DISTURBANCE OF THE MARINE BENTHIC HABITAT BY COMMERCIAL FISHING: IMPACTS AT THE SCALE OF THE FISHERY

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Abstract. Commercial fishing is one of the most important human impacts on the marine benthic environment. One such impact is through disturbance to benthic habitats as fishing gear (trawls and dredges) are dragged across the seafloor. While the direct effects of such an impact on benthic communities appear obvious, the magnitude of the effects has been very difficult to evaluate. Experimental fishing-disturbance studies have demonstrated changes in small areas; however, the broader scale implications attributing these changes to fishing impacts are based on long-term data and have been considered equivocal. By testing a series of a priori predictions derived from the literature (mainly results of small-scale experiments), we attempted to identify changes in benthic communities at the regional scale that could be attributed to commercial fishing.

Samples along a putative gradient of fishing pressure were collected from 18 sites in the Hauraki Gulf, New Zealand. These sites varied in water depth from ~17 to 35 m and in sediment characteristics from ~1 to 48% mud and from 3 to 8.5 µg chlorophyll *a*/cm³. Video transects were used for counting large epifauna and grab/suction dredge and core sampling were used for collecting macrofauna. After accounting for the effects of location and sediment characteristics, 15–20% of the variability in the macrofauna community composition sampled in the cores and grab/suction dredge samples was attributed to fishing. With decreasing fishing pressure we observed increases in the density of echinoderms, long-lived surface dwellers, total number of species and individuals, and the Shannon-Weiner diversity index. In addition, there were decreases in the density of deposit feeders, small opportunists, and the ratio of small to large individuals of the infaunal heart urchin, *Echinocardium australe.* The effects of fishing on the larger macrofauna collected from the grab/suction dredge samples were not as clear. However, changes in the predicted direction in epifaunal density and the total number of individuals were demonstrated. As predicted, decreased fishing pressure significantly increased the density of large epifauna observed in video transects. Our data provide evidence of broad-scale changes in benthic communities that can be directly related to fishing. As these changes were identifiable over broad spatial scales they are likely to have important ramifications for ecosystem management and the development of sustainable fisheries.

Key words: benthic communities, broad-scale changes; benthic community structure cf. fishing pressure; fishing impacts; habitat disturbance by commercial fishing; habitat disturbance, broad-scale effects; marine benthic habitats; New Zealand, Hauraki Gulf.

INTRODUCTION

Sustainable management of renewable natural resources should include a balance between exploitation and adverse effects on other components of the ecosystem. In marine ecosystems, the removal of target and non-target species and habitat disturbance by commercial fishing are probably the most important human impacts (Dayton et al. 1995). Commercial fishers exploit resources from near shore to deep water. Trawls and dredges potentially impact many species that live on or near the seafloor. In addition, the fishing gear physically disturbs the habitat as it is dragged across

the seafloor. Direct changes can result from the crushing of individuals or removal as by-catch (i.e., species caught in fishing gear other than the species being targeted by the fishers), while the partial excavation and damage of near-surface-dwelling organisms can attract mobile predator/scavengers (Britton and Morton 1994, Kaiser and Spencer 1994, Dayton et al. 1995). Further changes are possible due to habitat modification (Auster et al. 1996), changes in sedimentation pattern (Churchill 1989), or benthic algal production and nutrient cycling (Mayer et al. 1991).

The spatial extent and frequency of habitat disturbance by fishing influences the ecological impact. Fisheries statistics indicate that some regions are intensively fished. For example, some areas of the North Sea

and the northeastern shelf of the United States and Canada are on average completely covered by commercial fishing several times a year (de Groot 1984, Churchill 1989, Messieh et al. 1991, Auster et al. 1996). However, as fishers effectively target prey and exploit the habitat in a patchy manner, there is a great deal of spatial variation in fishing effort not detectable in the coarse spatial scale over which fisheries statistics are usually collected (Kaiser and Spencer 1996).

There is a general recognition of the need to consider the ecological impacts of commercial fishing (Jones 1992, Gislason 1994, ICES 1994), but identifying impacts is often obfuscated by the lack of environmental-impact assessment procedures in fisheries management. Lack of monitoring and adequate control sites make it very difficult to tease apart a posteriori any effect of habitat disturbance by fishing from spatial and temporal variability in benthic communities.

A number of small-scale experimental studies of bottom disturbance by commercial fishing gear have demonstrated local effects on benthic communities (e.g., Peterson et al. 1987, Bergman and Hup 1992, Eleftheriou and Robertson 1992, Thrush et al. 1995, Currie and Parry 1996). However, such effects are not always consistent across sites. For instance, there is a failure to detect the effect of experimental fishing disturbance in areas exposed to extreme natural disturbances (e.g., storms or very strong tidal flows; Hall et al. 1990, Brylinsky et al. 1994, Kaiser and Spencer 1996).

There are two reasons for a potential disparity between effects that can be demonstrated by small-scale field experiments and possible broader scale fishing effects. Firstly, by their nature, experiments occur on much smaller scales in space and time and are usually done in reasonably homogeneous habitats, whereas fishing occurs across habitats. Chronic effects of fishing disturbance may cumulate over long time periods. Secondly, recovery rates of benthic organisms are extremely dependent upon the area and proximity to recruit source areas; therefore, isolated and small experimental disturbances do not mimic fishing disturbances, which recover much more slowly than experimental plots (Hall et al. 1994, Thrush et al. 1996). Broader scale implications of fishing impacts have, however, been inferred a posteriori from benthic surveys and time-series data (Reise 1982, Holme 1983, Sainsbury 1988, Rice et al. 1989, Hutchings 1990, Langton and Robinson 1990, Witbaard and Klein 1994). Typically these studies indicate reductions in the density of large, long-lived epifaunal organisms that add heterogeneity to soft-sediment habitats. However, with any broad-scale environmental survey alternative hypotheses can always be found (Hall 1994).

The problems in trying to identify the broad-scale effects of habitat disturbance by fishing on benthic communities are that adequate information has not been collected from the outset, there are no adequate controls, and the appropriately scaled critical experi-

ments cannot be performed. The spatial heterogeneity in benthic community composition has daunted early attempts to identify broad-scale effects; however, this can be dealt with by treating variability as information rather than noise. Much of the variability in community structure in soft-sediment habitats on spatial scales of kilometers is related to changes in sediment grain size and organic content (e.g., Rhoads 1974, Warwick and Uncles 1980, Gray 1981, Pearson and Rosenberg 1987, Schaff and Levin 1994). Variability contributed by other factors that operate at the scale of sampling, but that cannot be measured (e.g., variation in oceanographic characteristics), can be accounted for with location (i.e., spatial) variables as surrogates. In our study, latitude, longitude, and water depth were used to locate sites in three-dimensional space. By using analytical procedures that incorporate these spatial and environmental (e.g., sediment grain size and organic content) factors (ter Braak 1988, McCullagh and Nelder 1989, Borcard et al. 1992, Legendre 1993, Borcard and Legendre 1994, Jongman et al. 1995) we are able to focus on changes in macrobenthic community structure in relation to fishing pressure rather than other factors operating at regional spatial scales.

