



Original Article

Short-term effects of bottom trawling and a storm event on soft-bottom benthos in the eastern Bering Sea

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A Before–After Control–Impact (BACI) experiment was conducted to investigate the effects of a commercial bottom trawl on benthic invertebrates in a sandy and previously untrawled area of the eastern Bering Sea. Six pairs of experimental and control corridors were sampled with a research trawl before and after four consecutive tows with the commercial otter trawl. A major storm event occurred during the experiment, and it was possible to differentiate its effect from that of the trawling using the BACI model. Species composition changed very little; *Asterias amurensis* and *Paralithodes camtschaticus* comprised over 80% of the total invertebrate biomass (kg ha^{-1}) during each year of the study. In general, the commercial trawl did not significantly affect the biomass of the benthic invertebrate populations. The trawling effect after 4–14 d was statistically significant in three of the 24 taxa that were analysed, which was, as expected, because of nothing more than random variation with $\alpha = 0.10$. Biomass immediately after the trawling disturbance was lower for 15 of the taxa and higher for the other nine, with a median change of -14.2% . Similarly, the effect of trawling on invertebrate biomass after one year was not statistically significant for any of the taxonomic groups ($p \geq 0.23$), indicating no evidence of a delayed response to the commercial-trawl disturbance. Further analysis suggests that storms have an overall greater effect on the benthos than do bottom trawls at this location. Both the numbers of taxa significantly affected by trawling and the storm (3 vs. 12), as well as the median sizes of these effects -14.2% vs. -22.0% , were greater for the storm event. Results from this study are combined with those from a related investigation of chronic trawling effects to propose an adaptive management strategy for the study region, including rotating area closures to mitigate for temporary trawling effects.

Keywords: adaptive management, BACI experimental design, Bering Sea, bottom trawl, marine fish habitats, natural disturbances, statistical power, storm effects, trawling effects.

Introduction

The quality and integrity of benthic habitats affect the productivity and sustainability of marine fisheries through indirect effects on important demographic parameters (Jennings and Kaiser, 1998; Johnson, 2007). For example, patterns of abundance in North Pacific groundfish respond to spatial and temporal variability in habitat factors that influence resource availability and use (McConnaughey and Syrjala, 2009; Kotwicki and Lauth, 2013). Recruitment success, the supply of food, exposure to predators, and the suitability of breeding and nursery areas are also related to benthic habitats, in general, but are subject to substantial change as a result of natural and anthropogenic disturbances (Hall, 1994; Jennings and Kaiser, 1998). These disturbances range from regular environmental fluctuations, such as those that are common in the intertidal, the surf zone, and high-current areas, to more destructive and less predictable processes associated with episodic storms, introduced

exotic species, and certain fishing activities. Of these, bottom trawling is a particular concern for marine habitats given the design of the gear, its manner of operation, and the widespread use.

Bottom trawls are designed to maintain direct contact with the seafloor for extended periods and are highly adaptable for use in areas with different substrates and vertical relief. For example, various bobbins, rollers and even truck tyres can be added to bare-wire ground gear to enable fishing on seamounts, in canyons, and in other forbidding areas. These hard-bottom areas generally support relatively diverse benthic communities and are thought to be particularly sensitive to physical disturbances (NRC, 2002; Williams *et al.*, 2010). Other less structured, soft-bottom areas are somewhat less sensitive, reflecting differences in the underlying physical regime and the specific biota that occur there (Collie *et al.*, 2000).

Impact studies in the marine environment typically focus on benthic invertebrates because of their key ecological roles as both

structural habitat and prey, and because as a group they demonstrate rather narrow affinities for particular seafloor properties (Gray, 1974; Snelgrove, 1999; McConnaughey *et al.*, 2000). Two primary types of field investigations are used to estimate bottom-trawling effects. Long-term (chronic) effects are examined by comparing heavily fished and unfished or lightly fished areas that are otherwise similar, whereas short-term (acute) effects are studied by comparing conditions before and after experimental trawling in an unfished area. The effects of bottom trawls are generally consistent with those identified for other types of disturbance (Pickett and White, 1985), including significant reductions in species diversity and populations, as well as reduced productivity of the benthos (Jennings and Kaiser, 1998; NRC, 2002; Barnes and Thomas, 2005). Physical effects on the seafloor may include reduced stability and structural complexity, altered bedforms, and biogeochemical changes (Mayer *et al.*, 1991; Schwinghamer *et al.*, 1998).

Multiple factors affect the sensitivity of an area to bottom-trawl disturbances and the community- and population-level responses that result. Ecological theory and empirical evidence suggest that the temporal history of disturbance and its spatial pattern affect both the magnitude of the impacts and the manner of recovery (Pickett and White, 1985; Auster and Langton, 1999; NRC, 2002). That is, previously disturbed areas are considered relatively insensitive to additional disturbances as compared with more pristine areas, where sizable effects are likely. This difference is attributed to the cumulative nature of the effects and the disproportionate impact of initial disturbance events. The species composition at a particular location will also influence the magnitude and direction of responses. Sessile, emergent, large-bodied, and fragile epifauna are especially vulnerable to injury and death. Other taxa tend to increase in abundance after trawling disturbances, including low-profile encrusting bryozoans that may benefit from relaxed competition for substrate (Asch and Collie, 2008) and certain mobile scavenger–predator populations, such as hermit crabs, sea stars, buccinid gastropods, and nemerteans, that respond opportunistically to increased availability of food (Ramsay *et al.*, 1998; McConnaughey *et al.*, 2000; Sparks-McConkey and Watling, 2001; Asch and Collie, 2008). The nature and magnitude of effects will also relate to the trawl configuration, especially characteristics of the ground-contact components (Rose *et al.*, 2010).

Although generalizations about sensitivity of habitats are insightful, the effects of trawling at a particular location are ultimately based on a complex set of factors that are in some cases poorly understood and difficult to estimate. Uncertainty about the response is illustrated by the numerous examples from carefully designed studies where anticipated results either were not detected or the outcomes were opposite to expectation (Collie *et al.*, 2000). Broad application of findings, although expedient, is further complicated by non-random selection of the study site(s) and imperfect experimental comparisons. As such, decision-making about trawling effects should depend on proper local studies that account for the unique ecology of a particular benthic community and relevant details of the fishing activity.

Bottom trawling in the eastern Bering Sea (EBS) has a relatively brief history of intensive development, beginning in 1954. Using well-documented fishing-effort data, the chronic effects of bottom trawling in a soft-bottom area of the EBS were evaluated by comparing adjacent heavily trawled and untrawled areas (McConnaughey *et al.*, 2000; McConnaughey *et al.*, 2005). That study revealed significant but mixed population-level differences in biomass and body sizes of benthic macrofauna, as well as significant community-level

effects, including reduced diversity, increased species dominance, and greater patchiness of epibenthic cover. Another study investigated both immediate and long-term effects of commercial bottom trawling in a shallow (20–30 m), high-energy, fine-sand area of the EBS (Brown *et al.*, 2005a; Brown *et al.*, 2005b). In general, granulometric properties and organic matter in the sediments were indistinguishable, a condition attributed to persistent surface-wave disturbances of greater magnitude than disturbances associated with commercial trawling. Similarly, changes in macrofauna density, biomass, diversity and richness were not detected within a week of an experimental trawling disturbance, however post-disturbance sampling was not always in the path of the trawl and this complicated interpretation of the results. Some long-term effects on diversity, richness, aggregate density, and biomass were detected, but the results were inconsistent for the two sampling periods.

The study presented here is part of an ongoing research program in Alaska to address essential fish habitat (EFH) mandates in the primary laws regulating marine fisheries management in the USA. Our objective was to quantify the immediate (after days) and delayed (after 1 year) effects of repetitive bottom trawling in a previously untrawled offshore area and to describe the recovery process for any significant impacts. Suggestions for habitat management in Bristol Bay are presented based on a synthesis of results from this study and the previous study of chronic trawling effects (McConnaughey *et al.*, 2000; McConnaughey *et al.*, 2005).

Methods

Study area

The study occurred inside the Crab and Halibut Protection Zone (CHPZ) located in the Bristol Bay region of the EBS (Figure 1). The history of commercial fishing there is well documented, and the absence of prior fishing disturbances eliminated a common confounding effect for studies of this kind (McConnaughey *et al.*, 2000). In general, Bristol Bay is relatively shallow (<60 m), has sandy substrates, and supports a rich invertebrate assemblage, as shown by annual bottom-trawl surveys conducted by the US National Marine Fisheries Service (NMFS; Lauth, 2011). A high level of natural disturbance is associated with strong tidal currents and severe weather events, including winter storm waves capable of disturbing the seafloor at depths to 94 m (Sharma, 1974; Marlow *et al.*, 1999; Brown *et al.*, 2005a).

