



No more detectable fishing effect on Northern Gulf of St Lawrence benthic invertebrates

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Trawling has been reported worldwide to alter seabed structure, and thus benthic habitats and ecosystems. Usually, a decrease in species richness and biomass is observed, and community structure is modified towards more opportunistic species. The Gulf of St Lawrence (Canada) has been intensely exploited since the 17th century, including net, longline, dredge and trawl fishing activities. Recently, the collapse of groundfish stocks induced a shift in fishing practices toward shrimp trawling, which is currently considered a sustainable fishing activity in the region. However, no long-term study has evaluated the potential effects of trawling disturbances on benthic mega-invertebrates. We investigated whether shrimp trawling had long- (ca. 20 years), mid- (ca. 10 years), and short-term (ca. 4 years) impacts on benthic mega-invertebrate taxa richness, biomass, and community structure. Scientific and fishery trawling data analyses showed that no significant long-, mid-, or short-term effect was detected on taxa richness. Significant but weak effects on biomass and community structure were detected at the mesoscale, i.e. at the scale of fishing grounds. In this long-exploited ecosystem, we suggest that a critical level of disturbance was attained by the first gear passages, which occurred decades ago and had irreversible impacts on the seabed by removing vulnerable taxa and structures that provided three-dimensional habitats. It is likely that benthic communities have subsequently reached a disturbed state of equilibrium on which current trawling disturbance has limited or no further impacts.

Keywords: benthic invertebrate community, Gulf of St Lawrence, multivariate analyses, shrimp, spatial scales, trawling disturbance.

Introduction

Fishing activities are known to impact marine ecosystems worldwide and have become an important environmental issue (Pauly *et al.*, 1998; Link *et al.*, 2010; Zhou *et al.*, 2010). Among these activities, trawling is assumed to be one of the most destructive, causing severe damage to seabed structure and benthic communities due to the passage of fishing gears and frequent bycatch (Jones, 1992; Tillin *et al.*, 2006; Thurstan *et al.*, 2010). Experimental, observational, and modelling methods have been used in studies in all parts of the world subjected to fishing to better understand the exact effects of fishing on benthic ecosystems. Although models do exist to predict the effects of fishing disturbance in relation to gear type, bottom type,

depth, and faunal composition (NRC, 2002), experimental and observational studies sometimes show diverging results according to the region studied. Thus, there is no exact and general disturbance theory associated with trawling because the impacts depend on the combination of fishing characteristics (trawling effort, more specifically distribution and intensity, gear type and selectivity, etc.) and environmental properties (initial structure of the seabed, presence of vulnerable species to trawling, fishing stock state, etc.), which differ from one region to another, and often from one period to another (Gray *et al.*, 2006; Jones *et al.*, 2008; Zhou *et al.*, 2010). In Australia for instance, Drabsch *et al.* (2001) and Svane *et al.* (2009) reported contradictory results regarding

trawling effects on the benthos. Tanner (2003) found an overall negative effect of trawling but suggested that trawling favours recruitment by suppressing competition. Pitcher *et al.* (2009) also suggested that trawling impacts species differently according to their vulnerability, and Brylinski *et al.* (1994) found only weak trawling impact on benthic communities in the Bay of Fundy (Canada). This panel of examples demonstrates, despite a large number of studies reporting negative impacts, the difficulty of assessing broad-spectrum trawling impacts on benthic communities. An accurate evaluation of commercial trawling impact in specific regions and for specific fisheries is therefore critical for the conservation of exploited stocks and natural populations and habitats.

The Estuary and Northern Gulf of St Lawrence (EGSL), Canada, is the natural outlet of one of the largest freshwater systems in the world, the Great Lakes, and has provided valuable fisheries for centuries, first to local populations, then to European immigrants attracted by the richness of these waters. Despite the long history of intense human use of the EGSL, especially through incessant fishing since the 18th century, it still supports diverse and productive fisheries that sustain the local economy (LaPan *et al.*, 2002; DFO, 2012a, b). Several intensive fishing activities have nevertheless occurred since the beginning of fishing in the EGSL. The walrus (*Odobenus rosmarus*) hunt drove the St Lawrence stock to extinction in the late 1700s (Sergeant, 1976). Among activities targeting fish, two centuries later several groundfish stocks are still experiencing difficulties in the EGSL, with fisheries either under moratorium (redfish) or operating under very low quotas (American plaice, witch flounder). The most well known, but still poorly understood, stock collapse is that of Atlantic cod (Myers *et al.*, 1997; Savenkoff *et al.*, 2007; Bundy *et al.*, 2009; Chassot *et al.*, 2009). Despite some attempts of the fisheries services to foster conservation since the late 1800s, collapses of several fish stocks may have been promoted by new technology that was progressively adopted by fishing fleets, encouragement to fish them by various governments, and a lack of scientific understanding of stock dynamics at that time (Walters and Maguire, 1996). It is also evident that groundfish stock collapses have further benefited invertebrate fisheries for lobster, crab, and shrimp (Hare and Dunn, 1993; Savenkoff *et al.*, 2006; Dufour *et al.*, 2010; DFO, 2012a). Such switch towards invertebrates is widespread in northern hemisphere fisheries and is usually indicative of overfishing (Pauly *et al.*, 1998; Jackson *et al.*, 2001; Anderson *et al.*, 2011). Increased interest in fishing shrimp in eastern Canada was due to the industry adapting to the harsh economic context brought about by the collapse of some fish stocks (e.g. cod). These collapses allowed invertebrate abundances to increase (Savenkoff *et al.*, 2006; Dufour *et al.*, 2010; Savard, 2012) and fishing activity thus refocused on species such as shrimp to maintain incomes (Gillett, 2008).