The deductive potential of any survey can be enhanced by testing a priori predictions (Eberhardt and Thomas 1991). Testing predictions that arise from small-scale experiments concerning differences in habitat heterogeneity, biodiversity, and life-history characteristics of resident species should, in combination with assessments of changes in community structure, provide a practical mechanism to scale up experimental results and assess the broad-scale consequences of fishing within marine ecosystems. In this paper we test a priori predictions derived from the literature of changes in population, taxonomic, and functional groups, as well as univariate community-level characteristics with changes in fishing pressure. We also assess the importance of fishing pressure in accounting for variation in community composition across a number of sites that differ in a variety of environmental characteristics.

PREDICTIONS

Results from experimental disturbance studies of soft-sediment habitats enable us to make predictions about changes in benthic communities that can be tested at larger scales. A common response of marine soft-sediment communities to increasing disturbance frequency and intensity is the increased abundance of small opportunistic species and juvenile life-history stages (see Hall et al. [1994] for recent review). Experimental studies of habitat disturbance by fishing provide other predictions. Bergman and Hup (1992) demonstrated 10–65% reductions in echinoderm, polychaete, and mollusk densities after trawling. Eleftheriou and Robertson (1992) in particular noted negative effects on heart urchin (*Echinocardium* sp.) densities. Thrush et al. (1995) observed larger reduc-

TABLE 1. Predicted changes in marine benthic communities along a gradient of decreasing habitat disturbance by trawling and dredging.

Decreasing densities or ratios
Scavenger density
Deposit-feeder density
Small-opportunist density
Ratio of polychaetes to molluscs
Increasing densities or ratios
Large epifauna density
Species diversity and richness
Long-lived near-surface-dweller density
Ratio of small/large individuals
Echinoderm density
Total number of individuals

tions in densities due to scallop dredging on a community dominated by polychaetes and bivalves than on one dominated by small crustaceans, but both communities exhibited decreased species richness and diversity. Currie and Parry (1996) reported a 20–30% decrease in infaunal abundance following commercial scallop dredging, with effects lasting up to 14 mo. Furthermore, reductions in the density of large long-lived epifaunal organisms, which add notable habitat heterogeneity to soft-sediment benthic communities, have been observed in a number of long-term studies and attributed to bottom fishing (Reise 1982, Holme 1983, Sainsbury 1988).

A report of the International Council for the Exploration of the Sea (ICES) working group on ecosystem effects of fishing activities (ICES 1994:34) also synthesized much of the available information on habitat disturbance in the North Atlantic to predict changes in benthic soft-sediment communities in areas protected from bottom fishing. They predicted that in protected areas: (1) the density, age, and size of shallow burrowing, epibenthic, and long-lived species should increase; (2) the density of demersal scavengers and the relative abundance of polychaetes to molluscs should decrease; and (3) species that burrow deeper than the depth to which fishing gear disturbs the sediment should be unaffected, although disturbances may still influence smaller, near-surface-dwelling juvenile stages. Based on the literature, we made a number of a priori predictions about how benthic communities may change along a gradient of bottom disturbance by fishing (see Table 1).

METHODS

The study was conducted in the inner Hauraki Gulf (37° S, 175° E), New Zealand (Fig. 1). The major finfishery in this area is focused on snapper (*Chrysophrys auratus*). Typical trawl gear used for snapper in the Hauraki Gulf consists of 480-kg trawl doors and a ground rope of 140–150 mm diameter rubber bobbins and steel balls, with a total ground rope mass (not including sweeps and bottom bridles) of 240 kg (Drury and Hartill 1993). Danish seine are also used to catch
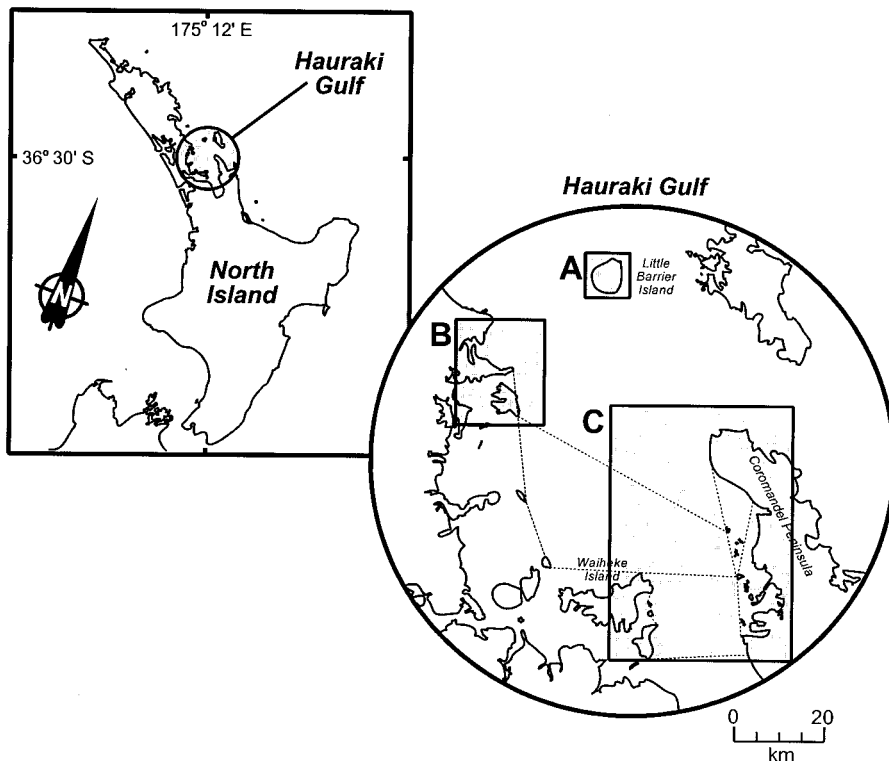

