Effects of Chronic Bottom Trawling on the Size Structure of Soft-Bottom Benthic Invertebrates

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Abstract. Chronic bottom trawling reduces benthic biomass, but it is generally unknown whether this represents a decrease in numbers of individuals or their mean body size. Because this distinction provides insight into the mechanisms of disturbance and recovery, we investigate the matter here. Using comprehensive historical effort data, adjacent untrawled (UT) and heavily trawled (HT) areas were identified along the boundary of a long-standing no-trawl zone in Bristol Bay, a naturally disturbed offshore area of the eastern Bering Sea. The study site was shallow (44–52 m) with a sandy substrate, ubiquitous bottom ripples, and strong tidal currents. A modified research trawl was used to collect 42 HT–UT paired samples of benthic infauna and epifauna. These data were used to compare mean sizes (kg) of 16 invertebrate taxa. On average, 15 of these taxa were smaller in the HT area, and the overall HT–UT difference in body size was statistically significant (P = 0.0001). However, individually, only the whelk Neptunea spp. (P = 0.0001) and Actiniaria (P = 0.002) were significantly smaller in the HT area after correcting for multiple tests. Mean size of red king crabs Paralithodes camtschaticus was 23% greater in the HT area (P = 0.17). Supplemental length–frequency data indicate that substantially fewer small red king crabs, rather than more large individuals, occupy the HT area (P = 0.0001). Finally, a large number of within-year, within-taxon comparisons of mean body size were made using 1982–2001 U.S. National Marine Fisheries Service trawl survey data collected in the same closed area. Overall, these comparisons indicate natural variability of body size in UT areas is large relative to the observed HT–UT differences due to chronic bottom trawling. Since active fishing in the HT area occurred 3 or more years before our field sampling program, our findings reflect conditions associated with an intermediate level of recovery.

Introduction

Commercial fishing with mobile gear is a rather unique form of disturbance, given its high frequency and widespread occurrence in the eastern Bering Sea (Figure 1). Recent expansions into previously unexploited (deep) and untrawlable (hard) grounds as a result of technological advances and declining catches in more traditional areas have heightened concern about possible environmental consequences. Whereas disturbance of the benthos with mobile fishing gear was once just a scientific curiosity (e.g., Caddy 1968), it is now the focus of a major international research effort with statutory mandates to consider possible adverse effects on biodiversity, seafloor habitats, and their associated fish stocks (Turner et al. 1999). Despite decades of intensive research, however, its overall impact on marine ecosystems and, in particular, fish production is largely unknown (Daan 1991; Rogers et al. 1998; Thrush et al. 1998; Auster and Langton 1999; Turner et al. 1999; NRC 2002).

Research to characterize mobile fishing gear effects is pursued using two main experimental approaches. Short-term (acute) effects are studied by comparing conditions in experimental corridors before and after a single pass or repeated passes of a trawl or dredge (e.g., Tuck et al. 1998). Occasionally, the recovery process is examined by resampling at a later date; these studies incorporate untrawled control corridors into the sampling program in order to account for natural variability during the study period (a before–after, control–impact design; Green 1979; Drabsch et al. 2001). Multiple trawled and control corridors are preferred (Lindegarth et al. 2000). This approach provides insights about the process of trawl disturbance and is the basis for most knowledge about trawling effects. Longer-term (chronic) effects are studied by comparing conditions in heavily fished and lightly fished or unfished areas and, as such, measure
cumulative effects of fishing (e.g., McConnaughey et al. 2000). These experiments are relatively uncommon because high-quality historical trawl effort data are frequently unavailable, and their designs are often flawed because the (unfished) “control” areas have previously been fished or they are fundamentally different than the corresponding experimental units (Hall et al. 1993; NRC 2002).