Shrimp fishing began in the EGSL in 1965, focusing on *Pandalus borealis* species (DFO, 2012b; Savard, 2012). The main fishing grounds were historically located off the North Coast, around Anticosti Island, and progressively migrated southward to follow changing shrimp distributions (DFO, 2012b; Savard, 2012). Today, fleets of trawlers from five provinces (Quebec, New Brunswick, Nova Scotia, Prince Edward Island, and Newfoundland) and seven First Nations, including 141 active licences in 2011, run most of the fishing activity in four main areas: the Estuary, the North Coast around Sept-Îles, around Anticosti Island, and the Esquiman Channel (DFO, 2012a; Savard, 2012). Several management measures ensure the sustainability of the shrimp fishery. These include a minimum mesh size of 40 mm and the use of the Nordmore grid

on trawls to ensure high gear selectivity, strongly reducing groundfish bycatches. To decrease impacts on the seabed at local scales, research has focused on fishing gear improvements (e.g. semi-pelagic doors; DeLouche and Legge, 2004; He *et al.*, 2006; Winger *et al.*, 2006; He and Winger, 2010), and camera-systems to better observe local impacts (Underwood *et al.*, 2012; Nguyen *et al.*, 2014). The shrimp fishery runs only from April to December, when females have already released their eggs. TAC (“total allowable catches”)-based management has been in effect since 1982 to limit fishing to protect the reproductive potential for the shrimp population, and stock assessments based on fishery and research surveys are done each year to follow stock dynamics (e.g. DFO, 2002, 2012a). The use of science advice based on peer reviews and meetings with the industry, resulting in scientific advices and risk assessments for fishing stocks, associated species, and benthic habitat sustainability, are used in a precautionary approach to determine annual TAC and evaluate the impact of trawling on benthic habitats (DFO, 2011, 2012c; Lévesque *et al.*, 2012). These measures have allowed TAC and landings to increase continuously in all four areas since the 1970s (from 1000 to 34 000 tons) indicating the healthy condition of the shrimp stock (DFO, 2012a). This demonstrated sustainability of the EGSL shrimp stock and fishery led to the “ecocertification” of the Gulf of St Lawrence northern shrimp fishery by the Marine Stewardship Council in 2008, which was renewed in 2014 (www.msc.org).

Although a preliminary risk assessment was done in the context of ecocertification re-assessment, no long-term study on the overall resilience of EGSL benthic invertebrate communities to fishing has been done. Three main approaches have been adopted in different parts of the world over the past couple of decades to investigate the impacts of fishing on benthic invertebrates: (i) experimental trawl studies to assess the immediate direct effects of the passage of fishing gear in lightly or unfished areas (Kaiser *et al.*, 1998; Collie *et al.*, 2000; Tanner, 2003; Pitcher *et al.*, 2009) with the calculation of recovery indices (Hiddink *et al.*, 2006a), (ii) comparative studies of benthic communities over gradients of fishing intensity (integrated over prolonged periods: Frid *et al.*, 1999; Burridge *et al.*, 2006; Tillin *et al.*, 2006; Reiss *et al.*, 2009), and (iii) mass-balance models (ECOPATH: Christensen and Pauly, 1992; inverse methodology: Vézina and Platt, 1988). Usually, reduced biomass, secondary production, and species diversity are associated with increased fishing disturbance (Hiddink *et al.*, 2006b; Tillin *et al.*, 2006; Reiss *et al.*, 2009). In Canada, local trawling experiments have revealed moderate physical and temporal effects on benthic sediments (Schwinghamer *et al.*, 1998), although the effects on epifauna may be more substantial (Prena *et al.*, 1999). Recent studies characterized fish and invertebrate communities of EGSL benthic ecosystems (Chouinard and Dutil, 2011; Lévesque *et al.*, 2012; Moritz *et al.*, 2013) but without focusing on fished species. In contrast, studies focusing on EGSL fished species have not included non-fished benthic taxa, focusing solely on specific commercial populations and stock dynamics (e.g. DFO, 2002, 2012a; Savenkoff *et al.*, 2006) or protected taxa (sponges and corals: Kenchington *et al.*, 2010; DFO, 2010, 2012b). Quantitative studies on the impacts of trawling on entire benthic communities are thus lacking for the EGSL, whereas increasing human activities in the marine area raise the need to assess any such impacts at a large scale and on the long term.

