^{*}	117.6	146.4	281
Urophycis spp.	UROSPP	20-25	8.8*	32.5	49.0	224
Macrozoarces americanus	MACAME	30	32.0^{*}	89.1	119.0	213
Citharichthys arctifrons	CITARC	13-15	10.8^{*}	18.8	29.7	120
Lepophidium profundorum	LEPPRO	20	85.5	85.5	115.0	117
Ophichthus cruentifer	OPHCRU	83.5	70.0^{*}	111.0	146.0	80
Gadus morhua	GADMOR	20-30	20.0^{*}	36.8	49.0	62
Peprilus triacanthus	PEPTRI	12-18	6.8*	15.2	45.0	61
Glyptocephalus cynoglossus	GLYCYN	22-35	13.5^{*}	30.0	47.5	40
Helicolenus dactylopterus	HELDAC	20	21.0^{*}	28.9	35.0	38
Enchelyopus cimbrius	ENCCIM	20	9.1*	26.7	47.0	35
Etropus microstomus	ETRMIC	10-12	14.7^{*}	23.6	29.0	26
Prionotus carolinus	PRICAR	20	11.1*	30.1	49.0	26
$Myoxocephalus\ octode cemspinos us$	MYOOCT	15	15.9^{*}	22.2	44.0	22
Scophthalmus aquosus	SCOAQU	9	9.1*	59.8	143.0	19
Paralichthys oblongus	PAROBL	10-12	9.4^{*}	15.8	37.0	15
Hippoglossoides platessoides	HIPPLA	18-34	20.1^{*}	23.7	26.1	13
Ophidion marginatum	OPHMAR	35 - 50	52.1^{*}	64.4	75.3	10
Stenotomus chrysops	STECHR	17	52	64.4	75	10
Sebastes spp.	SEBSPP	24	25.5^{*}	28.1	33.1	8
Lophius americanus	LOPAME	50	56.0^{*}	74.2	96.5	5
Melanogrammus aeglefinus	MELAEG	20	39.0	44.7	48.0	4
Centropristis striata	CENSTR	8.3	25.0	29.8	35.5	3
Hemitripterus americanus	HEMAME	19	27.0	28.0	29.0	2
Astroscopus guttatus	ASTGUT	20	9.8*	9.8	9.8	1
Monolene sessilicauda	MONSES	33	41.0	41.0	41.0	1
Pholis gunnellus	PHOGUN	30-35	39.0^{*}	39.0	39.0	1
Tautogolabrus adspersus	TAUADS	8	8.7*	8.7	8.7	1
Citharichthys cornutus	CITCOR	13 - 15	53.2	53.2	53.2	1
Pleuronectes americanus	PLEAME	10–13	81.2	81.2	81.2	1

cies collected at near-settlement sizes on the shelf (Table 3). Two species represented 88.9% of the age-0 fishes collected: yellowtail flounder (*Pleuronectes ferrugineus*, 67.8%) and silver hake (*Merluccius bilinearis*, 21.1%). Overall, densities of these dominant species on the shelf during peak settlement averaged 55.7 and 26.23 per 1000 m², respectively (Table 4), although maximum densities of 771.4 and 660.9 per 1000 m², respectively, occurred during peak settlement in individual tows. In addition to age-0 juveniles, both larval (n=267, <2% total), and adult (n=2765,

13.0% total) fishes were captured with the trawl. Of the 25 species collected at or near-settlement size, 11 included individuals smaller than predicted settlement size, based on published maximum larval size (Fahay, 1983).

Most (94%) age-0 fishes were collected in the summer and fall (Table 4). *P. ferrugineus* and *M. bilinearis*, the two dominant species, settled almost exclusively during summer and fall, respectively (Fig. 2). However, if species richness is considered rather than species abundance, summer and fall are still the primary

Table 4

Mean seasonal density $(fish/1000 m^2)$ of 21 abundant age-0 fishes over the entire continental shelf of the New York Bight. Winter and spring cruises are combined. Species are grouped by their season of highest density and only species with a density greater than 0.1 in at least one season are included.