Both natural and anthropogenic disturbances are relatively discrete events that disrupt ecosystem, community, or population structure and change resources, substrate availability, or the physical environment (Pickett and White 1985b; Lytle 2001). Their form varies from predictable environmental fluctuations to irregular destructive events. The magnitude of environmental effects generally increases with the intensity and spatial extent of the disturbance, while the persistence of these effects is closely related to the frequency of disturbances or, equivalently, the degree of recovery since the last event. All or parts of populations may be affected through collective effects on individuals, which are themselves influenced by characteristics such as body size, age, density of individuals, and their life histories. Community attributes such as richness, diversity, and structure may also be affected. Generally speaking, disturbances produce fragmented habitats that are structurally simple and populated by a relatively few small, short-lived, and highly productive (opportunistic) species that respond favorably to open space and newly available resources. Although subtidal communities do not respond to disturbances in a uniform way, responses of benthic systems to bottom trawling are generally consistent with disturbance theory (Pickett and White 1985b; Dayton et al. 1995). In particular, the physical effects of mobile fishing gear include winnowing, excavation, and resuspension of sediments; loss of physical features; and translocation of biogeochemical material at the sediment–water interface (Mayer et al. 1991; Fonteyne 2000). There also may be reductions of structural biota, altered relative abundances of species due to differential mortality and removals, loss of species from part of their normal range, altered predator–prey relationships, decreases and fragmentation of certain populations, and, presumably, higher-order food web and ecosystem effects (Lindeboom and de Groot 1998; NRC 2002). In general, these effects are thought to be cumulative and, thus, depend on the frequency of disturbance (NRC 2002). In some cases, effects may be delayed for a period of days or weeks (Kaiser and Spencer 1996; Mensink et al. 2000; Maguire et al. 2002) and, overall, the effects may persist for many years (Probert et al. 1997; NRC 2002).

Figure 1. Bottom trawl effort in the eastern Bering Sea (1973–2001). Endpoints for 400,776 individual tows recorded by fishery observers are summarized on a 25-km² grid. The rectangular outline indicates the location of the Crab and Halibut Protection Zone 1 in Bristol Bay.
Most biological research has targeted the specific changes in benthic invertebrate populations and community structure that occur when mobile fishing gear, particularly bottom trawls, contact the seabed. This focus on benthic invertebrates reflects their limited mobility and vulnerability to bottom-tending gear and observations that structurally complex seafloors are an important element of healthy, productive benthic systems (Kaiser et al. 1999a; Turner et al. 1999; Thrush et al. 2001) that are preferred by some (Sainsbury et al. 1997; Freese et al. 1999) but not all (Kaiser et al. 1999b; McConnaughey and Smith 2000; Else et al. 2001) groundfish. Effects are typically measured as changes in abundance (both biomass and numeric) or community structure (e.g., diversity or evenness). In some cases, mortalities according to sex and in situ density have been reported (Bergman and van Santbrink 2000). Studies that document gear effects have been (and remain) the primary research emphasis, despite a practical need for more interpretive work. This is because site-specific factors such as the resident species assemblage, substrate characteristics, water depth, gear type(s) used, and the disturbance history (natural or anthropogenic) influence the nature of the response to trawling (Collie et al. 2000).

Effects on the size structure of invertebrate populations are usually ignored. When size is addressed, it is typically limited to statements concerning gear selectivity and specific vulnerabilities (e.g., Bergman and van Santbrink 2000). In a few very cases, individual measurements of benthic invertebrates have been taken to examine possible effects along depth or established disturbance gradients (Hall et al. 1993; Collie et al. 1997), to compare epifaunal populations (Ramsay et al. 1996; Prena et al. 1999) and demersal fish diets (Kaiser and Spencer 1994) before and after experimental trawling, and to evaluate trawling effects on benthic production and faunal size structure (Jennings et al. 2001, 2002). This general inattention to size structure is problematic given the fundamental importance of body size in biological systems (Peters 1983; Calder 1984). Without information about the size structure of populations, simple measures of biomass or numeric abundance cannot fully address the mechanism of disturbance, the functional status of the benthos after trawling, and certain key processes (e.g., production) that influence recovery dynamics.

In this paper, we compare mean body sizes of 16 benthic invertebrate taxa in a chronically trawled area of the eastern Bering Sea with those in an adjacent untrawled area. We then consider the magnitude of observed differences in the context of natural size variability in these same taxa at untrawled locations elsewhere in Bristol Bay. This study is an elaboration of earlier work that compared invertebrate biomass in this same experimental area (McConnaughey et al. 2000).

Data and Methods

Study Area and Biological Sampling

The study area is located at the northeastern corner of a long-standing no-trawl zone in the Bristol Bay region of the eastern Bering Sea (now the Crab and Halibut Protection Zone 1, CHPZ1; Figure 2). This area is shallow (44–52 m) and is characterized by sandy substrates, ubiquitous bottom ripples, strong tidal currents (<1 m/s [2 knots]), and a rich invertebrate assemblage (Marlow et al. 1999; Smith and McConnaughey 1999; McConnaughey et al. 2000). The history of bottom trawling there was reconstructed using foreign regulations and catch statistics, international agreements, U.S. National Marine Fisheries Service (NMFS) enforcement and surveillance reports, the NORPAC fishery observer database (1973–1996; maintained at the NMFS Alaska Fisheries Science Center, Seattle), and details of historical and more recent regulatory closures, which collectively span the 40+ year history of Bering Sea trawl fisheries. From this analysis, we identified heavily trawled (HT) and untrawled (UT) areas straddling the CHPZ1 boundary. This pattern reflects a trawl prohibition first instituted by the Japanese in 1959 (Bristol Bay Pot Sanctuary, which included the subsequently designated CHPZ1; Forrester et al. 1978) and intensive fishing for yellowfin sole Pleuronectes aspera along the northern boundary of the closed area.

