

Effects of anthropogenic and natural disturbance on a recently settled continental shelf flatfish

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ABSTRACT: Concern over essential fish habitat characterization and conservation has directed attention toward the potential impact of mobile fishing gear on benthic ecosystems. However, previous findings do not necessarily extend to all environments, life stages, and/or gear types. The juvenile stage of benthic marine fishes is one such life stage that may be sensitive to disturbance. We examined the impact of commercial scallop dredge gear on a recently settled, continental shelf fish within the context of a sand sediment, storm-dominated system, the New York Bight. From June 1999 to July 2000, experimental manipulations with spatially replicated control-impact effects were used to investigate the immediate and longer-term consequences of a dredging event on young-of-the-year (YOY) yellowtail flounder *Limanda ferruginea* and its benthic nursery habitat. Contrary to expectation, *L. ferruginea* abundance did not decrease significantly immediately after dredging. Rather, at high-density sites, continued recruitment generated increases of smaller individuals across treatments. A significant decrease of older YOY *L. ferruginea* and available benthic prey was observed 3 mo later following a series of major natural perturbations (Hurricanes Dennis, Floyd, and Gert). Using concomitant buoy data, we also examined the physical regime of the region as it relates to important benthic settlement windows. Increased levels of natural disturbance during the fall and winter months appeared to play a critical role in shaping inner-mid-shelf seafloor architecture, effectively obscuring any longer term dredge-related signals. The results, overall, tend to highlight the vulnerability of New York Bight shelf habitats to multiple forms of disturbance.

KEY WORDS: Dredging · Juvenile fish · *Limanda ferruginea* · Disturbance · New York Bight · Nursery habitat · Storms · Submersible

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INTRODUCTION

In coastal marine environments, the presence of discrete microhabitats, substrates, and physical regimes exerts a profound influence on the recruitment, growth, and survival of local species (e.g. Wahle & Steenack 1991, Tupper & Boutilier 1995, Stoner et al. 1997). These features presumably constitute 'high quality' habitat wherein future reproductive potential is optimized (Gibson 1994, Beck et al. 2001). Further, the functional role of this quality varies with the spatial

scale under consideration (Levin 1992, Mullin 1993, Langton et al. 1995). Consequently, examples of habitat selection in marine systems range from small-scale obligatory relationships (Able & Musick 1976: inshore snailfish *Liparis inquilinus*) to complex spatio-temporal exchanges (Hare & Cowen 1996: bluefish *Pomatomus saltatrix*). However, life history information of this quality, at any scale, is lacking for a majority of benthic continental shelf fish species, particularly during the first year of life (USDOC 1996, Able & Fahay 1998, Collette & Klein-MacPhee 2002).

The evolving concept of what makes a fish habitat 'essential' is compounded by concern over impacts by mobile bottom fishing gear, the use of which is common out to (and beyond) the shelf edge and upper slope of coastal systems worldwide (Watling & Norse 1998). The real and potential ecological consequences of gear disturbance for a variety of continental shelf environments cannot be overstated (reviewed in Jennings & Kaiser 1998, Auster & Langton 1999). For example, a number of studies have convincingly documented real-time impacts of mobile gear on site-attached organisms (increased mortality, decreased biomass, recruitment failure) as well as on entire benthic communities (e.g. Eleftheriou & Robertson 1992, Currie & Parry 1996, Kaiser & Spencer 1996, Freese et al. 1999). Others have reported the effects of chronic fishing (reduced complexity, diversity, niche breadth) using historical fishing records and modern side-scan techniques as guideposts (e.g. Auster et al. 1996, Collie et al. 1997, Thrush et al. 1998, McConnaughey et al. 2000). More recent work has attempted to identify the causal mechanisms behind impact-related change through analyses of sediment chemistry and nutrient composition (Watling et al. 2001). In a broad sense, intuition concerning negative impacts of fishing gear has been well supported in the scientific literature (Collie et al. 2000).

Despite a growing number of case studies, generalized effects of fishing remain unclear due to significant gaps in knowledge from multiple habitats (outer continental shelves, deeper water), disturbance regimes (chronic natural, chronic anthropogenic), and biological communities (Collie et al. 2000). Interpreting experimental results from a given habitat is difficult, as only a small subset of variables can be measured and controlled for at one time (Lindegarh et al. 2000, Hewitt et al. 2001). To complicate matters, gear effects are often embedded within a background of natural disturbance on storm-dominated shelf systems (Hall 1994). For example, Churchill (1989) argued that wave-induced oscillatory currents constitute the main mechanism for sediment resuspension over portions of the inner-mid Middle Atlantic Bight continental shelf, while trawl-generated disturbance predominates at outer shelf-slope locales. Consequently, benthic species may vary widely in their response to disturbance through the complex interaction between habitat and life history (e.g. Kaiser et al. 1998, Lindholm et al. 1999). Benthic fishes regulated by one or more critical life-stage transitions (metamorphosis, settlement) may be particularly susceptible to habitat alteration. Conversely, certain families (flatfish) may become adapted to chronically disturbed environments contingent on their functional role in the ecosystem (Hall 1999). Thus, extrapolating previous findings to novel habitats and species is a risky proposition.

The New York Bight continental shelf is an appropriate biological and physical setting for investigating the intersection of habitat quality and physical disturbance. The shelf provides habitat for over 30 species of early-stage groundfish and many of their adult counterparts (Steves et al. 2000, Steves & Cowen 2000). Although infused with substantial stochastic variability, settlement patterns of local recruits are predictable in both a spatial and temporal sense (Sullivan et al. 2000). These shelf habitats also support active scallop and winter otter trawl fisheries that may account for elevated levels of anthropogenic disturbance out to and beyond the upper slope. Both components (nursery habitat, fishing grounds) are overlain on a seasonal, storm-driven system punctuated by rare, high magnitude events (hurricanes, winter storms; Butman 1987). The present study used a spatially replicated BACI (before-after-control-impact) experimental design (Underwood 1991, Green 1993) to investigate the effects of mobile, commercial scallop dredge gear on New York Bight young-of-the-year (YOY) yellow-tail flounder *Limanda ferruginea* and its benthic nursery habitat. The following 4 null hypotheses concerning the spatial and temporal effects of a single dredging event were considered: specifically, that there is no significant difference from before to after dredging in (H_1) YOY *Limanda ferruginea* abundance, (H_2) *L. ferruginea* size structure, (H_3) benthic habitat structure, and (H_4) benthic prey abundance. In order to account for potential sources of additional shelf-wide variability, the natural physical character of the region was described using concomitant NOAA buoy data and surficial sediment records. Finally, the input and active participation of the fishing community itself (fishing vessel [FV] 'Kathy Ann', Barnegat Light, New Jersey) was sought in order to foster a more balanced view of the potential outcomes of the experiment (Churchill 1998).

MATERIALS AND METHODS

Overview and sampling design. Three sites (45, 67 and 88 m water depth)¹ were selected near the southern limit of the New York Bight for a pre-dredge submersible survey, experimental scallop dredging, and 3

¹The original study design attempted to target recruits of several different species (*Limanda ferruginea*, *Merluccius bilinearis*, *Citharichthys arctifrons*) over a range of depths (mid to outer shelf). However, *Limanda ferruginea* (Sites 1 and 2) was the only YOY groundfish with appreciable densities during all experimental time steps. Although deeper depths rarely receive *L. ferruginea* recruits, portions of the benthic data from Site 3 were analyzed for comparison purposes

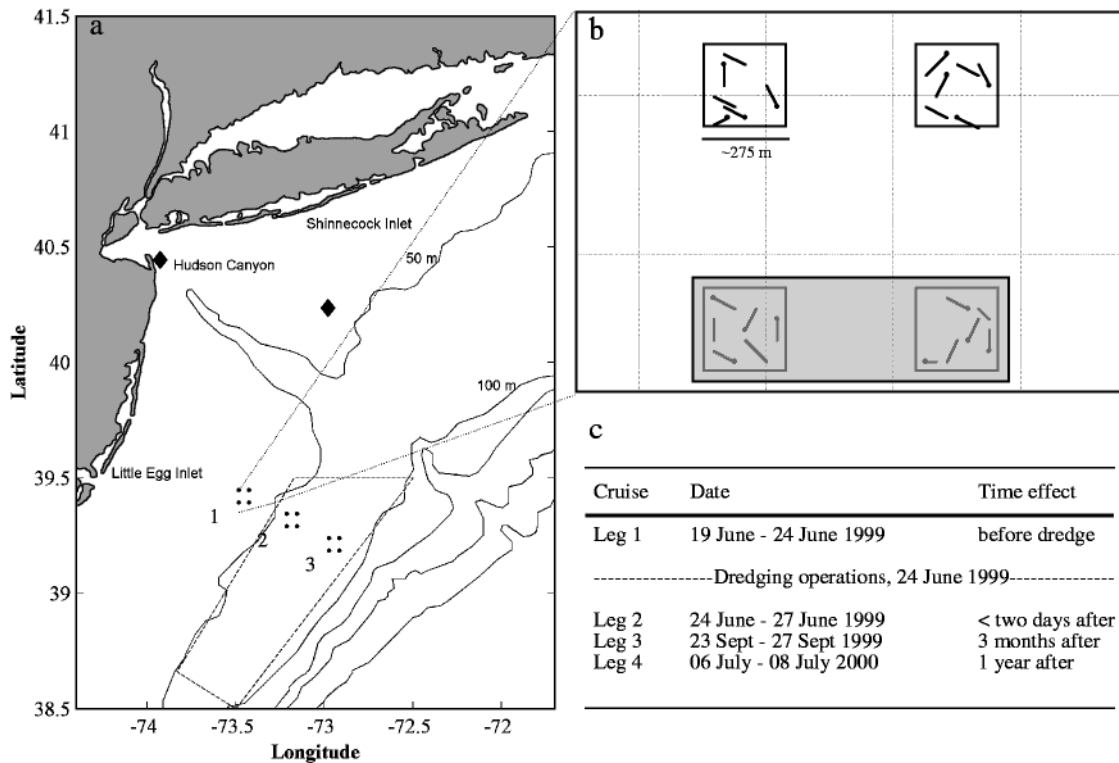


Fig. 1. (a) Locations of experimental dredging sites (::) on the New York Bight continental shelf. The trapezoidal box marks the boundary of the Hudson Canyon Closed Area. NOAA buoy locations are noted by ♦. (b) Detail of seafloor sampling at an individual site (Site 1, 45 m water depth) depicting experimental boxes (2 control, 2 impact) with component submersible transects (line) and benthic suction samples (point) (data from July 2000 mission). The shaded rectangle denotes the dredging corridor of FV 'Kathy Ann'. (c) Sampling dates and associated time effects

post-dredge surveys (<2 d, 3 mo, and 1 yr after impact; Fig. 1). To minimize potential confounding effects due to recent, unrelated trawling events, the 2 deep sites were located within the Hudson Canyon Closed Area (dashed box, Fig. 1a). Based on 1999 vessel monitoring system (VMS) data, it is possible that Site 1 was commercially trawled at least once in the months leading up to the experiment (NEFSC 2002). Of critical importance at each depth was the inclusion of multiple control and dredge treatments to reliably detect and interpret significant ecological effects. To this end, coordinates for four $275 \times 275 \text{ m}^2$ experimental boxes (each separated by at least 1 box length) were selected at all sites prior to sampling (Fig. 1b). From each quartet, 2 adjacent boxes were randomly chosen for experimental dredging, with the remaining 2 designated as controls. Surveys completed in each box at each time step consisted of: (1) an underwater visual census of YOY *Limanda ferruginea* and associated habitat using the submersible Delta (Delta Oceanographics), (2) beam trawl collections of recruits from the support vessel Atlantic Surveyor, (3) continuous, standard meteorological data downloaded from NOAA buoy stations, (4) a series of benthic 'cores' using the submersible's suction arm.

