Journal of Experimental Marine Biology and Ecology 344 (2007) 23 – 34

Journal of EXPERIMENTAL MARINE BIOLOGY AND ECOLOGY

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Comparison of trawled vs untrawled mud seafloor assemblages of fishes and macroinvertebrates at Coquille Bank, Oregon

Mark A. Hixon [a,*], Brian N. Tissot [b]

[a] *Department of Zoology, Oregon State University, 3029 Cordley Hall, Corvallis, Oregon 97331-2914, USA*

[b] *Program in Environmental Science and Regional Planning, Washington State University Vancouver, 14204 NE Salmon Creek Avenue, Vancouver, Washington 98686-9600 USA*

Received 13 September 2006; received in revised form 24 October 2006; accepted 18 December 2006

Abstract

We report the first quantitative comparison of trawled vs untrawled mud seafloor communities off the west coast of North America. Using a manned submersible, we ran visual transects at Coquille Bank, 25 km off the central coast of Oregon, USA, including six half-hour (mean length 1184 m) transects over mud seafloors 183–361 m deep. The shallowest transects were untrawled, whereas deeper transects were heavily trawled, as evidenced by extensive trawl-door tracks. Differences between trawled and untrawled seafloor assemblages were striking. We observed 23% more fish over untrawled compared to trawled seafloors, and recorded 27 fish species on untrawled bottoms, but only 19 species on trawled seafloors. Regarding benthic invertebrates, density of individuals was 6 times greater on untrawled compared to trawled bottoms. Nonetheless, we observed 11 taxa on trawled seafloors and only 6 taxa on untrawled bottoms. Principal components analysis (PCA) defined the untrawled assemblage as characterized by sea pens, ratfish, sablefish, ronquil, slender sole, and poacher. PCA defined the trawled assemblage as characterized by seastars, hermit crabs, bigfin eelpout, Dover sole, hagfish, and shortspine thornyhead. In untrawled areas, there was no correlation between sea-pen density and total fish density, whereas in trawled areas, there was a marginally inverse correlation between the density of trawl-door tracks and total fish density. The dominant fishes and macroinvertebrates on trawled seafloors are known mobile scavengers that may aggregate along trawl-door tracks. Sea pens that dominated untrawled bottoms are sessile, slow-growing, long-lived species that are likely to recover slowly from physical disturbance. We conclude that the observed differences between trawled and untrawled communities were the result of groundfishing activities rather than local environmental differences. Given that habitat considerations for groundfish management in this region focus exclusively on rocky seafloors, it seems prudent to consider the adverse effects of bottom trawling on mud seafloor ecosystems of the continental shelf and slope.

Keywords: Bottom trawling effects; Demersal fishes; Macroinvertebrates; Mud seafloors

1. Introduction

Approximately 75% of the global continental shelf is subjected to trawling and dredging (Kaiser et al., 2002). Numerous reviews examining empirical studies worldwide have concluded that bottom trawls have substantial deleterious effects on seafloor communities (e.g., Auster

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* Corresponding author. Tel.: +1 541 737 5364; fax: +1 541 737 0501.

E-mail address: hixonm@science.oregonstate.edu (M.A. Hixon).

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doi:10.1016/j.jembe.2006.12.026

and Langton, 1999; Norse and Watling, 1999; Collie et al., 2000; Kaiser et al., 2002, 2006; NRC, 2002; Thrush and Dayton, 2002; papers in Barnes and Thomas, 2005). In the United States, there appears to be consensus that bottom trawls not only directly affect the distribution and abundance of target and bycatch species, but also have strong collateral impacts on physical and biological fish habitat (Chuenpagdee et al., 2003). However, different seafloor types and benthic communities are affected to different degrees (Collie et al., 2000; Kaiser et al., 2002, 2006), and the acute impacts of trawling may differ from chronic impacts (Auster and Langton, 1999). Nonetheless, the National Research Council (2002) concluded that bottom trawling in general (1) reduces habitat complexity, (2) alters benthic communities, (3) reduces benthic productivity, and (4) most strongly affects fauna that live in regimes of low natural disturbance, especially soft-bodied, erect, sessile organisms inhabiting stable deep seafloors (e.g., sea pens on mud).

Along the west coast of North America, most studies of trawling impacts have been conducted on sandy seafloors off Alaska and have focused on invertebrates (Fig. 1). On pebble bottoms 206–274 m deep in the eastern Gulf of Alaska, Freese et al. (1999) demonstrated experimentally the single-pass, acute effects of trawling, including displacement of boulders and significant decreases in the densities of sponges and anthozoans. Densities of mobile invertebrates did not differ between treatments, although trawl damage to brittlestars was evident. On sand bottoms 44–52 m deep in the eastern Bering Sea, McConnaughey et al. (2000, 2005) documented chronic effects of trawling, including reduced benthic invertebrate size and species diversity, with erect sessile taxa, such as sponges and anemones, being particularly vulnerable. On high-energy sand bottoms 20–30 m deep in the southeastern Bering Sea, Brown et al. (2005) examined both chronic and acute effects of trawling, including chronic patterns of reduced macrofaunal density, biomass, and species richness. On sand bottoms 105–157 m deep in the Gulf of Alaska, Stone et al. (2005) found lower species richness and lower abundance of low-mobility species in trawled areas compared to areas closed to trawling.

