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Environmental associations and assemblage structure of shrimp species in the Gulf of St. Lawrence (Canada) following dramatic increases in abundance

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ABSTRACT: Decapod shrimps typically occupy lower trophic levels, often as omnivores, and many have high population turnover rates, which makes shrimp populations susceptible to changes in predator abundance and environmental change. The increased biomass of northern shrimp *Pandalus borealis* in many parts of the NW Atlantic has been associated with the collapse of predatory fish populations and changes in water temperature. In this study, we show that biomass of many shrimp species in the Gulf of St. Lawrence (Canada) increased between 4- and 100-fold between the late 1980s and mid-2000s. Multivariate analyses based on trawl survey data during a period of relative stability (2004–2015) that followed the increase revealed species assemblages that were strongly spatially structured and which were associated with depth and bottom water temperatures. Univariate analyses of the associations between individual species' densities and depth and temperature revealed that approximately half of the species had narrow temperature associations, suggesting that these species may be susceptible to projected warming of the ecosystem. Furthermore, all species in the northern Gulf of St. Lawrence will be affected by recent and ongoing increases in predator biomass. In contrast, predator biomasses continue to decrease in the southern Gulf of St. Lawrence.

KEY WORDS: Community structure · Shrimp · Predation release · Environmental associations

INTRODUCTION

Over the last few decades, both fisheries science and fisheries management have increasingly shifted their focus from a strictly single-species approach to one that considers harvesting and stock dynamics within the context of ecosystems (Hall & Mainprize 2004, Pikitch et al. 2004, Jennings & Rice 2011, Gascuel et al. 2016). Implementation of ecosystem-based fishery management (EBFM) needs to account for complex ecosystem dynamics having a multitude of interactions stemming from 3 main drivers: species interactions (often trophic), fishing, and environmental conditions (Tolimieri & Levin 2006, Jouffre et al. 2010, Murawski 2010, Rice 2011). Large amounts of data are required to quantify and assess relationships among species within an ecosystem, the spatial dynamics, and the effects of anthropogenic activities on ecosystem functioning. The lack of sufficient and appropriate data on structure and dynamics of critical ecosystem components remains one of the major obstacles for the implementation of EBFM. Charac-

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terizing species abundance and distribution, and identifying species assemblages, their major environmental correlates, and potential drivers constitute steps towards filling these gaps (Mahon & Smith 1989, Tolimieri & Levin 2006, Nogueira et al. 2013).

The Gulf of St. Lawrence (GSL) comprises 2 largely distinct ecosystems: a shallow shelf ecosystem in the south and one characterized by deep channels and an estuarine portion in the north (Ouellet et al. 2016). Commercial fishing in the GSL has been ongoing for centuries and was particularly intense between the 1960s and the early 1990s. In the early to mid-1990s, the populations of many large demersal fishes, such as Atlantic cod *Gadus morhua*, white hake *Urophycis tenuis*, and redfishes (*Sebastes* spp.), collapsed as a result of overfishing, in some cases combined with increases in natural mortality (Savenkoff et al. 2007a,b, Benoît & Swain 2008, Swain & Chouinard 2008, DFO 2011). Despite reductions in fishing mortality over the past 20 yr, many populations did not recover and some continue to decline (Swain & Benoît 2015). These changes have had profound effects not only on fisheries but also on the structure and functioning of both ecosystems, which have shifted from being dominated by large demersal fish predators to being dominated by small-bodied forage species and seals (Savenkoff et al. 2007a,b, Benoît & Swain 2008). Similar changes have been reported in the western Atlantic (Worm & Myers 2003, Bundy et al. 2009, Frank et al. 2011), Black Sea (Daskalov et al. 2007), and some coastal ecosystems (Jackson et al. 2001). Increases in northern shrimp *Pandalus borealis* abundance in the GSL and neighboring ecosystems have been attributed to release from predatory pressure by large demersal predators (e.g. Atlantic cod and redfishes) as well as environmental change (Koeller 2000, Lilly et al. 2000, Worm & Myers 2003, Frank et al. 2005, Dawe et al. 2012).

The purpose of this study was first to demonstrate that an increase in shrimp biomass in the GSL occurred for a number of shrimp species that are known to form important links to higher trophic levels in numerous ecosystems (Garrison & Link 2000, Lilly et al. 2000, Savenkoff et al. 2007a,b, Link & Idoine 2009, Pérez-Rodríguez et al. 2011). We then described shrimp assemblage structure, both spatially and in terms of species composition, and examined the influence of important available habitat variables (depth and bottom temperature) on assemblage composition and distribution, and individual species' densities. To our knowledge, this is one of the first examinations of shrimp assemblage structure and environmental associations in a large marine system (but see Hudon 1990, who presented the distribution of 18 shrimp species in the Canadian Eastern Arctic). This information also provides an important baseline that can be used to explain or detect changes in the shrimp community resulting from recent and projected ocean warming (Galbraith et al. 2016, Long et al. 2016) and projected recovery of predatory fish populations (DFO 2015a, 2016a).