Experimental dredging. Following the initial pre-dredge survey and associated collections (see 'Underwater surveys' below), the commercial scallop FV 'Kathy Ann' (Barnegat Light, New Jersey) was given the coordinates to each impact box and instructed to thoroughly dredge the bottom with rigging, orientation and gear deployment following standard fishing operations. Paired New Bedford-style dredges (4.6 m wide, 89 mm ring size) were used for all experimental treatments. Scallop dredging was conducted as one continuous corridor between random, adjacent impact boxes to allow for a complete and realistic coverage of the bottom (Fig. 1b). To record bycatch as well as verify fishing effort and configuration, an independent scientific observer was placed on-board throughout dredging operations. Once experimental dredging was completed at each site, post-dredge surveys were initiated immediately (pending ship transit time and completion of remaining pre-dredge work).

Underwater surveys. Generally, 6 to 8 underwater visual/Hi-8 video transects (~3 transects per observer per dive) were completed in each box for each time step to calculate YOY fish abundance and view associated habitat change (Fig. 1b). Transects were ran-

domly dropped from boxes where >6 replicates were completed (typically, during the pre-dredge survey) to maintain a balanced statistical design. Starting coordinates of individual transects were randomly chosen from the support vessel by a member of Delta Oceanographics with 2 caveats: transects needed to be within a given box and away from previously visited lines. Individual transects lasted 10 min, during which the observer counted all YOY fishes within an ~0.5 m² total field of view and noted their location in relationship to the submersible's laser light system (0.2 m apart on the bottom). A hand-held laser pointer was used to highlight cryptic individuals (partially buried flatfish) and note fine-scale habitat changes (color/rugosity/structure) for facilitated reviewing in the laboratory. After completing the third transect and collecting the final benthic 'core' (see 'Benthic sampling' below), the submersible and observer returned to the support vessel and all transects were re-inventoried for recently settled fishes from the Hi-8 tape (with the original observer and 2 additional scientists as viewers). All videos were analyzed a second and final time in the laboratory to confirm questionable ID's and/or disputed counts. Finally, distance traveled was calculated using surface-submersible fixes acquired at the start and endpoints of individual transects. Major changes in direction while underway (i.e. edge of box reached, strong current) were accompanied by a new fix and incorporated into the total distance calculation. Total area sampled was the distance traveled multiplied by the field of view width (referenced by the submersible laser lights from Hi-8 video).

Benthic fish collections. Collections of YOY *Limanda ferruginea* for length-frequency analysis and future otolith/growth studies were made by towing a 2 m beam trawl through each pair of treatment boxes following completion of submersible operations (see Steves et al. 2000, Sullivan et al. 2000 for trawl configuration). GPS bearings from the surface vessel were used to position the ship at the edge of each box before lowering the trawl to the bottom. Collections from dredge boxes were made coincident with each treatment corridor in case a box edge was reached before tow completion (see Fig. 1b). A fitted meter wheel and surface GPS positions were used as post-hoc verification of bottom coverage and tow duration. The total number of tows performed at each site varied, but was contingent on obtaining a minimum of 40 to 50 ind. treatment⁻¹ (generally 2 to 4 tows per box). All recruits collected during trawling were preserved in 95% ethanol and later measured in the laboratory to the nearest 0.01 mm with digital calipers (Mitutoyo). Damaged individuals as well as incidental catches of larvae were omitted from subsequent analyses.

Wave climatology and sediment transport calculations. Using NOAA buoy wave data, the frequency and magnitude of natural seabed disturbance was assessed as an additional source of variability to benthic habitats. Standard meteorological measurements (dominant wave period, T ; significant wave height, H) were obtained from NOAA Buoy 44025 (40.25° N, 73.17° W) and NOAA C-MAN station Ambrose Light (40.46° N, 73.83° W; Fig. 1a) for the period June 15, 1999 to July 15, 2000 (available at <http://seaboard.ndbc.noaa.gov/>). Buoy 44025 failed for a portion of the study (November 12, 1999, to March 8, 2000), therefore, Ambrose Light data were substituted using regression techniques on a full complement of data from both stations (January 1, 1998, to January 1, 1999). Concomitant wave parameters between sites were generally well correlated ($r = 0.7441$ for T , $r = 0.8833$ for H), with the dominant wave period tending toward a poorer fit at extreme values. Conditions at Ambrose Light were used in sediment transport calculations for 10 m depths, all other stations (50, 100, and 200 m) referenced conditions at Buoy 44025. To reduce high-frequency variability, all wave data were binned into 3 d averages (~130 bins for duration of experiment). Sediment types included in the analysis at each depth were: medium-coarse sand (10 m), medium-coarse sand (50 m), fine sand-silt (100 m), fine silt-mud (200 m).

Natural disturbance frequency and magnitude over the southwest portion of the New York Bight shelf under oscillatory flow (i.e. wave action) were calculated using wave climatology data. Specifically, the maximum near-bottom horizontal orbital velocity (U_m) was calculated to predict the probability of grain movement under varying wave, depth and sediment conditions. Using procedures outlined in Dyer (1986), U_m was calculated as:

$$U_m = H\pi/T \sinh(kh) \quad (1)$$

where h is the bottom depth, T is the dominant wave period, and k the wave number.

The near-bottom horizontal velocity was then used to calculate the maximum bottom-shear stress ($t_{o,m}$) as detailed in Madsen & Grant (1975):

$$\tau_{o,m} = 0.5\rho f_w U_m^2 \quad (2)$$

where ρ is the density of seawater and f_w a dimensionless wave friction factor (after Jonsson 1966).

A generally accepted parameter for estimating the initiation of sediment motion under oscillatory flow is the Shields parameter, Ψ . The maximum bottom shear stress subsequently was used to calculate the Shields parameter for each 3 d period at each of 4 depths (10, 50, 100, and 200 m):

$$\Psi = \tau_{o,m}/(\rho_s - \rho)gD \quad (3)$$

where ρ_s is the sediment density at a given depth, g is the acceleration due to gravity, and D is equal to the mean sediment diameter.

Finally, in order to estimate the initiation (or not) of grain motion, Ψ was plotted against a boundary Reynolds parameter:

$$R_* = U_* D / \nu \quad (4)$$

on a standard Shields diagram where U_* is the total friction velocity and ν is the kinematic viscosity. Transport occurs when Ψ exceeds the Shields curve threshold (Ψ_{TH}). Relevant transport parameters and units are presented in Table 1. Transport estimates under combined oscillatory wave/mean current conditions were not calculated in this analysis (see Grant & Madsen 1979).

Benthic infauna sampling. Finally, in order to assess potential changes in the prey base of *Limanda ferruginea*, sampling of benthic infauna was performed using a suction sampler connected to a rotating tray of paired 1 mm mesh bags. At the end of the first and third transects of each dive, the submersible was stopped and a 0.5 m diameter metal sampling ring randomly placed on the seafloor adjacent to the right viewport. The submersible's sampling arm was then used to suction off the top layer of sediment into one of the collection bags. In an attempt to standardize sampling depth and

effort between observers, samples were collected to a depth of approximately 6 cm for the duration of 30 s. A hand-held 35-mm camera was used to take before/after photos of each sampled ring for qualitative purposes. Upon return to the support vessel, sediments and associated animals were washed with seawater through a stacked series of sieves (final mesh size = 1 mm), picked on board, and preserved in a solution of 10% formalin/buffered seawater. In the laboratory, samples were transferred to 95% ethanol and major prey items of YOY juvenile *L. ferruginea* (gammarid amphipods, cumaceans, decapods, isopods; Bowman 1981) identified to the lowest resolvable taxonomic level. Due to the high percentage of damaged individuals, statistical tests were performed at the genus-level or higher.

Statistical considerations and analysis. Recently settled *Limanda ferruginea* and major prey-taxa abundance data were analyzed using a univariate 'repeated measures' ANOVA because individual boxes nested within treatments were re-sampled several times over the course of 1 yr (Green 1993, Underwood 1993). One advantage of this design is that tests of impact-related hypotheses are not based on the error derived from random sub-sampling within sites (in this case, treatment boxes; 'pseudoreplication', see Hurlbert 1984). Rather, measurement of error was derived from variability generated between treatment replicates over time. Random sub-sampling then allows for a valid test of whether within-treatment variation contains environmentally driven trends (i.e. a cautious interpretation of the main effects would then be warranted). The ANOVA design for the present study consisted of 3 factors: time (fixed), dredge (fixed), and box (random, nested within dredge). Homogeneity of abundance data were examined using Cochran's C -test and transformed, $\log(x+1)$, where appropriate. The main interaction of interest, dredge \times time, was tested using the time \times box (dredge) interaction as error. In order to objectively decompose the potential effect of dredging with time, single-df planned contrasts (nonorthogonal, adjusted Type 1 error) were carried out when the dredge \times time interaction was significant. The single factor time was also of interest as an indicator of seasonal effects. Since the pre-dredge survey was limited to a single time step, trends greater than 2 time steps were not considered. The size structure of *Limanda* recruits collected within each treatment was analyzed using a nonparametric Kolmogorov-Smirnov 2-sample test (Sokal & Rohlf 1995).

ANOVA, associated contrasts, and length-frequency analyses were performed using SYSTAT (Version 8.0, SSI). Wave climatology and sediment transport calculations were performed with the MATLAB software package (Version 6.0, The Mathworks).