FIG. 1. North Island of New Zealand, showing the areas sampled within the Hauraki Gulf.
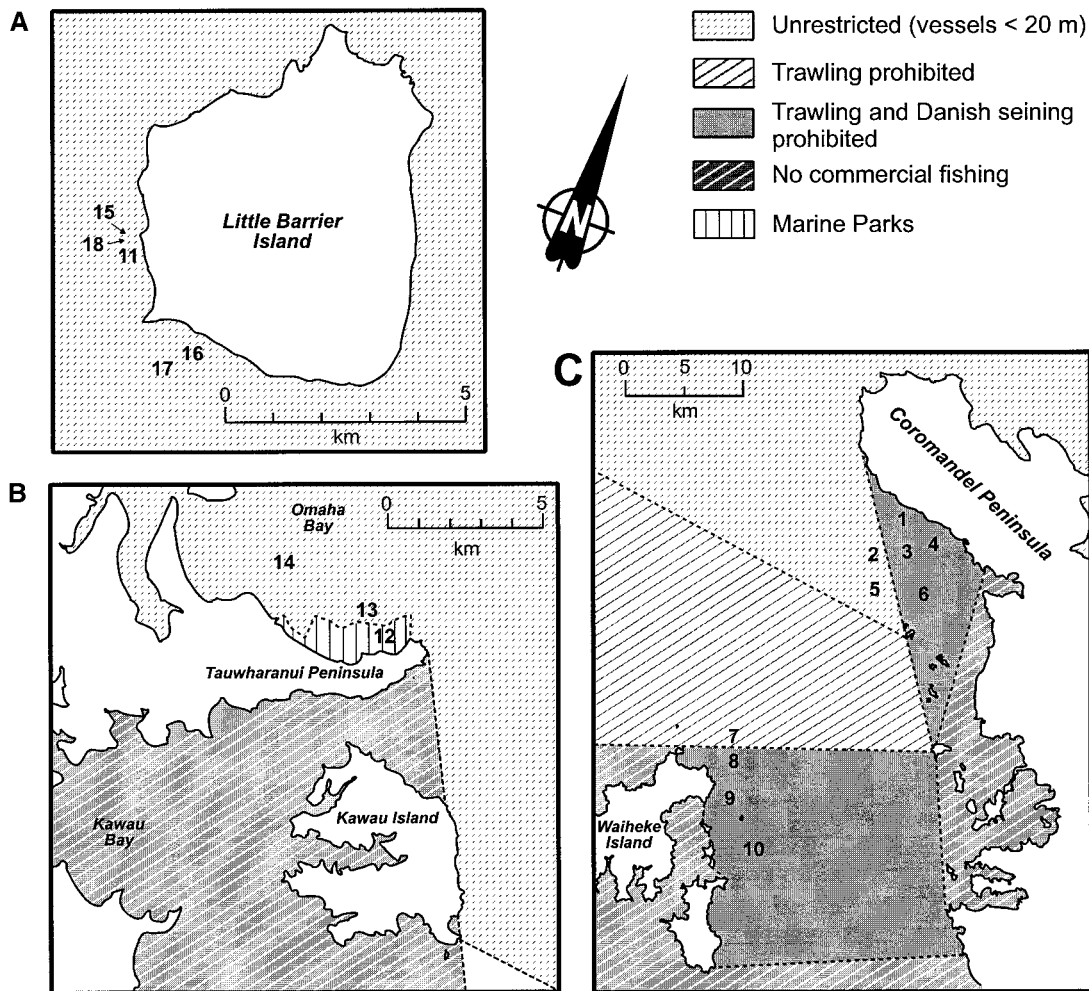
FIG. 2. Location of sites 1–18. For the geographic relations of panels A, B, and C, see Fig. 1. The key indicates restrictions to commercial bottom fishing in these areas. Sites 3, 4, 11, 13, 14, and 17 are dredged for scallops.

snapper; the ground rope of the seine net is of similar design to that used for trawling, but it is much lighter. Leaded seine ropes are also laid over kilometers of the seafloor and used to herd fish into the net. Scallops (*Pecten novaezelandiae*) are the major wildstock bivalve fishery in the inner Hauraki Gulf. Scallops are usually fished with a 2-m-wide box dredge, similar to that described by McLoughlin et al. (1991).

Fisheries statistics on the intensity of fishing were not appropriate to determine sites because these data are collected over much too broad a scale. However, we have attempted to estimate the spatial extent of disturbance by bottom trawling, Danish seining, and scallop dredging in the inner Hauraki Gulf (1568 km²), to provide some indication of the intensity of the fishery. In 1993 (the year prior to our study), 1568 km² was swept by bottom trawl gear (i.e., ground ropes, net, sweeps, bridles, and trawl doors), of which 719 km² was swept by ground rope at the front of the trawl net. To estimate the area swept by the Danish seine

fishery we assumed a rope 6000 m long shot in a circle and retrieved by the fishing boat at anchor. We estimate 8274 km² was swept in 1993. The total area encompassed by the traditional commercial scallop beds in the inner Hauraki Gulf is ~81 km². However, in recent years most of the fishing effort has been focused on beds off Little Barrier Island, Coromandel Peninsula, and Omaha Bay and these beds encompass an area of ~30 km² (see Figs. 1 and 2). We estimate scallop dredges swept 8.9 km² in the 1993/1994 season.

The snapper fishery in the Hauraki Gulf has recently been subject to a total fishing mortality, F_m, of ~0.20 (F_m = instantaneous rate of fishing mortality, Ricker 1975), about two thirds of which is due to commercial fishing. This rate of fishing pressure is modest by international standards for demersal fisheries, but pressure of this order has nevertheless reduced snapper stocks in the Hauraki Gulf well below B_{msy}, the biomass that can support the maximum sustainable yield (Annala and Sullivan 1997). Recent years have produced

TABLE 2. Habitat characteristics and fishing-pressure ranking for each site in the Hauraki Gulf, New Zealand. Site numbers are only a code to ensure sample sorting, and identification was done blind of site fishing-pressure rank. Fishing-pressure rank runs from the most (1) to the least (15.5) disturbed.

Site no.	Fishing-pressure rank	Depth (m)	Sediment chlorophyll a ($\mu g/cm^3$)	Sediment composition (% dry mass)		
				Hash†	Silt	Clay
1	11	22	7.27	5	28.0	13.0
2	5	14	5.65	2	29.0	10.0
3	8	22	8.37	2	34.0	14.0
4	4	32	8.45	8	21.0	20.0
5	7	24	4.30	3	27.0	19.0
6	9	17	6.75	14	28.0	16.0
7	6	35	4.06	28	10.0	5.0
8	12	23	4.38	8	8.0	6.0
9	15.5	25	7.22	67	11.0	3.0
10	15.5	18	5.65	2	31.0	8.0
11	2	21	5.20	22	0.1	1.0
12	10	18	3.0	10	0.2	1.0
13	8	17	8.48	8	0.4	0.4
14	3	25	6.23	27	0.3	0.3
15	13	21	7.17	8	0.4	1.0
16	14.5	17	5.97	31	0.2	1.0
17	1	23	4.33	25	0.2	1.0
18	14.5	20	7.11	93	0.1	1.0
Correlation with site rank						
r^2		0.0392	0.0286	0.0958	0.0022	0.0171
P		0.2096	0.5023	0.2113	0.8520	0.6053

† Hash = shell fragments >2 mm.

poor scallop landings from the Hauraki Gulf, stocks are heavily fished with an apparent $F_m \sim 1.0$. This is roughly equivalent to about 60% absolute mortality per year (Cryer 1994) and quite a high level of exploitation by international standards.