In the region managed by the Pacific Fisheries Management Council–federal waters off Washington, Oregon, and California–there has been only a single published study that compared trawled vs untrawled areas. Just south of Monterey Bay, central California, on mostly sandy seafloors along the 180 m depth contour, Engel and Kvitek (1998) compared a lightly trawled area just inside the 3 nmi offshore boundary of state

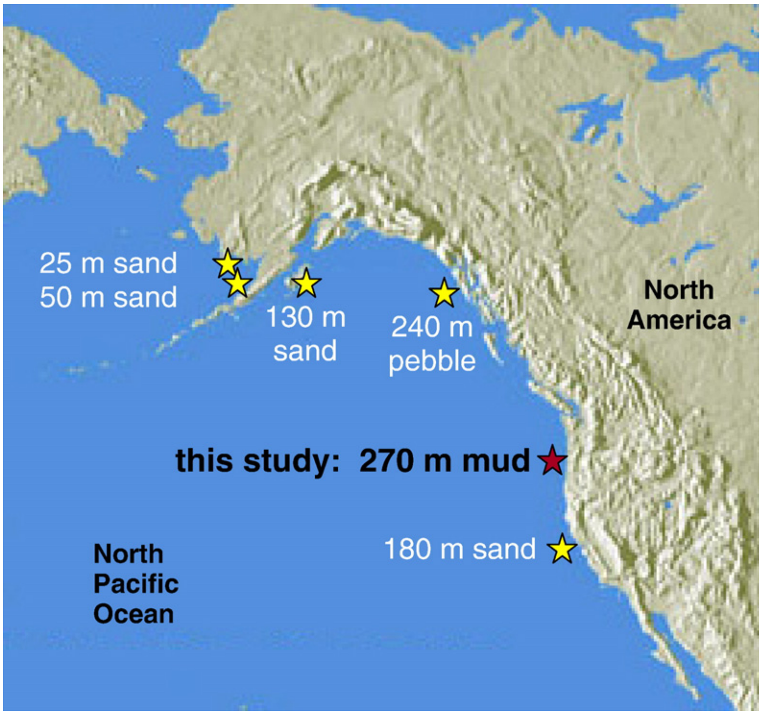

Fig. 1. Map of the west coast of North America, showing the general locations, approximate depths, and predominant seafloor types where studies of the effects of bottom trawling on seafloor communities have been published. See text for the details of each study.

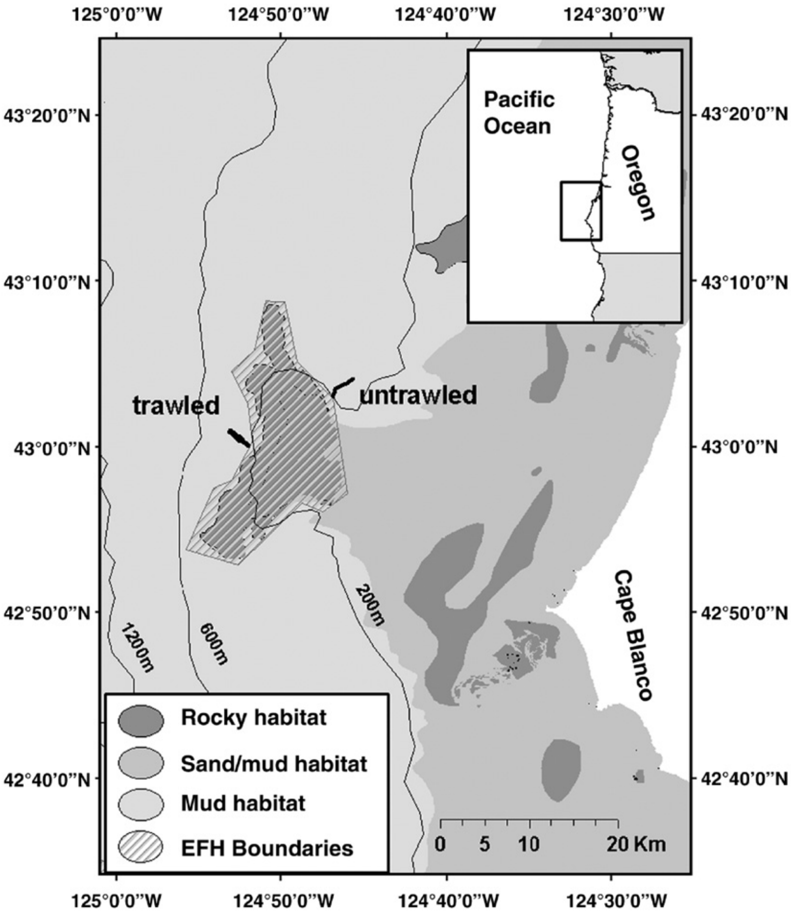

Fig. 2. Map of the study area, showing the locations of 4 trawled vs 2 untrawled non-overlapping submersible transects over mud seafloors adjacent to Coquille Bank, Oregon, in 1990, including the Essential Fish Habitat boundary established in 2005 (NMFS, 2005). Seafloor characterization courtesy of C. Goldfinger, Oregon State University. See Bellman et al. (2005) for a regional map.

waters to a highly trawled area just outside 3 nmi. Using a thorough combination of manned-submersible transects, bottom grabs, and experimental trawls–thereby examining both the chronic and acute impacts of trawling–they documented that the highly trawled seafloor had more trawl-door tracks, exposed sediment, and shell fragments, as well as fewer rocks and mounds than the lightly trawled areas. They also found higher densities of most epifaunal invertebrates in the lightly trawled area, yet higher densities of more infaunal oligochaetes, nematodes, brittlestars, and an amphinomid polychaete (common in the guts of commercially important fishes) in the heavily trawled area. They concluded that high-intensity trawling apparently reduced habitat complexity and biodiversity, while simultaneously increasing opportunistic infauna and the prey of some commercially important fishes.