Table 1. Relevant parameters used in calculations of sediment transport initiation. Standard meteorological data measurements (T , H) collected from NOAA Buoy 44025 and Ambrose Light

h	Water depth (m)
T	Dominant wave period (s) ^a
H	Significant wave height (m) ^b
Λ	Wavelength (m) ^c
k	Wave number ^d
Ψ	Shields parameter based on bottom stress
Ψ_{TH}	Threshold Shields number
$\tau_{o,m}$	Maximum boundary shear stress due to oscillatory motion ($\text{g cm}^{-1} \text{s}^{-2}$)
U_m	Maximum near-bottom horizontal orbital velocity (cm s^{-1})
f_w	Dimensionless friction factor ^e
ρ	Water density (g cm^{-3})
ρ_s	Sediment density (g cm^{-3})
g	Acceleration due to gravity (cm s^{-2})
R_*	Reynolds number
D	Mean grain diameter (cm)
U_*	Total friction velocity (cm s^{-1})
ν	Kinematic viscosity ($\text{cm}^2 \text{s}^{-2}$)

^aCalculated as the average of the highest $\frac{1}{3}$ of all wave heights during sampling period
^bCalculated as the period with the maximum wave energy
^cCalculated iteratively from T and h
^dCalculated from angular frequency, $2\pi/T$, and water depth, h .
^eAfter Jonsson (1966)

RESULTS

YOY *Limanda ferruginea* abundance (H_1)

Over the course of the entire experiment (June 1999 to July 2000), YOY *Limanda ferruginea* abundance at Site 1 varied significantly with time, exhibiting a short-term pattern consistent with a dredging effect (Fig. 2a; Table 2: overall ANOVA; Table 3: single df contrasts). Numbers of *L. ferruginea* increased significantly in all boxes <2 d after dredging, but decreased significantly across all treatments 3 mo later. Approximately 1 yr after the initial impact, abundances of new recruits (2000 yr class) were similar in magnitude to pre-dredge levels, with no significant time effect (Fig. 2a). The interaction between temporal and spatial trends in abundance at Site 1 reflected an effect consistent with a dredging impact (significant dredge \times time interaction; Table 2). The planned contrasts revealed a significant difference from before to <2 d after dredging—impact boxes increased with a greater overall magnitude than controls (Table 3). There was no significant time \times box (dredge) interaction indicative of significant variability between boxes within treatments over time

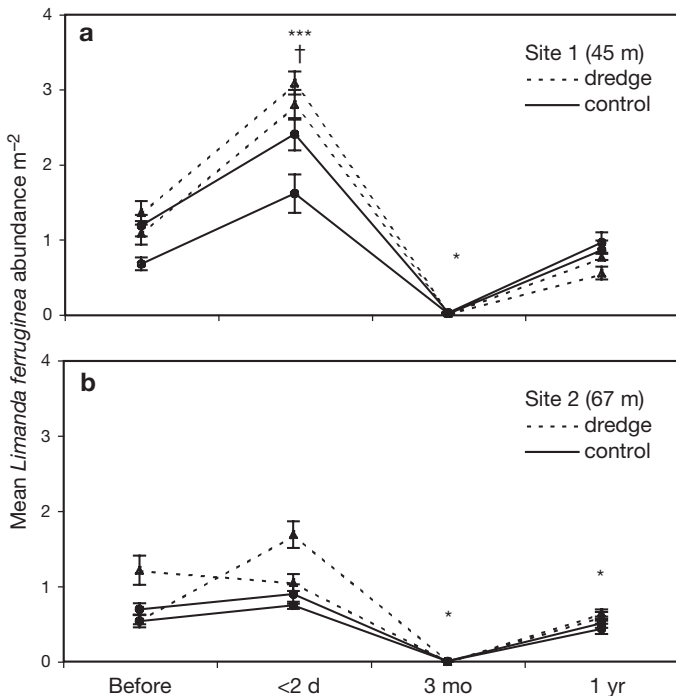


Fig. 2. *Limanda ferruginea*. Time series of young-of-the-year (YOY) abundance for Sites 1 (a) and 2 (b). Dashed lines indicate treatment boxes; solid lines, control. Note: x-axis values are not to scale to facilitate viewing of short-term effects. Error bars denote ± 1 SE for each box. Significant deviations from initial conditions are noted (* = time, † = dredge \times time; *p < 0.05; **p < 0.01; ***p < 0.001; †p < 0.05; ††p < 0.01; †††p < 0.001)

Table 2. ANOVA table for Site 1 testing the effect of scallop-dredge gear on young-of-the-year (YOY) *Limanda ferruginea* abundance. Effects of interest, 'time' and 'dredge \times time' are indicated in **bold** (after Green 1993). *p < 0.05, **p < 0.01, ***p < 0.001. Abundance data log(x+1) transformed

Source	df	MS	F-value	p
Dredge ^a	1	0.14	0.77	0.472
Box (dredge)	2	0.18	9.95	0.000***
Time ^b	3	5.91	168.07	0.000***
Dredge \times time ^b	3	0.20	5.72	0.034*
Time \times box (dredge)	6	0.04	1.94	0.082
Error	80	0.02		

^aBox (dredge) as Error 1
^bTime \times box (dredge) as Error 2

(Table 2). Overall, significant temporal variability from seasonal effects appears to have obscured any evidence of impact on scales greater than several months to 1 yr. On shorter time scales (<2 d), the effect was one of increased abundance with an embedded significant increase in dredged boxes (Fig. 2a).

Site 2 displayed lower overall temporal variability in abundance on time scales of <2 d than Site 1 (with no significant dredge effect), but similar patterns over several months to 1 yr (Fig. 2b; Table 4: overall ANOVA; Table 5: single df contrasts). *Limanda ferruginea* abundance appeared to increase from before to <2 d after dredging in the impact boxes—however, this trend was only exhibited by a single box and was lower in overall magnitude than the sustained increases of Site 1 (Fig. 2b). Further, the significant dredge effect, in the absence of a consistent dredge \times time effect, indicates controls may have differed from impact boxes irrespective of time (Table 4). This pattern was superimposed on a significant time \times box (dredge) interaction, signaling strong spatial variability between boxes within treatments over

Table 3. Single df contrasts of abundance for 'before' and successive 'after' time periods ('time' and 'dredge \times time') at Site 1. Final p-values were determined by sequential Bonferroni tests at 0.05 experimentwise error rate (Sokal & Rohlf 1997). Error = time \times box (dredge); *p < 0.05, **p < 0.01, ***p < 0.001

Source		df	MS	F-value	p
Time	Time1–time2	1	3.12	1560.00	0.001***
	Time1–time3	1	5.83	97.08	0.010*
	Time1–time4	1	0.25	7.65	0.109
Error	Time1–time2	2	0.00		
	Time1–time3	2	0.06		
	Time1–time4	2	0.03		
Dredge \times time	Time1–time2	1	0.07	33.98	0.028*
	Time1–time3	1	0.06	1.01	0.422
	Time1–time4	1	0.23	7.05	0.117
Error	Time1–time2	2	0.00		
	Time1–time3	2	0.06		
	Time1–time4	2	0.03		

Table 4. ANOVA table for Site 2 testing the effect of scallop-dredge gear on young-of-the-year (YOY) *Limanda ferruginea* abundance. Effects of interest, 'time' and 'dredge × time' are indicated in **bold** (after Green 1993). *p < 0.05, **p < 0.01, ***p < 0.001. Abundance data log(x+1) transformed

Source	df	MS	F-value	p
Dredge	1	0.36	39.84	0.024*
Box (dredge)	2	0.01	0.72	0.489
Time^b	3	2.22	22.16	0.001**
Dredge × time^b	3	0.07	0.65	0.610
Time × box (dredge)	6	0.10	7.99	0.000***
Error	80	0.02		

^aBox (dredge) as Error 1
^bTime × box (dredge) as Error 2

Table 5. Single df contrasts of abundance for 'before' and successive 'after' time periods ('time') at Site 2. Final p-values were determined by sequential Bonferroni tests at 0.05 experimentwise error rate (Sokal & Rohlf 1997). Error = time × box (dredge); *p < 0.05, **p < 0.01, ***p < 0.001

Source	df	MS	F-value	p	
Time	Time1-time2	1	1.85	1.33	0.368
	Time1-time3	1	3.46	36.85	0.026*
	Time1-time4	1	0.23	19.05	0.049*
Error	Time1-time2	2	1.39		
	Time1-time3	2	0.09		
	Time1-time4	2	0.07		

time (Table 4). Thus, at Site 2, *L. ferruginea* abundance exhibited a high degree of spatial variability among replicates (both time dependent and independent).

Recruits were rare or absent from the deepest location, Site 3; consequently, space and time trends were not analyzed.

Limanda size structure (H₂)

Beam trawl collections taken from control and impact boxes at Site 1 paralleled submersible-derived

abundance estimates and, additionally, revealed a size frequency shift toward smaller individuals (Fig. 3). The temporal change in abundance observed from the submersible at Site 1 immediately after dredging was reflected in the corresponding beam trawl catch. The total number of YOY *Limanda ferruginea* collected increased from 177 to 321 individuals in the impact boxes and from 118 to 236 in controls (Fig. 3a,b). A relatively constant fishing effort (combined area swept) was applied from before-to-after in both treatments (954.89 and 1125.13 m² for boxes 1 and 2, 974.84 and 1210.75 m² for boxes 3 and 4). Embedded within this abundance increase for impact treatments was also a

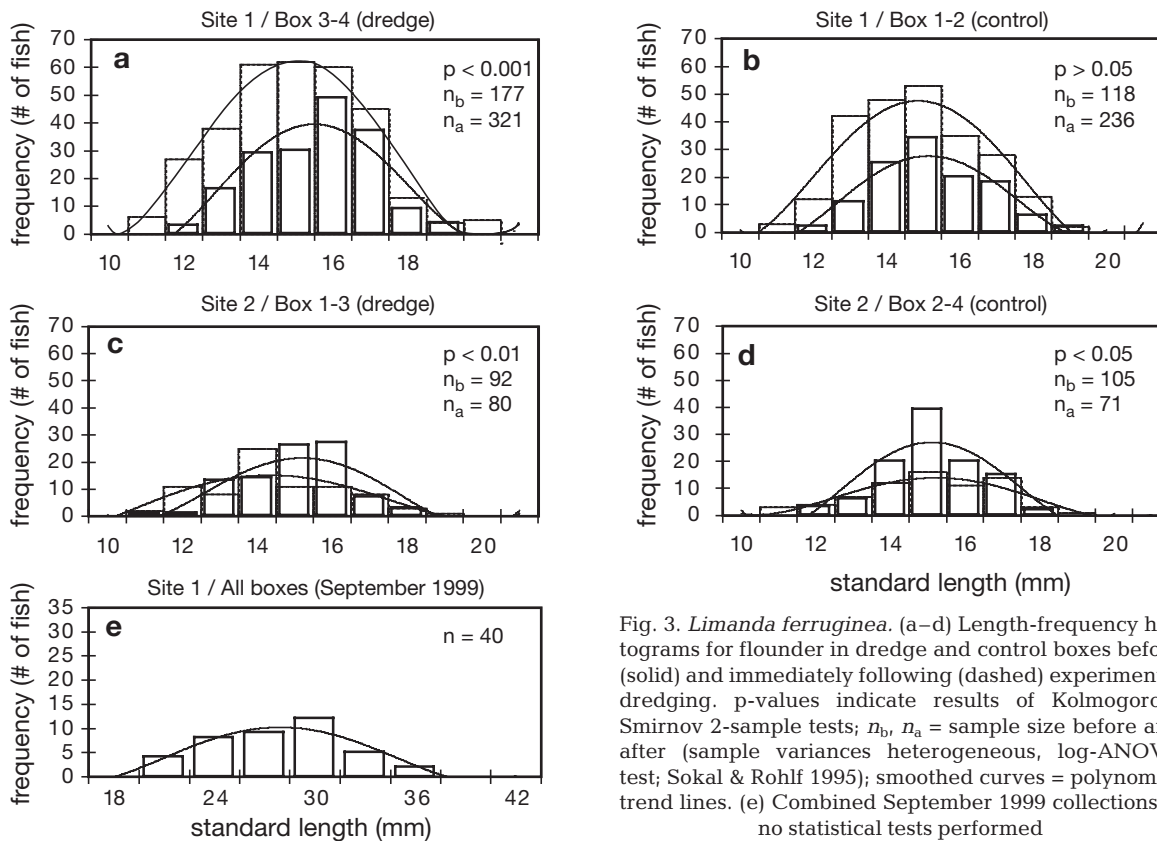


Fig. 3. *Limanda ferruginea*. (a-d) Length-frequency histograms for flounder in dredge and control boxes before (solid) and immediately following (dashed) experimental dredging. p-values indicate results of Kolmogorov-Smirnov 2-sample tests; n_b, n_a = sample size before and after (sample variances heterogeneous, log-ANOVA test; Sokal & Rohlf 1995); smoothed curves = polynomial trend lines. (e) Combined September 1999 collections—no statistical tests performed

significant, size-related shift toward smaller individuals (15.05 ± 1.54 mm standard length before, 14.44 ± 1.83 mm after, $p < 0.001$, K-S 2-sample test; Fig. 3a). Similar temporal trends in size were apparent in the control boxes, but were not significant (14.73 ± 1.51 mm before, 14.35 ± 1.67 mm after, $p > 0.05$, K-S test; Fig. 3b). September 1999 (3 mo after) catches were uncharacteristically low at Site 1 (mean standard length 26.33 ± 4.04 mm, $n = 40$: all boxes; Fig. 3e), mirroring the submersible observations.