The objective of this study was to evaluate the spatiotemporal impacts of trawling activities in the EGSL on benthic invertebrate megafaunal communities, i.e. to infer the spatial scale of action of fishing activities on several community properties. The present study focuses on the shrimp fishery as it represents the only trawling

activity occurring in the Northern Gulf of St Lawrence since 2007. Since the fishery uses trawls that may remove species other than shrimps, we expected to observe differences regarding biological communities in terms of diversity, biomass and structure between fished and unfished grounds. The accuracy of our fishing data allowed the investigation of several specific issues within the period covered by the data: (i) the restoration capacity of the community, i.e. the ability of taxa to re-establish quickly after trawling disturbances; (ii) the resilience of benthic communities, i.e. the ability of component taxa to recolonize the entire the whole trawled area and reorganize as a community; and (iii) whether taxa may restore their biomass between trawling disturbances to avoid trophic cascading effects on the rest of the benthic foodweb. These community properties were evaluated on long-, mid-, and short-term scales (20, 10, and 4 years, respectively). Based on current knowledge on the EGSL ecosystem and on trawling impacts on benthic invertebrates in general, we predict that some taxa are able to recolonize a towed area, and that the taxa composition will be different after trawling. Only species that are quick colonizers would re-settle quickly on the entire disturbed surface. We also predict that some taxa will be able to restore their biomass on the long term, but only if the respective total biomass of these taxa has not been extracted.

Method

Survey area and data

Survey area

The EGSL has two major connections with the Atlantic Ocean, through the Cabot and Belle-Isle straits, and receives significant freshwater inflows, mainly from the St Lawrence River (Figure 1a). The topography of the northern part of the Gulf is distinguished by three deep channels: Laurentian, Anticosti, and Esquiman, with a maximum depth of 535 m. A cold layer (-1 to 1°C) situated between 30 and 100 m separates warmer mixed surface (14°C in summer) and deep (6°C) layers. Estuarine circulation occurs by water flowing seaward in the surface layer and landward in the deep layers (Saucier *et al.*, 2003). The seabed of the EGSL is a mosaic of different sediment types, from fine mud to coarse rocks (Loring and Nota, 1973).

Fishery-independent biological scientific survey

Megafauna were sampled at >755 stations visited between 2006 and 2009, from 1 to 31 August (Figure 1a), using a stratified random sampling following predetermined depth strata (Doubleday, 1981; Gagnon, 1991). Station depth spanned from 24 to 512 m, and the minimal distance between two stations was 115 m. The samples were collected with a four-sided shrimp bottom trawl (Campelen 1800 type). The trawl was rigged with variable net mesh sizes (44–80 mm centre knot to centre knot) appropriate for each part of the trawl. The codend and the lengthening piece were also equipped with a 12.7 mm knotless nylon lining (McCallum and Walsh, 2002). The standard tow duration was 15 min on the bottom but was shorter in rare cases where the substrate was rougher. Only tows exceeding 10 min ($n = 755$) were used in analyses (Archambault *et al.*, 2012). Tow results (biomass) were standardized to 15-min tow durations.

Samples were sorted, taxa identified to the lowest possible practical level, and taxonomic names verified using the Integrated Taxonomic Information System (www.itis.gov). Because colonial organisms such as bryozoans and hydrozoans found in several

samples were too abundant to be enumerated, the wet mass of each taxon was recorded as an index of abundance. Photographs of total capture and of each identified taxon were recorded. Taxa not identified while at sea were preserved in 70% ethanol or frozen for later identification in the laboratory. Biomass estimates were standardized relative to catch per unit effort by dividing the mass of a taxon by the total area swept by the trawl. Biomass in the database was therefore expressed in kg km^{-2} .

Environmental data

The environmental variables that were previously found to be best related to overall benthic megafauna structure were used: depth, temperature, and oxygen saturation (Moritz *et al.*, 2013). These variables were taken from an extensive set of 103 water column, geographic, and physical data integrated in a 10×10 km cell grid over the EGSL (Dutil *et al.*, 2011).

Fishing data and variables used

The northern Gulf of St Lawrence is divided into two administrative Northwest Atlantic Fisheries Organization fishing areas, 4R and 4S. The estuary is covered by subareas 4Tp and 4Tq, which are part of area 4T that also comprises the southern part of the Gulf (Figure 1b). Data on bottom trawling were obtained using commercial logbook recordings reported for these four administrative