MATERIALS AND METHODS

Study area

The GSL (Fig. 1) is physically and topographically heterogeneous. The Laurentian Channel divides the Gulf into a deep northern and a shallow southern system (Koutitonsky & Bugden 1991). The northern GSL (nGSL) consists of 4 distinct areas: a shallow (<100 m) shelf on the west coast of Newfoundland; a shelf on Québec's North Shore characterized by uneven topography; the Laurentian Channel, which extends from Cabot Strait to the center of the Gulf and is up to 500 m deep; and the Esquiman Channel, which connects the Laurentian Channel to the Strait

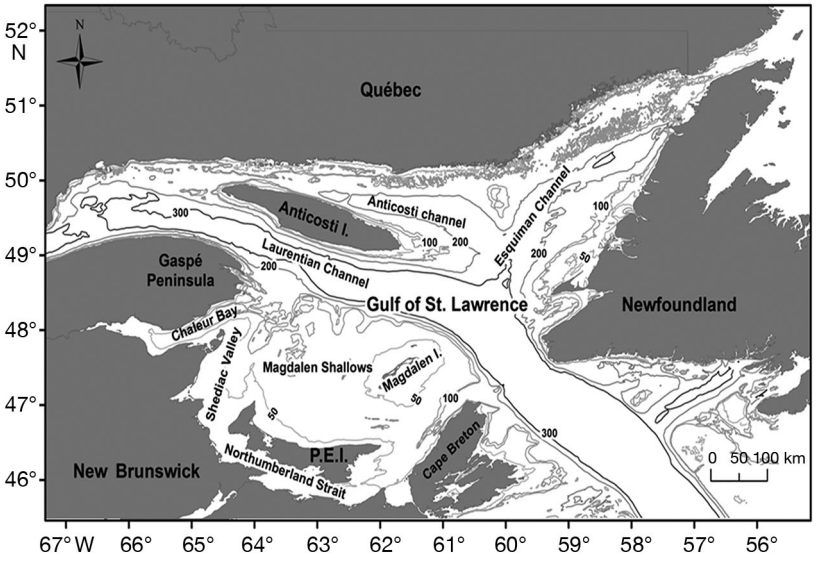


Fig. 1. Study area in the Gulf of St. Lawrence, showing the 50, 100, 200, and 300 m isobaths (grey lines). P.E.I.: Prince Edward Island

of Belle Isle to the north, with an average depth of 200 m. In contrast, the southern GSL (sGSL) consists of a large shelf area with depths mostly less than 100 m, bordered by the Laurentian Channel to the north and land otherwise.

The Gulf waters are generally characterized by 3 vertical layers during the ice-free season, and the intersection of these layers with the bottom strongly influences the bottom-habitat environmental conditions (Koutitonsky & Bugden 1991, Drinkwater & Gilbert 2004, Smith et al. 2006, Galbraith et al. 2016). During the summer, the surface layer generally extends to around 40 m and is characterized by a thermocline with surface temperatures exceeding 20°C at their peak in some nearshore areas. A cold intermediate layer (CIL) generally occurs between 40 and 120 m depths with water temperatures between −1.0 and 2°C. Below the CIL is a deep, cool, layer characterized by relatively salty waters with temperatures of 4–6°C year round. During the winter, the surface layer disappears, and near-freezing temperatures (around −1.7°C) extend from the surface to the top of the cool deep layer. Sea ice typically covers the Gulf beginning in early January, and icemelt can occur as early as March and as late as the end of May.

Data sources

Data on the biomass of shrimp species were obtained from fishery-independent bottom-trawl surveys carried out annually by Fisheries and Oceans Canada (DFO) in the nGSL in August and in the sGSL in September (for further description of the surveys see Chadwick et al. 2007). Both surveys follow a stratified-random survey design with stratification based on depth and geographic area. Except as noted below, most of the data for this study (specifically for the multivariate and environmental association analyses) cover the period from 2004–2015, which are the years for which information on the species composition of shrimp catches was available for both survey areas. During that period, approximately 140 trawl sets at sampling stations (hauls) were taken annually over the 38 strata of the nGSL survey that were regularly surveyed during the study period, and 170 in 27 strata in the sGSL survey. The number of hauls per stratum was approximately proportional to stratum surface area in each survey.