In contrast, Site 2 showed no appreciable increase in numbers from before to after dredging, but did show evidence of a shift toward smaller individuals in the impact treatment (14.56 ± 1.32 mm before, 13.98 ± 1.80 mm after, $p < 0.01$, K-S test; Fig. 3c,d). Total effort was similar between treatments for Site 2; however, it is important to recall that submersible-derived abundances from individual boxes (see 'YOY *Limanda ferruginea* abundance') exhibited highly significant spatial and temporal variability.

Due to low abundances of YOY *Limanda ferruginea*, Site 3 (all time periods) and September 1999 collections at Site 2 were not analyzed. July 2000 cohorts at Sites 1 and 2 were collected for future growth-related studies, but were not analyzed with respect to changes in size frequency and structure.

Benthic habitat structure (H_3)

Benthic habitat structure (as proxied by the frequency of natural seabed disturbance) was influenced by the interaction between depth, sediment size/density, and prevailing seasonal wave conditions. Aver-

Table 6. Multiple comparison among means of seasonal effects on wave parameters at Buoy 44025 (June 1999–July 2000). In top half of table dominant period was the dependent variable, in bottom half, significant wave height was the dependent variable. Probabilities were derived from Tukey's HSD test. Bold values indicate no difference detected

	Spring	Summer	Fall	Winter
Spring	–	0.013	0.864	0.000
Summer	0.000	–	0.001	0.000
Fall	0.091	0.000	–	0.000
Winter	0.013	0.000	0.000	–

age wave parameters (H , T) were significantly different between all seasons, except fall and spring (multiple comparison among means, Tukey's HSD test) when hurricane activity and several early spring storms, respectively, produced similar, elevated values of both parameters (i.e. September: 1.55 m, 8.99 s; April: 1.51 m, 7.74 s; Table 6, Fig. 4). Using a simple transport model based on wave oscillatory currents, inner shelf habitats (10 m water depth) were predicted to be disturbed by wave action during all seasons, 100% of the time. This frequency fell to 16.9% for mid-shelf sites (50 m), 3.1% at the shelf edge (100 m) and was nonexistent for deep, 200 m slope sites (0%) (Fig. 5). Virtually all of the transport occurring at and beyond the 50 m isobath was storm driven (either via late summer/fall hurricanes, or winter/early spring storms). For example, during a 3 d period coincident with the passage of Hurricane Floyd (September 1999), significant transport was calculated to occur seaward of the 100 m isobath (Fig. 6b). Typical winter/spring storm scenarios generated appreciable

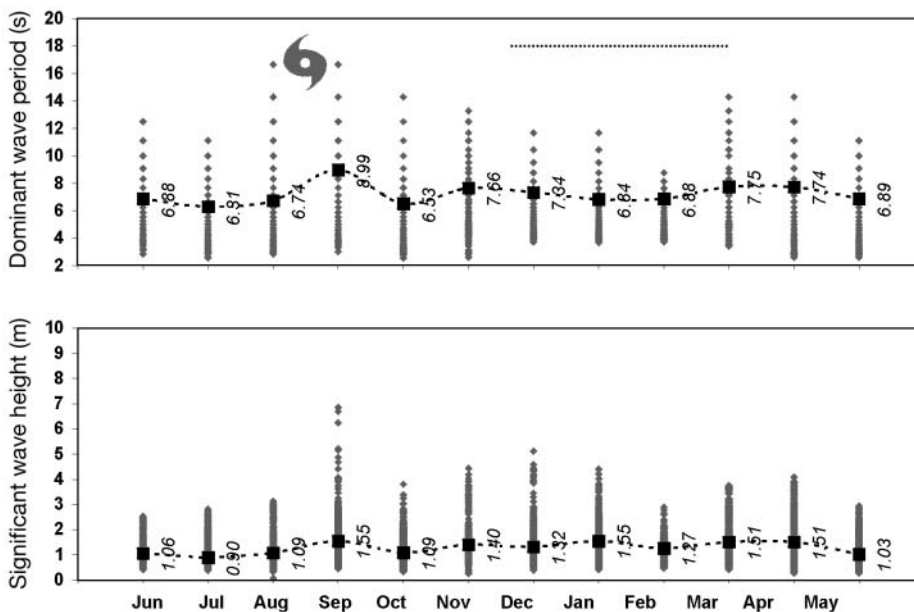


Fig. 4. Seasonal wave climatology for Buoy 44025 (south of Islip, Long Island) compiled from June 1999 to July 2000. Blocks denote mean monthly values. Individual points denote hourly values for each month. Horizontal dashed bar (top) corresponds to data derived from Ambrose Light (wave data). Hurricane symbol refers to period of intense storm activity (Hurricanes: Dennis, 24 Aug to 8 Sep; Floyd, 7 to 17 Sep; Gert, 11 to 23 Sep). Data source: NOAA National Data Buoy Center

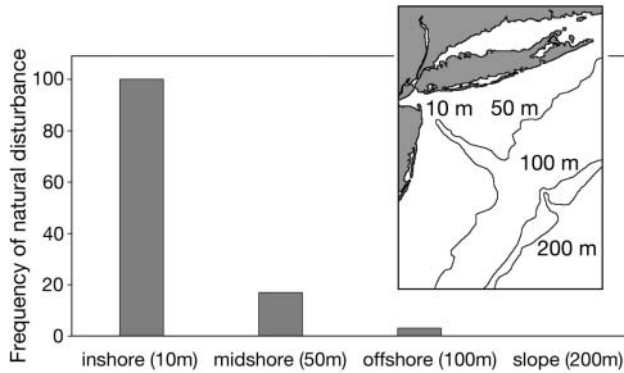


Fig. 5. Percent of time critical Shields threshold was exceeded for 4 depths (see map inset) on the New York Bight continental shelf (June 1999 to July 2000)

disturbance over 50 to 75% of the entire continental shelf (Fig. 6c). In contrast, the early summer months were the most quiescent with reduced transport occurring beyond the 50 m isobath (Fig. 6a) due to seasonal minima in H and T (July 0.90 m, 6.31 s; Fig. 5).

In situ observations from the submersible support the extent and magnitude of the seasonal sediment-transport predictions. In the wake of Hurricanes Dennis, Floyd and Gert (Leg 3, September 23 to 27, 1999), Sites 1 and 2 were characterized by highly irregular sand waves, occasionally reaching upwards of 50 to 60 cm in vertical relief (Fig. 7a). Previously extensive regions of amphipod tube mats were interspersed with characteristic excavations of bare silt/sand or filled-in shell hash. Bottom clarity at both sites was consistently turbid, indicating significant residual resuspended sediments. Although less dramatic, the deep (88 m) site displayed parallel rows of fresh, silty ripples on the order of 2 to 3 cm (height), reflecting the steep attenuation of wave orbital velocity with depth.

In contrast, the action of the scallop dredge (June 1999) produced a clear reduction in physical heterogeneity in treatment plots, such that the frequency of sand waves, tube mats, and biogenic depressions decreased relative to control plots (Fig. 7b,c; Sullivan et al. unpubl. data). Typical post-dredge landscapes (<2 d) consisted of extensive patches of clean, silty sand, interspersed with regular striations of shell hash, biogenic tubes and castings strained through the dredge teeth (Fig. 7d). Abundant mobile epifauna such as sand dollars were typically dislodged or buried under a thin layer of silt. Bottom coverage by the dredge appeared to be complete at all depths—with occasional patches of undisturbed sediment. Despite this vigorous surficial reworking, the overall impact of the dredge appeared to extend no farther than 2 to 6 cm below the sediment surface. Control plots remained unchanged with continuous patches of amphipod tube mats and sand dollars interspersed between

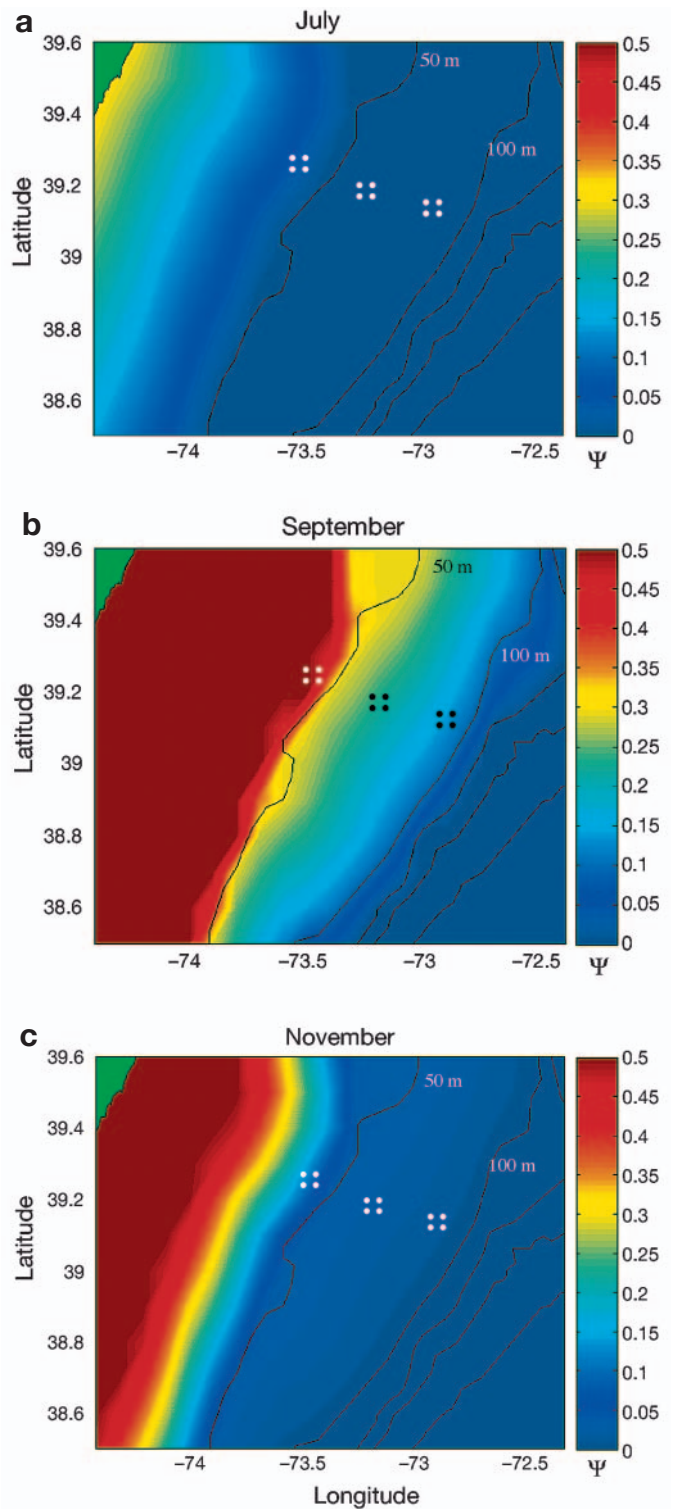


Fig. 6. Three-day average of the Shields parameter (ψ), over 3 study sites, in relation to critical Shields parameter (ψ_{TH} ; threshold at which sediment transport is initiated, dark blue and above on color bar) for representative seasons (1999 to 2000). 'September' depicts a 3 d period coincident with the passage of Hurricane Floyd. In this example, depths greater than ca. 125 m do not exceed the critical value (dark blue), therefore, no transport occurs