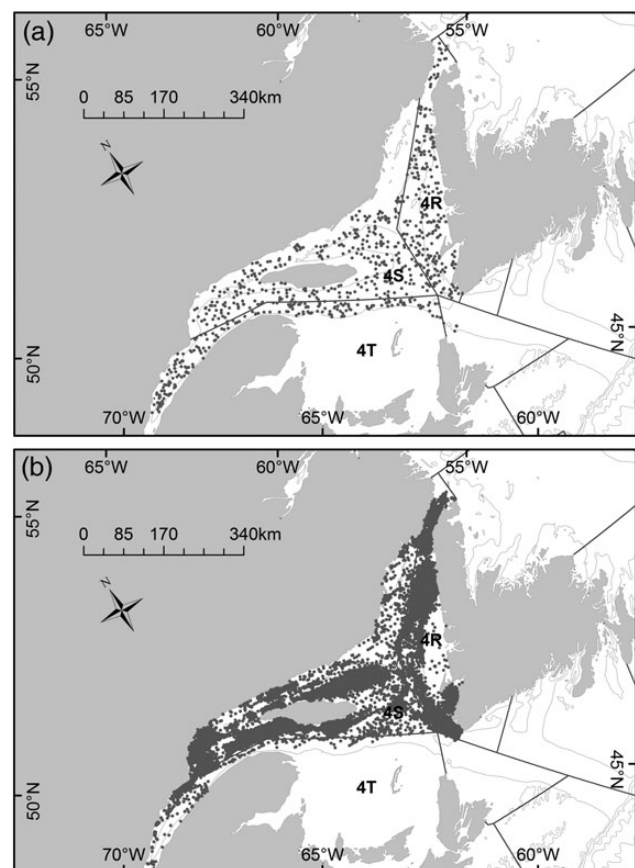


Figure 1. Map of the Estuary and Northern Gulf of St Lawrence (EGSL) depicting (a) biological survey sampling stations between 2006 and 2009, and (b) fishing tows (starting coordinates) between 1991 and 2009 in NAFO areas 4R, 4S, and 4T separated by grey segments. Bathymetric lines delineate the 200 m-depth isobath.

fishing areas during 1991–2009, provided by the Department of Fisheries and Oceans Canada (DFO). Beginning geographic coordinates of each tow during this period are shown in Figure 1b. The duration of fishing tows is on average 2–5 h at a speed of three knots, i.e. 5.5 km/h (J.-C. Brêthes, pers. comm.). The use of logbooks allows for standardized data to be recorded for fishing boats and administrative fishing areas. Fishers identity and boat names were kept confidential. Fishing data were pooled over the four areas for the analyses and separated into three periods to assess the relationships between fishing and megafauna: 1991–2009 (“long term”), 2000–2009 (“mid term”), and 2006–2009 (“short term”).

Three fishing-related variables of likely pertinence to megafauna ecology were considered in the analyses:

- (i) The fishing effort in number of tows per year, depicting how often fauna were perturbed (i.e. extracted from substrate, moved away), reflecting the restoration capacity of the communities: “Can any taxa re-settle quickly after a disturbance?”
- (ii) The fishing effort in hours per year, representing the seabed surface trawled: “Are the organisms able to recolonize the entire fishing-disturbed area?”
- (iii) The mass landed in kg per year, depicting how much biomass (mainly of shrimp, but also of bycatch) was extracted from the ecosystem: “Are the organisms of different taxa able to restore their biomass between two trawling events?”

Assigning fishing sampling data and biological sampling data to environmental data

Beginning coordinates of tows and sampling coordinates of biological data were integrated into the predefined 10 × 10 km-cell environmental grid. Because the study objective was to assess the effects of fishing on benthic organisms, cells containing neither fishing nor biological data, and cells containing fishing data only, were not included in further analyses. For the three fishing time scales considered (long, mid, and short term), number of tows, fishing effort, and mass landed within the same cell were summed. For biological data, total biomass, total number of taxa, and taxa composition per cell was recalculated if more than one sampling station fell into a given cell. Commercial fishing tows may not always overlay exactly scientific survey tows, but since trawling activities are concentrated in specific areas (Figure 1b), and given the surface towed by fishers during one tow (from 0.15 to 0.40 km²), it is very likely that trawling has, either the same year or in past years, affected the scientific surveyed areas towed.

Statistical analyses

All analyses were performed using the long-, mid-, and short-term fishing data on the 2006–2009 fauna dataset, using the statistical package R version 3.0.0, and libraries “vegan” and “raster”.

Multivariate and univariate analyses at large spatial scale

Multivariate ordination methods were used to evaluate the relationships between megafauna community structure and environmental and fishing variables. A preliminary variation partitioning (Peres-Neto *et al.*, 2006) was done to assess the effects of the environmental and fishery variables on the benthic invertebrate community data, and revealed that the environment mostly explained variation in benthic communities (Supplementary Table S1). Given this, partial redundancy analysis (partial RDA), used to assess the effects of a set

of variables on community structure conditioned by another set of variables, i.e. by removing the effects of the latter, was used to evaluate the relationships between fishery variables and benthic community structure, while controlling for environmental covariables. A permutation test (999 permutations) was used to test relationships between the stations and the fishing variables described by the first and second RDA axes. Before this analysis, megafauna data were Hellinger-standardized to decrease the mass of rare taxa and sites with many individuals (Legendre and Gallagher, 2001).

Further univariate analyses were done to focus on “fishing effort”. Linear regressions were used to evaluate the relationships between fishing effort and taxa richness and biomass, using Pearson’s correlation coefficient.

Multivariate analysis from fine to large spatial scales

Principal coordinates of neighbour matrix (PCNM) analyses were used to detect the spatial structure of the macrofauna data at all scales, and infer the scale of action of the three fishing variables on benthic fauna. PCNM analysis identifies if spatial structure at different scales is present in the response (here, faunistic) data. This spatial model is decomposed into submodels for each relevant scale, which are interpreted to reveal the relationships between the taxa and the fishing variables at these scales (Borcard and Legendre, 2002; Dray *et al.*, 2006).