Until the study reported here, virtually nothing was known of bottom-trawl effects on the predominant trawled habitat off the U.S. west coast: mud seafloors of the outer continental shelf. Seafloors off Oregon have been subjected to higher bottom-trawling effort than those off Washington and California (NRC, 2002). It has been estimated that an average of 6% of the fished continental shelf and slope area of Oregon was swept by groundfish and shrimp trawls more than once annually during the late 1990s, and 94% was swept less than once per year (NRC, 2002). Off nearby northern California, side-scan sonar mapping of trawl-door tracks revealed that the region was trawled an average of 1.5 times annually (Friedlander et al., 1999). Since the turn of the century, bottom trawling off the U.S. west coast has decreased substantially due to more stringent management measures (Bellman et al., 2005).

As part of a broad-scale exploratory study of possible oil-drilling sites on the outer continental shelf of Oregon in the late 1980s and early 1990s (Hixon et al., 1991; Hixon and Tissot, 1992; Pearcy et al., 1989; Starr et al.,

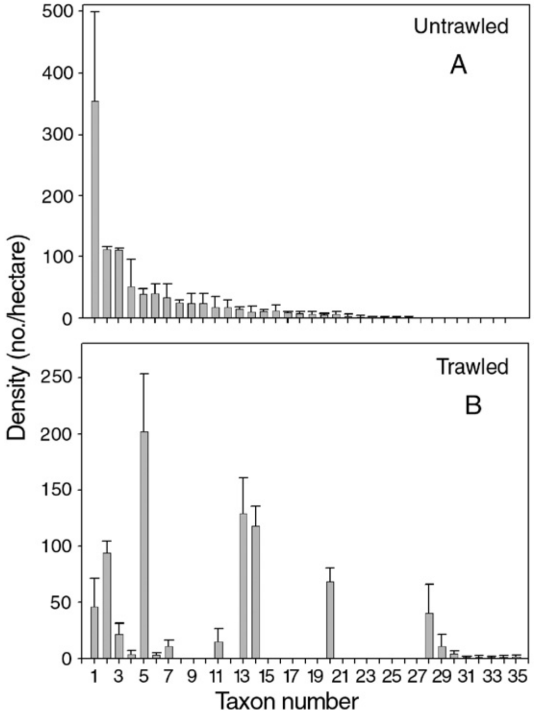

Fig. 3. Density of fish (mean number per hectare + 1 SE) in (A) untrawled and (B) trawled mud areas adjacent to Coquille Bank, Oregon. Species numbers are identified in Table 1. Samples sizes: untrawled area = two 30-minute transects; trawled area = four 30-minute transects. Note difference in *y*-axis scaling.

1996; Stein et al., 1992; Nasby-Lucas et al., 2002, we sampled Coquille Bank, Oregon, using the same manned submersible as Engel and Kvitek (1998) off California and both Freese et al. (1999) and Stone et al. (2005) off Alaska. Historically, there has been substantial bottom trawling for groundfishes and shrimp in the vicinity of Coquille Bank (NRC, 2002), although groundfish trawling has recently been relegated to less rocky locations by gear restrictions implemented in 2000 (Bellman et al., 2005).

During our studies, we ran visual transects over deep mud seafloors, some of which were clearly trawled and others untrawled, providing a limited yet serendipitous means of estimating trawl impacts in this poorly known habitat. Here we report a comparison of the demersal fish and epibenthic macroinvertebrate assemblages occupying these relatively disturbed and undisturbed seafloors.

2. Methods

2.1. Data collection

Coquille Bank, also known as the Bandon High Spot, is located about 25 km off the central Oregon coast

Table 1

Densities of demersal fish and epibenthic macroinvertebrates in untrawled vs trawled mud areas adjacent to Coquille Bank, Oregon, ranked by mean density in untrawled areas

No.	Taxon	Density (number/hectare)			
		Untrawled		Trawled	
		Mean	SE	Mean	SE
	Fishes				
1	*Lyopsetta exilis* (slender sole)	354	145	46	25
2	*Glyptocephalus zachirus* (rex sole)	111	4	94	11
3	Agonidae (poacher)	110	3	21	10
4	*Hydrolagus colliei* (spotted ratfish)	51	45	4	4
5	*Microstomus pacificus* (Dover sole)	39	9	202	51
6	*Anoplopoma fimbria* (sablefish)	40	15	3	2
7	Unidentified flatfish	33	22	10	6
8	*Rathbunella* sp. (unidentified ronquil)	26	4	–	–
9	*Sebastes alutus* (Pacific Ocean perch)	24	16	–	–
10	*Sebastes zacentrus* (sharpchin rockfish)	24	16	–	–
11	*Sebastes diploproa* (splitnose rockfish)	18	18	15	11
12	*Parophrys vetulus* (English sole)	18	12	–	–
13	*Lycodes cortezianus* (bigfin eelpout)	15	4	129	31
14	*Eptatretus* sp. (hagfish)	10	10	118	18
15	*Sebastes elongatus* (greenstriped rockfish)	11	3	–	–
16	*Agonus acipenserinus* (sturgeon poacher)	12	10	–	–
17	*Atheresthes stomias* (arrowtooth flounder)	9	2	–	–
18	Unidentified roundfish	8	3	–	–
19	*Merluccius productus* (Pacific hake)	7	4	–	–
20	*Sebastolobus alascanus* (shortspine thornyhead)	6	2	68	12
21	*Pleuronichthys* sp. (turbot)	7	4	–	–
22	Cottidae (sculpin)	4	4	–	–
23	*Raja kincaidii* (sandpaper skate)	3	3	–	–
24	*Sebastes* sp. (rockfish)	3	1	–	–
25	*Chilara taylori* (spotted cusk-eel)	2	2	–	–
26	*Citharichthys* sp. (sanddab)	2	2	–	–
27	*Sebastes crameri* (darkblotched rockfish)	2	2	–	–
28	*Lycodapus mandibularis* (pallid eelpout)	–	–	40	26
29	*Sebastes babcocki* (redbanded rockfish)	–	–	11	11
30	*Careproctus melanurus* (blacktail snailfish)	–	–	4	3
31	*Lycodes diapterus* (black eelpout)	–	–	1	1
32	*Raja rhina* (longnose skate)	–	–	1	1
33	*Eopsetta jordani* (petrale sole)	–	–	1	1
34	*Sebastes helvomaculatus* (rosethorn rockfish)	–	–	1	1
35	*Raja binoculata* (big skate)	–	–	2	2
	All fishes:	948	266	772	46