Experimental design

A Before–After Control–Impact (BACI) experiment was conducted to investigate the effects of an experimental disturbance of the seafloor with a commercial bottom trawl (Green, 1979; Schmitt and Osenberg, 1996; Pitcher *et al.*, 2009). The basic BACI model is a 2×2 factorial design in which the study area is divided into control and impact areas and sampling occurs before and after an experimental disturbance applied only in the impact areas. The intention is to isolate the effect of the impact by comparing populations before and after a disturbance, while adjusting for temporal variability observed in the associated control area (i.e. statistically testing for a time \times treatment interaction). A frequent criticism of BACI designs is a lack of spatial replication (Underwood, 1994). For this study, we controlled for environmental variability in the study area by establishing six parallel pairs of sampling corridors (i.e. a $2 \times 2 \times 6$ factorial design with the pairs treated as randomized blocks), three of which were oriented north–south and

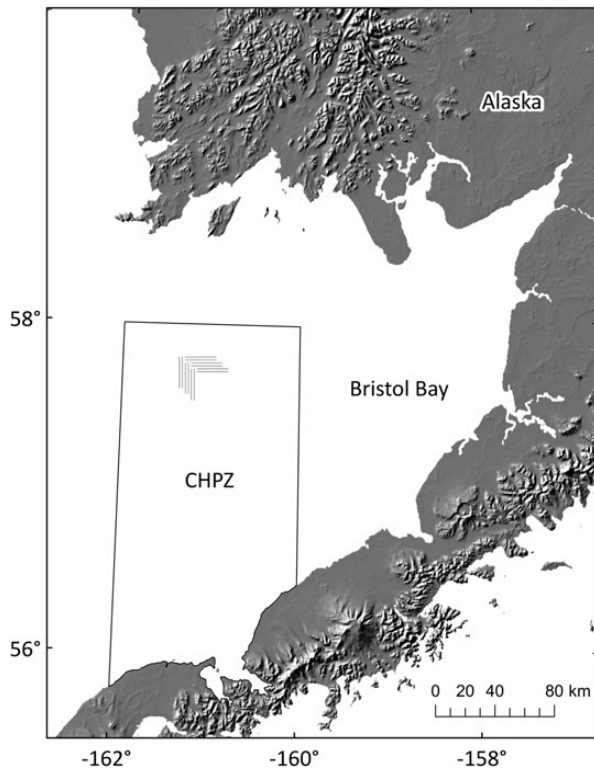


Figure 1. Layout of the six pairs of research corridors used for the Before–After Control–Impact study of bottom-trawl effects in the eastern Bering Sea. The corridors were 20.9 km long and 100 m wide, in keeping with commercial gear and fishing practices for the region. Each pair consists of an experimental (trawled) and a control (untrawled) corridor separated by 100 m. A previous study of chronic trawling effects was conducted along the northeastern boundary of the Crab and Halibut Protection Zone (CHPZ) that is closed to bottom trawling. In 1996, the CHPZ closure (27 172 km²) was superseded by the larger Nearshore Bristol Bay Trawl Closure Area (65 139 km²), where trawling is prohibited at all times east of 162°W, except for a small nearshore area that is open to trawling for yellowfin sole from 1 April to 15 June.

three were oriented east–west (Figure 1). Within each pair, one corridor was randomly selected to be fished with the commercial trawl (the impact or treatment), while the other was designated as its untrawled control.

Corridors were defined to represent historical bottom-trawling activity in the Bristol Bay region. The 100-m width was sufficient to contain both trawl doors and all other components of the commercial bottom trawl. The length was based on the average historical tow for the region outside the CHPZ closed area, corresponding to an average speed of 6.5 km h⁻¹ for an average duration of 3 h (NORPAC fishery observer database maintained at the Alaska Fisheries Science Center, Seattle, Washington; $n = 81\ 189$ tows). The resulting length of a corridor was adjusted to 20.9 km to accommodate an integer number of sampling stations ($n = 14$) with 100-m buffers between them. The stations were each 1400 m long and 100 m wide. The overall number of corridor pairs was determined by the required number of sampling stations for the planned number of sampling events.

Four discrete events were defined for biological and physical sampling in the corridors, namely before the commercial-trawl impact (B), immediately after the impact (A1), one year after the

Table 1. Results of the *a priori* sample-size analysis used to design the current BACI trawling experiment.

| Taxonomic group | Proportion | Mean | CV | Minimum n |
|-----------------------------------|------------|-------|------|-------------|
| <i>Asterias amurensis</i> | 1.00 | 53.10 | 0.32 | ≤5 |
| <i>Boltenia</i> | 1.00 | 4.43 | 0.44 | ≤5 |
| <i>Bivalvia</i> (empty shells) | 1.00 | 0.19 | 0.60 | 8 |
| <i>Pagurus ochotensis</i> | 1.00 | 1.40 | 0.64 | 9 |
| Gastropoda (eggs) | 1.00 | 0.16 | 0.67 | 11 |
| Actiniaria | 1.00 | 1.90 | 0.97 | 18 |
| <i>Crangon</i> | 1.00 | 0.15 | 1.21 | 28 |
| <i>Neptunea</i> | 0.98 | 2.31 | 0.61 | 9 |
| Gastropoda (empty shells) | 0.98 | 0.49 | 1.28 | 32 |
| <i>Hyas</i> | 0.93 | 0.18 | 0.77 | 12 |
| <i>Paralithodes camtschaticus</i> | 0.90 | 2.90 | 2.69 | ≫40 |
| Paguridae ^a | 0.86 | 0.34 | 1.46 | >40 |
| <i>Oregonia gracilis</i> | 0.81 | 0.05 | 1.07 | 24 |
| <i>Gersemia</i> | 0.79 | 0.11 | 0.89 | 18 |
| <i>Styela rustica</i> | 0.64 | 0.04 | 1.37 | 39 |
| <i>Aplidium</i> | 0.62 | 0.14 | 1.24 | 31 |
| Bryozoa | 0.52 | 0.08 | 1.32 | 36 |
| <i>Cucumaria</i> | 0.50 | 0.19 | 1.53 | >40 |

Estimates are based on 42 samples from a prior trawl-effects study using the same sampling gear in a nearby unfished area. Taxonomic groups are those represented in at least one half of the samples (i.e. Proportion) from the previous study, along with the mean cpue (kg ha⁻¹) and coefficient of variation (CV) for those samples. Minimum sample sizes (n) needed to detect a 50% reduction with 0.80 power in a two-sample experiment were estimated with a statistical bootstrap analysis. ^aIncludes *Pagurus capillatus*.

impact (A2), and a final sampling event reserved for a future date (ultimately not used in this study). Prior to fieldwork, sampling stations for all events were randomly selected without replacement. The sampling sequence in the field was based on logistical considerations.

A statistical bootstrap analysis was developed to estimate the sample size required to detect a 50% change in biomass due to the commercial trawling, using a two-sample experimental design with the level of significance $\alpha = 0.10$ and statistical power of 0.80. Empirical distributions of catch per unit effort (cpue, kg ha⁻¹) from a prior study using the same sampling gear in a nearby, unfished area were used (McConnaughey *et al.*, 2000). Based on a criterion that specimens appeared in at least 50% of the 42 samples in that prior study (designed to exclude taxa with large numbers of zeros), 18 of the 24 taxa ultimately included in this study were part of that analysis. Among those 18 taxa, the calculations yielded an estimated sample size of $n \leq 18$ per sample for nine taxa, $24 \leq n \leq 39$ for six taxa, and $n > 40$ for the remaining three taxa (Table 1). Based on available sea time and other resources, a decision was made to conduct the present experiment with 36 stations per event, 18 each in the control and the impact corridors. For a $2 \times 2 \times 6$ BACI design with three stations in each corridor per event, the sample size is comparable with a two-sample experiment with 18 observations per sample.

Commercial trawl

The commercial trawl used for the experimental disturbance was a NETS 91/140 two-seam Aleutian combination otter trawl, rigged and deployed in a manner consistent with common practices of the Pacific cod fleet in Alaska (NET Systems Inc. USA, Bainbridge Island, Washington). Thyboron model 120 conventional V-design trawl doors were used. The ground contact parts, in order from the doors to the net, consisted of 27-m bare-wire sweeps (which remained mostly off-bottom), 82-m wire sweeps covered with

7.6-cm rubber disks, and 27-m wire bridles covered with 7.6-cm rubber disks. The trawl footrope was 43-m long with a combination of 46-cm diameter rubber disks ($n = 15$) and bobbins ($n = 16$) separated by 84-cm wide spacers made up of 20-cm diameter rubber disks. This footrope weighed ~ 700 kg in water, 60% of which was from steel components, including cylindrical weights, chain and toggles. This averaged 23 kg of weight per contact surface (disk or bobbin). The forward 6.8-m segments on either side were detached from the net in a flying-wing configuration. The headrope was a 28-m steel cable with 18 36-cm diameter floats, corresponding to 327 kg of buoyancy.

A mechanical bottom-contact sensor was mounted on the footrope and an acoustic net mensuration system (Scanmar AS, Åsgårdstrand, Norway), with sensors mounted on the headrope, the trawl wings and the doors, monitored gear performance while trawling and provided measurements for calculating the area swept by the gear.

The experimental disturbance in the impact corridors consisted of four consecutive passes down the centre at $6.5\text{--}6.9$ km h^{-1} . The tows were in alternating directions to produce a homogeneous disturbance with respect to the weight of the codend (catch) on the seafloor. The catch from each commercial haul was estimated on-deck to the nearest ton and was then dumped at least 2000 m from the study corridors.

Sampling and sample processing

The study was conducted aboard a 47-m chartered commercial bottom-trawl vessel, the FV "Ocean Explorer." The "Ocean Explorer" is powered by a 1764-hp main engine and is fitted with a variable pitch propeller and propeller nozzle. The vessel has been active in both bottom- and midwater-trawl fisheries in Alaska since 1986.

Field operations in 2001 consisted of sampling sediments and benthic invertebrates in all corridors prior to the experimental disturbance (event B), then commercial trawling in the impact corridors, followed by sediment and invertebrate sampling in all corridors (event A1). The experiment was continuously executed over the period 15 June to 13 July, with the exception of limited activities during a 5–6-d storm just after the A1 sampling began. On average, 10 d elapsed between the time a corridor was disturbed with the commercial trawl and the time the A1 sampling event was completed (range 4–14 d). In 2002, sediment and invertebrate sampling for the A2 event occurred over the period 18–28 June, corresponding to a lapse of ~ 1 year since the experimental disturbance.