We were able to rank areas of the Gulf in terms of potential habitat disturbance by commercial bottom trawling and dredging. Ranking was based on fisheries legislation that limits the use of particular types of fishing gear (dredges and trawls) in certain areas (Fig. 2). Information from fisheries managers also enabled us to identify areas with different histories of exploitation by the scallop fishery. For example, areas on the southwest side of Little Barrier Island (Fig. 2A) are heavily exploited, except in the vicinity of gravel/cobble patches and reefs; the area around site 9 (Fig. 2C) has not been exploited in the last decade; the area around site 4 is regularly exploited by scallop fishers, but nearby areas are less intensively exploited. In developing the ranking we considered scallop dredging to disturb the seafloor more than trawling or Danish seining, because of the focus on specific scallop beds and the nature of the fishing gear. The ranking developed from this information does not order sites by habitat characteristics (Table 2) or by latitude ($r^2 = 0.0597$, $P = 0.3286$) and longitude ($r^2 = 0.0392$, $P = 0.4310$). Eighteen sites were sampled in the summer (i.e., December–January) of 1994 (Fig. 2, Table 2).

Sampling techniques

High-resolution side-scan sonar (Klein 595; Klein Associates, Inc., Sonar, Salem, New Hampshire, USA) was used to survey the seafloor to identify sites at various locations throughout the Gulf with different environmental conditions and levels of fishing activity. In total, the side-scan was run over a distance of 150 km. The side-scan sampled at 500 kHz, with a range of 100 m on either side of the tow fish. Allowing for poor signal return, this provided us with transects 150 m wide. Although dependent on surface wave conditions, we could confidently resolve individual objects on the seafloor of ~ 4 m² (e.g., rocks, dredge tracks) or repeatable patterns of smaller objects (e.g., sand waves, horse mussel patches). In areas considered as potential sites, 3 km² of the seabed was surveyed. We used this technique to determine the broad-scale homogeneity of habitats and thereby qualitatively assess the representativeness of the smaller-scale intensive sampling strategies to be nested within sites (see next two paragraphs).

A remotely operated vehicle (ROV) was used to conduct video transects of the seafloor at each site to estimate the density of large epifauna. The video camera was mounted obliquely to the bottom of the ROV. Four lasers mounted in a 20 cm × 20 cm array around the video camera were used to provide scaling and estimates of area covered on each transect. At least two transects were recorded at each site with the ROV positioned <1 m off the bottom and traveling between 0.06 and 0.16 m/s. Video footage was only analyzed if: the image was in focus; the scale lasers could be seen and were not badly skewed (i.e., differences between the distance delineated by the top and bottom pairs of lasers was <10% of the distance delineated by

the bottom pair [Grassle et al. 1975]); and surface characteristics (>10 mm in diameter) could be identified. Usable sections of each transect were viewed and large epifauna in major taxonomic groups (sponges, starfish, scallops, and horse mussels) were counted as they crossed the 20-cm line delineated by the bottom pair of lasers, thus avoiding problems caused by skewness of the image. The length of useable parts of the transects was calculated at the same time by counting the number of 20-cm strips observed (i.e., counting the number of times the frame was moved forward the distance delineated by the bottom pair of lasers).

Macrofauna were sampled from the central area of each site. Five randomly located grab (muddy sites) or suction-dredge (sandy sites) samples ($25 \times 25 \times 20$ cm deep) were collected to assess the density of large macrofauna (≥ 2 mm). Fifteen randomly located core samples (10 cm diameter, 12 cm deep) were collected at each site by divers to assess the density of smaller macrofauna (≥ 0.5 mm). Grab samples, but not core samples, were collected at sites 7 and 8 due to time/ water-depth restrictions. Core samples, but not suction-dredge samples, were collected at sites 12 and 18 due to high current velocity. Data from the two macrofaunal sampling strategies were treated separately. All samples were preserved in 70% isopropanol and 0.1% Rose Bengal in seawater. In the laboratory macrofauna were sorted, identified to the lowest practical taxonomic level, and counted. Taxa were aggregated into functional groups based on personal observations, available local information (e.g., Morton and Miller 1973, Pridmore et al. 1990), or general descriptions found in the literature (e.g., Ronan 1978, Fauchauld and Jumars 1979, Sloan 1980, Jangoux 1982). We classified long-lived animals as those with a potential to live >3 yr; opportunistic species were defined according to Grassle and Grassle (1974) and Pearson and Rosenberg (1978).

Divers also collected surficial sediment samples (0– 2 cm depth) that were bulked by site for subsequent analysis of sediment grain size and chlorophyll content. Samples for grain size were digested in 6% hydrogen peroxide for 48 h to remove organic matter, and dispersed using calgon (0.5% [mass : volume] sodium hexametaphosphate) before being sampled by wet sieving and pipette analysis (Gatehouse 1971) at 1 ϕ intervals from 10 to -1 ϕ. (Phi is a standard measure of sediment particle size, $-\log_2$[diameter in millimeters].) Chlorophyll samples were kept in the dark and frozen until analysis. Chlorophyll was extracted from a subsample of the sediment by boiling in 95% ethanol, and the extract processed using a spectrophotometer. An acidification step was used to correct for phaeopigment interference. The amount of chlorophyll a in the extract was calculated using the equations of Sartory (1982).

Statistical analyses

Partial canonical correspondence analysis (ter Braak 1986, 1998, ter Braak and Prentice 1988) was used to assess the importance of fishing pressure on the macrobenthic community structure. This approach eliminated all the co-variables and related the residual variation in the community data specifically to fishing-pressure rank (see Borcard et al. 1992, Borcard and Legendre 1994). Co-variables used in the partial canonical correspondence analysis were sediment characteristic variables: chlorophyll a (μg/cm^3), shell hash (shell fragments >2 mm), silt, and clay (all as percentage sediment dry mass); location variables: seconds of latitude (East) and longitude (South); and water depth (m). Analyses were performed using CANOCO (ter Braak 1987).