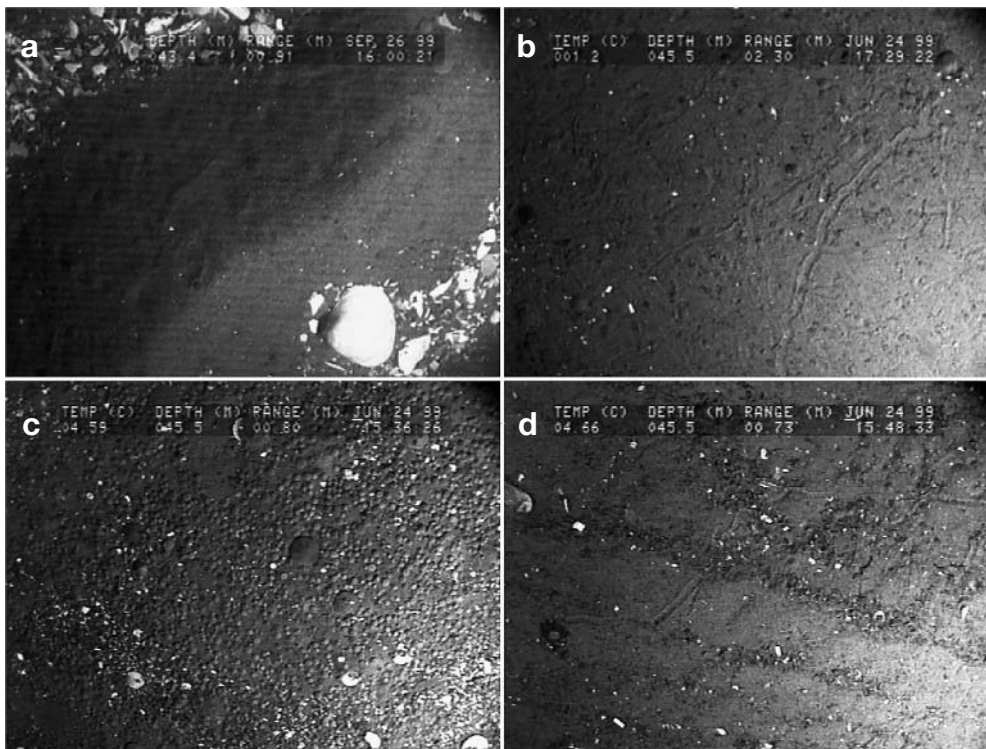


Fig. 7. (a) Storm wave crest (center) and adjacent debris-filled troughs (top left, bottom right) generated during September 1999 at Site 1. (b) Animal trails left in upper layer of recently disturbed silt from scallop dredge. (c) Dense patches of recently recruited sand dollars adjacent to a dredged box. (d) Linear striations of amphipod tubes and sand dollar recruits combed from dredge gear teeth

Table 7. ANOVA summary table for major prey items of YOY-juvenile *Limanda ferruginea*. Significant p-values are indicated in bold. Note: metamorphosing individuals typically consume a combination of copepods (not quantified) and small amphipods (Bowman 1981)

Site Source	df	Amphipods			Cumacea ^c			Decapoda			Isopoda		
		MS	F-values	p	MS	F-values	p	MS	F-values	p	MS	F-values	p
45 m													
Dredge ^a	1	40214.38	0.44	0.577	714.92	0.13	0.755	117.13	0.07	0.816	40.53	0.10	0.780
Box(dredge)	2	92042.19	1.88	0.163	5584.82	4.82	0.012	1679.91	7.70	0.001	399.61	5.46	0.007
Time ^b	3	102033.81	7.51	0.019	18572.31	12.48	0.005	1800.95	6.33	0.027	455.00	7.55	0.018
Dredge × time ^b	3	25361.50	1.87	0.236	223.18	0.15	0.926	657.51	2.31	0.176	39.45	0.66	0.609
Time × box(dredge)	6	13593.12	0.28	0.945	1488.76	1.28	0.283	284.65	1.31	0.273	60.25	0.82	0.558
Error	48	48924.76			1159.93			218.18			73.22		
67 m													
Dredge ^a	1	495758.88	0.44	0.575	0.09	1.59	0.334						
Box(dredge)	2	1127558.06	6.19	0.004	0.06	0.11	0.897						
Time ^b	3	647715.26	1.43	0.325	1.12	3.15	0.108						
Dredge × time ^b	3	911772.31	2.01	0.214	0.17	0.48	0.711						
Time × box(dredge)	6	453914.31	2.49	0.035	0.36	0.67	0.671						
Error	48	182037.96			0.53								
88 m													
Dredge ^a	1	198625.79	4.49	0.168									
Box(dredge)	2	44256.01	0.63	0.539									
Time ^b	3	65511.90	1.27	0.366									
Dredge × time ^b	3	105695.34	2.05	0.209									
Time × box(dredge)	6	51574.07	0.74	0.625									
Error	34	70206.89											

^aBox(dredge) as Error 1; ^bTime × box(dredge) as Error 2; ^cSite 2 Cumacea log(x+1) transformed

regular fields of sand waves. No evidence of a dredging impact of any kind was apparent in September 1999 or July 2000.

Benthic prey abundance (H_4)

Prey items of YOY *Limanda ferruginea* retrieved from the suction samples failed to exhibit a positive or negative change consistent with a dredging impact—but did reflect significant seasonal variability (contingent on depth) (Fig. 8, Table 7). Benthic cores at all 3 sites were dominated by amphipods (Table 8). Taxa with low abundances at a given site (Site 2: decapods, isopods; Site 3: cumaceans, decapods, isopods) were omitted from the analysis. At Site 1, patterns of prey

abundance (amphipods, cumaceans, decapods, isopods) were characterized by significant variation over time with synchronous declines in late September (Fig. 8). This trend parallels submersible and beam-trawl derived estimates for *L. ferruginea*. Although no impact-related effect was uncovered, it is important to note the high degree of variability between sampling locations independent of time (significant box [dredge] interaction for cumaceans, decapods, isopods; Table 7). The seasonal pattern was similar at Site 2 for amphipods; however, time-related trends were accompanied by appreciable between-box variability (time \times box [dredge]; Fig. 8, Table 7). Conversely, seasonal patterns for cumaceans at Site 2 and amphipods at Site 3 were less pronounced with relatively stable abundances over time (Fig. 8, Table 7). In summary, major

variations in the prey base of YOY juveniles occur seasonally (time) with additional variability generated between sampling locations (box [dredge] and time \times box [dredge]). Seasonal effects were most pronounced at the shallow Site 1 and decreased in significance with depth. No functional relationship was apparent between prey abundance and dredging with time. A power analysis of the before-after time step at Site 1 revealed the overall power to detect a dredge-related impact as moderate-low (reduction in mean abundance of 30 and 50%, respectively: amphipods 35 and 51%; cumaceans 24 and 39%; isopods 18 and 34%; decapods 36 and 47%). This result is largely a reflection of the limited carrying capacity of the submersible (maximum 2 cores per dive) as well as the inherent natural patchiness of individual taxa.

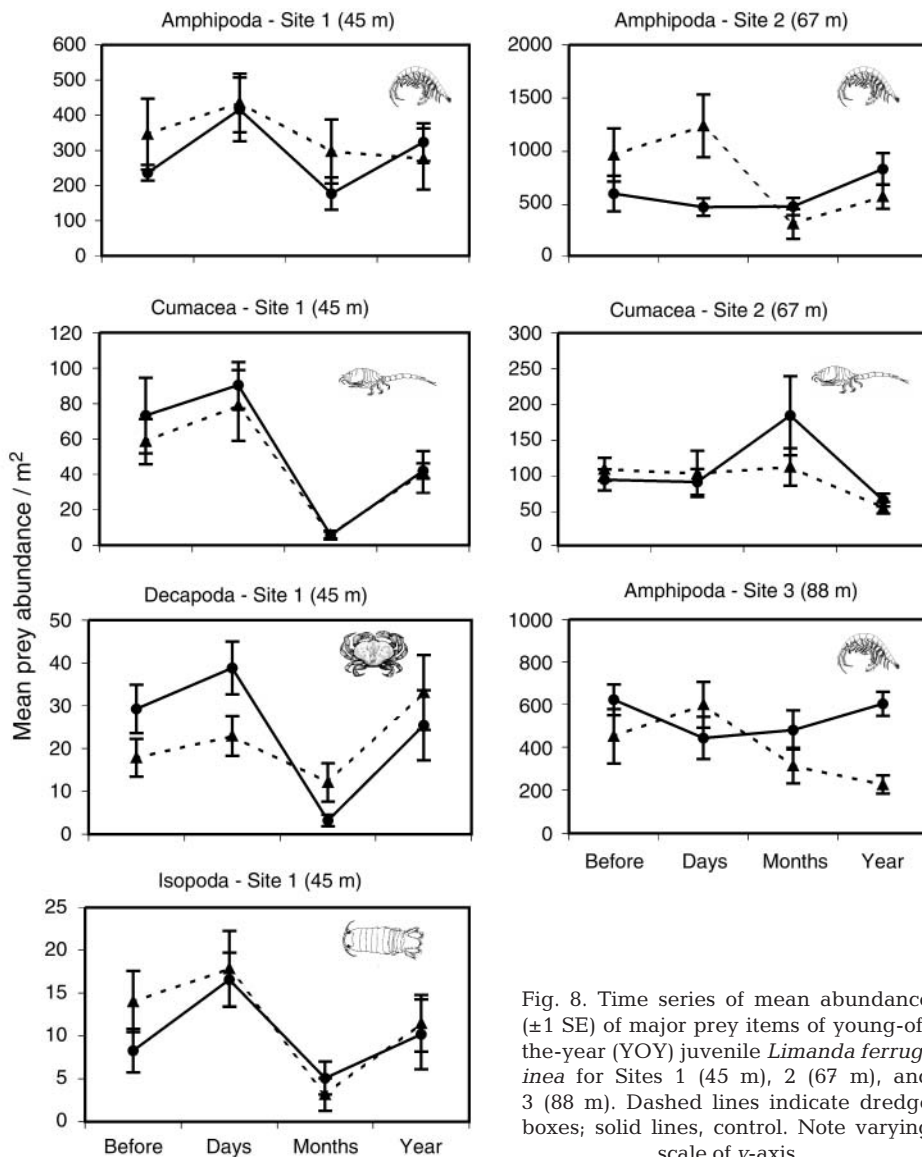


Fig. 8. Time series of mean abundance (± 1 SE) of major prey items of young-of-the-year (YOY) juvenile *Limanda ferruginea* for Sites 1 (45 m), 2 (67 m), and 3 (88 m). Dashed lines indicate dredge boxes; solid lines, control. Note varying scale of y-axis