A total of 42 HT–UT paired stations were established in 3.4-km² (1-nautical-mi²) cells straddling the CHPZ1 boundary (Figure 2). Adjacent stations were paired to account for a possible east–west environmental gradient in this poorly surveyed area (D. Hill, Pacific Hydrographic Branch, National Oceanic and Atmospheric Administration Office of Coast Survey, personal communication). Each pair was sampled by one of two 38-m-chartered stern trawlers (1.137-kW [1,525-hp] sister ships, the F/V Arcturus and F/V Aldebaran) using matching NMFS 83-112 survey trawls modified to improve catchability and retention of benthic fauna (McConnaughey et al. 2000). Biota were collected between 31 July and 6 August 1996 with 15-min tows at 1.5 m/s (3 knots) through the center of each preselected cell. Benthic fauna in the catch were identified to the lowest practicable taxon and were then separately weighed on a motion-compensating balance and enumerated while at sea. Acoustic net mensuration and a global positioning system were used to standardize catches according to area swept (average net width for this study was 14.7 m). For each taxon that could be both weighed and counted, mean size (kg) was calculated for each haul as the ratio of total biomass (kg) and the total number of individuals in the catch. Hermit crabs (family Paguridae) were weighed in their shells after
removing attached biota. Carapace lengths for all specimens of red king crab *Paralithodes camtschaticus* were measured to the nearest mm using calipers.

**Statistical Analysis**

**Heavy Trawling Effect on Body Size**

Prior to analysis, catch data were lumped into larger taxonomic groups for consistency with biomass data used in previous analyses (McConnaughey et al. 2000). Not all taxa were caught in all tows. To preserve the paired-station design of the experiment, only those pairs in which a given taxon occurred in both of the samples were included in the analysis, resulting in the exclusion of some data. Observed positive correlation in the data confirmed the importance of the paired design. Statistical analysis using linear models showed no statistically significant differences between the catches of the two boats; hence, data from the two boats were pooled for analysis. In order to better align type I and type II error levels, \( \alpha \) was set equal to 0.10 (supporting arguments by Peterman [1990], Dayton et al. [1995], Mapstone [1996], and Nester [1996]). Given the nature of the data (paired observations, skewed distribution), the Wilcoxon signed rank test was used to test whether the difference between mean body size in the HT and the UT areas differed from zero. A Bonferoni correction for multiple tests was applied (Miller 1981). In addition, a randomization test was designed to examine the overall effect, if any, of trawling on all taxa. The test was constructed to test the null hypothesis that the across-taxa average difference in HT–UT mean size was equal to zero. For each taxon, the mean size difference was calculated for the observed data and for 9,999 pseudo-random permutations of the data for each HT–UT pair. These means produced a distribution for each taxon that was used to generate a randomization test for that taxon, the results of which were consistent with the results of the Wilcoxon signed rank tests. To construct the simultaneous test of all taxa, the 10,000
means per taxon were normalized within taxa—to give equal weight to each taxon—and then summed across taxa. Thus, the 10,000 pseudo-random sums of normalized means formed the distribution for the randomization test.

To examine the individual carapace length measurements for red king crabs, simple histograms were used to look at the difference in the size distributions from the UT and HT areas. The Kolmogorov–Smirnov two-sample test was used to evaluate statistical significance.

Natural Size Variability
For comparison with experimental results, we estimated natural size variability of benthic invertebrates by examining catches at 14 of the 17 standard NMFS trawl survey stations located within the CHPZ1 closed area (Nebenzahl 2001; Figure 3). Three stations containing the northern boundary, and other stations located outside the closed area, were excluded to avoid confounding effects of commercial bottom trawling. Prior to our analysis, NMFS survey catch data were lumped into larger taxonomic groups in order to be consistent with the mean body size data from this study. For each year from 1982 to 2001, we calculated the absolute value of the pair-wise differences in mean size for all stations where a specific taxon was caught. Absolute value was used because we had no reason to expect one station would have a greater or lesser mean size than another station within the untrawled area. These differences were then collected across years to generate an empirical distribution of differences in mean size based on natural variability among stations. The location of the absolute value of each HT–UT difference within its corresponding empirical distribution was then determined.