			Winter 1996–	
	Summer 1996	Fall 1996	Spring 1997	Summer 1997
Summer				
Pleuronectes ferrugineus	55.68	0.53	_	1.29
Citharichthys arctifrons	3.84	2.25	0.66	0.09
Macrozoarces americanus	0.94	0.36	0.16	0.20
Gadus morhua	0.40	0.03	0.14	_
Helicolenus dactylopterus	0.09	0.03	_	0.26
Peprilus triacanthus	0.24	0.04	_	0.17
Glyptocephalus cynoglossus	0.21	0.03	_	0.05
Enchelyopus cimbrius	0.21	0.03	_	0.05
$Myoxocephalus\ octode cemspinos us$	0.11	0.07	0.11	0.09
Fall				
Merluccius bilinearis	0.07	26.23	1.04	0.22
Liparis inquilinus	1.19	1.89	0.09	1.75
Urophycis spp.	0.26	1.88	1.05	0.07
Lepophidium profunforum	0.09	0.77	_	_
Ophichthus cruentifer	0.02	0.61	_	0.11
Etropus microstomus	0.11	0.40	0.79	0.05
Paralichthys oblongus	0.06	0.13	—	0.05
Winter-Spring				
Raja erinacea	0.60	0.56	0.90	0.54
Prionotus carolinus	0.04	0.22	0.46	_
Centropristis striata	_	0.15	0.20	_
Ophidion marginatum	_	_	0.11	_
Scophthalmus aquosus	0.02	0.07	0.11	0.05

time of settlement on the shelf (Fig. 2). Although many species settled between August and October, *Macrozoarces americanus* and *Gadus morhua* settled, and *Raja erinacea* hatched, on the shelf starting in midwinter.

Juvenile fish were colleced at all 21 stations sampled. Mean depths of all species of age-0 fish, weighted by abundance, are shown in Figure 3. Although the depth distributions cover the entire depth range of the surveyed shelf, for convenience of discussion we separate species into three depth groups (inner, middle, and outer shelf; Table 5). Inner shelf species included two flounders (Etropus microstomus and Paralichthys oblongus), searobin (Prionotus carolinus), and fourbeard rockling (Enchelyopus cimbrius). Little skate (*Raja erinacea*) was collected on the inner shelf at sizes near to hatching size. Midshelf settlers were dominated by Pleuronectes ferrugineus but also included large numbers of inquiline snailfish (Liparis inquilinus) and phycid hakes (Urophycis spp.). The dominant fish that settled on the outer shelf were silver hake (Merluccius bilinearis), Gulf Stream flounder (*Citharichthys arctifrons*), margined snake eel (*Ophichthus cruentifer*), fawn cusk eel (*Lepophidium profundorum*), and black-bellied rose fish (*Helicolenus dactylopterus*).

Generally, distributions along depth (Fig. 3A) and salinity (Fig. 3B) gradients showed similar but inverse trends; this finding was expected because of high correlation between bottom depth and bottom salinity. Weighted average distributions with respect to bottom temperature (Fig. 3C) did not show similar trends; seasonal variation in temperature and the presence of minimum temperatures midshelf during the summer precludes temperature and depth trends from being similar. Midshelf species such as *P. ferrugineus* and *Liparis inquilinus*, which settle in summer, had the coldest mean temperatures of collection. Outer-shelf species found in slope water had slightly warmer preferences, and those of inner-shelf species were even warmer.

Individual year classes were distinct, based on length frequencies for the more abundant species (Fig. 4–6). For several species (e.g. *P. ferrugineus* and



M. bilinearis), large decreases in abundance were observed following initial settlement, whereas abundance decreased at a more modest rate for other species such as *C. arctifrons*, *Macrozoarces americanus*, and *L. inquilinus*.