Table 1 (*continued*)

No.	Taxon	Density (number/hectare)			
		Untrawled		Trawled	
		Mean	SE	Mean	SE
Invertebrates					
1	*Stylatula* spp. (sea pen)	19,342	9725	4	3
2	*Allocentrotus fragilis* (fragile urchin)	627	627	855	505
3	*Lopholithodes foraminatus* (brown box crab)	49	2	13	6
4	Paguridae (hermit crab)	8	0	1019	455
5	*Pandalus* spp. (prawn)	1	1	–	–
6	*Cancer* sp. (cancer crab)	2	2	–	–
7	*Mediaster aequalis* (red seastar)	–	–	597	201
8	*Parastichopus* spp. (sea cucumber)	–	–	393	120
9	*Rathbunaster / Pycnopodia* (sunstar)	–	–	322	68
10	*Luidia foliolata* (mud star)	–	–	32	15
11	unidentified anemone	–	–	5	3
12	*Henricia* sp. (blood star)	–	–	2	2
13	*Octopus* sp. (octopus)	–	–	1	1
All invertebrates:		20,029	9100	3242	602

Taxon numbers provide legend for Figs. 3 and 5. Samples sizes: untrawled area = two 30-minute transects; trawled area = four 30-minute transects.

between the city of Bandon and Cape Blanco (Fig. 2). This low-lying rocky outcrop is composed of low-relief ridges of claystone, siltstone, and sandstone (Kulm and Fowler, 1974), characterized by our submersible observations as highly eroded, exfoliating, slab-like boulders, mostly covered by a thin layer of sediment. Extending to within 100 m of the surface, the bank is surrounded by mud (clay to silt grain size, Greene et al., 1999), with the offshore edge bordering the continental slope. In 2005, the rocky portions of the bank were designated as Essential Fish Habitat for rockfishes and other groundfishes by the U.S. National Marine Fisheries Service (NMFS, 2005).

During 23–26 September 1990, we used the 2-man submersible *Delta* to make 12 daylight dives at Coquille Bank. Three of these dives were over mud bottoms several kilometers off the bank and therefore clearly accessible to bottom trawls: one (2 transects) in an untrawled area 183–215 m deep, and two (4 transects) in a heavily trawled area 274–361 m deep (Fig. 2). At these depths in this region, water motion is minimal. Relative trawling intensity was obvious, based on trawl-door tracks that crossed the path of each submersible transect. In the trawled area, trawl-door tracks occurred at a density of 110 per hectare (range 13–322), whereas no tracks were observed in the untrawled area.

Each of the three dives examined here occurred in the afternoon at least an hour before sunset, minimizing possible effects of diurnal changes in the behavior and movements of fish and mobile invertebrates. The submersible held one pilot and one observer, and two different submersible pilots and three different observers made these dives. The scientific observers had participated in the broader project together for the previous 3 years with the same pilots, and had developed standardized transect methods to minimize personal sampling bias as much as possible.

Non-overlapping visual belt transects were adapted from methods long used for SCUBA surveys on shallow reefs (Brock, 1954, 1982; Ebeling, 1982; Sale and Sharp, 1983; Butler et al., 1991). The view through the two forward portholes of the sub, which transected the fore ballast tank, provided a continuous visual field of the seafloor that was 2.3 m wide as the sub cruised 2 m off the bottom. This bracketed visual field dictated the width of our belt transects for calculating densities of groundfish and epibenthic macroinvertebrates. During each dive, we ran a two half-hour transects, separated by a 10–15 min “quiet period” to determine the effect of the sub on fish behavior (see below). Overall, each dive lasted about 2 h, including transit time between the surface and seafloor.

For mapping transect paths, we used a Trackpoint II system by positioning the support vessel directly above the sub every 10–15 min, then noting latitude and longitude using Loran-C (the study being conducted before GPS was available). The Trackpoint II system is an ultra-short baseline acoustic tracking system that triangulates position from a single transponder. The error of this system associated with individual fixes is very small in relation to the length of our transects. Using these fixes, we calculated the approximate length of each half-hour transect, which averaged 1184 m (SD = 100 m, $n = 6$).

During each transect, the pilot maintained the sub approximately 2 m above the bottom, and radioed depths and miscellaneous observations to the support vessel. The observer verbally tape-recorded data on the species, size class (to the nearest dm TL), and abundance of all visible demersal fish. To estimate fish lengths and to provide an external scale for photography, we suspended a 0.3 m fiberglass rod (marked in decimeter intervals) by a chain into the transect path. A visual record of the transect path was provided by both VHS videotape (with timed data logger and audio track) and automated 35-mm still photos taken every 30 s, which were subsequently used to identify and enumerate dominant benthic macroinvertebrates in the same way the fish transects were conducted. Immediately following each dive, the observer transcribed the data on