DISCUSSION

This field investigation into the effects of mobile fishing gear on *Limanda ferruginea* recruit abundance and essential fish habitat structure revealed 3 primary results: (1) an initial post-dredge increase

Table 8. Rank order of major amphipod genera by site from benthic core samples. Classification follows Dickinson et al. (1980)

Amphipod genera	Number	% of total
Site 1		
<i>Unicola</i>	2465	62.77
<i>Erichthonius</i>	470	11.97
<i>Phoxocephalus</i>	312	7.94
<i>Ampelisca/Byblis</i>	184	4.69
<i>Paraphoxus</i>	174	4.43
<i>Monoculodes</i>	145	3.69
<i>Protohaustorius</i>	47	1.20
Site 2		
<i>Ampelisca/Byblis</i>	4835	56.55
<i>Unicola</i>	2681	31.36
<i>Erichthonius</i>	332	3.88
<i>Photis</i>	244	2.85
<i>Phoxocephalus</i>	146	1.71
Site 3		
<i>Ampelisca/Byblis</i>	3259	88.66
<i>Unicola</i>	276	7.51
<i>Photis</i>	90	2.41

of recently-settled *L. ferruginea* immediately following gear disturbance, (2) strong seasonal trends in both YOY *L. ferruginea* and benthic invertebrate abundance, and (3) significant habitat reworking by wave action out to, and beyond, the mid-continental shelf. These 3 findings suggest that the New York Bight shelf is a physically dominated system subjected to extensive seasonal reworking by natural processes. In this context, a single dredging event has only a minimal impact on recently settled recruits and associated habitat. Taken individually (below), each point suggests that the settlement dynamics of local benthic species may be shaped, in part, by individual morphology and behavior, preferred nursery habitat and depth, as well as the magnitude and timing of natural processes.

Dredging response on time scales of less than 2 d

Conservatively, the complex interaction between settlement magnitude, substrate availability, and recruit activity levels appears to be driving short-term patterns in recently settled *Limanda ferruginea* abundance. Scientific impartiality aside, it was difficult to envision a 400 kg mobile scallop dredge having any impact other than a negative one on a sedentary, early stage benthic fish. For example, Collie et al. (2000) recently used a meta-analytical approach to examine trends in impact and recovery rates binned by gear, location, habitat, and biological class. Not a single scenario offered a 'positive' short-term response to

dredging (i.e. change in abundance over 1 d)—although longer-term trends tended to vary with physical setting. Because of the present study's atypical result (significant, positive dredge effect over <2 d at Site 1), it is worth evaluating the possible mechanistic reasons for this response.

First, due to the sheer magnitude of the settlement event itself, additional individuals may have successfully recruited between the final pre- and initial post-dredge survey. This would explain the simultaneous increase of recruits (with time) in both Site 1 treatments. The occurrence of smaller-sized individuals based on length-frequency data tends to support this notion with increased abundances in all boxes (accompanied by an embedded, significant size-related shift in dredged boxes). Accordingly, the significant, higher magnitude increase exhibited by the dredge treatments could be the byproduct of newly available settlement habitat (i.e. flat, homogenized sand), thus, creating a 'match' between recruitment and percent cover of a preferred substrate (Cushing 1975, Auster & Langton 1999).

Second, observed distributions could be the result of technical artifacts rather than any realistic recruitment-oriented premise (Benedetti-Cecchi et al. 1996, Thompson & Mapstone 1997, Kulbicki 1998). Scientific observers may have become more competent with time at observing small, cryptic organisms (i.e. improved search technique and image), in essence, 'under sampling' the pre-dredge portion of the experiment. Increased recruit activity levels (after disturbance) could render the same, exaggerated effect in dredged treatments. However, after initial viewing and reviewing of video transects (with multiple, independent observers), the former scenario appears unlikely. Further, beam trawl catches tended to mirror prevailing submersible-derived observations. Nevertheless, it was difficult to quantitatively discount the possibility of a stress-induced response leading to increased recruit detection.

A final scenario involves opportunistic feeding and/or emigration from non-experimental habitats. Numerous studies have suggested that disturbance events attract scavengers and other mobile predators due to sudden, highly available pulses of organic matter and benthic prey (Caddy 1973, Murawski & Serchuk 1989, Ramsay et al. 1998). Overall response magnitude, however, tends to reflect the scaled, physiological limitations of individual species (Kaiser & Spencer 1994). In this study, boxes were designed to minimize edge effects from outlying *Limanda ferruginea* recruits. Given the scaling relationship between box length (~275 m) and average recruit length (~10 to 15 mm), the chance of an edge-related result integrating over an entire box area is unlikely.

Site 2 displayed a similar temporal pattern to that of Site 1 (increased abundance following dredging); however, the effect was only observed in a single dredged box. This significant between-box variability rendered the main effect of interest negligible. Rather than traditional sample size considerations, this phenomenon is probably attributable to asynchronous spatial and seasonal ecological variance (see recent work by Drabsch et al. 2001, Schratzberger et al. 2002 for macro and meiofaunal communities).

Overall, the large abundance of settling recruits may have masked any functional dredge-induced response at any of the experimental sites. This saturation of nursery habitats has been observed previously for *Limanda ferruginea* in the New York Bight (Steves et al. 2000, Sullivan et al. 2000) and may function as a bet-hedging strategy against an array of patchy microhabitats (MacCall 1990). In the present study, the fate of these recruits in the weeks immediately following the dredging event is unknown.

Seasonal response

Abundances of YOY *Limanda ferruginea* and associated benthic prey items (amphipods, cumaceans, decapods, isopods) were dramatically reduced in September 1999, resulting in a highly significant seasonal effect. For the benthic infauna, this pattern was distinct in the mid-shelf region and more ambiguous at offshore sites. Although statistical power was moderate, the seasonal component clearly overshadowed any appreciable dredge-induced response (either negative or positive). These findings are similar in scope to recent experimental work by Schratzberger et al. (2002), which concluded that seasonal variability dominated patterns of meiofaunal abundance on fishing grounds in the southern North Sea. In the present study, observations were collected approximately 1 wk after a series of intense, late summer disturbances (Hurricanes Dennis, Floyd, and Gert). Based on previous work in the New York Bight region, there are several explanations for the abundance patterns observed in the wake of these storms.

First, the synchronous declines between older YOY flounder and benthic prey may have been the by-product of increased physical stress. On the continental shelf proper, it is assumed that local populations are adapted to deal with some minimal threshold of wave stress (Hall 1994), with large-scale community change driven by acute, episodic events (i.e. Ebeling et al. 1985: kelp forests; Underwood 1999: rocky intertidal). As benthic habitats in this study were reworked extensively out to the 100 m isobath and beyond, individuals occupying heavily disturbed mid-shelf sites were

likely exposed to prolonged, high-energy conditions. Direct physical measurements taken from the coastal mixing and optics experiment during the passage of Hurricanes Edouard and Hortense (fall 1996, Southern New England shelf, 70 m water depth) provide a detailed glimpse into the environmental changes associated with a disturbance of this magnitude (Dickey & Williams 2001). During the passage of both storms, *in situ* ADCP (Acoustic Doppler Current Profiler) mooring data revealed current velocities in the upper 35 m approaching $>65 \text{ cm s}^{-1}$ (Chang et al. 2001). On the seafloor, tripod measurements recorded 10-fold increases in average wave orbital velocities, while integrated optical instrumentation documented benthic sediments and detritus re-suspended $<30 \text{ m}$ from the ocean surface (Gardner et al. 2001, Chang et al. 2001). Perhaps most impressively, significant sediment transport was first observed as the system traveled approximately 900 km south of the study site. In this respect, even relatively distant storms have the potential to invoke a major stress on the benthic constituents of a marine ecosystem.

A second, related seasonal phenomenon acting on YOY *Limanda ferruginea* in the New York Bight is the mid-shelf cold pool, a body of isolated winter water typically located between the 40 and 70 m isobaths (Steves et al. 2000). Recently settled *L. ferruginea* exhibit a high degree of inter-annual fidelity to the cross-shelf breadth and extent of this cold cell, with settlement magnitude dependent on absolute bottom temperature (Sullivan et al. 2000). Typically, the cold pool gradually warms over the course of the summer until fall bottom and surface temperatures approach equilibrium (Houghton et al. 1982). However, wave action from large-scale tropical storms and hurricanes may contribute to an early de-stratification (Chang & Dickey 2001). During the 1996 settlement season, a turnover event initiated by Hurricanes Edouard and Hortense was linked with magnitude-order declines in YOY *L. ferruginea* abundance on the New York Bight shelf (Steves et al. 2000).

Unfortunately, the direct impacts of storms on benthic organisms (either from physical or temperature related stress) are difficult to document and probably vary widely with trophic level. Increased turbidity and turbulence have been implicated as factors in decreased prey detection and foraging success (Weissburg & Zimmer-Faust 1993, Benfield & Minello 1996, Gregory & Levings 1998), as well as depressed levels of benthic production (Emerson 1989, Nelson et al. 1999). However, wave disturbance is not necessarily negative and may depend on an organism's functional role as predator or prey. Pile et al. (1996) observed an increase in juvenile blue crab *Callinectes sapidus* survival during and after a major tropical storm in Ches-

peake Bay, and related this trend to decreased foraging success by predators (moderated by a sudden temperature drop and/or increased turbidity). In the present study, it is unclear whether short-term episodic stress or longer-term demographic trends are responsible for the seasonal minima in abundance. Arrival to benthic nursery habitats often coincides with a complex array of density-dependent processes that significantly modify abundances throughout the first year of life (Sissenwine 1984, Gibson 1994). In this respect, attributing cause and effect to 'before-after' snapshots may foster a misleading interpretation of the actual dynamics of the system (Underwood 1991, 2000). However, dramatic storm activity observed in September 1999 appeared to have no significant effect on the following year's new recruits, as well as the overall distribution of benthic habitat types.