Generalized linear-modeling techniques (McCullagh and Nelder 1989, Crawley 1993) were used to test the various a priori predictions about changes to populations, taxonomic and functional groups, or univariate measures of community structure down the gradient of fishing pressure (Table 1). Models with different error structures (normal, Poisson, negative binomial) and link functions (identity and log) were run and the model fit was evaluated by half-normal plots of standardized Pearson and deviance residuals together with plots of residuals vs. predicted values. Results are presented for model error structures and link functions that resulted in the best fit. The initial model included fishing-pressure rank of each site, location variables, and sediment-characteristic variables. The most parsimonious model was derived by backward selection with a $P \geq 0.15$ exit criteria. Terms were only removed from the model if doing so did not result in a significant increase in deviance (Crawley 1993). Analyses were performed using SAS Institute (1993) and SAS/Insight (1993) procedures.

Because of obvious limitations of the sampling gear, not all of the predictions were tested on all of the data— effects on large epifauna were tested on video count and grab/suction dredge data; effects on small opportunistic species were only tested on core data; and effects on the ratio of small/large individuals were tested on *Echinocardium australe* densities from the core data (i.e., the only abundant and ubiquitous animal with a large size range).

Results

Side-scans of potential sites adjacent to Little Barrier Island (Fig. 2) revealed distinct variability in sediment structure on a kilometer scale, with sand/gravel, cobble, and mega-ripple areas. A high incidence of scallop dredge marks were noted in some areas. Largely homogeneous areas of sandy sediment with some patches of mega-ripples were found in Omaha Bay. Off Waiheke Island a large horse mussel bed (*Atrina zealandica*) was found; outside of this bed sediments were homogeneous and fine grained. Areas off Coromandel Peninsula revealed a featureless fine-grained background, except for a horse mussel bed in the vicinity of site 1. Occasional trawl door tracks were observed
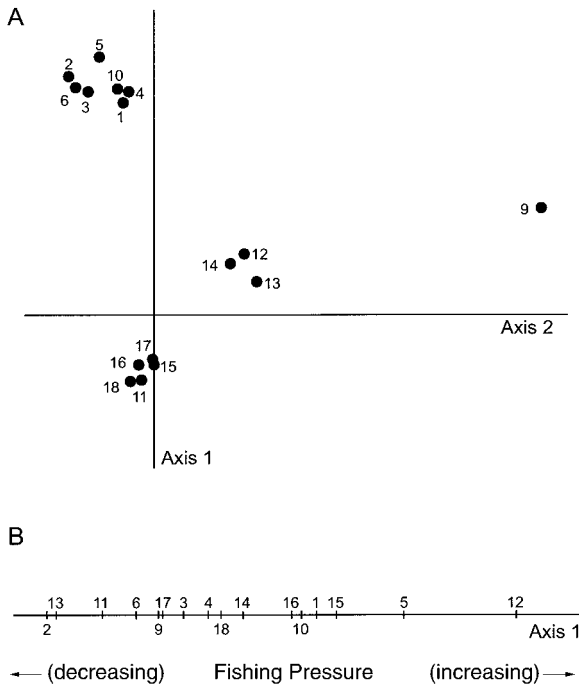
A

B

FIG. 3. (A) Correspondence analysis of core data (only axes 1 and 2 are shown; they account for 19.3% and 13.6% of the variability, respectively.) (B) Partial canonical correspondence analysis showing distribution of sites relative to fishing-pressure rank.
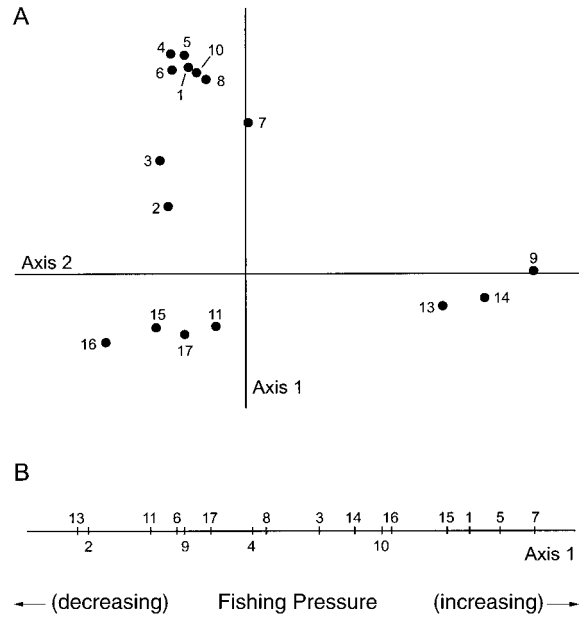
A

B

FIG. 4. (A) Correspondence analysis of grab/suction dredge data (only axes 1 and 2 are shown; they account for 19.1% and 16.4% of the variability, respectively.) (B) Partial canonical correspondence analysis showing distribution of sites relative to fishing-pressure rank.

in the sediments around sites 2 and 5. These observations concur with our site fishing-pressure ranks.

Multivariate analyses

The first four axes of the initial unconstrained correspondence analysis accounted for 54% of the variation in the core data and 60% of the variation in the grab/suction dredge data. Figs. 3A and 4A show positions of the sites on the first two axes. Partial canonical correspondence analyses peel away the variability due to geographic location and sediment characteristic co-variables. The remaining variability was significantly related to site fishing-pressure rank (correlation = 0.91, P = 0.0270; correlation = 0.92, P = 0.0203 for the core and grab/suction dredge data, respectively). Figs. 3B and 4B show the partial canonical correspondence analysis axis related to fishing pressure, with site numbers superimposed. Fishing-pressure rank accounted for 15% and 20% of the variability in community structure in the core and grab/suction dredge data, respectively. There is a high degree of consistency in the ordering of sites between the two ordinations (remember, core data only were collected from sites 17 and 26 and grab data only from sites 9 and 10). The only differences between ordinations based on core and grab/suction dredge data are some flips in the position of adjacent sites.

Tests of predictions: video data

Counts of specific epifaunal groups from the video transects were extremely patchy, therefore statistical analysis was only performed on the total density of epifauna from each site. As predicted (Fig. 1), decreased fishing pressure significantly increased the density of large epifauna (Table 3).

Tests of predictions: core data

As expected from general benthic literature, location and sediment grain-size characteristics were often important in accounting for variation between sites (Table 4). Of the 10 predictions relevant to testing with the core data, fishing pressure was an important factor in all of our models except the density of scavengers and

TABLE 3. The effect of decreasing fishing pressure on density of total epifauna counts derived from video transects.