For species such as P. ferrugineus and L. inquilinus that settled during the summer (Fig. 4), the cohort could be followed for the entire first year after settlement (June 1996–July 1997). For other species that did not settle in the summer (Figs. 5 and 6), the cohort from the previous year was observed until the new cohort settled in the fall, winter, or spring. Inferred growth rates from the length-frequency distributions varied from two millimeters per month for species such as P. ferrugineus and L. inquilinus (Fig. 4), to about 15 mm per month for Merluccius bilinearis (Fig. 5) and Macrozoarces americanus (Fig. 6).

Cross-shelf movement between and within settlement and nursery areas was evident for some species but not for others. *Pleuronectes ferrugineus, Etropus microstomus*, and *Lepophidorum profundorum* are examples of species with consistent mean depths of distribution during their first year after settlement (Fig. 7, A–C). However, *M. americanus* exhibited a gradual migration towards deeper waters, whereas *C. arctifrons* and *Merluccius bilinearis* moved rapidly after settlement to waters about 30 meters deeper for the remainder of the first year (Fig. 7, D–F).

Habitat characteristics

Bottom temperatures in the NYB were dynamic (Fig. 8), and seasonal shifts in temperature were more varied at nearshore stations (5-20°C at the 25-m isobath) than at offshore stations (7–11°C at 90 m). Midshelf bottom temperatures showed a moderate seasonal range (4.3-14°C at 50 m). During the summer, bottom temperatures were stable, and there was only a slight increase of about 1°C per month. The highest rate of increase in bottom temperatures was recorded at the inshore stations: 8°C between August and September, associated with an early fall turnover in 1996. This was followed by the highest rate of cooling $(-3^{\circ}C)$ at the same nearshore locations between the September and October cruises. During fall turnover, the bottom temperatures increased by about 4°C per month over the midshelf, for a total of 8°C in two months. Following this



warming trend, temperatures decreased by about 1°C per month until they reached their minimum in April. Late winter bottom temperatures in 1997 were not as cold as midshelf temperatures during summer 1996.

Salinity was a more conservative hydrographic variable than temperature. Variation in seasonal bottom salinity was slight; all cruises had a salinity range of approximately 31-35.5 psu. Bottom salinities were lowest inshore near inlets (station 1) and the Hudson River (station 15). The correlation between bottom salinity and bottom depth was high (r=0.87). Higher bottom salinities (>34 psu) off-shore showed some fluctuation in their distribution on the outer shelf associated with similar fluctua-

tions in warmer bottom temperatures. These warm, high-salinity bottom waters are representative of slope water intrusions (Churchill, 1985; Flagg et al., 1995).

The total catch of benthic organisms from the trawl varied greatly between stations, but there were generally three major groups or types of trawl samples. Groups were delineated to some extent by the depth at which they were collected. Inner-shelf stations (<40 m) typically included such organisms as the common sea star (*Asterias forbesi*) and fig sponge (*Suberites ficus*). Gammarid amphipods, sand shrimp (*Crangon septemspinosa*), and northern moon snail (*Euspira heros*) constituted much of the rest of the nonfish fauna collected there. Sand dollar (*Echina*- rachnius parma) and valves of surf clams (Spisula solidissima) dominated the midshelf group (40-70 m) of benthic organisms. Shell hash collected midshelf consisted of fine fragments of sand dollar tests and larger pieces of clam valves. Small, recently settled rock crabs (Cancer borealis) were found in high numbers (>100 per 5-min trawl) during the summer in this type of sample. Margined sea stars (Pontaster tenuispinus) and sea scallops (Placopecten magellanicus) made up most of the trawl catch for deeper outer-shelf stations (70-90 m). Young pandalid shrimp (Pandalus montagui) constituted a large fraction (30-90%) of samples from these stations in late summer and fall. Larger crustaceans such as American lobsters (Homarus americanus) and large rock crabs (C. borealis) were occasionally abundant (>10 per 5-min trawl) at these stations. Several were collected during each cruise.

Table 5

Mean density (fish/1000 m²) of 21 abundant age-0 fishes within each of three depth strata: inner shelf (<40 m), middle shelf (41–70 m), and outer shelf (71–95 m) across all sampling periods. Species are grouped by stratum of their highest abundance; only species from Table 4 are included.