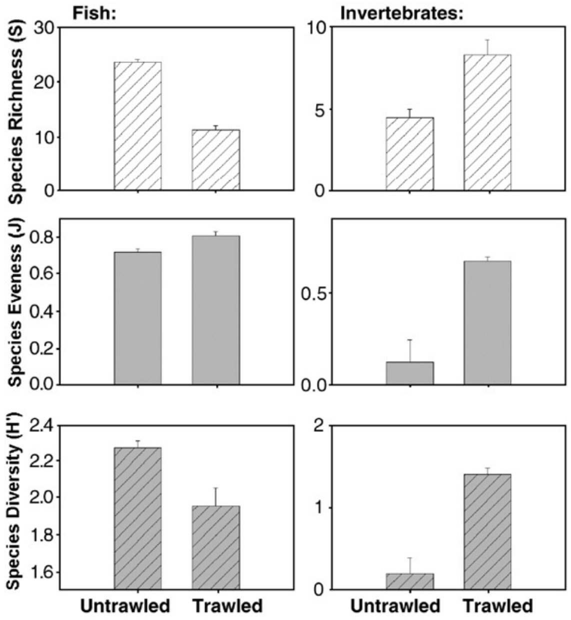

Fig. 4. Species diversity indices (mean + 1 SE) for fishes and macroinvertebrates in untrawled and trawled areas adjacent to Coquille Bank, Oregon.

fishes, as well as incidental data on macroinvertebrates and seafloor type, from the tape recorders into a computerized database.

We attempted to determine the extent to which fish were differentially repelled by or attracted to the submersible by comparing their behavior just before and after "quiet periods." Between each pair of transects on the same dive, we would rest the sub on the seafloor and turn-off all lights and motors for 10–15 min. Turning-on the lights at the end of these periods invariably showed that the local distribution and abundance of fishes had not changed appreciably, suggesting that the presence of the submersible *per se* caused little sampling bias due to rapid attraction or avoidance by fish. At the very least, whatever such bias existed was consistent between dives.

2.2. Data analysis

Overlap in species composition and relative abundance between trawled and untrawled assemblages was measured using the Percent Similarity Index ($\mathrm{PSI} = \sum \min [p_{xi}, p_{yi}] \times 100$, where p_{xi} and p_{yi} are the proportions of individuals of the ith species in assemblages x and y, Wolda, 1981). Species diversity was examined as richness (S = number of species), evenness or equitability of relative abundances (Pielou's $J = H' / \ln S$, Pielou, 1969), and composite diversity, which integrates both richness and evenness (Shannon–Wiener $H' = -\sum p_i \ln p_i$, where p_i is the proportion of individuals of the ith species, Pielou, 1966). Differences between assemblages were so great that a variety of other diversity indices showed the same patterns as those reported here, indicating that the choice of index did not alter data interpretation.

Principal components analysis was used to examine joint patterns of variation in abundance among fish and macroinvertebrate species at the assemblage level in trawled vs untrawled areas. Data were transformed to log scale and analysis performed on the correlation matrix (Dillon and Goldstein, 1984).

We explored two post-hoc synthetic hypotheses by simple correlation analysis: (1) in the untrawled area, that sea pens provided biogenic habitat for fishes, thereby increasing fish densities, and (2) in the trawled area, that trawling directly or indirectly reduced local fish density. Each pair of 30-minute transects was subdivided arbitrarily into twelve 5-minute sections. For the untrawled area, sea-pen and fish densities were then correlated among transect sections, and for the trawled

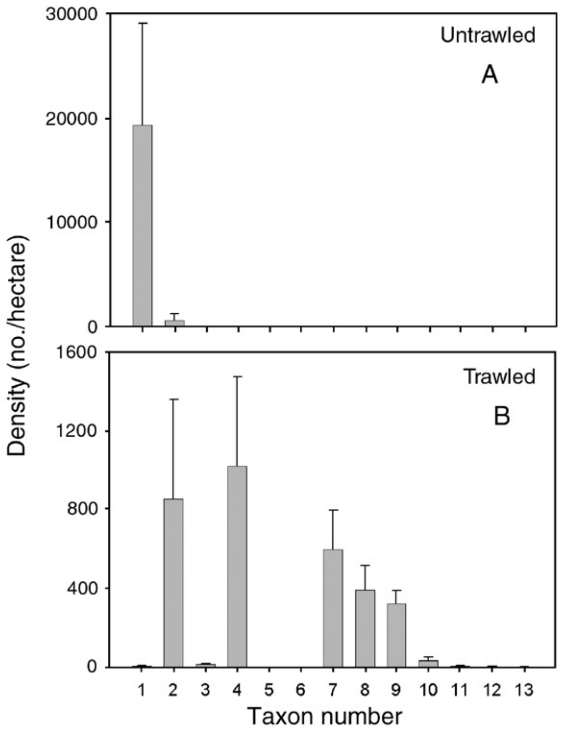

Fig. 5. Density of epibenthic macroinvertebrates (mean number per hectare + 1 SE) in (A) untrawled and (B) trawled mud areas adjacent to Coquille Bank, Oregon. Taxon numbers are identified in Table 1. Sample sizes: untrawled area = two 30-minute transects; trawled area = four 30-minute transects. Note difference in y-axis scaling.

area, frequencies of trawl-door tracks and fish densities were correlated.

3. Results

3.1. Fish abundance, species composition, and diversity

We observed 23% more fish over untrawled mud seafloors (mean±SE=948±266 fish/hectare) compared to trawled mud seafloors (772±46 fish/hectare) (Table 1). Untrawled seafloors were dominated numerically by three species that accounted for 61% of the fish seen: slender sole (*Lyopsetta exilis*), rex sole (*Glyptocephalus zachirus*), and an unidentified poacher (Agonidae) (Fig. 3A). In contrast, trawled seafloors were dominated by three species that accounted for 59% of the fish seen: Dover sole (*Microstomus pacificus*), bigfin eelpout (*Lycodes cortezianus*), and hagfish (*Eptatretus* sp.) (Fig. 3B).