Factors	P†	a_i‡
Fishing pressure	0.0330	1.860
Longitude	0.0245	−0.947
Latitude	0.0923	−0.227
Depth	0.0434	2.490
% Hash	0.0502	−1.100
% Silt	0.0764	0.220
% Clay	0.0716	−1.150

Notes: The most parsimonious model (Poisson errors with log-link function) is presented. Pearson's χ^2/df ratio = 0.91. The χ^2 for goodness of fit = the Pearson statistic.
† Type-3 probability level.
‡ Coefficient in $y = c + a_1$var 1 + $a_2$var 2 + . . . $a_n$var n, where y = total epifaunal count and c is a constant.

TABLE 4. Results of test of predictions using core data. Generalized linear models were used to test predictions about the effect of decreasing fishing pressure on macrofaunal groupings. The results presented are the most parsimonious models.

Macrofaunal group	Model type†	Factors	P‡	a_i§ estimate
Deposit feeders	PL‖, 34.929	Fishing pressure	0.0810	−0.0446
		Longitude	0.1087	−0.0308
		Latitude	0.1874	−0.0108
		% Hash	0.0028	0.0144
		% Clay	0.1906	−0.0520
Echinoderms	PL‖, 3.986	Fishing pressure	0.0037	0.1597
		Longitude	0.0156	−0.0690
		Latitude	0.0735	0.0242
		Depth	0.0007	0.1660
		Chl. *a*	0.0135	−0.2370
		% Silt	0.0001	0.0108
Ratio of small to large *Echinocardium*	NL 0.503	Fishing pressure	0.0536	−0.2440
		Latitude	0.1360	0.0520
		% Hash	0.0103	0.0682
Long-lived surface dwellers	PL‖, 16.211	Fishing pressure	0.0776	0.0929
		Longitude	0.0089	−0.0602
		Latitude	0.0306	0.0270
		Depth	0.1298	0.0732
		% Hash	0.0001	0.0281
		% Silt	0.0019	0.0675
Ratio of polychaetes to mollusks	NL, 0.765	Fishing pressure	0.0211	0.0545
		Latitude	0.0292	−0.0130
		Depth	0.0019	0.0879
		% Hash	0.1155	−0.0073
		% Silt	0.0160	−0.0197
Scavengers	PL‖, 19.334	Longitude	0.0001	−0.0403
		Latitude	0.1742	−0.0078
		Chl. *a*	0.1270	0.0993
		% Hash	0.0007	0.0095
Small opportunists	PL‖, 23.540	Fishing pressure	0.0620	−0.0559
		Longitude	0.0020	−0.0633
		Chl. *a*	0.2313	0.1426
		Carbon	0.0020	0.4720
		% Hash	0.0017	0.0149
		% Clay	0.0114	−0.2350
Shannon-Weiner diversity index	NI, 0.766	Fishing pressure	0.0128	0.0535
		Latitude	0.0001	0.0295
		Depth	0.0085	0.0659
Total number of individuals	BL, 26.660	Longitude	0.0001	−0.0487
		Latitude	0.0001	−0.0172
		Depth	0.0218	−0.0502
		% Hash	0.0001	0.0131
Total number of species	PL, 2.925	Fishing pressure	0.0346	0.0204
		Longitude	0.0183	−0.0114
		Latitude	0.0559	0.0044
		Depth	0.0651	0.0201
		% Clay	0.0152	−0.0204

 † PL = Poisson errors with log link; NL = normal errors with log link; NI = normal errors with identity link; BL = negative binomial with quadratic errors with log link. The number given after the model type is either the model r^2 (for NI or NL) or the Pearson's χ^2/df ratio (for PL or BL).
 ‡ Type-3 probability level.
 § a_i coefficient as in Table 3.
 ‖ Using a quasi-likelihood response distribution (McCullagh and Nelder 1989).

total number of individuals. Fishing pressure was a significant factor ($\alpha = 0.05$) for the density of echinoderms, polychaete to mollusk ratio, Shannon-Weiner diversity index, and total number of species. In addition, we tested the prediction that the ratio of small to large *Echinocardium australe* would increase with fishing pressure. A lower proportion of smaller individuals was found with decreasing fishing pressure, although the level of evidence for this relationship ($P = 0.0536$) did not reach $\alpha < 0.05$. In seven out of eight cases

where fishing contributed to the most parsimonious model, the sign of the parameter estimate was consistent with our a priori prediction. The only exception was the polychaete/mollusk ratio, which was positively correlated with decreased fishing pressure.

Tests of predictions: grab and suction dredge data

The densities of deposit feeders, total number of individuals, and epifauna were all influenced by fishing-pressure rank (Table 5), although not all of these re-

TABLE 5. Results of test of predictions using grab/suction dredge samples. Generalized linear models were used to test predictions about the effect of decreasing fishing pressure on macrofaunal groupings. The results presented are the most parsimonious models. Abbreviations and further details are as in Table 4.

Macrofaunal group	Model type	Factors	P	a_i estimate
Deposit feeders	PL†, 27.387	Fishing pressure	0.0066	0.122
		Longitude	0.0001	−0.0884
		Latitude	0.0005	0.0457
		Chl. a	0.0067	−0.579
		% Hash	0.0003	0.0425
Echinoderms	PL†, 17.370	Longitude	0.0025	0.0726
		% Clay	0.0011	0.0866
Epifauna	NI, 0.335	Fishing pressure	0.0628	4.7800
		Longitude	0.0465	−1.8700
Long-lived surface dwellers‡	PL†, 42.249			
Ratio of polychaetes to molluscs	PL†, 146.652	Latitude	0.0890	−0.0271
		Depth	0.0025	−0.1707
Scavengers	PL†, 74.670	Longitude	0.0041	−0.0433
		% Hash	0.0453	0.0238
Shannon-Weiner diversity index	NI, 0.901	Longitude	0.0028	−0.0483
		Depth	0.0271	0.0604
		% Hash	0.0357	0.0174
		% Silt	0.0099	0.0626
		% Clay	0.0006	−0.1500
Total number of individuals	PL†, 134.300	Fishing pressure	0.0534	0.0935
		Longitude	0.0001	−0.0749
		Latitude	0.0150	0.0347
		Chl. a	0.0230	−0.5050
		% Hash	0.0111	0.0319
Total number of species	LI, 0.565	Longitude	0.0051	−1.1600
		% Hash	0.0423	0.6080

† Using a quasi-likelihood response distribution (McCullagh and Nelder 1989).

‡ No adequate statistical model developed.

lationships were significant at the $\alpha < 0.05$ level. In each case, decreased fishing pressure was associated with increases in density. This is consistent with our a priori predictions for epifauna and total number of individuals, but contrary to our prediction for deposit feeders. Fishing-pressure rank was not a factor that contributed to the most parsimonious model for the density of echinoderms or scavengers, the polychaete/mollusk ratio, the Shannon-Weiner index, or the total number of species. No adequate model could be developed to explain the density variation of long-lived surface dwellers. For models with Poisson errors, comparison of the Pearson's χ^2/df ratio for models derived from the core and grab/suction dredge data (Tables 4 and 5) indicates that models based on grab/suction dredge data generally were not as adequate as models based on core data.