	Inner shelf	Middle shelf	Outer shelf
Inner shelf			
Raja erinacea	1.01	0.81	0.03
Etropus microstomus	0.88	0.01	_
Prionotus carolinus	0.21	0.11	0.01
Paralichthys oblongus	0.12	0.03	_
Enchelyopus cimbrius	0.10	0.06	0.08
Scophthalmus aquosus	0.09	0.01	_
Ophidion marginatum	0.06	—	—
Middle shelf			
Pleuronectes ferrugineus	15.31	49.81	2.25
Liparis inquilinus	0.03	1.94	1.11
Urophycis spp.	0.83	0.84	0.58
Macrozoarces americanus	0.03	0.79	0.69
Gadus morhua	0.16	0.38	0.01
Glyptocephalus cynoglossus	0.02	0.23	0.01
Peprilus triacanthus	0.05	0.19	0.05
Myoxocephalus			
octodecemspinosus	_	0.11	0.01
Centropristis striata	0.04	0.10	_
Outer shelf			
Merluccius bilinearis	0.40	5.42	14.69
Citharichthys arctifrons	0.29	0.64	5.63
Lepophidium profundorum	_	_	0.68
Ophichthus cruentifer	_	_	0.51
Helicolenus dactylopterus	—	—	0.14

Other groups of macrobenthos were ubiquitous. Hermit crabs and cancer crabs of intermediate sizes were found throughout the stations sampled. Although they dominated the midshelf, sand dollars were also collected at inner-shelf stations. Other large benthic fauna such as horseshoe crabs (*Limulus polyphemus*) and spider crabs (*Libinia emarginata*) were collected, but these collections were sporadic.

Species assemblages and environmental variables

Four canonical axes, each representing a linear combination of the environmental data, were calculated from the data set. These four axes together accounted for 36.7% of the variation in species abundance and 82.1% of the cumulative variation, in relation to the total variation explained by the environmental variables. A summary of eigenvalues and the variance accounted for by each axis is given in Table 6A. The variance explained by the entire ordination, as well as the first axis, was more significant than expected by chance, as calculated by a Monte Carlo permutation test (n=99 iterations, P=0.01 for both tests).

Interpretation of the relationships between environmental variables and the CCA axes involves determining which variables are most correlated to the axes. One intuitive and effective method of accomplishing this is to examine an ordination plot of environmental variables (Fig. 9). Environmental variables with large components along a CCA axis have high correlations to that axis. However, the results of the ordination with 25 environmental variables were difficult to interpret because of inherent covariability of variables with one another (Fig. 9, A–B).

Forward selection of environmental variables resulted in selection of five environmental variables (bottom temperature, depth, the relative abundance of scallops, longitude, and the relative abundance of margined sea stars). Eigenvalues of the forward selection of these five variables (Table 6B) are predictably lower than for the CCA with all 25 variables included (Table 6A). However, 59% of the variability explained with all 25 variables included was explained by these five environmental variables alone. Temperature represented 23% of the entire variability explained by the environmental data, depth contributed 18%, scallop abundance explained 8%, and longitude and margined sea star abundance combined explain an additional 5%. The remaining variables, which did not add significantly to the resulting explanation, each explained less than 4% of the variation. Because only five variables were selected, the four synthetic gradients (CCA axes) are each highly correlated with one of the environmental variables (Table 6A). Thus, to some extent each axis



is a proxy for the environmental variable to which it is highly correlated.

Examination of species-environment biplots revealed relationships between environmental variables and species distributions. The species-environment biplot for the first two axes represents the majority of the species-environment relationships that resulted from the partial CCA (Fig. 9C). The importance of depth and temperature to these two canonical axes (see Table 7) indicates that temperature and depth are the two most important determinants of the species data. Inner-shelf species such as *Stenotomus* chrysops, Paralichthys oblongus, Centropristis striata, and Etropus microstomus are located near the upper right-hand quadrant of the ordination (positive values for both of the first CCA axes). Outershelf species, such as the rockfishes, Sebastes spp., and Helicolenus dactylopterus and the snake and cusk eels (Ophichthus cruentifer and L. profundorum) are found in the lower right-hand quadrant (positive CCA 1 and negative CCA 2). Species from the middle shelf, particularly Pleuronectes ferrugineus and Liparis inquilinus, are located near the origin of the ordination diagram.