Frequency and magnitude of seabed disturbance

The frequency of occurrence and relative magnitude of anomalous events can potentially offer valuable insight into the dynamics of a particular ecosystem (even while confounding experimental treatment effects) (Hurlbert 1984, Dayton et al. 1992, Turner et al. 1993). In this study, the disturbance events (Hurricanes Dennis, Floyd, and Gert) were of such a remarkable intensity and spatial coverage that it shifted our perception of how shelf communities are structured on seasonal time scales. Further, the subsequent recovery of the system provided an equally powerful contrast between the resilience of inner-mid continental shelf habitats and the potential precariousness of low disturbance, outer shelf locales.

The natural disturbance regime of a continental shelf ecosystem can partially be estimated by examining the sequential distribution of bottom types with depth. Sediment sequences in the New York Bight apex, for example, represent the endpoint of thousands of years of local atmospheric forcing, with the 10 to 20 m isobath marking typical wave base conditions ($\sim \Lambda/2$, where Λ is wavelength) (Vincent et al. 1981). Unfortunately, the notion of 'wave base' approximates an average set of conditions and does not provide insight into the frequency, magnitude and seasonality of anomalous events. For example, Komar et al. (1972) found symmetrical ripple marks at depths of over 200 m off of the Oregon coast corresponding with characteristics of long period storm waves (15 s period). Using a sequence of bottom photographs, Butman & Moody (1983) similarly documented the shelf-wide effects (Georges Bank to Delaware Bay) of a winter Northeaster on Middle Atlantic Bight sediment transport and gross bottom morphology. On Georges Bank, winter storms occur on

average every 10 d (December to March), marked by less-frequent periods of intense activity that rework habitats well seaward of the median wave base.

Sediment transport calculations in this study estimated transport initiation over and beyond the 100 m isobath, with frequent disturbance occurring out to the mid-continental shelf (50 m isobath). The former scenario was verified by submersible observations of surface wave ripples at depths >80 m approximately 4 d after the passage of Hurricane Gert. By way of contrast, the mid-shelf sites (45 and 67 m) were considerably reworked with highly irregular ridge (0.5 m in height) and trough topography characterized by disorganized tube mats and a scarcity of mobile megafauna. This contrast between mid- and outer-shelf disturbance regimes reflects the exponential attenuation of wave orbital velocities with depth. Perhaps even more striking than the sheer magnitude of the bedforms themselves was their complete reworking over the course of the following 6 mo, such that July 2000 conditions mirrored average summer seafloor topography (low relief sand waves). Thus, the frequency of winter storms has an appreciable effect on longer-term patterns of seafloor architecture. In general, these results are similar to more detailed calculations by Vincent et al. (1981) and represent the logical extension of work by DeAlteris et al. (1999) for estuaries and inner continental shelf environments.

It is important to note that this experiment did not specifically address the effects of chronic, mobile gear disturbance on seafloor habitats (see Kaiser et al. 2000, McConnaughey et al. 2000). Rather, a single, intense dredging event was embedded within the larger context of seasonal, wave-generated disturbance. Vessel monitoring as well as NMFS sea sampling data clearly identify the New York Bight shelf as a major center of frequent, repeated trawling activity (Auster & Langton 1999, NEFSC 2002). Chronic trawling has the potential to modify, remove and replace substrates critical for growth and survival (Watling & Norse 1998), as well as shift the overall composition of benthic communities (Collie et al. 1997). Although logistically difficult, in order to truly scale the relationship between dredging and natural processes, future comparisons must be made on the scale of the actual fishery, rather than a single event (Collie et al. 2000). Nevertheless, the findings of this study suggest that the effects of bottom trawling may be less critical in storm-dominated, sand-sediment environments.

SUMMARY

In conclusion, the goal of this study was to quantify the short (<2 d) and longer-term (3 mo to 1 yr) effects of

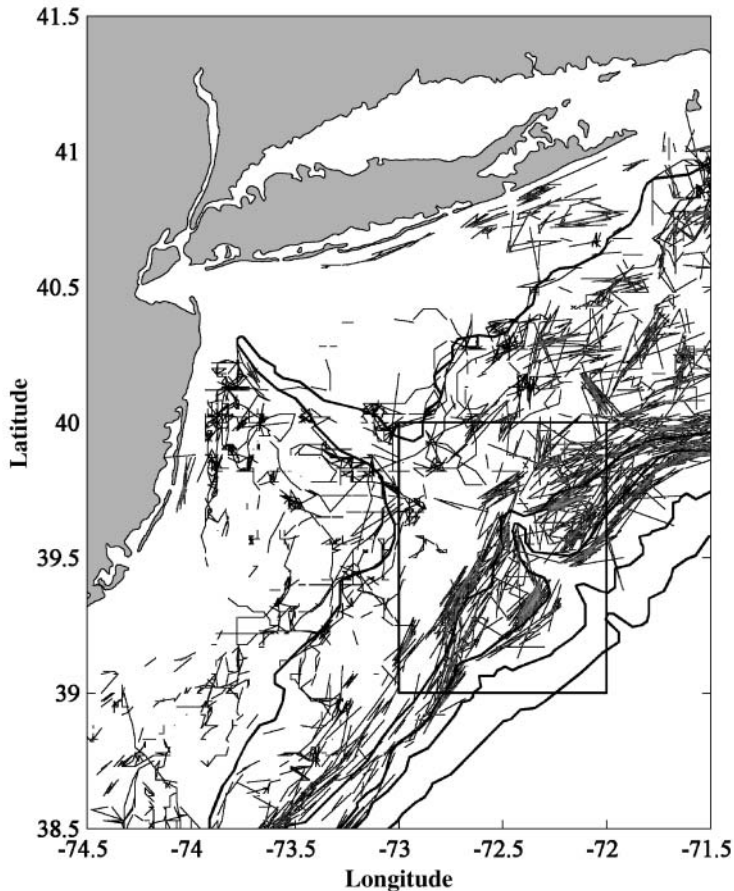


Fig. 9. Aggregations of mobile fishing gear sets (black lines: scallop dredges; grey lines: otter trawls) for the New York Bight continental shelf and shallow slope, 1989 to 1994. Data were compiled and plotted from the National Marine Fisheries Service sea sampling database. The rectangle corresponds to Statistical Area 616—a sub-region of particularly intense trawling activity

a dredging event on essential fish habitat using a common, recently settled flatfish *Limanda ferruginea* as the target species. YOY *L. ferruginea* settling onto New York Bight continental shelf nursery grounds exhibited short-term increases in abundance from anthropogenic disturbance, presumably through the alteration of available settlement habitat (H_1 , H_2). However, these distributional and structural changes were relatively short-lived given the sequence of frequent, intense natural disturbance events during the fall and winter months (detectable through standard wave measurements and corresponding changes in seafloor architecture; H_3). Accordingly, flounder recruits and components of their benthic prey-base exhibited strong seasonal variability of a greater overall scale and magnitude than that created by mobile scallop dredging alone (H_1 , H_4). Taken as a whole, these findings highlight the relative vulnerability of various shelf habitats to multiple forms of seafloor dis-

turbance. If one considers the dominant distribution and abundance of trawl operations in the New York Bight (Fig. 9), future studies should address the relative susceptibility of low energy, high relief outer shelf habitats to mobile fishing gear impacts.

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LITERATURE CITED

- Able KW, Fahay MP (1998) The first year in the life of estuarine fishes in the Middle Atlantic Bight. Rutgers University Press, New Brunswick, NJ
- Able KW, Musick JA (1976) Life history, ecology, and behavior of *Liparis inquilinus* (Pisces: Cyclopteridae) associated with the sea scallop, *Placopecten magellanicus*. Fish Bull 74:409–421
- Auster PJ, Langton RW (1999) The effects of fishing on fish habitat. Am Fish Soc Symp 22:150–187
- Auster PJ, Malatesta RJ, Langton RW, Watling L and 5 others (1996) The impacts of mobile fishing gear on seafloor habitats in the Gulf of Maine (Northwest Atlantic): implications for conservation of fish populations. Rev Fish Sci 4: 185–202
- Beck MW, Heck KL Jr, Able KW, Childers DL and 9 others (2001) The identification, conservation, and management of estuarine and marine nurseries for fish and invertebrates. Bioscience 51:633–641
- Benedetti-Cecchi L, Airolidi L, Abbiati M, Cinelli F (1996) Estimating the abundance of benthic invertebrates: a comparison of procedures and variability between observers. Mar Ecol Prog Ser 138:93–101
- Benfield MC, Minello TJ (1996) Relative effects of turbidity and light intensity on reactive distance and feeding of an estuarine fish. Environ Biol Fish 46:211–216
- Bowman RE (1981) Food of 10 species of northwest Atlantic juvenile groundfish. Fish Bull 79:200–206
- Butman B (1987) The effect of winter storms on the bottom. In: Backus RH (ed) Georges Bank. MIT Press, Cambridge, MA, p 74–78
- Butman B, Moody JA (1983) Observations of bottom currents and sediment movement along the US east coast continental shelf during winter. In: McGregor BA (ed) Environmental geologic studies on the United States Mid and