Results
Approximately 176 ha of seabed were sampled with 84 tows of the modified bottom trawl. Overall, 12.5 metric tons of invertebrate megafauna representing 92 distinct
taxa (including empty shell and egg case categories) were processed for an average catch of 71.0 kg/ha. For comparison, this is considerably more than the average catch (0.69 kg/ha) reported for 13-km sets in a 120–146-m deep, sandy area on the Grand Banks of Newfoundland (net width = 20 m; Prena et al. 1999).

### Heavy Trawling Effect on Body Size

Mean individual size could be determined for 16 of the invertebrate taxa that were caught. Nine motile epifaunal taxa (five crab, two starfish, one snail, and one shrimp), four infaunal bivalves, and three sedentary epifaunal groups (anemones, a sea cucumber, and a compound colonial tunicate) were represented. Two additional taxa were excluded because of low sample size: the bivalve *Siliqua* spp. (*N* = 3 pairs) and the basket star *Gorgonocephalus caryi* (*N* = 2 pairs). Overall, 8 of 16 invertebrate taxa were caught in at least 31 pairs, while the other 8 were represented in 6–19 pairs (Table 1).

The mean sizes of the whelk *Neptunea* spp. (*P* = 0.0001) and species from the order Actiniaria (*P* = 0.002) were significantly smaller in the HT area (Table 1). The mean size of *Crangon* spp. (*P* = 0.05) was also smaller in the HT area; however, the result was not statistically significant after a Bonferoni correction for multiple tests (*α´* = 0.006). Twelve additional taxa were also smaller in the HT area, albeit, not significantly smaller. Observed HT–UT differences ranged from –4% (*Asterias amurensis*, *Hyas* spp., and *Serripes* spp.) to –68% (*Tellina* spp.). Overall, the weighted-average effect for the infaunal group (–31.1%) exceeded that for the sedentary (–16.1%) and the motile (–9.1%, excluding *P. camtschaticus*) groups. The overall HT–UT difference in body size was statistically significant (*P* = 0.0001).

The mean body size of the red king crab was 23% greater in the HT area (*P* = 0.17; Table 1). This was the only exception to the overall pattern of smaller size in the HT area. An examination of carapace length (CL) frequencies indicated this mean effect was primarily due to the presence of fewer small crabs rather than more large individuals in the HT area (Figure 4; *P* < 0.0001 that there is no difference in the two CL distributions). A single pod of juveniles (*N* = 588, or >50% of all specimens caught; mean CL = 62 mm) caught in the UT area was excluded from the paired analysis because the corresponding HT sample was zero. Including those measurements in the CL distribution does not qualitatively change the conclusions.

### Natural Size Variability

A total of 10,018 within-year, within-taxon comparisons of mean body size were made using 1982–2001 NMFS trawl survey data collected in the CHPZ1 closed area. Overall, these comparisons indicate natural vari-

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### Table 1

Mean body size (kg) of 16 invertebrate taxa sampled in the untrawled (UT) and heavily trawled (HT) areas. Percentage difference represents the HT treatment effect (HT–UT) divided by the UT value. The biomass percentage difference is after McConnaughey et al. (2000). Simultaneous consideration of all taxa based on a randomization test indicated the HT–UT differences were significantly different from zero (*P* = 0.0001). Significance level of Wilcoxon results is 0.006 after Bonferoni correction for experiment-wise error (*α* = 0.10).