For each sampling event, benthic invertebrates were sampled at three stations in each corridor ($n = 36$ total) with a modified Eastern 83–112 bottom trawl, the standard sampling gear used by NMFS for fish and invertebrate surveys in the EBS since 1982. This trawl has a 25-m headrope and a 34-m footrope. A tickler chain and a 3.8-cm stretch-mesh liner were added to improve the catchability and retention of benthic invertebrates (McConnaughey *et al.*, 2000). This gear effectively samples patchily distributed organisms over large areas, and its opening is not likely to clog with large specimens. It was towed diagonally across a station for 15 min at 5.6 km h^{-1} so as to include areas disturbed by all parts of the commercial-trawl gear. Similar to the commercial trawl, a mechanical bottom-contact sensor and acoustic net mensuration system monitored gear performance while trawling and provided measurements for calculating the area swept by the gear. A microbathythermograph (model XL-200, RBR Ltd, Ottawa, Canada)

attached to the trawl continuously measured depth and water temperature. Prior to trawl sampling, surficial sediment properties were sampled once at each of two randomly selected 100×100 m sites within each station using a standard 0.1 m² van Veen grab. A calibrated ultrashort baseline (USBL; Trackpoint II Plus, Ashtead Technology, Aberdeen, Scotland) system interfaced to an integrated navigation system installed on the vessel provided accurate subsurface positioning of the commercial trawl and sampling gear with respect to the corridors and stations. The USBL transponder was placed in a net bag centred on the head rope of each trawl and was attached to the deployment line just above the arms of the grab sampler.

Benthic invertebrates caught in each haul of the sampling trawl were fully processed at sea by sorting specimens to the lowest possible taxon and weighing them on a motion-compensated electronic balance. Biogenic substrate (i.e. empty gastropod and bivalve shells and identifiable egg masses) was also processed in order to provide a more complete characterization of the benthos. Prior to analysis, some of the catch data were aggregated into larger groups of similar species in order to resolve taxonomic inconsistencies and limit the number of zero catches (cf. McConnaughey *et al.*, 2000; McConnaughey *et al.*, 2005; Table 2). Standardized catches (cpue) for the i (th) tow and the j (th) taxonomic group were then calculated as:

$$cpue_{ij} = C_{ij} / (NW_i \times DF_i), \quad (1)$$

where C_{ij} is the weight of the catch, NW_i is the average net width while on-bottom, and DF_i is the distance fished.

The grab samples were processed in the laboratory to describe the physical and chemical characteristics of sediments associated with each invertebrate sample. Sediment texture and the grain size distributions were obtained by the sieve-pipette method and described with standard statistical parameters expressed in units of φ (i.e. $-\log_2$ of particle diameter in mm; Folk, 1974), including mean φ , sorting (the standard deviation of φ), skewness and kurtosis, as well as the percentages by weight of gravel, sand, silt and clay. Mean φ represents the centre of gravity for the grain-size distribution, while the sorting coefficient is a measure of size variation (by convention, poorly sorted samples have a relatively high degree of variation). Both parameters affect basic sediment properties such as porosity, permeability and compaction, and thus could explain differences in benthic invertebrate abundances within the study area at the times of sampling. Skewness and kurtosis index the symmetry and peakedness of the particle-size distribution, which may relate to depositional sources and history. The concentrations (% dry weight) of total nitrogen (N%) and organic carbon (C%) were determined for carbonate-free sediments. The concentrations of stable isotopes of carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$), measured as the deviation from a reference standard in parts per thousand (ppt), were analysed with standard laboratory methods (Naidu *et al.*, 1993; Naidu *et al.*, 2000).

Analysis

The statistical model for the BACI analysis was fit using PROC GLM in SAS/STAT 9.2 software (SAS Institute Incorporated, 2009):

$$y_{ijkm} = \mu + \theta_i + \beta_j + \gamma_{ij} + \delta_k + \varepsilon_{ijkm}, \quad i = B, A; j = C, I; \quad (2)$$

$$k = 1, \dots, 6; \text{ and } m = 1, 2, 3,$$

Table 2. Taxa caught in the study corridors during 2001 and 2002, along with a common group name and the constituent taxa.

| Group name | Common name | Constituents | Proportion |
|---------------------------------|---------------------|---|------------|
| Actiniaria | Misc. anemones | Actiniaria | 0.50 |
| Amphipoda | Misc. amphipods | Amphipoda Gammaridae <i>Caprella</i> sp. | 0.22 |
| <i>Aplidium</i> spp. | Tunicate (compound) | <i>Aplidium</i> sp. <i>Aplidium</i> new species a | 0.94 |
| Ascidacea | Tunicates | | 0.00 |
| Asteroidea | Sea stars | <i>Henricia</i> sp. <i>Leptasterias polaris</i> | 0.00 |
| <i>Asterias amurensis</i> | Sea star | | 1.00 |
| Bivalvia | Clams | <i>Hiatella arctica</i> <i>Yoldia</i> sp. <i>Cyclocardia</i> sp. <i>Clinocardium</i> sp. <i>Pododesmus</i> sp. | 0.17 |
| Bivalvia (empty shells) | Biogenic substrate | | 1.00 |
| <i>Boltenia</i> sp. | Tunicate (stalked) | <i>Boltenia</i> sp. <i>Boltenia ovifera</i> | 1.00 |
| Bryozoa | Bryozoans | | 1.00 |
| Buccinidae | Buccinid whelks | <i>Colus</i> sp. <i>Volutopsius</i> sp. <i>Beringius</i> sp. <i>Plicifusus</i> sp. <i>Plicifusus kroyeri</i> <i>Buccinum</i> sp. | 0.28 |
| <i>Chionoecetes bairdi</i> | Crab | | 0.89 |
| <i>Chionoecetes opilio</i> | Crab | | 0.06 |
| Crangonidae | Shrimp | <i>Crangon</i> sp. <i>Argis</i> sp. | 0.94 |
| <i>Cucumaria fallax</i> | Sea cucumber | | 0.56 |
| <i>Echiura</i> sp. | Spoon worms | | 0.06 |
| <i>Erimacrus isenbeckii</i> | Crab | | 0.17 |
| <i>Eunoe</i> spp. | Scale worms | <i>Eunoe nodosa</i> <i>Eunoe depressa</i> | 0.39 |
| <i>Evasterias echinosoma</i> | Sea star | | 0.00 |
| Gastropoda | Misc. live snails | Gastropod unident. <i>Natica</i> sp. <i>Crepidula</i> sp. | 0.28 |
| Gastropoda (eggs) | Snail eggs | | 0.94 |
| Gastropoda (empty shells) | Biogenic substrate | | 0.94 |
| <i>Gersemia</i> sp. | Soft coral | <i>Gersemia</i> sp. <i>Gersemia rubiformis</i> | 1.00 |
| <i>Gorgonocephalus eucnemis</i> | Basket star | | 0.78 |
| <i>Hyas</i> sp. | Crab | <i>Hyas coarctatus</i> <i>Hyas lyratus</i> | 0.72 |
| Isopoda | Misc. isopods | | 0.06 |
| <i>Macoma</i> sp. | Clam | <i>Macoma</i> sp. <i>Macoma nasuta</i> | 0.67 |
| <i>Mactromeris</i> sp. | Clam | <i>Mactromeris</i> sp. <i>Mactromeris polynyma</i> | 0.83 |
| Mytillidae | Mussels | <i>Modiolus modiolus</i> <i>Musculus discors</i> <i>Mytilus</i> sp. | 0.06 |
| <i>Neptunea</i> spp. | Neptunid whelks | <i>Neptunea borealis</i> <i>Neptunea lyrata</i> <i>Neptunea ventricosa</i> <i>Neptunea heros</i> | 1.00 |
| <i>Notostomum cyclostomum</i> | Sea leach | | 0.06 |
| Ophiuroids | Brittle stars | <i>Ophiura</i> sp. Ophiuroid unident. | 0.00 |

Continued

Table 2. Continued

| Group name | Common name | Constituents | Proportion |
|-----------------------------------|------------------------|--|------------|
| <i>Oregonia gracilis</i> | Crab | | 0.89 |
| Paguridae | Misc. (hermit) crabs | <i>Pagurus</i> sp. <i>Pagurus aleuticus</i> <i>Pagurus confragosus</i> <i>Labidochirus splendescens</i> | 0.89 |
| <i>Pagurus capillatus</i> | (Hermit) crab | | 1.00 |
| <i>Pagurus ochotensis</i> | (Hermit) crab | | 1.00 |
| Pandalidae | Misc. pandalid shrimp | <i>Pandalus borealis</i> <i>Pandalus goniurus</i> | 0.44 |
| <i>Paralithodes camtschaticus</i> | Crab | | 1.00 |
| Polychaeta | Misc. polychaetes | Polychaeta (class) | 0.17 |
| Polychaeta (tubes) | Empty polychaete tubes | | 0.78 |
| Porifera | Sponge | | 0.28 |
| Sand dollars | Sand dollars | sand dollar unident. <i>Echinarachnius parma</i> | 0.33 |
| <i>Serripes</i> sp. | Cockle | <i>Serripes</i> sp. <i>Serripes groenlandicus</i> | 0.33 |
| <i>Siliqua alta</i> | Clam | | 0.00 |
| Sipuncula | Peanut worms | | 0.00 |
| Skate (egg cases) | | | |
| <i>Styela rustica</i> | Tunicate (attached) | | 0.67 |
| <i>Tellina</i> sp. | Clam | | 0.00 |
| <i>Tritonia diomedea</i> | Nudibranch | | 0.00 |

Taxa were selected for statistical analysis if the proportion of impact stations ($n = 18$) where the taxon was caught prior to the commercial-trawl disturbance was ≥ 0.50 .

where y_{ijkm} denotes a cpue observation for time (event) i , treatment j , corridor pair k , and station m ; μ denotes the base mean expected value; θ_i denotes the expected time effect (Before vs. After); β_j denotes the expected treatment effect (Control vs. Impact); γ_{ij} denotes the expected time \times treatment interaction (the trawling effect); δ_k denotes the expected block effect (corridor pairs); and ε_{ijkm} is the random component of the observation from each of the three selected sampling stations within the corridor during the given sampling event. With constraints on the parameter estimates of:

$$\theta_B = \beta_C = \gamma_{BC} = \gamma_{AC} = \gamma_{BI} = \delta_6 = 0, \quad (3)$$

μ becomes the expected value in the sixth control corridor before the disturbance and γ_{AI} is the trawling effect. Note that the subscript A may reference either event A1 or event A2, depending on which data are being analysed with the event-B data.