- North Atlantic outer continental shelf area, 1980–1982, Vol III. Final report to US Bureau of Land Management, New York
- Caddy JF (1973) Underwater observations on tracks of dredges and trawls and some effects of dredging on a scallop ground. *J Fish Res Board Can* 30:173–180
- Chang GC, Dickey TD (2001) Optical and physical variability on timescales from minutes to the seasonal cycle on the New England shelf: July 1996 to June 1997. *J Geophys Res (C Oceans)* 106:9435–9453
- Chang GC, Dickey TD, Williams AJ (2001) Sediment resuspension over a continental shelf during Hurricanes Edouard and Hortense. *J Geophys Res (C Oceans)* 106:9517–9531
- Churchill JH (1989) The effect of commercial trawling on sediment resuspension and transport over the Middle Atlantic Bight continental shelf. *Cont Shelf Res* 9:841–864
- Churchill JH (1998) Sediment resuspension by bottom fishing gear. In: Dorsey EM, Pederson J (eds) *Effects of fishing gear on the sea floor of New England*. Conservation Law Foundation, Boston, p 134–137
- Collette BB, Klein-MacPhee G (2002) *Bigelow and Schroeder's Fishes of the Gulf of Maine*, 3rd edn. Smithsonian Institution Press, Washington, DC
- Collie JS, Escanero GA, Valentine PC (1997) Effects of bottom fishing on the benthic megafauna of Georges Bank. *Mar Ecol Prog Ser* 155:159–172
- Collie JS, Hall SJ, Kaiser MJ, Poiner IR (2000) A quantitative analysis of fishing impacts on shelf-sea benthos. *J Anim Ecol* 69:785–798
- Currie DR, Parry GD (1996) Effects of scallop dredging on a soft sediment community: a large-scale experimental study. *Mar Ecol Prog Ser* 134:131–150
- Cushing DH (1975) *Marine ecology and fisheries*. Cambridge University Press, Cambridge
- Dayton PK, Tegner MJ, Parnell PE, Edwards PB (1992) Temporal and spatial patterns of disturbance and recovery in a kelp forest community. *Ecol Monogr* 62:421–445
- DeAlteris J, Skrobe L, Lipsky C (1999) The significance of seabed disturbance by mobile fishing gear relative to natural processes: a case study in Narragansett Bay, Rhode Island. *Am Fish Soc Symp* 22:150–187
- Dickey TD, Williams AJ (2001) Interdisciplinary ocean process studies on the New England Shelf. *J Geophys Res (C Oceans)* 106:9427–9434
- Dickinson JJ, Wigley RL, Brodeur RD, Brown-Leger S (1980) Distribution of gammaridean amphipoda (crustacea) in the Middle Atlantic Bight region. NOAA Tech Rep NMFS SSRF-741:1–46
- Drabsch SL, Tanner JE, Connell SD (2001) Limited infaunal response to experimental trawling in previously untrawled areas. *ICES J Mar Sci* 58:1261–1271
- Dyer KR (1986) *Coastal and estuarine sediment dynamics*. John Wiley & Sons, New York
- Ebeling AW, Laur DR, Rowley RJ (1985) Severe storm disturbances and reversal of community structure in a southern California kelp forest. *Mar Biol* 84:287–294
- Eleftheriou A, Robertson MR (1992) The effects of experimental scallop dredging on the fauna and physical environment of a shallow sandy community. *Neth J Sea Res* 30:289–299
- Emerson CW (1989) Wind stress limitation of benthic secondary production in shallow, soft-sediment communities. *Mar Ecol Prog Ser* 53:65–77
- Freese L, Auster PJ, Heifetz J, Wing B (1999) Effects of trawling on seafloor habitat and associated invertebrate taxa in the Gulf of Alaska. *Mar Ecol Prog Ser* 182:119–126
- Gardner WD, Blakey JC, Walsh ID, Richardson MJ and 7 others (2001) Optics, particles, stratification, and storms on the New England continental shelf. *J Geophys Res (C Oceans)* 106:9473–9497
- Gibson RN (1994) Impact of habitat quality and quantity on the recruitment of juvenile flatfish. *Neth J Sea Res* 32:191–206
- Grant WD, Madsen OS (1979) The threshold of grain motion under oscillatory flow in a laboratory wave channel. *J Sediment Petrol* 49:287–294
- Green RH (1993) Application of repeated measures designs to environmental impact and monitoring studies. *Aust J Ecol* 18:81–98
- Gregory RS, Levings CD (1998) Turbidity reduces predation on migrating juvenile Pacific salmon. *Trans Am Fish Soc* 127:275–285
- Hall SJ (1994) Physical disturbance and marine benthic communities: life in unconsolidated sediments. *Oceanogr Mar Biol Annu Rev* 32:179–239
- Hall SJ (1999) *The effects of fishing on marine ecosystems and communities*. Blackwell Science, London
- Hare JA, Cowen RK (1996) Transport mechanisms of larval and pelagic juvenile bluefish (*Pomatomus saltatrix*) from South Atlantic Bight spawning grounds to Middle Atlantic Bight nursery areas. *Limnol Oceanogr* 41:1264–1280
- Hewitt JE, Thrush SE, Cummings VJ (2001) Assessing environmental impacts: effects of spatial and temporal variability at likely impact scales. *Ecol Appl* 11:1502–1516
- Houghton RW, Schlitz R, Beardsley RC, Butman B, Lockwood Chamberlin J (1982) The Middle Atlantic Bight cold pool: evolution of the temperature structure during summer 1979. *J Phys Oceanogr* 12:1019–1029
- Hurlbert SJ (1984) Pseudoreplication and the design of ecological field experiments. *Ecol Monogr* 54:187–211
- Jennings S, Kaiser MJ (1998) The effects of fishing on marine ecosystems. *Adv Mar Biol* 34:201–352
- Jonsson IG (1966) Wave boundary layers and other friction factors. *Proc 10th Conf Coastal Eng, Am Soc Civ Eng* 1:127–148
- Kaiser MJ, Spencer BE (1994) Fish scavenging behavior in recently trawled areas. *Mar Ecol Prog Ser* 112:41–49
- Kaiser MJ, Spencer BE (1996) The effects of beam-trawl disturbance on infaunal communities in different habitats. *J Anim Ecol* 65:348–358
- Kaiser MJ, Edwards DB, Armstrong PJ, Radford K, Lough NEL, Flatt RP, Jones HD (1998) Changes in megafaunal benthic communities in different habitats after trawling disturbance. *ICES J Mar Sci* 55:353–361
- Kaiser MJ, Ramsay K, Richardson CA, Spence FE, Brand AR (2000) Chronic fishing disturbance has changed shelf sea benthic community structure. *J Anim Ecol* 69:494–503
- Komar PD, Neudeck RH, Kulm LD (1972) Observations and significance of deep-water oscillatory ripple marks on the Oregon continental shelf. In: Swift DJP, Duane DB, Pilkey OH (eds) *Shelf sediment transport: process and pattern*. Dowden, Hutchinson and Ross, Stroudsburg, PA, p 601–620
- Kulbicki M (1998) How the acquired behaviour of commercial reef fishes may influence the results obtained from visual censuses. *J Exp Mar Biol Ecol* 222:11–30
- Langton RW, Auster PJ, Schneider DC (1995) A spatial and temporal perspective on research and management of groundfish in the northwest Atlantic. *Rev Fish Sci* 3:201–229
- Levin SA (1992) The problem of pattern and scale in ecology. *Ecology* 73:1943–1967
- Lindgarth M, Valentinsson D, Hansson M, Ulmestrand M

- (2000) Interpreting large-scale experiments on effects of trawling on benthic fauna: an empirical test of the potential effects of spatial confounding in experiments without replicated control and trawled areas. *J Exp Mar Biol Ecol* 245(2):155–169
- Lindholm JB, Auster PJ, Kaufman LS (1999) Habitat-mediated survivorship of juvenile (0-year) Atlantic cod *Gadus morhua*. *Mar Ecol Prog Ser* 180:247–255
- MacCall A (1990) Dynamic geography of marine fish populations. University of Washington Press, Seattle
- Madsen OS, Grant WD (1975) The threshold of sediment movement under oscillatory water wave: a discussion. *J Sediment Petrol* 45:360–361
- McConnaughey RA, Mier KL, Dew CB (2000) An examination of chronic trawling effects on soft-bottom benthos of the eastern Bering Sea. *ICES J Mar Sci* 57:1377–1388
- Mullin MM (1993) Webs and scales: physical and ecological processes in marine fish recruitment. Washington Sea Grant Program, University of Washington Press, Seattle
- Murawski SA, Serchuk FM (1989) Environmental effects of offshore dredge fisheries for bivalves. ICES 1989 Satutory Meeting. The Hague, Netherlands
- NEFSC (Northeast Region Essential Fish Habitat Steering Committee) (2002) Workshop on the effects of fishing gear on marine habitats off the Northeastern United States. October 23–25, 2001, Boston, Massachusetts. Northeast Fish Sci Cent Ref Doc 02-01, Woods Hole, MA
- Nelson JR, Eckman JE, Robertson CY, Marinelli RL, Jahnke RA (1999) Benthic microalgal biomass and irradiance at the sea floor on the continental shelf of the South Atlantic Bight: spatial and temporal variability and storm effects. *Cont Shelf Res* 19:477–505
- Pile AJ, Lipcius RN, Van Montfrans J, Orth RJ (1996) Density-dependent settler-recruit-juvenile relationships in blue crabs. *Ecol Monogr* 66:277–300
- Ramsay K, Kaiser MJ, Hughes RN (1998) Responses of benthic scavengers to fishing disturbance by towed gears in different habitats. *J Exp Mar Biol Ecol* 224:73–89
- Schratzberger M, Dinmore TA, Jennings S (2002) Impacts of trawling on the diversity, biomass and structure of meiofauna assemblages. *Mar Biol* 140:83–93
- Sissenwine MP (1984) Why do fish populations vary? In: May RM (ed) Exploitation of marine communities. Springer-Verlag, New York, p 59–95
- Sokal RR, Rohlf FJ (1995) Biometry, 3rd edn. WH Freeman, New York
- Steves BP, Cowen RK (2000) Settlement, growth, and movement of silver hake, *Merluccius bilinearis*, in nursery habitat on the New York Bight continental shelf. *Mar Ecol Prog Ser* 196:279–290
- Steves BP, Cowen RK, Malchoff MH (2000) Settlement and nursery habitats for demersal fishes on the continental shelf of the New York Bight. *Fish Bull* 98:167–188
- Stoner AW, Mehta N, Lee TN (1997) Recruitment of *Strombus veligers* to the Florida Keys reef tract: relation to hydrographic events. *J Shellfish Res* 16:1–6
- Sullivan MC, Cowen RK, Able KW, Fahay MP (2000) Spatial scaling of recruitment in four continental shelf fishes. *Mar Ecol Prog Ser* 207:141–154
- Thompson AA, Mapstone BD (1997) Observer effects and training in underwater visual surveys of reef fishes. *Mar Ecol Prog Ser* 154:53–63
- Thrush SF, Hewitt JE, Cummings VJ, Dayton PK and 6 others (1998) Disturbance of the marine benthic habitat by commercial fishing: impacts at the scale of the fishery. *Ecol Appl* 8:866–879
- Tupper M, Boutilier RG (1995) Effects of habitat on settlement, growth, and postsettlement survival of Atlantic cod (*Gadus morhua*). *Can J Fish Aquat Sci* 52:1834–1841
- Turner MG, Romme WH, Gardner RH, O'Neill RV, Kratz TK (1993) A revised concept of landscape equilibrium—disturbance and stability on scaled landscapes. *Landscape Ecol* 8:213–227
- Underwood AJ (1991) Beyond BACI: experimental designs for detecting human environmental impacts on temporal variations in natural populations. *Aust J Mar Freshw Res* 42:569–587
- Underwood AJ (1993) The mechanics of spatially replicated sampling programmes to detect environmental impacts in a variable world. *Aust J Ecol* 18:99–116
- Underwood AJ (1999) Physical disturbance and their direct effect on an indirect effect: responses of an intertidal assemblage to a severe storm. *232:125–140*
- Underwood AJ (2000) Importance of experimental design in detecting and measuring stresses in marine populations. *J Aquat Ecosyst Stress Recov* 7:3–24
- USDOC (US Department of Commerce) (1996) Magnuson-Stevens Fishery Conservation and Management Act as amended through October 11, 1996. NOAA Technical Memorandum, NMFS-F/SPO-23
- Vincent CE, Swift DJP, Hillard B (1981) Sediment transport in the New York Bight, North American Atlantic Shelf. *Mar Geol* 42:369–398
- Wahle RA, Steneck RS (1991) Recruitment habitats and nursery grounds of the American lobster *Homarus americanus*: A demographic bottleneck? *Mar Ecol Prog Ser* 69:231–243
- Watling L, Norse EA (1998) Disturbance of the seabed by mobile fishing gear: a comparison to forest clearcutting. *Conserv Biol* 12:1180–1197
- Watling L, Findlay RH, Mayer LM, Schick DF (2001) Impact of a scallop drag on the sediment chemistry, microbiota, and faunal assemblages of a shallow subtidal marine benthic community. *J Sea Res* 46:309–324
- Weissburg MJ, Zimmer-Faust RK (1993) Life and death in moving fluids: hydrodynamic effects on chemosensory-mediated predation. *Ecology* 74:1428–1443

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