PCNM base functions, the descriptors of spatial relationships, were obtained by principal coordinate analysis of a truncated matrix of the Euclidean distances among all scientific survey sampling sites ($n = 755$). The significant base functions were then selected using forward selection (an automated method for selecting significant variables, adding variables into the model in decreasing order of significance) with detrended fauna data. A preliminary ANOVA performed on an RDA of fauna data vs. geographic coordinates revealed a significant spatial trend in the benthic community data (linear trend between geographic coordinates and taxa distribution). These data were therefore detrended by regressing all variables on the geographic coordinates and retaining the residuals for the forward selection. Arbitrary spatial scale submodels were built with combinations of significant base functions resulting from the forward selection. RDAs were performed for each submodel, using the PCNM base functions as explanatory variables, and each one was subsequently used to predict taxa structure depending on each spatial scale submodel. A forward selection was applied to the predicted values against fishing variables to infer the importance of these on benthic community structure at the different submodel spatial scales. Year effects were not included in the statistical models.

Results

Community structure

The six dominant taxa in terms of biomass are very similar in fished and non-fished grounds (Supplementary Table S2a). The shrimp *Pandalus borealis* and Actinaria (sea anemones) represent the greatest part of the biomass for all three periods, followed by the shrimp *Pandalus montagui* for most of the periods. *Ctenodiscus crispatus*, a seastar, is consistently one of the six most dominant taxa in non-fished grounds but never in fished grounds. Conversely, Pennatulacea (sea pens) and Porifera (sponges) are found in fished grounds but not in non-fished grounds at mid- and short-term time scales. A similarity percentage analysis revealed that taxa contribution between fished and non-fished grounds is similar for the three periods (Supplementary Table S2b). The taxa

Table 1. Results of partial redundancy analyses (RDA removing environmental effects) using Hellinger-transformed megafaunal biomass and fishery data on the long, mid, and short term.

| | Long term | | | | Mid term | | | | Short term | | | |
|----------------|-----------|-------|-------|---------|----------|-------|-------|---------|------------|-------|-------|---------|
| | D.f. | Var | F | Pr (>F) | D.f. | Var | F | Pr (>F) | D.f. | Var | F | Pr (>F) |
| Number of tows | 1 | 0.004 | 5.824 | 0.01** | 1 | 0.003 | 4.957 | 0.01** | 1 | 0.002 | 3.263 | 0.01** |
| Fishing effort | 1 | 0.002 | 2.680 | 0.01** | 1 | 0.001 | 1.946 | 0.05* | 1 | 0.002 | 3.115 | 0.01** |
| Mass landed | 1 | 0.001 | 2.237 | 0.05* | 1 | 0.001 | 1.279 | 0.18 | 1 | 0.001 | 0.908 | 0.55 |

Statistical significance: *0.01 < p ≤ 0.05; **0.001 < p ≤ 0.01.

Table 2. Results of PCNM analysis showing regression coefficients of significant fishing variables detected at different spatial scales of variability for the long, mid, and short term.

| | Very large 200 > km | Large 200 – 100 km | Meso 100 – 50 km | Small 50 – 20 km | Very small 20 < km |
|----------------|---------------------|--------------------|------------------|------------------|--------------------|
| Long term | | | | | |
| Number of tows | | 0.02** | 0.03** | 0.01** | |
| Fishing effort | 0.007* | 0.01* | | | |
| Mass landed | 0.01* | | 0.013** | 0.009** | 0.006* |
| Mid term | | | | | |
| Number of tows | | 0.008** | 0.028** | 0.006* | |
| Fishing effort | | 0.032** | 0.012* | 0.006* | |
| Mass landed | 0.01** | | | | 0.006* |
| Short term | | | | | |
| Number of tows | | 0.03** | | 0.009** | 0.008* |
| Fishing effort | | 0.004* | | | |
| Mass landed | 0.008* | | | | |

Bold font highlights the five largest R^2 of the table.

Statistical significance: *0.01 < p ≤ 0.05; **0.001 < p ≤ 0.01.

contributing most to community dissimilarity (Supplementary Table S2b) are identical with those dominating the community for at least one period (Supplementary Table S2a).

Partial RDAs computed for each period indicate that the number of tows is consistently best correlated with benthic community structure, followed by the effect of fishing effort (Table 1). Mass landed is correlated with benthic community structure only on the long term. However, all relationships (R^2) are very weak, suggesting that fishing has only a minor effect on overall community structure after removing the effects of the environment.

PCNM analysis shows that fishing is significantly related to community structure at different spatial scales, although, as for RDAs, relationships (R^2) are weak (Table 2). The strongest R^2 values are observed at large and meso scales, i.e. at the scales of fishing grounds (from 50 to 200 km). The number of tows is, again, the variable that is most often correlated with community structure for the three periods, as well as fishing effort on the mid term. Whereas the number of tows is never significant at very large scales, the mass landed is. This variable is also less and less significant at the different spatial scales when going from long to short terms.