<table>
<thead>
<tr>
<th>Taxon</th>
<th>Mean body size (kg)</th>
<th>Biomass % difference</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>HT</td>
<td>UT % difference</td>
</tr>
<tr>
<td><strong>Motile</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Asterias amurensis</em></td>
<td>0.1007</td>
<td>0.1049</td>
</tr>
<tr>
<td><em>Crangon</em> spp.</td>
<td>0.0018</td>
<td>0.0021</td>
</tr>
<tr>
<td><em>Evasterias</em> spp.</td>
<td>0.8584</td>
<td>0.9862</td>
</tr>
<tr>
<td><em>Hyas</em> spp.</td>
<td>0.0664</td>
<td>0.0691</td>
</tr>
<tr>
<td><em>Neptunea</em> spp.</td>
<td>0.1215</td>
<td>0.1496</td>
</tr>
<tr>
<td><em>Oregonia gracilis</em></td>
<td>0.0351</td>
<td>0.0373</td>
</tr>
<tr>
<td><em>Paguridae</em></td>
<td>0.0687</td>
<td>0.0737</td>
</tr>
<tr>
<td><em>Pagurus ochotensis</em></td>
<td>0.0642</td>
<td>0.0680</td>
</tr>
<tr>
<td><em>Paralithodes camtschaticus</em></td>
<td>1.2948</td>
<td>1.0536</td>
</tr>
<tr>
<td><strong>Sedentary</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Actinaria</em></td>
<td>0.1722</td>
<td>0.2106</td>
</tr>
<tr>
<td><em>Aplidium</em> spp.</td>
<td>0.2379</td>
<td>0.2809</td>
</tr>
<tr>
<td><em>Cucumaria</em> spp.</td>
<td>0.4520</td>
<td>0.5029</td>
</tr>
<tr>
<td><strong>Infauna</strong></td>
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<td></td>
</tr>
<tr>
<td><em>Macoma</em> spp.</td>
<td>0.0270</td>
<td>0.0321</td>
</tr>
<tr>
<td><em>Mactromeris</em> spp.</td>
<td>0.0446</td>
<td>0.1000</td>
</tr>
<tr>
<td><em>Serripes</em> spp.</td>
<td>0.0426</td>
<td>0.0442</td>
</tr>
<tr>
<td><em>Tellina</em> spp.</td>
<td>0.0262</td>
<td>0.0830</td>
</tr>
</tbody>
</table>
ability of body size in untrawled areas is large relative to the observed HT–UT differences due to chronic bottom trawling (Table 2). On average (weighted by the number of comparisons), spatial differences in body size exceeded the observed trawling effect in 91% of the comparisons involving sedentary taxa, 81% of those for motile taxa, and 22% of those for infauna. In this latter case, the composite result is most applicable to the bivalve *Mactromeris* sp. (*N* = 563) because sample sizes for the other three taxa in this group (*N* = 19 total) were quite low. Overall, 78% of all spatial differences in body size exceeded the HT–UT difference observed in the 16 benthic invertebrate taxa considered.

**Discussion**

Body size directly affects the fitness of individuals, thereby influencing the structure and function of populations, communities, and ecosystems (Peters 1983; Calder 1984; Blanckenhorn 2000). Although easily measured, it is rarely considered in the context of mobile fishing gear effects. To our knowledge, there is only one other study set that has investigated effects of chronic trawling on body size and its possible ecological consequences (Jennings et al. 2001, 2002; Duplisea et al. 2002). In our case, the observed effects were generally consistent with theoretical expectations but were probably limited in magnitude by several factors. First, the study area has a relatively high level of natural disturbance (McConnaughey et al. 2000), and there is general consensus that sandy areas with strong tidal flow are less sensitive to mobile gear effects (Hall 1994; Thrush et al. 1998; Collie et al. 2000; Gordon et al. 2002; NRC 2002). Also, our findings probably reflect conditions associated with an intermediate stage of recovery since active fishing in the HT area declined to a very low level prior to field sampling in 1996 (only five tows during 1993–1995). Moreover, trawl intensities for Alaskan waters are low relative to other shelf areas in the United States (NRC 2002) and Europe (Rijnsdorp et al. 1998). Although the intensity level at our study area is only moderate for the eastern Bering Sea shelf as a whole, the concentrated pattern of trawling along the CHPZ1 boundary, nevertheless, suggests an intensity that is higher than would ordinarily result from more randomly oriented effort (Figure 2).

The overall HT–UT difference was statistically significant (*P* = 0.0001), reflecting the fact that 15 of the 16 invertebrate taxa we examined were smaller in the more highly disturbed HT area (two of which were individually significant at *P* < 0.006, the Bonferroni-cor rected α; Table 1). The binomial likelihood of observing at least 15 of 16 taxa showing a decrease in mean size by chance alone is highly unlikely (*P* = 0.0003). Reduced body size is a common response to stress, pollution, or disturbance by a very diverse set of fauna from a variety of terrestrial and aquatic systems. These include responses to size-selective predation and organic enrichment by marine sediment assemblages (Raffaelli et al. 2000), pesticide stress on freshwater zooplankton (Hanazato 1998), land management disturbances on carabid beetles (Ribera...
et al. 2001), and nutritional stress in Steller sea lions *Eumetopias jubatus* (Calkins et al. 1998). Overall, reduced body size is a general expectation for stressed ecosystems (Odum 1985).