The origin represents the mean for each environmental variable, and those means are weighted by species abundance. Because of the numerical dominance of *P. ferrugineus* in the samples, its mean temperature and depth of collection is driving the location of the origin. Consequently, the location of *P. ferrugineus* is just slightly left of the origin. The mean depth distribution of *P. ferrugineus*, however, was midshelf and thus its abundance did not skew the species distributions about the second axis, CCA 2.

One of the largest effects of the forward selection of variables is that the third and fourth CCA axes (Fig.

9D) now have definite environmental correlates. When 25 variables were used during full CCA, no one variable stood out as a clear contributor to the variation along these axes (Fig. 9B). With the abundance of scallops being the important environmental gradient describing the third CCA axis, one important species association is made clear: the abundances of juvenile inquiline snailfish and scallops. The fourth CCA axis, representative of longitude, accounted for only 5% of the total environmental explanation of the species patterns. This pattern might be considered as the subtle variation among the three transects (west, central, and east).



Discussion

Many commercially and ecologically important species of demersal fishes in the NYB settle onto the continental shelf throughout the course of the year. In some cases settlement densities on the shelf may rival those of nearshore and estuarine species. For example, at some stations yellowtail flounder (*P. ferrugineus*) was found to have settlement densities as high as the long-term average for a congeneric estuarine species, plaice (*Pleuronectes platessa*), at approximately one per m^2 (Modin and Phil, 1994). Yet given the large areal extent of *P. ferrugineus* settlement on the shelf, its relative total abundance is potentially much larger. Similarly dense settlement may occur within portions of the shelf environment for other species such as *Merluccius bilinearis*. Even for those species collected in relatively low numbers, the large areas of NYB in which they settle suggests that total numbers are substantial.

Evidence that settlement does occur on the shelf is from two sources. The minimum size of collected



age-0 fishes (Table 3; Figs. 4–6) were near (and occasionally below) that reported for size at the end of the larval stage (Fahay, 1983). Moreover, although the total contribution of larvae to the trawl catch was low (<2% of numeric abundance), the presence of these specimens in our samples strengthens the assertion that they were collected near first settlement. Most fish larvae collected were metamorphosing or post-flexion flounder, particularly *P. ferrugineus*. Larvae from nondemersal fish species known to be present in the water column at this time of year (Kendall and Naplin, 1981; Cowen et al., 1993; Cho, 1996) were not collected by the trawl. Collected larvae, there-

fore, were likely taken near the bottom rather than during the deployment or recovery of the net.

Compared with settlement areas, nursery areas for groundfishes on the continental shelf are more problematic to define. Gibson (1994) described nursery habitat as being an area where the scope for growth is enhanced for settled juveniles. Scope for growth is a function of habitat quality and quantity, but these parameters, particularly quality, are difficult to measure. Nursery habitats are generally spatially and temporally species-specific, but two or more species may have similar nurseries. Within a single species, nursery and settlement habitats may



occur in the same area, include just a slight overlap with one another, or may be entirely separate spatial entities. Although association with settlement habitat is not a given, an area in which postsettled juvenile fishes persist and grow prior to first spawning must be considered to be nursery habitat. Evaluation of nursery habitat quality requires the comparison of growth rates among stations for individual settlement cohorts (Sogard, 1992; Jenkins et al., 1993)—information not presented in our study. For many species, however, growth certainly occurs on the shelf after settlement (Figs. 4–6).