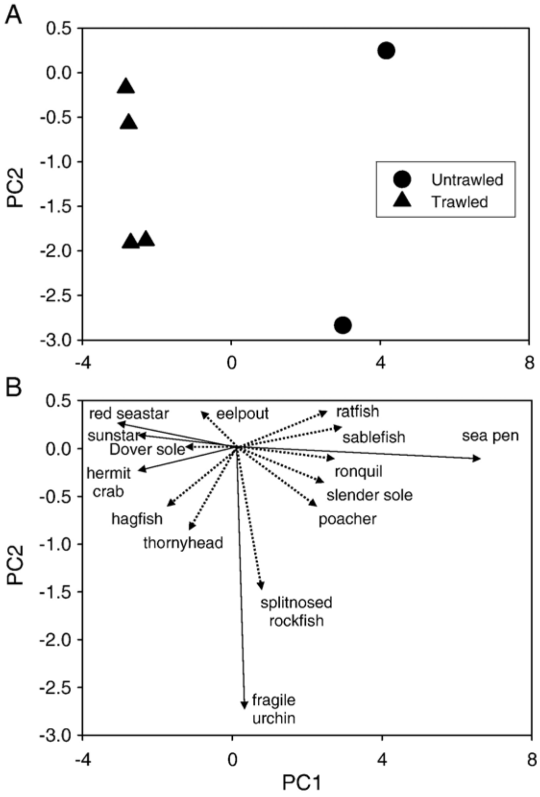

Fig. 6. Principal components analysis of demersal fish and epibenthic macroinvertebrate assemblages in untrawled and trawled mud areas adjacent to Coquille Bank, Oregon. (A) Ordination of 2 untrawled transects and 4 trawled transects. (B) Major component variable loading vectors for fishes (dotted vectors) and macroinvertebrates (solid vectors).

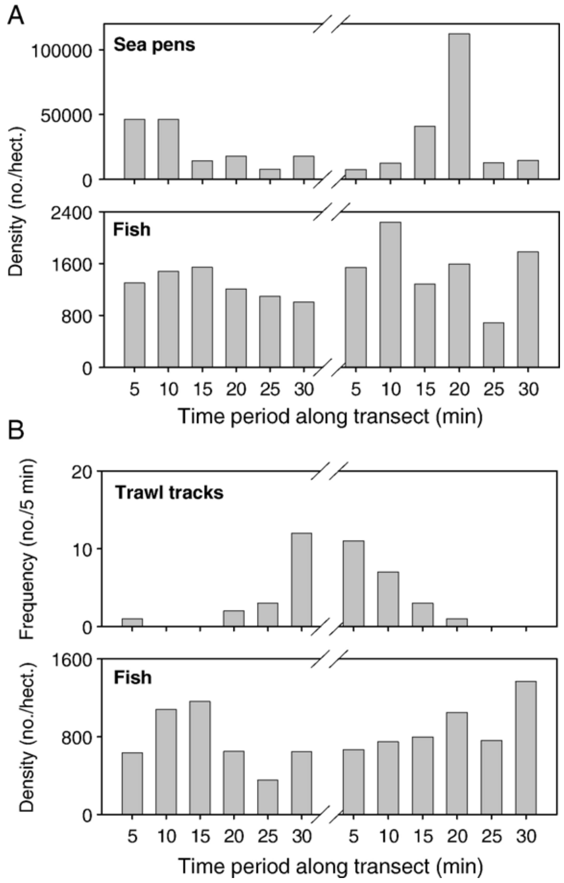

Fig. 7. Relationship between (A) sea-pen density and fish density in the untrawled area, and (B) trawl-track frequency and fish density in the trawled area adjacent to Coquille Bank, Oregon, each for the single pair of transects during which all such data were enumerated. Each *x*-axis value represents the end-point of each 5-minute section of each 30-minute transect.

Overlap in species composition between trawled and untrawled areas was remarkably low, with 16 species found only over untrawled bottoms and 8 species found only over trawled bottoms (Table 1, Fig. 3). Consequently, overall percent similarity (PSI) of the two fish assemblages was only 31.9%.

A total of 27 species of fish were seen over untrawled bottoms, yet only 19 species over trawled bottoms (Table 1, Fig. 3). At the scale of transects, fish species richness (*S*) over untrawled seafloors (24 species, SEM=1) was more than double that over trawled seafloors (11 species, SEM=1). Fish species evenness was slightly less on untrawled bottoms (*J*=0.72, SEM=0.02) than trawled bottoms (*J*=0.81, SEM=0.02), yet composite species diversity was substantially greater over untrawled seafloors (H'=2.27, SEM=0.04) than trawled seafloors (H'=1.96, SEM=0.10) (Fig. 4).

3.2. Invertebrate abundance, species composition, and diversity

Epibenthic macroinvertebrates were over 6 times more abundant on untrawled mud seafloors (mean ± SE = 20,029 ± 9100 invertebrates/hectare) than on trawled seafloors (mean ± SE = 3242 ± 602 invertebrates/hectare) (Table 1). Untrawled bottoms were strongly dominated numerically by 30–50 cm high sea pens (*Stylatula* spp.), which accounted for over 95% of all recorded invertebrates (Fig. 5). In stark contrast, sea pens were nearly absent (4 orders of magnitude less abundant) on trawled bottoms, which were dominated by five taxa that combined accounted for 87% of all invertebrates seen: hermit crabs (Paguridae), fragile urchin (*Allocentrotus fragilis*), red seastar (*Mediaster aequalis*), sea cucumbers (*Parastichopus* sp.), and sunstars (*Rathbunaster/Pycnopodia*) (Fig. 5).

As with fishes, overlap in invertebrate species composition between trawled and untrawled assemblages was remarkably low, with 2 taxa found only on untrawled seafloors and 7 taxa found only on trawled bottoms (Table 1, Fig. 5). As a result, as well as due to the strong dominance of sea pens on untrawled seafloors, overall percent similarity (PSI) between these assemblages was an extremely low 4.2%.