When our results are considered in combination with biomass differences reported previously, it is possible to draw general conclusions about the overall status of these populations (McConnaughey et al. 2000; Table 1). In most cases, biomass was also reduced as a result of heavy trawling, suggesting a general population decline (Actiniaria, Aplidium spp., Crangon spp., Cucumaria spp., Macoma spp., Neptunea spp., Oregonia gracilis, pagurids, Pagurus ochotensis, Serripes spp., Tellina spp.; Table 1). In a few cases, greater overall biomass accompanied the observed body-size reduction, suggesting a proliferation of relatively small individuals in the HT area (*A. amurensis, Evasterias spp., Hyas spp., Mactromeris spp.*). The mean size of the red king crab was larger in the HT area. This was the only exception to the pattern of smaller individuals in the HT area. Since biomass in the HT area was lower than that in the UT area, the red king crab response to chronic bottom trawling appears to be fewer individuals of greater mean size.

In order to gain insight into the ecological significance of our findings, it is important to consider our results in the context of natural variability of body size. Overall, the effect of chronic trawling on body size was relatively modest when compared with natural spatial variability in a large, adjacent area closed to commercial trawling. More than three-fourths of all within-year size differences for a 20-year period exceeded the HT–UT difference, whereas a comparatively large effect is indicated by a relatively low percentage in the last column of the table. Maximum natural difference is the most extreme natural difference in mean size observed among all possible within-year pairs of 14 standard NMFS survey stations in the CHPZ1 area closed to trawling.

### Table 2

The heavily trawled–untrawled (HT–UT) effect size compared to all possible within-year (1982–2001) differences in mean body size at 14 National Marine Fisheries Service (NMFS) survey stations in the Crab and Halibut Protection Zone 1 area closed to trawling. A relatively modest effect of chronic trawling on body size is indicated when natural (spatial) differences in body size frequently (i.e., high percentage) exceed the HT–UT difference, whereas a comparatively large effect is indicated by a relatively low percentage in the last column of the table. Maximum natural difference is the most extreme natural difference in mean size observed among all possible within-year pairs of 14 standard NMFS survey stations in the CHPZ1 area closed to trawling.

<table>
<thead>
<tr>
<th>Taxon</th>
<th>HT–UT Maximum difference (kg)</th>
<th>Number of comparisons</th>
<th>Natural difference &gt; HT–UT difference (%)</th>
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<tr>
<td><strong>Motile</strong></td>
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<td><em>Mactromeris</em> spp.</td>
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BOITOM TRAWLING EFFECTS ON SOFT-BOTTOM INVERTEBRATE SIZE STRUCTURE

als or damage by trawl gear is the simplest explanation and is consistent with the pattern of lower mortalities in smaller individuals and species of megafauna (Bergman and van Santbrink 2000). These authors conclude that smaller megafauna are primarily affected by disturbances of the sediment with possible suspension into the water column and relocation, whereas larger specimens suffer mortalities as a result of direct physical contact with the gear. Since the HT area has been disturbed repeatedly over many years, it is also reasonable to consider possible changes in habitat quantity and quality. Protective cover in the HT area is relatively sparse due to reduced epibenthic biomass that is both more patchy and less diverse than in UT areas (McConnaughey et al. 2000). This condition may be particularly limiting for larger individuals of “naked” motile epifauna (e.g., shrimp and some nonpagurid crabs) that are consumed by actively searching visually oriented, benthic-feeding groundfish, such as yellowfin sole; McConnaughey and Smith 2000). Intensive predation by starfish and crab that favor disturbed areas (McConnaughey et al. 2000; this study) may augment the effect of selective but incomplete removals of larger bivalves by trawls. For the neptunids studied here, high predation and selective removals or damage by trawling may act synergistically to induce smaller body sizes in the HT area. Trussell and Nicklin (2002) demonstrated increased shell thickness (and strength), accompanied by decreased body mass and length, in an intertidal snail Littorina obtusata (also known as yellow periwinkle) exposed to persistent crab predation. Inducible responses such as this require a temporally and spatially unpredictable cue, as is typical of trawling disturbances and associated scavenger influxes.