The benthic invertebrate groups included in this analysis were those with non-zero cpues at $\geq 50\%$ of the stations in the impact corridors before the commercial trawl disturbance (event B; $n = 24$ taxa; Table 2). The distributions of the cpue observations were highly skewed. To better meet the assumptions of the linear-model analysis, based on a Shapiro–Wilk goodness-of-fit analysis, a fourth-root transformation was applied to the cpue data before calculating tests of statistical significance.

The statistical analysis of commercial-bottom-trawl effects on each taxon was based on the significance of the time \times treatment interaction term in the BACI model [Equation (2)]. Both the immediate effects of the impact (i.e. B vs. A1) and possible delayed responses to the impact (i.e. B vs. A2) were examined with significance tests based on Type III sums of squares and appropriate statistical contrasts. Physical and chemical covariates for each station were added to the basic model to see if they would reduce unexplained variability in the cpue data and thus improve the ability to detect effects of the experimental disturbance. Covariates were

evaluated in four groups (in order to avoid potential data-mining consequences of looking simultaneously at 14 different covariates), namely depth and bottom water temperature, the sediment grain-size distribution parameters, the sediment size-class percentages, and the sediment chemistry properties.

The *a posteriori* statistical power for the trawling effects was examined with a method based on the non-central F distribution and the observed random variation in the cpue data (adapted from Murphy and Myors, 1998). The objective was to determine the *a posteriori* power for any level of trawling effect. First, using hypothetical values of the non-centrality parameter λ ranging from 0–11, a power curve was generated with R 2.13.0 software (R Development Core Team, 2011) for a test of the null hypothesis of no trawling effect (i.e. $\lambda = 0$), with a significance level $\alpha = 0.10$ and 1 and 63 degrees of freedom. This yielded power values from 0.10–0.95 across the range of λ . Next, the relationship between the non-centrality parameter and the trawling effect was determined. Based on the BACI model [Equation (2)], an estimate of the non-centrality parameter for the F distribution of the trawling effect parameter was calculated as:

$$\hat{\lambda} = \frac{18 \hat{\gamma}_{AI}^2}{4 MS_{Error}}, \quad (4)$$

where $\hat{\gamma}_{AI}$ is the estimate of the trawling effect for a particular taxon, and MS_{Error} is the mean square error. (The coefficient 18 results from the six pairs of corridors \times three stations per corridor, and the coefficient 4 is from the basic 2×2 BACI design.) Solving Equation (4) for $\hat{\gamma}_{AI}$ provides trawling-effect values corresponding to hypothetical values of the non-centrality parameter, thereby allowing translation of the power curve into a function of hypothetical values of trawling effects. Finally, to facilitate comparisons among taxa, the hypothetical trawling effects were converted to percentages. Using parameter estimates from Equation (2) and averaging over the six pairs of corridors, an estimate of the

after-impact cpue with a zero trawling effect was made as $\hat{\mu} + \hat{\theta}_A + \hat{\beta}_I + (\sum_k \hat{\delta}_k / 6)$. Dividing the hypothetical trawling-effect values γ_{AI} by this result yields trawling-effect values as a percentage of the estimated after-impact cpue if there were no trawling effect:

$$\text{Trawling Effect \%} = \frac{\gamma_{AI}}{\hat{\mu} + \hat{\theta}_A + \hat{\beta}_I + (\sum_k \hat{\delta}_k / 6)} \times 100\% \quad (5)$$

The power curves, now expressed as functions of the percentages, were used to estimate, for each taxon, the *a posteriori* power of the test as a function of the percentage change in the cpue due to trawling. For each taxon, this observed percentage change was calculated both with the untransformed cpue data and with the fourth-root-transformed data (Figure 2). A linear model with a zero intercept was used to estimate the fourth-root scale percentage equivalent to a 50% trawling effect with the untransformed cpue data. Consequently, the *a posteriori* powers presented to detect a 50%

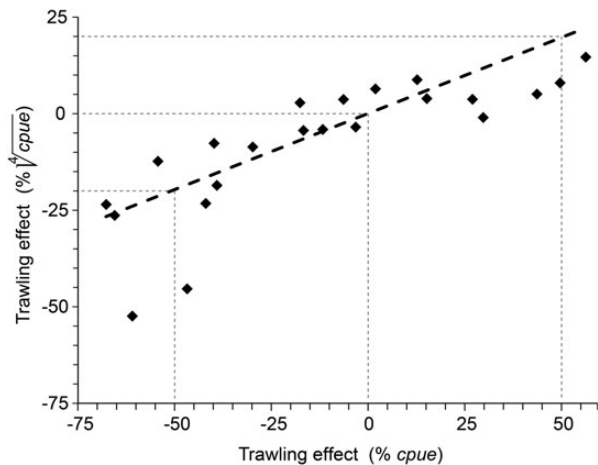


Figure 2. Linear regression through (0,0) showing the association between trawling effects on the untransformed (cpue) and transformed ($\sqrt[4]{\text{cpue}}$) scales. The line was used in the BACI power analysis to estimate the percentage change in transformed cpues that is comparable with a 50% change in untransformed cpues. The relationship is based on data for 22 of the 24 taxa analysed in this study. Two taxa (Bryozoa and *Macoma* sp.) were omitted because the estimated values for the cpue data were 1.5 and 3.5 orders of magnitude greater than the values for the other taxa; the estimated effects for $\sqrt[4]{\text{cpue}}$ data were comparable with the other taxa.

change in cpue were actually calculated as the power to detect a 20% change on the fourth-root scale. These power functions were also used to estimate the minimum detectable effect (MDE) for each taxon. This is the minimum trawling effect that would have achieved the targeted power (0.80) given the sample size used, the observed variability in the data, the null hypothesis of a zero trawling effect, and the specified level of significance ($\alpha = 0.10$).

Results

Field operations

In 2001, 36 trawl samples and 72 grab samples were collected both before and after the commercial-trawl disturbance; a further set of samples was collected in 2002, for a grand total of 108 invertebrate samples and 216 sediment samples evenly divided among the corridors. In 2001, four passes with the commercial trawl were completed in each of the impact corridors, with an estimated total catch of 110 t, composed primarily of northern rock sole (*Lepidopsetta polyxystra*) and yellowfin sole (*Limanda aspera*).

Study area characteristics

The study area was relatively shallow, with cold bottom waters and mostly sandy substrates (Table 3). Overall, depths ranged from 45–57 m (mean 51.6), with slightly deeper waters to the southwest and bottom temperatures from 4.1–5.5°C. (overall mean 4.6°, with 4.7° in 2001 and 4.6° in 2002). Surficial sediments were mostly homogeneous fine sands, with a nearly symmetrical to positively skewed distribution of particles. Sand was the predominant size grade, ranging from 91.3–98.7%. The remaining fraction included up to 2.1% gravel, 3.0% silt and 7.6% clay. The mean ϕ of the grain-size distribution averaged 2.33 (fine sand). The sorting coefficient averaged 0.46 (well sorted), skewness averaged 0.18 (positively skewed toward fine particles), and kurtosis averaged 1.85 [(very leptokurtic or peaked, according to Folk (1974)].

The concentrations of organic carbon and nitrogen were relatively low for marine shelf sediments, and the stable isotopes of carbon and nitrogen indicate that most of the sediment organic matter was derived from marine sources (Table 3; S. Naidu, University of Alaska Fairbanks, pers. comm.). Nitrogen by weight averaged 0.02% (range 0.01–0.10%), while organic carbon averaged 0.20% (range 0.09–0.39%). The stable isotope $\delta^{15}\text{N}$ averaged 5.64 ppt (range 1.16–7.82 ppt) and $\delta^{13}\text{C}$ averaged -22.11 ppt (range -25.33 to -19.49 ppt).

Biological samples

A total of 84 distinct invertebrate taxa were collected in the research trawl samples; 67 of these were represented in 2001 (events B and A1) and 60 occurred in 2002 (event A2; Table 2). The overall catch rate of

Table 3. Summary of physical and chemical characteristics of the study area.

| | Gravel % | Sand % | Clay % | Silt % | Mean ϕ | Sorting | Skewness | Kurtosis | N % | C % | $\delta^{15}\text{N}$ | $\delta^{13}\text{C}$ | C/N | Depth (m) | Temperature (°C) |
|----------------|----------|--------|--------|--------|-------------|---------|----------|----------|------|------|-----------------------|-----------------------|-------|-----------|------------------|
| Average | 0.11 | 97.60 | 1.25 | 1.05 | 2.33 | 0.46 | 0.18 | 1.85 | 0.02 | 0.20 | 5.64 | -22.11 | 8.46 | 51.6 | 4.5 |
| Std. Deviation | 0.27 | 0.90 | 0.97 | 0.41 | 0.23 | 0.09 | 0.58 | 1.42 | 0.01 | 0.05 | 1.10 | 0.61 | 1.94 | 2.8 | 0.2 |
| Minimum | 0.00 | 91.32 | 0.02 | 0.14 | 1.02 | 0.22 | -0.74 | 0.22 | 0.01 | 0.09 | 1.16 | -25.33 | 3.90 | 45.0 | 4.1 |
| Maximum | 2.08 | 98.73 | 7.61 | 3.04 | 2.58 | 1.01 | 5.63 | 10.66 | 0.10 | 0.39 | 7.82 | -19.59 | 17.00 | 57.0 | 5.5 |

Surficial sediment properties are summarized with two grab samples at each invertebrate sampling station not previously disturbed by the commercial trawl ($n = 72$ stations). Bottom depths ($n = 108$) and bottom temperatures ($n = 95$ of 108) were measured with a bathythermograph attached to the sampling trawl.

benthic invertebrates decreased 15.8% from 2001 (152.0 kg/tow, $n = 72$) to 2002 (128.0 kg/tow, $n = 36$), corresponding to a reduction of 23.9 kg per tow (Table 4). The invertebrate species composition in the study area changed very little over the course of the study. The two most abundant invertebrate taxa, comprising over 80% of the total biomass from all stations ($n = 108$), were *Asterias amurensis* (the purple-orange sea star; 59.8% in 2001 and 58.6% in 2002) and *Paralithodes camtschaticus* (the red king crab; 23.7% and 23.3%, respectively). Nine of the ten most abundant taxa by weight in 2001 were also ranked in the top 10 for 2002. The exception was the compound tunicate *Aplidium* spp., which dropped from eighth most abundant in 2001 (1.2%) to 12th in 2002 (0.4%); the Crangonidae (grass shrimp) moved from 13th in 2001 (0.3%) to ninth position in 2002 (1.0%).