The nGSL survey was conducted by the Canadian Coast Guard Ship (CCGS) 'Alfred Needler' using a URI shrimp trawl from 1991–2005 and has been conducted annually since 2004 by the CCGS 'Teleost' using a Campelen 1800 shrimp trawl (details on the vessels and trawls in Bourdages et al. 2007). The sGSL survey was conducted by the 'EE Prince' from 1971–1985 using a Yankee 36 trawl, and by the 'Lady Hammond' (1985–1991), CCGS 'Alfred Needler' (1992–2002, 2004–2005), and CCGS 'Teleost' (since 2004), all using a Western IIA trawl (details on the vessels and trawls in Benoît 2017). The survey catch values for total shrimp catches in the sGSL and for the 3 most abundant species in the nGSL (*Pandalus borealis*, *P. montagui*, and *Pasiphaea multidentata*) were adjusted for the changes in gear and vessel based on results from comparative fishing experiments (Benoît & Swain 2003, Benoît 2006, Bourdages et al. 2007). These data adjustments were used to standardize the data series. Catchability adjustments for other species in the nGSL could not be estimated due to small sample sizes and because many of those species appear to have been poorly sampled by the URI shrimp trawl (Supplement 1 at www.int-res.com/articles/suppl/m596p095_supp.pdf). All catches were standardized for tow length. Survey operations in the sGSL survey switched from day-only to 24 h in 1985, although this change did not seem to affect the relative catchability of species-aggregated shrimp biomass (Benoît & Swain 2003). The 2003 sGSL survey was undertaken by an uncalibrated vessel that did not complete the survey; therefore, the data for that year were not used. Although the data from each survey are considered to be part of standardized series, the non-calibrated differences in fishing gear between surveys means that the data from the 2 surveys cannot be combined directly, though the spatial structure and trends in abundance can be compared. For consistency, the abundance data were examined separately in the analyses and their interpretation.

The species composition of shrimp catches in each survey haul was established based on sorting, either at sea (nGSL survey; since 1991) or in the laboratory from frozen samples (sGSL; since 2002), of the total shrimp catch (for catches ≤1 kg) or from a 1–2 kg subsample from the well-mixed total shrimp catch. The size of subsamples, which constitutes a large fraction of the catch of the average haul (see Fig. 2), was established based on the time available for the work and has been found to produce consistent estimates of species composition at individual sampling locations. Sub-sampling was incomplete in 2002 in the sGSL. This, combined with the aforementioned issues with the 2003 sGSL survey and the poor and uncalibrated catchability for many species in the nGSL prior to 2004 (Supplement 1), were the reasons that

analyses of species-level data were limited to 2004–2015. Two subspecies, *Eualus gairmardii belcheri* and *E. g. gairmardii*, were identified in the nGSL survey but not the sGSL survey. The catches of these 2 subspecies were therefore combined.

Catch numbers and biomass were recorded for the majority of catches in the nGSL survey (>92%), while only biomass was recorded for the remaining catches. Catch numbers were not available for most sGSL surveys. This did not pose a problem for the multivariate analyses described below which were based on catch biomasses. However, catch numbers were required for the analyses of individual species' environmental associations, and these values were calculated using biomass and species-specific mean individual wet weights. Individual shrimp sizes are not measured in these surveys except for *P. borealis* in the nGSL survey.

Data on the bottom depths and temperatures were available for each tow during sGSL surveys. Temperature values were not available for 562 of the 1639 tows in the nGSL survey, but depths were recorded. Hauls with temperature values in the nGSL were considered to be representative of all hauls both spatially and as a function of depth (Figs. S2 & S3 in Supplement 2). Temperature values for the remaining hauls were estimated using the model described in Supplement 2. Temperature and depth are important variables shaping the assemblage structure of shrimp communities (Hudon 1990). They are taken here as key components of the habitat of the shrimp species of the Gulf of St. Lawrence, acknowledging that other characteristics such as the sediment type are also important but could not be evaluated because contemporary data of sufficient resolution were not available.

Analyses

Long-term trends in shrimp biomasses

Indices of relative biomass (kg tow^{-1}) were calculated using the standard estimators for the stratified mean and standard error (Krebs 1989). For the nGSL survey, both total and species-specific indices were calculated for 1991–2015. For the sGSL survey, a total biomass index was calculated for 1971–2015 and by species for 2004–2015. Though it was not possible to directly estimate the species composition of shrimp catches in the sGSL survey prior to 2004, we inferred which species may have contributed to observed increases in shrimp biomass by examining spatial patterns in those catches and relative catch size compared to the post-2004 period when species-level data were available.