Discussion

The potential importance of changes in benthic communities due to habitat disturbance by commercial fishing is often discounted because impacts have not been well documented. Biological effects are difficult to identify due to the complexity and variability in benthic communities (Messieh et al. 1991, Gislason 1994, Hall 1994). Combining modern statistical techniques with testing of appropriate and ecologically important a priori predictions, we were able to attribute broad-scale

changes in macrobenthic communities to fishing disturbance. These effects were documented from a region that is locally important to coastal fishers. However, our estimates of the area potentially swept by trawls, seines, and dredges indicate that the frequency of disturbance is probably much lower in the Hauraki Gulf than in other parts of the world (e.g., areas of the North Sea and the northeastern shelf of the United States and Canada; de Groot 1984, Churchill 1989, Messieh et al. 1991, Auster et al. 1996). Stronger effects might be expected in such areas; however, detection could be difficult as it may be hard to allocate sites to a gradient of fishing pressure.

The development of the fishing-intensity ranking used in our analyses, although based on local legislation and information provided by fisheries managers, obviously has a degree of subjectivity. This subjectivity is likely to be greatest in the allocation of middle-order ranks. To assess this effect we re-ran our analysis swapping some middle-order ranks; this made no substantive change to our results. The fact that significant relationships could be identified between site fishing-pressure ranking and community structure or various ecological parameters indicates that at least a near-monotonic relationship exists. In this case, were we able to characterize fishing pressure by more sophisticated means than a simple ranking, we could expect an even better fit. However, this was the best approach

possible given the lack of appropriate reference sites and the mismatch between the spatial scales over which fishing-effort statistics are collected and the scales used to identify impacts on benthic communities.

Multivariate techniques are commonly used to reveal changes in benthic communities that may be directly or indirectly attributed to human impacts (e.g., Clarke and Green 1988, Warwick et al. 1991, Olsgard and Hasle 1993, Warwick 1993, Olsgard and Gray 1995, Ellis and Schneider 1997, Turner et al. 1997). Our multivariate analysis based on core or grab/suction dredge samples accounted for only 54% and 60% of the variation in the core and grab/suction dredge data, respectively. Nevertheless these ordinations are still informative. Unexplained variance is due to noise (probably variability at different scales to those encompassed in the sampling program), sampling error, and numerical problems with estimation error in correlation coefficients and fitted values (ter Braak 1986). After accounting for the influence of location and sediment characteristics, 15% (core) and 20% (grab/suction dredge samples) of the variability was attributed to fishing. We consider these to be ecologically significant effects on the macrobenthic communities occurring over a spatial extent of 80 km and a range of habitat types. The weaker effect of fishing-pressure rank on the core data vs. the grab/suction dredge data most likely reflects the differences in the assemblages sampled by the two techniques. The core data were numerically dominated by small polychaetes and crustaceans, whereas the grab/suction dredge data were dominated by larger crustaceans and mollusks.

Most of the a priori predictions were supported by univariate analysis of the core data. Along a putative gradient of decreasing fishing pressure we observed: increases in the density of echinoderms and long-lived surface dwellers; increases in the total number of species and the Shannon-Weiner diversity index; and decreases in the density of deposit feeders, small opportunists, and the ratio of small to large *Echinocardium australe.* Variation in the polychaete/mollusk ratio was contrary to that predicted. Preliminary results from studies of gravelly habitats on Georges Bank (northeast Atlantic) and off the Isle of Man (Irish Sea) also failed to identify a decrease in the polychaete-to-mollusk ratio with decreased habitat disturbance by fishing (ICES 1996). This may indicate that attributes of individuals other than taxonomic affiliation are important. Evidence for the predicted changes in the larger macrofauna collected by the grab/suction dredge sampling was not so strong. Often fishing-pressure rank was not an important factor in the statistical models for these samples. However, predicted changes in the epifaunal density and the total number of individuals were demonstrated. Contrary to our prediction, decreased fishing pressure positively affected the density of deposit feeders. Failure of the prediction concerning deposit feeders indicates that factors other than feeding mode are in-

fluencing the distribution of large macrofauna. For example, increasing the density of epifauna that add to the three-dimensional complexity of undisturbed habitats can, under certain flow regimes, lead to the deposition of fine sediments potentially favoring increased deposit-feeder abundance (Nowell and Jumars 1984, Nalesso et al. 1995, Green et al. 1998).

It is unclear why there should be such a disparity in our predictive ability as tested by the core and grab/suction dredge data, especially as slightly stronger effects were apparent for the grab/suction data in the multivariate analysis. Re-analysis of the data using the generalized linear modeling, but omitting the sites for which only one type of data was collected, did not change the outcome of the results. Due to bottom time limitations of divers, we were only able to collect 5 suction dredge samples at each site, in contrast to the 15 cores. This lower sample size resulted in a less precise estimate of site means even though much larger areas of sediment were sampled by the grab/suction dredge sampling than by core sampling. Imprecise estimates of data points for trend analysis can confound the identification of trends (Thrush et al. 1994). Multivariate analyses that identify changes to a suite of taxa with various life-history characteristics and sensitivities to disturbance are often more sensitive than univariate analysis.

We did not identify a role for fishing pressure in accounting for the density of scavengers. Observations of epifaunal and demersal scavengers attracted to areas recently disturbed by trawls or dredges is one of the most consistent observations from experimental studies. For example, diet composition for gurnard and whiting (*Aspitrigla cuculus, Eutrigla gurnardus* and *Merlangius merlangus*) in fished areas indicates these bottom-feeding fish are preferentially feeding on fauna damaged by trawling (Kaiser and Spencer 1994). Ramsay et al. (1996) demonstrated changes in the density, size, and gut content of the hermit crab *Pagurus bernhardus* in recently trawled areas compared to adjacent undisturbed areas (although the sympatric *P. prideaux* did not show a significant response to the trawling disturbance). However, the presence of scavengers exploiting dead, damaged, or exposed macrofauna is likely to be a very transient phenomenon, and such short-term events are most likely only apparent in intensive small-scale studies. A very high intensity and frequency of disturbance would be needed before such patterns would emerge from broad-scale surveys.

The predictions we tested have important ecological ramifications for changes in the structure and function of benthic communities. For example, fishing disturbance is unlikely to affect adult animals that live deep within the sediment; such species are often important in biogenic sediment modification. However, juvenile stages living nearer to the sediment surface can be directly affected, and in the long term this results in lower densities of adults.