Table 4. Total catches with the sampling trawl for the 24 taxa used in the BACI analysis.

| Taxonomic group | 2001 ($n = 72$ stations) | | | 2002 ($n = 36$ stations) | | |
|-----------------------------------|---------------------------|--------------|------|---------------------------|--------------|------|
| | Catch (kg) | %Total catch | Rank | Catch (kg) | %Total catch | Rank |
| <i>Asterias amurensis</i> | 6542.05 | 59.8 | 1 | 2701.16 | 58.6 | 1 |
| <i>Paralithodes camtschaticus</i> | 2589.90 | 23.7 | 2 | 1075.10 | 23.3 | 2 |
| <i>Boltenia</i> sp. | 366.20 | 3.3 | 3 | 72.19 | 1.6 | 8 |
| <i>Neptunea</i> spp. | 362.85 | 3.3 | 4 | 178.48 | 3.9 | 3 |
| Gastropoda (empty shells) | 196.81 | 1.8 | 5 | 77.33 | 1.7 | 7 |
| <i>Pagurus ochotensis</i> | 154.99 | 1.4 | 6 | 116.05 | 2.5 | 4 |
| <i>Gorgonocephalus eucnemis</i> | 136.66 | 1.2 | 7 | 103.84 | 2.3 | 5 |
| <i>Aplidium</i> spp. | 132.94 | 1.2 | 8 | 20.40 | 0.4 | 12 |
| <i>Pagurus capillatus</i> | 108.40 | 1.0 | 9 | 79.10 | 1.7 | 6 |
| Bivalvia (empty shells) | 72.80 | 0.7 | 10 | 27.34 | 0.6 | 10 |
| <i>Gersemia</i> sp. | 44.05 | 0.4 | 11 | 22.46 | 0.5 | 11 |
| Gastropoda (eggs) | 35.65 | 0.3 | 12 | 18.18 | 0.4 | 13 |
| Crangonidae | 35.32 | 0.3 | 13 | 45.40 | 1.0 | 9 |
| <i>Chionoecetes bairdi</i> | 29.30 | 0.3 | 14 | 7.07 | 0.2 | 17 |
| <i>Cucumaria fallax</i> | 28.52 | 0.3 | 15 | 10.61 | 0.2 | 15 |
| <i>Hyas</i> sp. | 14.23 | 0.1 | 16 | 4.07 | 0.1 | 19 |
| Bryozoa | 12.74 | 0.1 | 17 | 12.14 | 0.3 | 14 |
| <i>Mactromeris</i> sp. | 11.21 | 0.1 | 18 | 8.46 | 0.2 | 16 |
| Actiniaria | 10.90 | 0.1 | 19 | 3.84 | 0.1 | 20 |
| <i>Macoma</i> sp. | 10.18 | 0.1 | 20 | 0.36 | 0.0 | 31 |
| Paguridae | 9.36 | 0.1 | 21 | 4.75 | 0.1 | 18 |
| <i>Styela rustica</i> | 6.13 | 0.1 | 22 | 3.71 | 0.1 | 21 |
| Polychaeta (tubes) | 5.84 | 0.1 | 23 | 3.28 | 0.1 | 23 |
| <i>Oregonia gracilis</i> | 3.43 | 0.0 | 26 | 2.06 | 0.0 | 25 |
| Others ^a | 20.23 | 0.2 | | 10.80 | 0.2 | |
| Total | 10 940.67 | 100.0 | | 4 608.19 | 100.0 | |

The 2001 summary includes control and impact corridors sampled before (event B) and immediately after (event A1) the commercial-trawl disturbance. The 2002 summary includes control and impact corridors sampled 1 year after the disturbance (event A2). ^aOthers includes all taxa caught during the trawl sampling but not with sufficient frequency to be included in this study.

BACI model analysis

In general, the cpues of benthic invertebrates were not significantly affected by the commercial trawl. Immediately after the experimental disturbance (event A1), the trawling effect was statistically significant in only three of the 24 taxa that were analysed (Actiniaria, $p = 0.083$; *Boltenia* sp., $p = 0.044$; *Pagurus capillatus*, $p = 0.087$; Table 5). This number of significant results is consistent with the expected number of significant results at $\alpha = 0.10$ (2.4) because of nothing more than random variation. Cpue immediately after the trawling disturbance was lower for 15 of the taxa and higher for the other nine, with an overall median change of -14.2% .

The significances of the main effects in the BACI model were examined because the time \times treatment interaction (the trawling effect) was non-significant (Table 5). The time effect compares cpues before and after the disturbance [θ_A , Equation (2) but with the interaction term γ_{ij} omitted]. The time effect for the period from before (B) to immediately after the commercial-trawling disturbance (A1) was statistically significant for 12 of 24 taxonomic groups (Table 6). This indicates a change in cpue over time unrelated to the experimental treatment. Biomass decreased in all cases except for *P. camtschaticus* and *Macoma* sp., and, overall, seven of the eight motile taxa and three of the four non-motile groups showed a significant negative change in cpue. The treatment effect compares cpues between the control and impact corridors [β_j , Equation (2) without γ_{ij} in the model]. Like the trawling effect, it was significant for only three of the 24 taxa, which is consistent with the expected number of significant results that would be produced by nothing more than random variation (Table 6). This indicates that, overall, there was no statistically significant difference between the impact and control corridors; the smallest p -value was 0.012. The block factor [δ_k ; Equation (2) without γ_{ij} in the model] examines mean cpues in the corridor pairs. It was statistically significant for 14 of the 24 taxonomic groups, indicating that these models accounted for cpue differences across the study area (Table 6) that were unrelated to the commercial-trawl disturbance.

In some cases, there were statistically significant relationships between cpues and the environmental covariates during the B–A1 interval. However, the inclusion of the covariates never accounted for enough of the cpue variability so that a non-significant trawling effect became statistically significant, or vice versa. Among 72 models fit to examine the influence of the three sediment-covariate groups (sediment size distribution, sediment size-class percentage, and sediment chemistry), only seven yielded a statistically significant association, in keeping with the expected number of significant results (7.2) that would arise from nothing more than random variation. Associations between cpues and the depth and bottom-water-temperature covariates were statistically significant for 12 taxonomic groups. In this case, 13 missing observations due to equipment malfunction would have substantially reduced the number of observations in the BACI model, effectively reducing statistical power for the primary analysis. Since the focus of this study was the effects of trawling on benthic invertebrate biomass, the environmental covariates were excluded from further consideration.

It is important to consider the *a posteriori* statistical power of the non-significant bottom-trawling effects (Peterman, 1990), recalling that power is the likelihood of acquiring data sufficiently extreme to reject the null hypothesis (in this case, no trawling effect) given the variability in cpue data and the assumption that a specified alternative to the null hypothesis is true (in this study, that trawling yields a 20% change in the fourth-root-transformed cpues). Data were

Table 5. Results of the BACI analysis of immediate (after 4–14 d) and delayed (after 1 year) effects on cpue (kg ha^{-1}) of the experimental trawling disturbance only.