Taxa richness and biomass

Only weak, though significant, relationships are found between fishing effort and taxa richness for the three periods considered (Figure 2). However, some specific years (e.g. 2008, Supplementary Figure S2a) do show a stronger negative relationship between taxa richness and fishing effort. Interestingly, when considering the three periods of interest, non-fished areas (log fishing effort + 1 = 0, Figure 2a) display nearly the same range in mean taxa richness as fished areas (log fishing effort + 1 > 0, Figure 2a), highlighting that overall taxa richness does not differ between fished and non-fished grounds (also demonstrated by Supplementary Figure S1a). The same lack of overall difference between fished (log fishing

effort + 1 > 0) and non-fished grounds (log fishing effort + 1 = 0) appears for biomass (Figure 2b–f and Supplementary Figure S1b and c), but the positive correlation between biomass and fishing effort on the long and short terms is statistically significant (p < 0.001, Figure 2b). This relationship is supported within specific years (e.g. 2008, Supplementary Figure S2b) and suggests that the higher the fishing pressure, the more biomass is produced by the ecosystem. Supplementary data, Figures S1b, c and S2b, c indicate that this is actually an artefact of fishers' behaviour that emerges in fishing data: most of the benthic biomass is composed of shrimp *P. borealis*, and, when removing *P. borealis* from the analysis, fishing effort is no longer correlated with biomass (Supplementary Figure S2c). This positive relationship depicts the evident fact that fishing activity is mostly concentrated in areas with a large biomass of shrimp. This and the non-significant difference in biomass between fished and non-fished grounds (Supplementary Figure S1b and c) demonstrate that fishing effort has no significant impact on megafauna taxa other than species *P. borealis*.

Discussion

This study highlights weak relationships between shrimp fishery variables and EGSL benthic megafauna diversity, suggesting that shrimp trawling may have very little impact on present EGSL communities. Although this may be contradictory to common sense and previous studies on fishing impacts (e.g. Collie *et al.*, 2000; Svane *et al.*, 2009; but see Brylinsky *et al.*, 1994), several factors may explain the apparent insensitivity of the EGSL to trawling.

High fishing gear selectivity

High gear selectivity combined with high shrimp biomass in EGSL waters (DFO, 2012a) could explain why trawling has little effect on benthic communities. Indeed, we could not detect strong