For several of the species collected during this study in the NYB, nursery and settlement habitats are synonymous. For example, *P. ferrugineus*, *E. microstomus*, and *L. profundorum* were limited in their distributions, remaining unchanged from settlement throughout the first year of life (Fig. 7, A–C). Several other species, *M. bilinearis*, *C. arctifrons*, and *M. americanus* (Fig. 7, D–F) showed some movement in depth between settlement and nursery areas, as well as some indication of within-nursery migration across the shelf. Toole et al. (1997) observed similar migration between the settlement and nursery areas of Dover sole (*Microstomus pacificus*) and suggested that such movements were actively pursued by the juveniles, but the ultimate migratory cues remained unclear.

Within the NYB, several environmental gradients describe the spatial and temporal distributions of settlement habitats. Species-environment relationships from the ordination analysis reveal that temperature and depth explain most of the among-species variance in habitat associations. Previous studies of adult fishes in the NYB have shown the importance of temperature and depth in describing species assemblages (Colvocoresses and Musick, 1984). This is in contrast to the west coast of the United States, where fish habitat associations have been studies extensively for rockfish (Sebastes spp.) and to a lesser extent for flatfish. There, for many species, more importance has been attributed to geological features such as sediment size and bathymetric heterogeneity (Pearcy, 1978; Stein et al., 1992; Adams et al., 1995). Considering the higher level of geological diversity on the West Coast than in the NYB, this conclusion is not surprising.



Ordination of the 25 environmental variables with (\mathbf{A}) the first two and (\mathbf{B}) the third and fourth canonical axes. Seasonal variables (Spring, Summer, Fall, and Winter) are plotted as points, all other variables as vectors. Environmental variable codes are explicated in Table 2. Species-environment biplots are given in (\mathbf{C}) for the first two axes and in (\mathbf{D}) for the third and fourth axes of the partial CCA. Species codes are defined in Table 3. The relative rank of a species with respect to an environmental variable can be determined by extending a line perpendicular from the environmental vector to the species.



Other variables such as salinity, the abundance of benthic organisms, mean sediment size, as well as the proximate location of other essential habitats (e.g. estuaries), were correlated to distance offshore and depth and are thus possible contributors to observed habitat preferences. It is doubtful that a species would prefer habitat based on distance offshore or depth alone because both variables are spatial indices and as such, they can have no direct effect on habitat quality. The indirect effects of these spatial variables on habitat quality may be associated with how they correlate with the distribution of

Table 6

(A) Results from the CCA including all 25 environmental variables. The sum of all canonical eigenvalues (2.187) was 44.7% of the total inertia (4.891). (B) Results of the CCA with forward selection (5 environmental variables) and season treated as a covariable. The sum of the unconstrained eigenvalues (3.825) is 78.2% of the total inertia, indicating that the seasonal component contributed 21.8% of the variance. The sum of all canonical eigenvalues (0.636) is 16% that of the sum of all unconstrained eigenvalues and 13% of total inertia. See text for explanation of terms.

	Axes				
	1	2	3	4	Total inertia
A					
Eigenvalues	0.809	0.464	0.284	0.238	4.891
Species-environment correlations	0.961	0.873	0.704	0.691	
Cumulative percentage variance of species data	16.5	26.0	31.9	36.7	
of species-environment relation	37.0	58.2	71.2	82.1	
Sum of all unconstrained eigenvalues					4.891
Sum of all canonical eigenvalues					2.187
В					
Eigenvalues	0.269	0.230	0.078	0.047	4.891
Species-environment correlations	0.721	0.735	0.518	0.365	
Cumulative percentage variance					
of species data	7.0	13.0	15.1	16.3	
of species-environment relation	42.3	78.5	90.8	98.3	
Sum of all unconstrained eigenvalues (after fitting covariables)					3.825
Sum of all canonical eigenvalues (after fitting covariables)					0.636

important factors or combinations of factors, or with both. For example, age-0 inquiline snailfish (L. inquilinus) are found almost exclusively in association with the presence of sea scallops, with which they have their inquiline relationship (Able and Musick, 1976). The distribution of these fishes on the mid to outer shelf is therefore not necessarily directly affected by any physiological response to depth or distance offshore; rather, they are probably most affected by their dependence on sea scallops for shelter. The distribution of scallops in turn may be affected by such variables as temperature, salinity, circulation pattern, and the production of phytoplankton (Stewart and Arnold, 1994). Temperature, however, may have a direct effect on the quality of habitat for a given species because many physiological functions such as respiration, metabolism, and growth are directly controlled by changes in temperature (Neill et al., 1994).