| Taxonomic group | Immediate trawling effects | | | | | | Delayed trawling effects | | | | | |
|-----------------------------------|----------------------------|---------------------|---------|-----------------|-------|-------|--------------------------|---------------------|---------|-----------------|-------|-------|
| | Percent | Kg ha^{-1} | S.E. | <i>p</i> -value | Power | MDE % | Percent | Kg ha^{-1} | S.E. | <i>p</i> -value | Power | MDE % |
| Actiniaria | –61 | –0.0614 | 0.0336 | 0.083 | 0.17 | 187 | –9 | –0.0052 | 0.0346 | 0.780 | 0.14 | 248 |
| <i>Aplidium</i> spp. | 56 | 0.2117 | 0.2857 | 0.504 | 0.24 | 137 | –1164 ^a | 0.2239 | 0.2437 | 0.317 | 0.12 | 324 |
| <i>Asterias amurensis</i> | 50 | 9.5258 | 13.7299 | 0.585 | 0.39 | 91 | –17 | –5.2528 | 14.2240 | 0.850 | 0.39 | 92 |
| Bivalvia (empty shells) | 27 | 0.0867 | 0.1131 | 0.605 | 0.87 | 45 | –19 | –0.0743 | 0.1034 | 0.401 | 0.87 | 45 |
| <i>Boltenia</i> sp. | –30 | –0.6182 | 0.3884 | 0.044 | 1.00 | 26 | 14 | 0.1174 | 0.3623 | 0.607 | 0.97 | 35 |
| Bryozoa | 1967 | 0.0359 | 0.0573 | 0.818 | 0.39 | 92 | 89 | 0.0767 | 0.0720 | 0.899 | 0.56 | 69 |
| <i>Chionoecetes bairdi</i> | –42 | –0.0827 | 0.0808 | 0.490 | 0.16 | 210 | –46 | –0.0645 | 0.0694 | 0.584 | 0.17 | 195 |
| Crangonidae | 13 | 0.0190 | 0.0583 | 0.409 | 0.59 | 66 | –15 | –0.0884 | 0.0902 | 0.907 | 0.86 | 45 |
| <i>Cucumaria fallax</i> | –47 | –0.0514 | 0.1120 | 0.516 | 0.11 | 436 | 31 | 0.0381 | 0.1178 | 0.682 | 0.11 | 448 |
| Gastropoda (eggs) | 2 | 0.0034 | 0.0652 | 0.629 | 0.44 | 83 | 5 | 0.0102 | 0.0627 | 0.719 | 0.43 | 84 |
| Gastropoda (empty shells) | –18 | –0.2223 | 0.3233 | 0.806 | 0.53 | 72 | –24 | –0.2675 | 0.3415 | 0.720 | 0.49 | 77 |
| <i>Gersemia</i> sp. | –3 | –0.0065 | 0.0688 | 0.682 | 0.76 | 53 | 45 | 0.0946 | 0.0752 | 0.386 | 0.83 | 48 |
| <i>Gorgonocephalus eucnemis</i> | –54 | –0.6999 | 0.5046 | 0.541 | 0.26 | 126 | –26 | –0.3798 | 0.4621 | 0.934 | 0.29 | 114 |
| <i>Hyas</i> sp. | –17 | –0.0102 | 0.0403 | 0.874 | 0.19 | 171 | 90 | 0.0233 | 0.0389 | 0.961 | 0.15 | 223 |
| <i>Macoma</i> sp. | –5997 ^a | 0.1138 | 0.1028 | 0.348 | 0.11 | 462 | –307 ^a | 0.0057 | 0.0324 | 0.722 | 0.12 | 417 |
| <i>Mactromeris</i> sp. | 44 | 0.0130 | 0.0382 | 0.882 | 0.16 | 213 | –32 | –0.0333 | 0.0544 | 0.578 | 0.17 | 192 |
| <i>Neptunea</i> spp. | –40 | –0.8353 | 0.6971 | 0.312 | 0.84 | 47 | –19 | –0.5144 | 0.7292 | 0.881 | 0.85 | 47 |
| <i>Oregonia gracilis</i> | 30 | 0.0041 | 0.0090 | 0.971 | 0.19 | 169 | –27 | –0.0078 | 0.0144 | 0.693 | 0.17 | 190 |
| Paguridae | –68 | –0.0510 | 0.0456 | 0.308 | 0.22 | 144 | 4 | –0.0412 | 0.0479 | 1.000 | 0.26 | 125 |
| <i>Pagurus capillatus</i> | –39 | –0.2682 | 0.1924 | 0.087 | 0.58 | 67 | –43 | 0.5553 | 0.2347 | 0.272 | 0.35 | 99 |
| <i>Pagurus ochotensis</i> | –12 | –0.1134 | 0.2209 | 0.548 | 0.90 | 42 | 86 | 0.0503 | 0.2665 | 0.676 | 0.95 | 37 |
| <i>Paralithodes camtschaticus</i> | 15 | 2.3484 | 2.6382 | 0.438 | 0.99 | 31 | –1 | –0.1253 | 2.5706 | 0.945 | 0.97 | 35 |
| Polychaeta (tubes) | –6 | –0.0022 | 0.0223 | 0.891 | 0.19 | 168 | –29 | –0.0146 | 0.0209 | 0.675 | 0.22 | 145 |
| <i>Styela rustica</i> | –66 | –0.0257 | 0.0210 | 0.411 | 0.16 | 200 | 146 | 0.0310 | 0.0220 | 0.226 | 0.14 | 250 |

Percent changes in cpue were calculated with untransformed data, whereas analyses to determine statistical significance of the change and a *posteriori* power to detect a 50% change attributable to the trawling were performed with fourth-root-transformed data. The minimum detectable effect (MDE) for this study is the estimated minimum change in cpue attributable to trawling that was detectable with 0.80 statistical power. Bold-faced probabilities (*p*-values) indicate statistical significance of the trawling effect at $\alpha = 0.10$. ^aThe BACI models do not constrain the cpue estimates to be positive values, resulting in unrealistic estimates of percentage change (i.e. Percent) in some cases. Equation (5) was used to calculate Percent. For each of the three cases identified, the estimate for the denominator was a very small negative number, whereas the estimate of the trawling effect in the numerator was positive and of a much greater magnitude, yielding estimates of Percent less than –100%.

available to estimate sample sizes for 18 of the 24 taxa analysed with the BACI model (Table 1). In general, the results of the BACI power analysis were as expected for the differences between the *a priori* estimates of sample size and the 18 samples actually collected. Nine of the 18 taxa were estimated to require 18 or fewer observations per sample to achieve the desired 0.80 power (Table 1). For five of these, a *posteriori* power was >0.75 (Figure 3), effectively satisfying the experimental design objective. The other four taxa, however, fell well short of the power objective, each with a power between 0.17 and 0.45. For the five taxa with relatively high a *posteriori* power, the ratio of the coefficients of variation for data from the current study and the previous study used to design the BACI experiment (i.e. CV_c/CV_p) was between 0.66 and 1.38. For the other four in this group, this ratio increased to between 1.32 and 2.25, which substantially reduced the ability to detect the targeted 50% change in cpue due to trawling. For a sample size of 18, six of the other nine taxa had *a priori* power estimates between 0.55 and 0.70, each estimated to require between 24 and 39 observations per sample to achieve the desired 0.80 power. Their *a posteriori* power estimates for the experiment were between 0.16 and 0.59. The final three taxa had *a priori* power estimates between 0.35 and 0.43 for a sample size of 18, requiring over 40 observations per sample to achieve the targeted power. Not unexpectedly, two of these had very low *a posteriori* power, but the third, *P. camtschaticus*, showed a very high 0.99 *a posteriori* power. This result was traced to a dramatic fivefold decline in the CV from the prior study to the

current study, which resulted from one particularly large observation in the former (a not uncommon phenomenon for this species; Dew, 1990). The six taxa with insufficient prior data for sample size calculations also had low a *posteriori* power, between 0.11 and 0.58. For the B–A1 interval, the MDE values as a percentage of the estimated after-impact cpue ranged from a 26% effect for *Boltenia* sp. to a 462% effect for *Macoma* sp. (Table 5). As such, it was possible to detect a 26% increase or decrease in cpue for *Boltenia* sp., whereas a greater than fourfold increase in cpue was required for *Macoma* sp. (since decreases cannot exceed 100%, a decrease in cpue could not be detected for *Macoma* at the specified level of power).

The effect of the trawling disturbance on cpue after one year (event A2) was not statistically significant for any of the taxonomic groups ($p \geq 0.23$; Table 5). Cpue was lower for 15 of the taxa and higher for the other nine, with an overall median change of –15.9%. The statistical power to detect a 50% change in cpue was remarkably similar to the power to detect the same change in the B vs. A1 case, as were the MDE percentages, which ranged from 35% for both *Boltenia* sp. and *P. camtschaticus* to 448% for *Cucumaria fallax* (Table 5). As such, there was no evidence of a delayed response to the commercial-trawl disturbance. Once again, the significances of the main effects in the BACI model were examined because the time \times treatment interaction (the trawling effect) was non-significant (Table 5). The time effect for the B–A2 period was statistically significant for 12 of the 24 taxonomic

Table 6. Results of the BACI analysis of immediate (after 4–14 d) and delayed (after 1 year) effects of time (Before vs. After), treatment (Control vs. Impact), and the block (six spatial replicates) factors on cpue (kg ha^{-1}), based on a model without the time \times treatment interaction.

| Taxonomic group | Immediate main effects | | | | | | Delayed main effects | | | | | |
|-----------------------------------|------------------------|---------------------|---------|--------------|--------------|--------------|----------------------|---------------------|---------|--------------|---------|--------------|
| | Time | | | p-value | p-value | p-value | Time | | | p-value | p-value | p-value |
| | Percent | Kg ha^{-1} | S.E. | | | | Percent | Kg ha^{-1} | S.E. | | | |
| Actiniaria | −0.9 | −0.000 5 | 0.017 1 | 0.873 | 0.520 | <0.001 | −20.8 | −0.012 1 | 0.017 2 | 0.825 | 0.426 | 0.002 |
| <i>Aplidium</i> spp. | −23.1 | −0.190 0 | 0.142 3 | 0.247 | 0.912 | 0.173 | −70.4 | −0.579 5 | 0.121 7 | <0.001 | 0.798 | 0.009 |
| <i>Asterias amurensis</i> | −34.6 | −14.893 0 | 6.837 1 | 0.023 | 0.589 | 0.062 | −24.8 | −10.679 2 | 7.063 8 | 0.088 | 0.237 | 0.480 |
| Bivalvia (empty shells) | −22.0 | −0.097 8 | 0.056 4 | 0.015 | 0.143 | 0.020 | −26.4 | −0.117 2 | 0.051 5 | 0.013 | 0.949 | 0.638 |
| <i>Boltenia</i> sp. | −24.9 | −0.566 4 | 0.196 5 | 0.004 | 0.265 | 0.122 | −61.9 | −1.407 4 | 0.179 9 | <0.001 | 0.173 | 0.001 |
| Bryozoa | −57.8 | −0.056 9 | 0.028 5 | 0.003 | 0.925 | 0.579 | 48.9 | 0.048 1 | 0.036 1 | 0.023 | 0.859 | 0.194 |
| <i>Chionoecetes bairdi</i> | −30.0 | −0.056 4 | 0.040 4 | 0.024 | 0.794 | 0.322 | −54.6 | −0.102 7 | 0.034 7 | 0.007 | 0.587 | 0.038 |
| Crangonidae | −36.0 | −0.085 5 | 0.028 9 | 0.033 | 0.797 | 0.068 | 130.4 | 0.309 5 | 0.045 1 | <0.001 | 0.339 | 0.921 |
| <i>Cucumaria fallax</i> | −72.4 | −0.178 6 | 0.055 7 | 0.002 | 0.976 | 0.009 | −48.5 | −0.119 8 | 0.058 5 | 0.110 | 0.340 | 0.216 |
| Gastropoda (eggs) | 4.2 | 0.007 8 | 0.032 4 | 0.755 | 0.331 | <0.001 | 16.8 | 0.031 4 | 0.031 1 | 0.439 | 0.308 | <0.001 |
| Gastropoda (empty shells) | 7.8 | 0.079 3 | 0.161 0 | 0.501 | 0.865 | 0.045 | −8.6 | −0.087 5 | 0.170 2 | 0.841 | 0.451 | 0.513 |
| <i>Gersemia</i> sp. | −18.7 | −0.049 2 | 0.034 1 | 0.143 | 0.212 | 0.377 | 2.9 | 0.007 6 | 0.037 8 | 0.809 | 0.969 | 0.076 |
| <i>Gorgonocephalus eucnemis</i> | 66.1 | 0.371 2 | 0.254 1 | 0.452 | 0.092 | <0.001 | 120.6 | 0.677 1 | 0.230 4 | 0.029 | 0.298 | <0.001 |
| <i>Hyas</i> sp. | −21.9 | −0.018 9 | 0.020 0 | 0.771 | 0.439 | 0.133 | −43.3 | −0.037 4 | 0.019 3 | 0.388 | 0.534 | 0.619 |
| <i>Macoma</i> sp. | 32.3 | 0.014 2 | 0.051 5 | 0.044 | 0.228 | 0.009 | −90.3 | −0.039 8 | 0.016 1 | <0.001 | 0.953 | 0.179 |
| <i>Mactromeris</i> sp. | −32.4 | −0.023 7 | 0.019 0 | 0.172 | 0.808 | 0.409 | 38.1 | 0.028 0 | 0.027 0 | 0.712 | 0.372 | 0.667 |
| <i>Neptunea</i> spp. | −50.3 | −1.332 1 | 0.349 7 | 0.001 | 0.593 | <0.001 | −18.8 | −0.497 5 | 0.363 2 | 0.610 | 0.190 | <0.001 |
| <i>Oregonia gracilis</i> | −29.8 | −0.006 6 | 0.004 5 | 0.005 | 0.862 | <0.001 | 14.2 | 0.003 2 | 0.007 2 | 0.086 | 0.564 | 0.001 |
| Paguridae | −55.6 | −0.039 0 | 0.022 8 | 0.025 | 0.288 | 0.007 | −18.6 | −0.013 0 | 0.023 9 | 0.982 | 0.964 | 0.021 |
| <i>Pagurus capillatus</i> | −2.3 | −0.013 8 | 0.096 9 | 0.441 | 0.099 | 0.001 | 59.7 | 0.356 3 | 0.121 5 | 0.082 | 0.261 | 0.022 |
| <i>Pagurus ochotensis</i> | 7.5 | 0.061 2 | 0.109 8 | 0.441 | 0.837 | 0.007 | 71.9 | 0.583 1 | 0.132 2 | <0.001 | 0.404 | 0.001 |
| <i>Paralithodes camtschaticus</i> | 46.8 | 5.337 2 | 1.316 9 | <0.001 | 0.577 | 0.268 | 13.2 | 1.503 0 | 1.275 2 | 0.137 | 0.782 | 0.366 |
| Polychaeta (tubes) | −3.2 | −0.001 0 | 0.011 0 | 0.751 | 0.812 | 0.637 | 23.9 | 0.007 6 | 0.010 4 | 0.121 | 0.972 | 0.660 |
| <i>Styela rustica</i> | 8.4 | 0.0027 | 0.0105 | 0.734 | 0.012 | 0.943 | 41.1 | 0.013 0 | 0.011 1 | 0.564 | 0.630 | 0.670 |