Patterns of macroinvertebrate diversity were nearly opposite those of fishes. A total of 6 invertebrate taxa were observed on untrawled seafloors, and 11 taxa on trawled seafloors (Table 1). At the scale of transects, invertebrate richness was less on untrawled bottoms (average of 5 taxa, range 4–5) than on trawled bottoms (average of 8 taxa, range 6–10). Invertebrate evenness was also less on untrawled seafloors ($J = 0.12$, SEM = 0.12) than on trawled seafloors ($J = 0.67$, SEM = 0.02), so composite diversity followed the same pattern: $H' = 0.20$ (SEM = 0.20) on untrawled bottoms and $H' = 1.40$ (SEM = 0.08) on trawled bottoms (Fig. 4).

3.3. Assemblage-level comparisons

Principal components analysis (PCA) revealed strong separation of trawled and untrawled assemblages along the first axis, which explained 79% of the total variance (Fig. 6A), and species loadings on this axis clearly distinguished these assemblages (Fig. 6B). The untrawled assemblage showed large positive loadings on the first PCA axis for sea pens, spotted ratfish (*Hydrolagus colliei*), sablefish (*Anoplopoma fimbria*), ronquil (*Rathbunella* spp.), slender sole, and poacher. In contrast, the trawled assemblage was characterized by large negative loadings on the first PCA axis for red seastars, sunstars, hermit crabs, bigfin eelpout, Dover sole, hagfish, and shortspine thornyhead (*Sebastolobus alascanus*). The second PCA axis accounted for only 11% of the total variance and largely contrasted differences among replicates in both trawled and untrawled areas in the abundances of fragile urchin and splitnose rockfish (*Sebastes diploproa*) (Fig. 6).

3.4. Association of sea pens and trawl-door tracks with fish density

At the untrawled area, there was no correlation between sea-pen density and total fish density among transect segments ($r = 0.11$, $p = 0.73$, Fig. 7A). However, at the trawled area, there was a marginally significant inverse correlation between the density of trawl-door tracks and total fish density ($r = -0.55$, $p = 0.06$); most trawl-door tracks were encountered near the middle of the hour-long pair of transects, where fish densities tended to be relatively low (Fig. 7B).

4. Discussion

4.1. General patterns

Empirical reviews (e.g., Auster and Langton, 1999; Norse and Watling, 1999; NRC, 2002; Thrush and Dayton, 2002) and meta-analyses (e.g., Collie et al., 2000; Kaiser et al., 2002, 2006) have concluded that, worldwide, bottom trawling has substantial impacts on benthic epifauna in stable deep mud habitats similar to those at Coquille Bank, Oregon. Our findings, the first for deep mud seafloor communities off the west coast of North America, are consistent with this general conclusion. Despite low sample sizes and other constraints of our limited and serendipitous study, the differences between trawled and untrawled assemblages at Coquille Bank were striking. Relative to untrawled bottoms, obviously trawled areas supported not only substantially fewer individuals and species of groundfish, but also an overall order of magnitude fewer epibenthic macroinvertebrate individuals. These patterns were similar to those documented for invertebrates on chronically trawled, shallower, and sandy seafloors off Alaska (McConnaughey et al., 2000; Brown et al., 2005; Stone et al., 2005). However, unlike these previous studies, we also documented a greater diversity of epibenthic macroinvertebrates in trawled areas.

The most striking pattern was the high density of sea pens in the untrawled area and their virtual absence in the trawled area. However, within the untrawled area, there was no correlation between the density of sea pens and the local density of fish, suggesting that sea pens do not provide an obvious biogenic habitat for demersal fishes, at least among patches at the scales we sampled (100 s of m). Nonetheless, within the trawled area, there was a marginally significant inverse correlation between the density of trawl-door tracks and the local density of fishes, suggesting that higher trawling intensity is associated with lower fish abundance. This pattern could be caused directly by the removal of fish by trawls and/or indirectly by habitat alteration due to trawling.

4.2. Correlation or causation?

A potential weakness of our study is its opportunistic and correlative nature. Our data were extracted from a broader study that did not focus on trawling effects *per se* (Pearcy et al., 1989; Hixon et al., 1991; Hixon and Tissot, 1992; Stein et al., 1992; Starr et al., 1996; Nasby-Lucas et al., 2002). Even though sites for the trawled and untrawled "treatments" were not replicated, replicate transects within each site revealed that differences between trawled and untrawled areas were both obvious and substantial. Although site replication is always desirable from a statistical viewpoint, lack of such replication does not necessarily invalidate the results of field studies, especially studies undertaken at large spatial scales that show strong differences among treatments and are logistically difficult to replicate (Oksanen, 2001).

The most rigorous means of testing the acute impacts of bottom trawling is a replicated Before–After-Control-Impact design, in which similar yet isolated sites are compared both before and after trawling occurs at some (impact sites), but not others (control sites) (NRC, 2002). Like all observational studies of the chronic impacts of trawling, our post-hoc comparison of sites that were obviously heavily trawled vs not trawled necessarily relied on the assumption that these sites were similar before the onset of trawling. Although the trawled and untrawled sites occurred at non-overlapping depth ranges, albeit at similar distances from the rocky portions of Coquille Bank, the assumption of pre-trawling similarity is nonetheless reasonable for at least five reasons. First, all species we observed are known to occur at all depths we sampled (invertebrates: McCauley and Carey, 1967; Tissot et al., 2006; fishes: Miller and Lea, 1972; Hart, 1973; Love et al., 2002). Second, the mud substratum was identical and the slope similar at untrawled and trawled sites.