Temperature and depth not only seem to provide the best description of the overall variance within this data set, but, along with salinity and time of year, form the basis for the hydrographic description of the NYB. In general, the bottom waters of

Table 7

Weighted correlations between the five environmental variables selected during the CCA with forward selection and the axes of from the analysis. Numbers in bold indicate the strongest correlation for each of the four axes. See Table 2 for meaning of environmental variable codes

Axis	Temp	Z	Scall	Long	Marg
CCA 1	0.8262	0.4257	-0.0796	0.3723	0.6508
CCA 2	0.4932	-0.7895	0.1636	-0.2067	-0.5973
CCA 3	-0.0819	0.1485	0.9711	-0.0620	0.1028
CCA 4	0.0863	-0.3690	-0.1399	-0.8822	-0.0934

the NYB can be broken down by location into three regions: inner-shelf waters, middle shelf (cold pool), and outer shelf. This breakdown of the continental shelf for the NYB is consistent with that of other shelf systems (McRoy et al., 1986; Werner et al., 1997). During the summer, waters overlaying these regions of the shelf are divided by two frontal features: the inner front, dividing the inner and middle shelves, and the middle front, dividing the middle and outer shelves. A third front, the shelf-break front, separates the outer shelf from the continental slope (McRoy et al., 1986). These three hydrographic features can be utilized as an effective means for describing the general nursery areas for groundfishes within the NYB.

Differences in environmental conditions occur not only along the shelf, but also temporally. Patterns in surficial sediments and bathymetry change on the order of hundreds to thousands of years. These characteristics are relatively stable in their distributions on the shelf. Other factors such as benthic faunal distributions may change from year to year but should remain unvarying during the first year of a fish's life. Hydrographic variables and the presence of ephemeral predator and prey species, however, may change on a seasonal or even daily basis. The scale and extent to which these variables change are important in understanding the nature of the settlement and nursery areas.

The turnover of the cold pool in the fall represents an abrupt change in bottom temperature that subsequently may have biological significance. In our study, higher mean catch of age-0 P. ferrugineus corresponded to the distribution of the cold pool, and catch dropped dramatically in the fall as bottom temperature increased during cold pool turnover. For a species with a preference for low temperatures, increased temperature may be a density-independent source of mortality. In at least one case, an increase in mortality of larval P. ferrugineus on Georges Bank has been associated with an increase in temperature from a warm-core ring (Colton, 1959). Although such abrupt temperature fluctuations at greater depths are not common, they may occasionally occur near the edge of the shelf in some areas, perhaps associated with Gulf Stream meanders (Able et al., 1993). Able et al. (1993) found a temperature increase of 6°C over a two-day period, and they suggested that such temperature fluctuations may cause a cessation of feeding for tilefish, Lopholatilus chamaeleonticeps. In contrast, some species may benefit from increased bottom temperatures associated with turnover. For example, in our study, settlement of M. bilinearis did not peak until after turnover, when bottom temperature was greater than 9°C. Likewise, spawning distribution for Atlantic croaker (*Micropogonias undulatus*) in the southern portions of the MAB has a positive association with the presence and location of warmer waters coincident with the cold pool turnover (Norcross and Austin, 1988).

This study and another from Georges Bank (Frank et al., 1992) indicate that the distribution of *P. fer-* rugineus corresponds well with bottom temperature. The presence of *P. ferrugineus* is negatively correlated with bottom temperature in the NYB, with highest abundance in the coldest waters ($<8^{\circ}$ C). However, on the Grand Banks the correlation with temperature was positive, with most fish collected above the warmest bottom waters ($>3^{\circ}$ C). Juveniles from the Grand Banks, however, were collected off the bottom, and highest abundances were found just below the thermocline, in waters closer to 6°C. Temperatures between 4° and 8°C have been noted as the preferred temperatures for older *P. ferrugineus* (Scott, 1982; Ross and Nelson, 1992; Walsh, 1992), and the evidence from these studies suggests that this may be true for age-0 *P. ferrugineus* as well.