Changes in cpue after the commercial-trawl disturbance were calculated with untransformed data, whereas analyses to determine statistical significance of the main effects were performed with fourth-root-transformed data. Bold-faced probabilities (p -values) indicate statistical significance of the factor at $\alpha = 0.10$.

groups, again indicating a change in cpue over time unrelated to the commercial trawling (Table 6). Cpue decreased in six cases and increased in the other six cases. The time effect for eight of these 12 taxa was also significant during the preceding B–A1 interval. In four cases, the effect was negative during both intervals, in three it switched from negative to positive, and in one from positive to negative. The median percentage change for all 24 taxa during B–A2 was -2.9% . The treatment effect was not statistically significant for any of the 24 taxa (Table 6), indicating there was no difference between the impact and control corridors during the B–A2 interval; the smallest p -value was 0.173. The block effect was statistically significant for 12 of the 24 taxonomic groups, indicating there were differences in the mean cpues of the six corridor pairs (Table 6). The block effect for eight of these 12 taxa was also significant during the B–A1 interval.

Discussion

This study investigated the effects of four consecutive passes of a commercial bottom trawl on populations of benthic invertebrates in a previously untrawled area of the EBS. It was conducted to supplement a previous investigation of chronic trawling effects in the same general area and, considered together, to provide additional guidance for regional habitat management.

The relatively shallow study area (Figure 1) with well-sorted fine-sand substrates, is characterized by a high level of natural disturbance. Although the intensity of the single experimental disturbance event here was relatively high for experiments of this type (Pitcher *et al.*, 2009), it did not significantly affect the biomass of benthic invertebrates either immediately after or one year after the trawling disturbance was completed (Table 5). The median estimated change in cpue for the 24 taxa examined was -14.2% , with mixed responses by the individual taxa; cpues for 15 of the taxa decreased during B–A1 and nine increased, with the same levels of response for the B–A2 interval. In 11 cases, negative changes in the B–A1 interval were either less negative or became positive one year later (A2), collectively suggesting some reversal of the non-significant effects.

The robust experimental methods used to isolate the effects of trawling during both time intervals support the conclusion of no effect and minimize the likelihood of a Type II error. The sampling trawl effectively sampled patchy organisms, and the calibrated USBL system enabled accurate placement of sampling devices and the commercial trawl, thereby ensuring the intended statistical comparisons. The BACI experimental design was spatially replicated (Lindegarh *et al.*, 2000), the block factor accounted for corridor-pair differences when they were present, time effects unrelated to the experimental disturbance were removed, and the results indicate that treatments were effectively randomized across the blocks

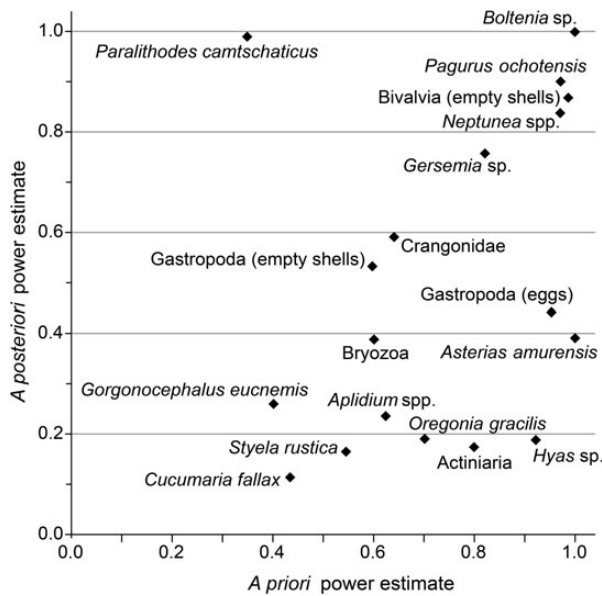


Figure 3. *A posteriori* power estimates to detect a 50% change in cpue for a $2 \times 2 \times 6$ BACI design with observations at three stations per corridor per sampling event (i.e. 18 observations per treatment; present study) compared with the *a priori* power estimates to detect a 50% change in a two-sample experiment with 18 observations per sample (based on a statistical bootstrap analysis used to design the BACI experiment).

(Table 6). Physical covariates were examined, but their effects were inconsequential. Statistical power analyses were performed, both to design the experiment and to evaluate the observed results (Tables 1 and 5).

Storm effects

Differentiating storm-related effects on the benthos from effects due to bottom trawling is difficult and frequently complicates the interpretation of experimental results (Hall-Spencer and Moore, 2000). In the absence of statistically significant experimental results, the relative importance of storms may involve subjective consideration of general weather patterns, characteristics of surficial sediments, and the general diminution of surface-wave effects with depth. In our case, there was a major storm event during A1, and a significant time factor was observed for 12 taxa during the B–A1 interval (Table 6). Considering that depths in the study area are well within the reported 94-m limit reported for storm-wave disturbance of the seabed in this area (Sharma, 1974), it is reasonable to attribute the significant time factors to the storm. Moreover, simple comparisons of the numbers of taxa significantly affected by trawling (three; Table 5) and the storm (12; Table 6), and the relative sizes of these effects, suggest that storm events have an overall greater effect on the benthos than do bottom trawls at this location. Overall, the median reduction in cpue for all 24 taxa due to the storm (–22.0%; Table 6) was substantially more than the size of the median effect due only to trawling (–14.2%; Table 5). In particular, the biomass of ten surface-dwelling or easily displaced taxa decreased after the storm, while two other taxa increased (event A1; Table 6). The decreases may have been the result of passive transport from the area, similar to colonial tunicates observed rolling along the bottom after trawling (Brown *et al.*, 2005b), or perhaps burial in shifting sands. On the other hand, the small, deposit-

feeding bivalve *Macoma* may have become more available to the sampling gear after storm currents reworked surficial sediments and exposed them (Hall, 1994). Greater access to preferred prey (Jewett and Feder, 1982) may have attracted more *P. camtschaticus* to the area, a common response for predators and scavengers after trawling disturbances. Similarly, there were 12 taxa with significant time effects during the B–A2 interval (Table 6). This time, the responses were evenly split between positive and negative changes in mean cpue. Once again, the numbers of taxa significantly affected by trawling (zero; Table 5) and by time indicate that the natural dynamics of invertebrate populations can exceed the effects of a single series of bottom-trawl disturbances when compared after one year. In this case, however, the median reduction in cpue for all 24 taxa due to time (–2.9%; Table 6) was quite small compared with the median effect due only to trawling (–15.9%; Table 5). This contrast with the B–A1 result could be because the mostly negative effects of multiple storms were offset by more positively directed processes such as recruitment, immigration and growth.