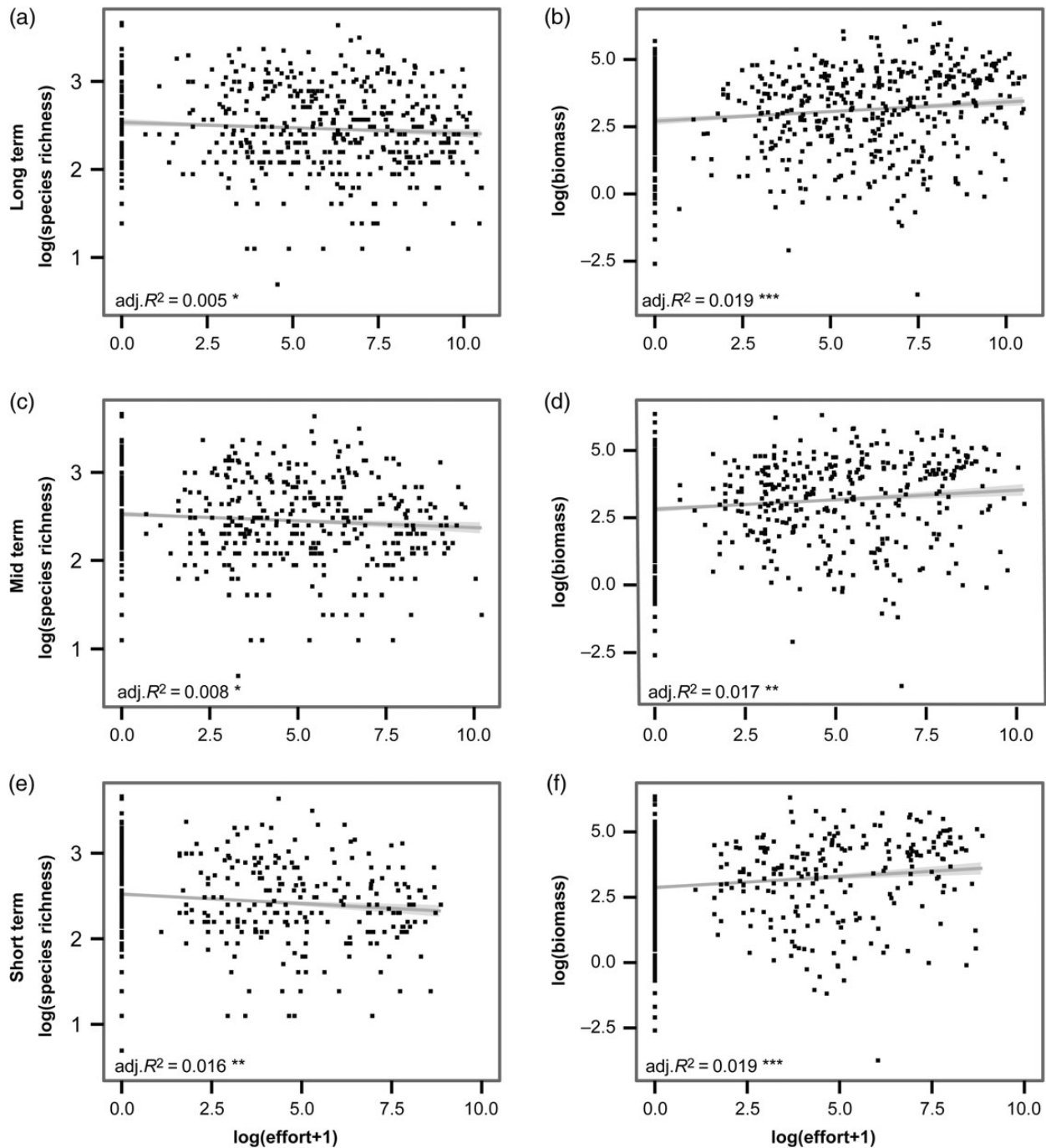


Figure 2. Linear relationships between taxa number, biomass, and cumulated fishing effort (in cumulated hours per period) on the long, mid, and short term. Logarithms were calculated and plotted for graph clarity. Adjusted R^2 and significance levels are given ($^*0.01 < p \leq 0.05$; $^{**}0.001 < p \leq 0.01$; $^{***}p \leq 0.001$).

differences in community structure between fished and non-fished areas. Bycatches of small fish in shrimp trawls are regularly examined by observers at sea, and were estimated in the EGSL in 2012 at 69 taxa, representing, for example, 150 tons of capelin, 64 tons of herring, 23 tons of Atlantic cod, and 15 tons of redfish (Savard, 2013), for the 34 000 tons of shrimp landed. Bycatches therefore represent only 1% of total catches, demonstrating the high selectivity of the gear used (arising from technological advances, Isaksen et al.,

1992; Hannah et al., 1996) and the high efficiency of the fishing industry to target shrimp.

Geographic location of fishing grounds and vulnerable taxa distribution

Of the recorded 69 bycatch taxa (Savard, 2013), only sponges and sea pens (soft corals of the Pennatulacea family) are protected taxa (Fuller et al., 2008; FAO, 2009). However, although they were

present on fishing grounds, these organisms are rarely caught in shrimp fishing nets, representing only 247 and 199 kg, respectively, in 2012 (Savard, 2013). Sea pens are found in deep areas that are unsuitable for large, mature fished shrimp, and are therefore not impacted by the shrimp fishery, which is located far from or at the edge of sea pen habitats (DFO, 2012c; Savard, 2012). The case for sponges is slightly different. Kenchington *et al.* (2010) showed that sponges could be strongly affected by trawling, being caught in nets and thrown back in the water elsewhere by fishers sorting catches on boats. Sponge fields are most vulnerable to the first passing of trawls, and some fields on EGSL fishing grounds have therefore been devastated long ago from EGSL fishing grounds (Kenchington *et al.*, 2010; DFO, 2012b). However, fields located in grounds that were deserted by the fishing industry from the 1980s, such as on the north coast of Anticosti Island, when fishing effort migrated south to follow the evolving shrimp distribution, do show some level of recovery (DFO, 2012b). Thus, it has been concluded in recent scientific advice for shrimp ecocertification renewal that the shrimp fishery in the Gulf does not threaten vulnerable sponge and sea pen species in their current distributions (DFO, 2012c). Our study also demonstrates that the shrimp fishery is not likely to threaten other non-vulnerable taxa inhabiting benthic habitats in the Gulf.

Shrimp ecology

The shrimp fishery and non-exploited benthic communities may have unexpectedly benefited from some characteristics of shrimp ecology. First, although considered a benthic taxon, shrimp are not permanently located on the seabed. They walk and swim to search for dead material on the bottom to feed on during the day (corresponding to the period when it is fished), migrating up the water column at night to feed on planktonic organisms (DFO, 2002; Savenkoff *et al.*, 2006). Bundy *et al.* (2000) consider that only 30% of the shrimp diet is benthic, compared with 70% being pelagic. Consequently, shrimp has limited competitive and trophic interactions (only indirect or weak) with other megafaunal benthic species, partly explaining the lack of a relationship between shrimp biomass decrease in fishing grounds and the biomass of the rest of the community. It is therefore likely that removing great amounts of shrimp from the benthic ecosystem by trawling does not directly affect, positively or negatively, other species sharing the seabed (by trophic cascade) since they are not direct space or food competitors of shrimp.

Second, shrimp change sex over the course of their life cycle (Savenkoff *et al.*, 2006). Males reach sexual maturity after 2.5 years, and become mature females 2–3 years later. Because females are older and carry eggs, they are larger than males and thus are targeted by the fishery. Females migrate to shallower waters in winter, deserting areas where younger (immature or male) individuals are located, such as the southern part of the EGSL and the deep channels where vulnerable sea pen species are located (DFO, 2002; Kenchington *et al.*, 2010). Therefore, the timing of the opening of shrimp fishery in spring, following breeding, and the natural location of females in mid-depth waters allow fishing to be periodically concentrated in restricted areas (Figure 1b) that are distant from or only partly overlap existing vulnerable sea pen and sponge grounds.