We can only speculate as to the basis of the red king crab result. Rose (1999) reported low injury rates for red king crabs passing under commercial trawl footropes, which, combined with the 3-year lapse in active trawling in the HT area, suggests that indirect or habitat-related effects may be most important in this case. Indeed, earlier work (McConnaughey et al. 2000) indicates that heavy trawling in the study area results in a more patchy and less structured habitat with lower overall diversity of sediment taxa. For unknown reasons, these conditions may be better suited to larger rather than small crabs. Moreover, if we assume that abundance and habitat suitability are positively associated, then the fact that more crabs were found in the UT area suggests that the untrawled habitat was somehow more suitable overall (N$_{'HT}$ = 288, N$_{'UT}$ = 121 for 33 sample pairs; N$_{'HT}$ = 886, N$_{'UT}$ = 126 when all 74 samples are included). Alternatively, the HT–UT difference in abundance may be entirely unrelated to the presence or absence of trawling. Historical data from NMFS trawl surveys indicate that Bristol Bay red king crabs typically are less abundant in the HT area north of the CHPZ1 boundary (58°N) and substantially more abundant to the south. If a large-scale, temporally stable, north–south, habitat suitability gradient exists in this area and is detectable over the relatively short distances separating the HT and UT station pairs, then we might expect to catch more crabs south of the HT–UT boundary regardless of treatment effects. Consistent with the idea that suitable crab habitat exists south rather than north of 58°N is the fact that the northern boundary of the no-trawl Bristol Bay Pot Sanctuary established by the Japanese in 1959 extended northward no further than 58.17°N.

Our ability to comment on the ecological consequences of smaller invertebrates in the Bering Sea is very limited. However, some illustrative examples are possible and we feel these clearly demonstrate the complex dependencies and interdependencies that structure the benthos there. Empty shell constitutes most of the hard substrate in these soft-bottom areas. It has previously been argued that less empty gastropod shells in HT areas may have cascading consequences for hermit crabs, snail eggs, and, ultimately, for the snails themselves (McConnaughey et al. 2000). This shell not only serves as the primary substrate for snail egg attachment, but most of the sedentary megafauna in this area, including Aplidium spp. and the actiniarians (sea anemones) attach to shells or shell fragments. If shell size is mechanically reduced and dispersed by repeated trawling, it follows that the mean size of attached epifauna could be reduced as well. Furthermore, the occurrence of smaller living neptunid whelks (and their shells) in the HT area could exacerbate a possible shortage of pagurid shelters and may explain the observed reduction in hermit crab size.

Despite considerable research to document changes in benthic populations and communities as a result of bottom trawling, it is generally true that the mechanisms and, especially, the consequences of these disturbances are poorly understood. Even when actual vulnerabilities to mobile gear are reasonably well known, specific outcomes may still be unpredictable. For example, although whelks are reported to have very low direct mortality rates by virtue of their thick, rounded shells (Fonds 1994), they are very sensitive to chronic trawling in this area of the Bering Sea, nevertheless (McConnaughey et al. 2000; Table 1). This suggests that indirect effects on habitat are at least as important as the more direct effects of removals and injury, and perhaps more so in some cases. Clearly, improved knowledge of invertebrate biology and life histories and, in particular, their ecological roles and linkages would be beneficial since almost all research on fishing gear disturbances measures effects in terms of these species. However, in many cases, particularly in Alaskan waters,
this information may not be available. As a result, unless change per se is deemed undesirable, it can be argued that we are generally unable to state whether changes due to trawling are harmful or not, and, thus, cannot provide objective technical guidance to resource managers concerned about possible adverse effects on fish and shellfish habitat. Until such time as informed management is possible, the National Research Council (NRC 2002:3) advises that:

Fishery managers should evaluate the effects of trawling based on known responses of specific habitat types and species to disturbances by different fishing gears and levels of fishing effort, even when region-specific studies are not available. The lack of area-specific studies on the effect of trawling and dredging gear is insufficient justification to postpone management of fishing effects on seafloor habitat. The direct responses of benthic communities to trawling and dredging are consistent with ecological predictions based on disturbance theory. Predictions from common trends observed in other areas provide useful first-order approximations of fishing effects for use in habitat management. As more site-specific information becomes available on the fine-scale distribution of fishing effort and habitat distribution, those estimates should be revised.

Notwithstanding the need for precautionary management and the general consistency between mobile fishing gear effects and disturbance theory, the proposed interim strategy may be impractical. In their seminal work on patch dynamics and disturbance theory (which incidentally is included in the list of references for the National Research Council document), Pickett and White (1985a:377) argue that:

Predictions from first principles, which treat all taxa, ecological systems, or situations as equivalent particles without an accrued history, such as are possible in physics, are not likely to be productive in the study of disturbance. Organisms, communities, populations, and ecosystems vary, have a history, and are subject to the vagaries of climatic and geological background. Thus the sorts of predictions we can make about disturbance are mechanistic—those that take into account the peculiarities of a particular system and situation.