Third, Collie et al.'s (2000) meta-analysis indicated that post-trawl recovery of mud-bottom benthic assemblages requires at least a year, suggesting that trawled invertebrate communities at Coquille Bank were maintained in an altered state by repeated disturbance. Indeed, Kaiser et al. (2002) concluded that impacts by trawls at intervals of 4–5 years may be enough to cause habitat loss and structural change, although Kaiser et al. (2006) found that otter trawls have less severe impacts that other kinds of towed bottom gear. Benthic recovery times would be even longer where the dominant organisms are extremely slow growing (Norse and Watling, 1999; NRC, 2002; Thrush and Dayton, 2002).

Fourth, differences in macroinvertebrate species composition and relative abundance between sites were consistent with the effects of trawling documented in other systems. In particular, soft-bodied, erect epibenthic invertebrates have low resistance and resilience to trawling (NRC, 2002). More specifically, meta-analyses (Collie et al., 2000; Kaiser et al., 2002) suggest that, in terms of relative declines, sea pens and relatives (Anthozoa) are more strongly affected by trawls and dredges than sea urchins (Echinoidea), which in turn are more strongly affected than seastars (Asteroidea). In our study, the density of sea pens was 4 orders of magnitude less on trawled seafloors, where they were nearly absent, compared to untrawled areas, where they were obvious dominants. Sea pens are known to be slow-growing and long-lived (up to 50 yr: Wilson et al., 2002), a life history that is incompatible with repeated physical disturbance (Norse and Watling, 1999; NRC, 2002; Thrush and Dayton, 2002). In contrast to relatively sensitive sea pens, mobile and less susceptible sea urchins and seastars, among other taxa, dominated trawled seafloors at Coquille Bank.

Fifth, patterns of species composition and relative abundance between trawled and untrawled sites were consistent with the ecology and life history of resident groundfishes, mobile macroinvertebrates, and their prey. The fishes that dominated untrawled seafloors are known to consume mostly epibenthic prey that could be removed or damaged by passing trawls. On deep soft bottoms off Oregon, both slender sole and rex sole focus on crustaceans, especially amphipods (Kravitz and Pearcy, 1977; Pearcy and Hancock, 1978), and poachers in general also consume small epibenthic crustaceans (Brodeur and Livingston, 1988; Tokranov, 1992). In contrast to untrawled seafloors, the fishes that dominated trawled bottoms are known scavengers and/or consumers of infaunal invertebrates. Such predators may be attracted to mud bottoms disturbed by repeated trawling.

The three most abundant species in trawled areas were Dover sole, bigfin eelpout, and hagfish. Dover sole on deep mud bottoms off Oregon are known to consume mostly infaunal polychaete worms (Pearcy and Hancock, 1978; Gabriel and Pearcy, 1981). Kaiser et al. (2002) note that Dover sole and similar flatfishes are more chemosensory than other more visually oriented flatfishes, and so would be the favored foraging type on repeatedly disturbed mud seafloors. North Pacific eelpout (*Lycodes* sp.) in general eat a variety of small invertebrates, including polychaetes (Livingston and Goiney, 1983; Lang et al., 2003). Hagfish in general are well-documented scavengers (Martini, 1998), and both hagfish and eelpout have been documented aggregating at deep seafloor disturbances (Dayton and Hessler, 1972). It seems probable that benthic prey could be flushed or exposed by passing trawls, attracting these fishes, similar to the conclusions of Engel and Kvitek (1998) for sand-bottom communities off California (see Auster and Langton, 1999, for a general review of this phenomenon, and Kaiser and Spencer, 1994, for a specific example). Additionally, many of the hagfish we observed were in burrows, with only their heads exposed, which may provide refuges from passing trawls. Alternatively or additionally, these three species may have been differentially attracted to the furrows created by trawl doors.

Regarding invertebrates, most of the species that dominated trawled bottoms at Coquille Bank–hermit crabs, seastars, urchins, and sea cucumbers–are highly mobile scavengers and/or may be morphologically resistant to trawl damage (Brusca and Brusca, 1990; Kaiser and Spencer, 1995; Lauerman, 1998; Freese et al., 1999). The probable exception to this generality is the fragile urchin, a deposit feeder (Boolootian et al., 1959; McCauley and Carey, 1967) that is probably susceptible to trawl damage. However, urchins are quite mobile and could readily recolonize trawl-door tracks. On shallow sand seafloors in the Bering Sea, Brown et al. (2005) also documented that mobile invertebrate scavengers were more abundant in chronically trawled areas. This aggregative response of scavenging predators to disturbed seafloors may explain the greater diversity of epibenthic macroinvertebrates we detected in trawled portions of Coquille Bank. Altered habitat structure, in terms of the furrows created by trawl-door tracks, may also have attracted more species.

4.3. Conclusions

Given these considerations, we conclude that the observed differences between trawled and untrawled demersal fish and epibenthic macroinvertebrate communities on deep mud seafloors adjacent to Coquille Bank were the result of gear impacts of groundfishing activities rather than local environmental differences. These differences suggest that the effects of bottom trawling along the west coast of North America are similar to those documented on deep soft-sediment seafloors elsewhere in the world. Given that gear restrictions and Essential Fish Habitat designations for groundfishes along the west coast of the United States currently focus on rocky seafloors and ignore soft bottoms (Bellman et al., 2005; NMFS, 2005), it seems prudent to consider the adverse impacts of bottom trawling on mud-seafloor ecosystems of the continental shelf and slope.

Acknowledgments

We thank the crews of the *RV William McGaw* and the submersible *Delta*, especially pilots D. Slater and R. Wicklund, for logistical support. We are grateful to W.H. Barss and D.L. Stein for serving as fellow fish observers, S.V. Benech for assisting in invertebrate identifications, C. Bianchi and J. Bright for enumerating invertebrates, and C. Goldfinger for seafloor mapping. We thank two anonymous reviewers for their helpful comments on the manuscript. This research was supported by the Minerals Management Service, Department of the Interior, under MMS agreement No. 14-12-0001-30445, and the National Undersea Research Program. **[SS]**

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