Resilience and equilibrium of a disturbed environment

Our findings that shrimp fishing does not affect benthic communities in the EGSL may be supported by the high–low-energy

environment hypothesis. High and low-energy environments host, respectively, specialist species with small ranges and generalist species with large ranges (Bonn *et al.*, 2004) and are, respectively, more and less prone to undergo stresses. On the one hand, low-energy environments are likely to be more sensitive to bottom fishing because their fauna are not adapted to the regular disturbance (e.g. waves) of high-energy environments. On the other hand, low-energy environments should be less sensitive to reductions in available energy, such as that done by fishing of one species, than high-energy environments (Powell and Lenton, 2013). Several reasons indicate that the EGSL is a low-energy environment, and thus likely to be resilient, in term of biomass withdrawal, to fishing. First, sheltered estuaries and gulfs, including several part of the St Lawrence, are considered as low-energy environments (Owens and Frobel, 1977; Jackson *et al.*, 2002). Second, shrimp trawling grounds are located at depths spanning from 200 to 300 m (DFO, 2012b). These areas are characterized by fine-grain well-sorted sediments, weak bottom currents, homogeneous warm temperatures, and high seabed uniformity (Dutil *et al.*, 2011), which is typical of low-energy environments (Nicolodi *et al.*, 2013). We also note that shrimp trawling grounds are located in areas with low potential to host diverse benthic megafaunal communities (DFO, 2012b; Lévesque *et al.*, 2012; Moritz *et al.*, 2013) usually associated with high habitat complexity, characteristic of high-energy environments (e.g. shallow coastal areas with breaking waves and straits with strong currents, Shields *et al.*, 2011).

A physical aspect also supports the hypothesis that the EGSL benthic environment has reached a new equilibrium after repeated disturbances due to fishing. In some coastal areas where habitat is heterogeneous (Moritz *et al.*, 2013), the very first passing of trawls may have greatly disturbed the substrate by removing the largest physical objects that originally created three-dimensional habitats for benthic communities. No data on this variable exist but it is well known that exploratory fishing in new areas may lead to nets being destroyed by becoming stuck on hard substrates. In the channels, three-dimensional structure is much more homogeneous due to past smoothing of passing glaciers (Dionne and Bernatchez, 2000; Hetu and Gray, 2000; Piper and DeWolfe, 2003) and is less likely to be damaged by trawl passages. In the EGSL fishing grounds, homogenization of the substrate due to repetitive tows may have altered community structure from that which existed centuries ago, before trawl fishing. Although it is likely impossible that three-dimensional habitats develop in the future, it is encouraging to observe that some taxa removed by nets may reappear (e.g. sponges off north Anticosti Island) in fishing grounds currently deserted by fishers (DFO, 2012b).

No detectable fishing effect: back to a pristine stage?

Although current shrimp trawling has no detectable effects on macroinvertebrates in the EGSL, is it unlikely that a pristine stage, like that reported centuries ago, would be restored at human scale. This would be possible only (i) if the seabed gets its physico-chemical properties back and (ii) if all original species successfully recolonize the surface by settlement of new recruits and reproduce efficiently to ensure species persistence. However, given that three-dimensional structure has been irretrievably changed in some locations (i.e. blocks removed) and given the strong link between sediment size and species identities (particularly for specialist species, which are characteristics of undisturbed environments: Devictor *et al.*, 2008), a proportion of the original species present centuries ago

would probably not be able to recolonize the area and/or maintain at high levels of biomass. The positive recolonization observed at human scale is the sponge grounds around Anticosti Island that has been reappearing within 10–20 years, after trawling effort has moved south. Some species (e.g. small polychaetes) can also re-settle quickly after natural and anthropic disturbances (Jennings *et al.*, 2002). However, we cannot conclude that a pristine stage can be recovered in the EGSL if only a few species like sponges and polychaetes, or the most resistant species and strong colonizers, can re-settle efficiently. Instead of expecting a pristine stage to recover, effort should be dedicated to properly manage the existing ecosystem to prevent it from being overexploited again, and protect relevant productive and diverse areas while possible.

Future directions

Apart from sponges and sea pens, the two vulnerable taxa that are monitored, and the well-known commercial species that are taken as bycatch, few data exist on the state of other non-fished benthic megafaunal species in the EGSL. Although interactions between shrimp and predatory fish species are clearly evident (Savenkoff *et al.*, 2006), interactions with benthic ecosystem components may require more attention to quantify relationships between shrimp, and thus its fishing, and benthic ecosystem functioning. In our study, we found that shrimp trawling does not alter overall EGSL megafaunal diversity. We suggest that future analyses further examine species-specific effects of the shrimp fishery on ecosystem stability, while maintaining stock and risk assessments run by DFO to adjust conservation objectives and management plans. This can be done through ongoing, or even increasing, scientific survey efforts by DFO to allow the creation of datasets that may be used for long-term species-specific and community analyses. Finally, to complement these data and evaluate large-scale fishing impacts on benthic community functioning, we recommend recording life-history and functional traits of species caught in future scientific survey samples. Tillin *et al.* (2006) found some effects of chronic bottom trawling disturbance on the functional composition of marine invertebrate communities, in particular regarding mobility and diet of the species present, and trawling areas are also inhabited by smaller species (Jennings *et al.*, 2001). These findings provide cues on which functional traits to record to possibly detect a spatio-temporal relationship between trawling and ecosystem functioning in the EGSL.

Supplementary data

Supplementary material is available at the *ICESJMS* online version of the manuscript.

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