Perhaps the most ecologically important effects relate to changes in habitat complexity. The removal of organisms that add three-dimensional complexity to benthic habitats is potentially extremely destructive, as is the homogenization of sediment characteristics by the physical action of dredges and trawls. Both effects reduce spatial heterogeneity over a range of ecologically important scales. Only at a few sites in our study were epifauna sufficiently large and abundant to appreciably add to habitat complexity (e.g., horse mussels [*Atrina zelandica*] observed in video transects). Nevertheless, we demonstrated significant epifaunal losses with increasing fishing pressure. This is a very important observation because epifauna such as sponges, bryozoans, hydroids, sea fans, anemones, and bivalves, as well as topographic modifications due to feeding (by rays, starfish, etc.) and burrowing (e.g., pits and mounds made by bivalves, polychaetes, holothurians, etc.), and sediment features such as sand waves can all be reduced or eliminated by fishing. These features enhance habitat complexity and potentially play important roles in species interactions that include the provision of settlement substrates and refugia (Bradstock and Gordon 1983, Sainsbury 1988, Hutchings 1990, Auster et al. 1995, Auster et al. 1996).

Various theoretical studies indicate the importance of spatial heterogeneity at 0.1–1 km spatial scales. Such heterogeneity is theoretically a very important component of the function of ecological systems (Kolasa and Pickett 1991, Legendre 1993, Giller et al. 1994), with implications for the maintenance of diversity and stability at the population, community, and ecosystem level (e.g., De Angelis and Waterhouse 1987, Pimm 1991, Loehle and Li 1996). Empirical evidence on the >10-m scale has been hard to generate in sublittoral soft-sediment habitats due to logistical difficulties. Nevertheless, patchiness at smaller spatial scales has been demonstrated in field studies and often this scale of patchiness is generated by small-scale biological-disturbance events (Hall et al. 1994). But spatial mosaics that result from local biological-disturbance events, as well as the organisms that create them, can be obliterated by intense broader scale disturbances. Increasing the area subjected to habitat disturbance by commercial fishing and increasing the frequency and intensity of these events could result in an appreciable loss of habitat heterogeneity and substrate complexity in benthic communities.

Fishing effects may also be expected to be heterogeneous. Apart from the influence of biological and environmental factors on benthic-community response to disturbance, variations in the intensity of fishing effects are to be expected due to interactions among the size and mass of the gear, the power of the vessel, and the proficiency of the skipper. Variation in the frequency and intensity of storm disturbance of the seabed is also likely to interact with any fishing effects. Differences in the response to habitat disturbance by fish-

ing have been demonstrated in many different habitats/communities (Thrush et al. 1995, Kaiser and Spencer 1996). Our study was integrated over a variety of habitat types, ranging from sandy, wave-exposed areas to more sheltered muddy areas. In frequently and intensely stirred areas, only species able to tolerate these conditions, or those confined to refuges, will persist (Hall et al. 1990, Hall 1994). Areas with high flow velocities often support extensive beds of suspension feeders and tube builders and in wave-exposed areas these organisms play important roles in ameliorating the effects of storms by stabilizing the seabed and increasing critical velocities (e.g., Thrush et al. 1996). We predict these kinds of surface-dwelling organisms will be reduced with increasing disturbance by bottom fishing.

Current concerns about sustainability, ecosystem management, and maintenance of biodiversity emphasize the need to assess and manage the environmental impact of commercial fisheries. Marine environments are dynamic and complex, the knowledge base is small, and many changes are not noticed until it is too late for a rigorous demonstration of cause and effect. Often observations are at the wrong scale to identify connections between exploited species and habitat features. Fishery models often fail to include the potential role of interactions between habitat features and the survivorship of juveniles of exploited stocks. While to date there may be limited evidence for such connections, the potential role of such interactions cannot be discounted without appropriate testing, as the risks of destroying important settlement sites and nursery areas are too great. Potential indirect effects may also occur where fishing decreases the density of predators and effectively decouples juvenile survivorship from predation. Inevitably there is uncertainty, but management actions always are made in an uncertain environment. Importantly, the resolution of these issues depends upon the successful blending of fisheries management and marine ecology.

In this paper we have demonstrated a relationship between regional-scale changes in macrobenthic community structure and habitat disturbance by commercial fishing. However, unequivocally linking structural changes to changes in ecosystem function is difficult. Nevertheless the weight of evidence should be of concern to resource managers. The problem of identifying cause-and-effect relationships over broad scales emphasizes the value of a precautionary approach to environmental or fisheries management (Bodansky 1991, Ludwig et al. 1993, Dayton et al. 1995). An approach that emphasizes gathering appropriate information to identify the way and degree to which fishing changes marine ecosystems over broad spatial and temporal scales is essential for the identification of environmental risks to the sustainability of fishery resources and the ecosystems to which they belong. Adaptive-management strategies can be used as the basis of large experiments so that predictions of effects can be tested

(Walters and Holling 1990). Whatever the management strategies used, appropriate data need to be collected to document ecological changes. As this involves finding appropriate controls against which to assess effects of fishing pressure, marine protected areas (Agardy 1994) are very useful. A sustained commitment to data collection is necessary if we are to determine appropriate time scales over which to assess changes. Fortunately, determining degrees of impact to ecosystems, as well as the time scales of impact, will both lead to better determination of the ecological constraints needed for sustainable management. In turn, this process will help us to objectively weigh social and economic demands against the biological constraints within which a sustainable fishery must operate (e.g., Langton et al. 1996, Auster et al. 1997).

The approach used here to identify regional-scale changes in benthic communities resulting from habitat disturbance by fishing provides a balance between confidence in results and the generality of the findings. We hope that this approach will be tested in other situations. One major improvement in developing the ability to identify ecological changes would be the general provision of information to define the actual location and frequency of contact of different types of fishing gear with the seafloor.

Most of the world's commercial marine fisheries are fully exploited, and in fact many are declining (FAO 1995, 1997). Most of the fishing effort is concentrated on the continental shelf and slope depths, although deep-water species are also exploited. Thus fishing is by far the largest human impact on the marine environment (Hammer and Jansson 1993, Dayton et al. 1995, Griffis and Kimball 1996). Our data provide evidence that the fishing industry needs to first recognize these environmental impacts and then act decisively to reduce and mitigate them where appropriate. This broadening of perspective to include ecological effects is important not only as changes to the ecology may affect other resource users but also because fisheries are sustained by natural productivity, and adverse environmental effects may feed back to influence the sustainability of fisheries resources. Sustaining this industry while conserving marine resources will be a major challenge for fishers, fisheries and resource managers, and ecologists.

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