Besides P. ferrugineus, several other boreal species, American plaice (*Hippoglossoides platessoides*), haddock (Melanogrammus aeglefinus), and Atlantic cod (Gadus morhua), were collected in our samples from the cold pool. Although not as numerically dominant as *P. ferrugineus*, the presence of these species this far down the coast suggests that the cold pool may act as a temporary refuge from the warmer waters normally associated with lower latitude. Metapopulations of such species, wherein local populations occupy small areas of suitable habitat outside the main population, are a potential confounding factor to the management of these species (Bailey, 1997). In the extreme, these juveniles may not be viable additions to the population if environmental conditions are not suitable for them to reach maturity. Just as warm-core eddies and eddy streamers may bring expatriates into this area from the south in the summer (Hare and Cowen, 1991), the cold pool may allow boreal species to temporarily extend their range southward during the summer. It is possible that conditions may occasionally enhance survival in such potentially marginal habitats to the extent that success of the population year class is facilitated.

In our study, we used trawl data to describe the general distribution and large-scale habitat associations of age-0 fishes. The resolution obtainable from trawl data is limited to the area swept (about 700 m²). Such resolution is sufficient to determine differences between stations that are 10 km apart but not to deterine the heterogeneity in habitat within a station. In situ methods, including the use of manned submersibles, are required for these types of smallscale studies (see Auster et al., 1991, 1997; Adams et al., 1995). One other drawback of using a trawl to quantify fish abundance is that trawls are inherently poor at collecting all fishes present in a given area; gear selection is size- and species-specific. However, if gear selection is constant between sites, trawl samples should be comparable (Kuipers et al., 1992). The estimation of abundances. For a trawl to be efficient, demersal fishes must remain near the bottom. Recently settled juveniles of some species, such as *M. bilinearis*, have been shown to make nightly excursions away from the bottom to feed (Fahay, 1974). For a fusiform juvenile like *M. bilinearis* this ability is not surprising. However, the pleuronectiform P. ferrugineus has been collected well off the bottom on the Grand Banks, not only as larvae but also as juveniles (Frank et al., 1992). These "pelagic juveniles" were of the same size classes (10-34 mm) as the postmetamorphic flounder we collected on the bottom with a 2-m beam trawl in our study. In extensive studies in the MAB with comparable or larger midwater sampling gear, few P. ferrugineus larger than 15 mm were collected (Morse, 1989; Cowen et al., 1993). For the NYB, however, juvenile P. ferrugineus do not appear to exhibit such trawl-avoiding behavior. This regional difference in vertical distribution of >20-mm postmetamorphic young may be due either to differences in the temperature structure of the water column (i.e. depth of optimal temperature, as discussed above) or to some other unknown latitudinal difference in developmental rate, settlement size, or behavior (Miller et al., 1991; Fuiman and Higgs, 1997; Osse and Boogaart, 1997).

In summary, age-0 demersal fishes utilize the continental shelf of the NYB as both settlement and nursery habitat. According to our findings, the shelf of the NYB can be divided into three broad nursery areas (inner, middle, and outer shelves) and can be described by species assemblage as well as by hydrography. There is a need for more research concerning the quality of habitats for age-0 fishes in the NYB. Information on smaller-scale variation in habitat for age-0 fishes may be just as revealing as that for larger macrobenthos (see Auster et al., 1991). Manned submersibles may be used to determine such small-scale habitat associations, even for small juveniles. Differences in growth rates of given species among habitats should also shed light on habitat quality within the NYB. Nursery habitats play an important role in the life history of marine fishes, and knowledge gained about the distribution and quality of these areas for commercially important offshore species should help to improve management of these areas..

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