If we are to advance beyond purely descriptive studies of mobile fishing gear effects, a mechanistic and scalable interpretive framework is needed. To this end, the ability to make predictions is an essential prerequisite to theory development, and to be efficient at it, we must clearly define the parameters of interest (e.g., production or diversity; Pickett and White 1985a). Although this will undoubtedly require more study and discussion, an existing body of knowledge may be applicable to the task. Allometry is the study of change in the proportions (size) of various parts of an organism as a consequence of development or growth (Peters 1983; Calder 1984). Calder refers to it as the “biology of scaling.” This is a mature discipline with hundreds of empirical relationships between individual body size and a broad array of organismic properties (e.g., anatomy, physiology, and reproduction) for animal groups ranging from Protozoa to mammals. In the context of our present study, for example, allometry predicts that animal density, population production (i.e., the ratio of production to biomass, P/B), and incidence of successful defenses by prey generally increase with decreasing body size, while standard metabolic rate, ingestion rate, individual growth rate, social dominance, prey size, locomotory speed, and foraging radii/territory size generally decrease with decreasing body size. Expressions of these differences may confer competitive advantages that restructure benthic communities, and it has been argued that the main determinant of variation in species composition in epifaunal communities (specifically subtidal communities) is the degree to which residents surviving a disturbance influence invasion of the patch created (Connell and Keough 1985). For example, Ramsay et al. (1996) suggest that larger specimens of the common hermit crab Pagurus bernhardus gain significant amounts of extra food by rapidly moving into recently-trawled areas and excluding smaller individuals that arrive later. In instances when disturbances are frequent and the supply of food is greater and nonlimiting, a broader range of crab sizes may populate the area (Ramsay et al. 1997). At a larger scale, substantial increases in abundance of North Sea flatfishes (Rijnsdorp et al. 1996) and perhaps certain Bering Sea species such as rock sole Lepidopsetta spp. (McConnaughey 1995) may in some way be related to sustained high levels of trawling effort and disturbance-related shifts to smaller, highly productive prey that are preferred by these small-mouthed predators. The end result of trawling disturbances and selective removals may be systems where small fish feed on small food items, as postulated by Jennings et al. (2002).

If estimates of population size are available, allometric equations can be used to predict various population rates, and if the size structure of the populations is known, these relations can be applied to describe processes at the community and ecosystem levels (Peters 1983). A preliminary effort by Daan (1991) evaluated the potential impact of fishing by comparing published P/B ratios with estimated total mortalities. Because size structure information was not available, a homogeneous assemblage of individuals was assumed. He concluded that it is unlikely that the North Sea benthic community as a whole is presently under severe pressure by the beam trawl fleet. More
recently, benthic production was calculated using new allometric relationships and size data collected at locations with different levels of “relative fishing effort” (Jennings et al. 2001, 2002; Duplisea et al. 2002). These authors concluded that epifaunal production (and biomass) were not significantly related to trawling disturbance and, while the infaunal P/B ratio rose with increased disturbance, overall production decreased, reflecting the selective removal of larger individuals and increased relative production of smaller animals. This infaunal result is entirely consistent with allometric predictions, as is Daan’s (1991) conclusion about minimal impacts by the beam trawl fleet. Recalling selective losses of large individuals by mobile fishing gear (Bergman and van Santbrink 2000), Peters (1983:181) states, in terms of community rates of energy or material flow:

The importance of individual animals and size classes declines with size. Community processes are dominated by smaller species. Therefore, removal of larger species and individuals may have little effect on the rest of the community, and destruction of the smallest size classes could be disastrous.

Obviously, additional factors such as size-based reproductive value must be considered in any complete analysis of mobile fishing gear effects on benthic habitats. Unfortunately, despite the new, higher-level perspective that allometric studies provide, additional progress will be constrained by the general absence of body size data for noncommercial benthic invertebrates. It is interesting to note that this situation is not unique to the study of mobile fishing gear effects. In fact, “the significance of size is pointed out periodically, often with the criticism that zoologists fail to give this preeminent factor sufficient attention” (reviewed by Calder 1984). Fortunately, these data are readily collected and the situation is easily remedied with some additional effort.

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References


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