Other studies in sandy offshore areas have also found that natural disturbances or seasonal effects can exceed those due to trawling or dredging. These studies include the Western Bank (70-m depth; Kenchington *et al.*, 2006), the New York Bight (45–88 m; Sullivan *et al.*, 2003), the North Sea (39–59 m; Schratzberger *et al.*, 2002), and the Grand Banks (120–146 m; Schwinghamer *et al.*, 1998; Gordon *et al.*, 2002). In general, the effects on physical habitat characteristics were immediate but short-lived, and the majority of benthic invertebrates were unaffected by trawling or dredging. Whereas it is episodic winter storms and summer hurricanes that dominate these particular areas, conditions in the EBS are capable of resuspending sediments on a daily basis throughout the year (Brown *et al.*, 2005a). Since frequently suspended sediments are more susceptible to resuspension than undisturbed sediments (Schoellhamer, 1996), and given some species adapt to shifting sands (e.g. sand lances, *Ammodytes* spp.; Diaz *et al.*, 2003) while others do not (e.g. juvenile scallops, *Placopecten magellanicus*; Thouzeau *et al.*, 1991), the frequency and severity of storms will be important variables affecting species composition. Considering species-specific differences in vulnerability to trawls and the unique trawling histories for different areas, the effects of bottom trawling will most likely be complex, site-specific, and difficult to predict, even for habitats considered to be equally sensitive.

Synthesis with chronic effects study

The present study involving four passes of a trawl did not produce significant effects of trawling, whereas the previous investigation of longer-term trawling at a nearby location in the EBS detected significant changes in biomass, diversity, niche breadth, and mean body size of soft-bottom benthos (McConnaughey *et al.*, 2000; McConnaughey *et al.*, 2005). Over 390 000 commercial-trawl positions were summarized to identify 42 pairs of heavily trawled (HT) and untrawled (UT) stations straddling a long-standing closed area boundary (Figure 1). In this case, a multivariate analysis indicated a significant difference in biomass of benthic invertebrates in the two areas; both positive ($n = 7$) and negative ($n = 22$) changes in mean cpue were reported for taxa represented in at least 25% of the samples. For 11 of the 16 benthic invertebrate species with biomass and body-size estimates available, it was determined that both measures were reduced by heavy trawling, suggesting a general decline in the population. In four cases, greater overall biomass accompanied the average body-size reduction, indicating a proliferation of relatively small individuals in the HT area.

P. camtschaticus was the only exception to the pattern of smaller individuals in the HT area. In this case, mean body size was greater in the HT area, due to substantially fewer small crabs in the HT area than in the UT area. Since biomass in the HT area was lower than in the UT area, the effect of chronic bottom trawling on *P. camtschaticus* was fewer individuals with a greater mean size. From a community perspective, the HT benthos was less diverse, was dominated by *A. amurensis*, had less emergent epifauna and less biogenic substrate (shell), resulting in reduced structural complexity and greater patchiness.

Close proximity of the two study areas and the use of identical sampling gear allow a direct comparison of results from these studies. Biomass of characteristically vulnerable epibenthos was reduced shortly after trawling (event A1) and also after decades of intense trawling; this included anemones (Actiniaria), sessile tunicates (*Boltenia* sp.), sea cucumbers (*C. fallax*), soft corals (*Gersemia* sp.), basket stars (*Gorgonocephalus eucnemis*), neptunid snails (*Neptunea* spp.), and hermit crabs (Paguridae, *Pagurus ochotensis*), as well as important biogenic substrate (empty gastropod shells) (Figure 4). These persistent negative effects may have been maintained by continued trawling and perhaps by positive feedback mechanisms acting on ecologically linked taxa (McConnaughey et al., 2000). Conversely, the predator *A. amurensis* maintained elevated biomass over time, an effect that may have been reinforced by its dominant status in the community (McConnaughey et al., 2000). Temporary increases observed for other predators (Crangonidae, *Oregonia gracilis*, *P. camtschaticus*) in the present study, however, were reduced to levels substantially below unfished areas after decades of trawling. This reversal suggests a (threshold) trawling intensity exists (Kaiser, 1998; McConnaughey et al., 2000) beyond which reduced structural complexity or other changes in HT areas have negative consequences for these taxa.

Ecological consequences

Effective management of bottom-trawl effects on fishery production and sustainability should ultimately be guided by the ecological consequences of changes in the benthic invertebrate community, not just statistical significance. However, worldwide success at

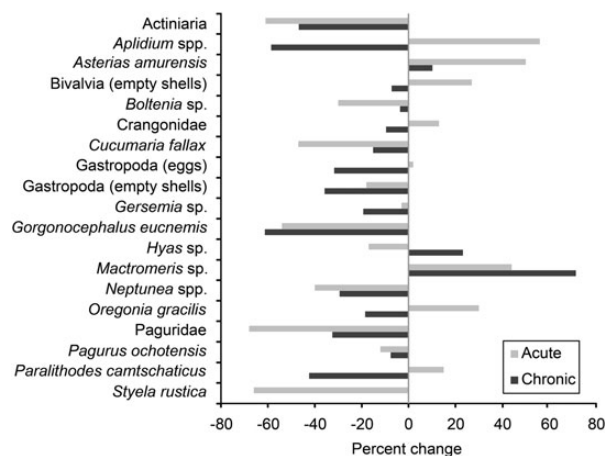


Figure 4. Changes in the biomass (kg ha^{-1}) of benthic invertebrate taxa 4–14 d after four consecutive passes of a commercial trawl (acute effects; present study) and after decades of intensive trawling by the fishery (chronic effects; McConnaughey et al., 2002). The chronic effect for *Styela rustica* was 0%.

interpreting the consequences of trawling is quite limited because relatively little is known about the ecology of individual benthic invertebrate species, let alone about their complex linkages and dependencies with managed populations. Three field studies confirm the likelihood that substantial changes in managed fish populations will accompany changes in the benthos due to trawling. Sainsbury (1988) observed a shift in fish community composition associated with removal of large epibenthos by pair trawling. Although overall fish biomass was unaffected, snappers and other species that associated with sponges and corals were replaced by species that occupy open sand. Dell et al. (2013) investigated the ecological effect of prawn trawling on the benthos by examining stomach contents of common demersal fishes. Differences in food habits were identified for seven of eight species of benthic fish predators when regions with different fishing intensities were compared, suggesting a change in benthic prey availability due to intensive fishing. The eighth species was a prey generalist, and the effects were non-significant in that case. Similarly, Hiddink et al. (2011) found bottom-trawl fisheries may have a negative effect on the length-weight condition of some but not all target species by reducing the abundance of their benthic prey. Another study, however, highlights the need to consider bottom-trawling effects in the context of natural variability. In this case, statistically significant effects on body sizes of benthic invertebrates in a chronically trawled area of the EBS were identified, but found to be relatively small when compared with natural variability in a large, adjacent area closed to commercial trawling (McConnaughey et al., 2005).

Empirical relationships between benthic invertebrates and managed populations may provide useful insights, if not mechanistic understandings, about the ecological consequences of trawling disturbances. A mathematical model has been developed to evaluate the effects of fishing on benthic habitats in Alaska (Fujioka, 2006). The model examines reductions of specific habitat types at equilibrium, for various levels of fishing intensity and different recovery rates, but does not consider the consequences of these reductions on the productivity of associated species. For this purpose, basin-scale habitat-utilization models already developed for managed populations in the EBS (e.g. McConnaughey and Syrjala, 2009) could be extended to include benthic-invertebrate predictors, thereby providing a means to estimate population-level responses to experimentally determined effects of trawling. Regardless of model structure, it will be necessary to devise a “common currency” for summarizing the various positive and negative changes in invertebrate (and fish) populations that occur. Ultimately, the statistical and ecological analyses, combined with an understanding of the local recovery dynamics, will be the basis for informed management actions about the effects of trawling on the benthos.

Fish habitat management in Bristol Bay

Bristol Bay is a highly productive area that has previously supported sizable trawl fisheries for *L. aspera* and other commercially valuable species (Chitwood, 1969; Forrester et al., 1978; Fisher, 1980). Despite recent surveys that indicate high concentrations of adult *L. aspera* in the area (Lauth, 2011), most of Bristol Bay has been closed to bottom trawling in order to protect the extremely patchy habitat of juvenile *P. camtschaticus* (Ackley and Witherell, 1999). New information about the habitats of *L. aspera* and juvenile *P. camtschaticus*, however, suggest the degree of spatial overlap may be smaller than originally thought. Highest densities of adult *L. aspera* are found on sand substrates in the EBS (McConnaughey and Smith, 2000), whereas juvenile *P. camtschaticus* habitat consists

of rocks, shell hash, and epifauna associated with gravel-cobble substrates that are typically found closer to shore (Armstrong *et al.*, 1993). As such, it may be possible to reduce the geographic extent of the existing closure, particularly if significant bycatch of other non-target species is preventable (Figure 1). To this end, the Japanese successfully instituted a no-trawl sanctuary that protected the *P. camtschaticus* brood stock in Bristol Bay for decades, i.e. until regulations were relaxed and significant bycatch of highly aggregated sexually mature females occurred during the early 1980s (Dew and McConnaughey, 2005). It therefore seems prudent, prior to a resumption of trawling, to institute a new protective closure that accounts for recent changes in the crab brood stock's distribution (Armstrong *et al.*, 1993). Undesirable bycatch of other valuable species, such as halibut and salmon, may be controllable with gear modifications (e.g. Rose and Gauvin, 2000).

A system of intermittent spatial closures may be practical for managing benthic habitat in high-energy soft-bottom areas like Bristol Bay (McConnaughey *et al.*, 2000; Fujioka, 2006), given the relative insensitivity to bottom trawls and the potential for limiting bycatch. In particular, a group of fishing zones could be established in Bristol Bay with subsets opened to bottom trawling on a rotating basis. Individual zones, scaled for efficient fishing operations, would be closed after reaching a predetermined level of trawl-related impact, at which point previously closed (recovered) fishing zones would be brought into production, and the newly closed zones would go fallow until recovered. Particularly sensitive areas or those prone to considerable bycatch, as discussed above, could be excluded from the group of zones *a priori*. Prior to fishing operations, the threshold trawling intensity for closing a zone to fishing should be determined (Auster, 2001), based on a consensus (ultimately an understanding) of what constitutes significant ecological effects. Conditions in the open and closed areas could be monitored by the existing bottom-trawl survey, while a coordinated research program would provide general scientific support for adaptive management decisions.

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