Standardized biomass indices for the major groundfish predators of shrimp were estimated in the same manner as for shrimp, based on the data collected during the surveys. Indices were estimated for the 2 major predator populations that occur in the sGSL, i.e. sGSL Atlantic cod and sGSL white hake, and the 2 major populations in the nGSL, i.e. redfishes and nGSL Atlantic cod.

Shrimp assemblage structure

Assemblage composition and environmental associations (below) were examined for the 2004–2015 period for both the nGSL and sGSL. Changes over time were not examined because there was little evidence for these changes over the 2004–2015 period based on preliminary analyses (see Supplement 3, Fig. S4).

Multivariate ordination methods were used to investigate the shrimp species assemblage structure. A fourth-root transformation was applied to all standardized tow-specific catch data to reduce the influence of the few highly abundant species and to support the importance of the rare ones (Somerfield & Clarke 1997, Jørgensen et al. 2005). The similarity in community composition among hauls was calculated using the Bray-Curtis index (Bray & Curtis 1957, Field et al. 1982).

Spatial patterns in community composition were examined using survey strata as the spatial unit. Strata encompass relatively homogenous habitats by their definition, and are a sufficiently small scale to characterize spatial patterns in assemblage structure, while ensuring that there are sufficient sample sizes to do so accurately. The observation units were individual hauls which ensured that variability in the composition of catches was fully expressed in the analyses. We tested for possible differences in species composition among survey strata using an ANOSIM randomization test (Clarke & Warwick 2001). The distance matrix generated after ANOSIM was used to perform hierarchical cluster analyses using complete linkage to define groups of strata. In addition to the cluster analysis, the distance matrix was ordinated using non-metric multidimensional scaling (nMDS) to visualize the spatial groupings of shrimp assemblages. In all cases, stress levels were ≤0.1 and were acceptable for a 2-dimensional nMDS plot (Clarke & Warwick 2001, McCune & Grace

2002). A similarity percentage analysis (SIMPER; Clarke 1993, Clarke & Warwick 2001) was performed to identify the species contributing most to the dissimilarity between groups. Species with ratios of average similarity or dissimilarity to standard deviation, r > 1.5, were considered to be typical (in similarity analyses) or discriminatory (in dissimilarity analyses) (Clarke & Warwick 2001).

To identify species assemblages and to examine the spatial patterns of shrimp species associations, cluster analysis was also performed based on a Bray-Curtis similarity matrix with species as samples. Catch data were subjected to a complete linkage hierarchical cluster analysis (Primer CLUSTER analysis). The groups of species were formed according to 2 criteria, the similarity index and the results of the similarity profile analysis (Primer SIMPROF procedure). The similarity profile permutation test was used as a stopping rule for *a posteriori* subdivision of a group of species (Clarke & Gorley 2006, Clarke et al. 2008). nMDS was also carried out using the same similarity matrix as for the cluster analysis, to visualize the spatial structure (on a stratum basis) of the groups of species.

Temperature and depth associations of assemblages

Stepwise distance-based linear model permutation tests (DistLM, McArdle & Anderson 2001) were used to identify the contribution of temperature and depth in explaining the variation in shrimp assemblage composition. Assumptions of the model were verified, confirming that no data transformations were required (Legendre & Legendre 1998, Anderson et al. 2008)

All multivariate analyses (nMDS, SIMPER, ANOSIM, DistLM) were performed using the PRIMER v6 package (Clarke & Gorley 2006) with the PERMANOVA+ add-on (Anderson et al. 2008).

Temperature and depth associations of individual species

The associations between shrimp abundance (numbers tow^{-1}) and depth (m) and temperature (°C) were described for each species and survey separately using generalized additive modeling (GAM; Wood 2006). The goal of that modeling was not to find models that best predict abundance but rather to describe how abundance is predicted to vary marginally with depth and with temperature, to support the interpretation of the multivariate analyses. The analyses were undertaken on catch numbers rather than biomass because of the availability of suitable models for counts that can accommodate zero catches and occasional large catches, here negative binomial (NB) models.

For each species and survey, the models were of the form:

$$Y_i \sim \mathrm{NB}(\mu_i, k) \quad (1)$$

$$\mathrm{E}(Y_i) = \mu_i = \exp\,[\beta_0 + s(X_i) + \log(\gamma_i)] \quad (2)$$

$$\mathrm{var}(Y_i) = \mu_i + \mu_i^2/k \quad (3)$$

where Y_i is the catch in tow i, $\mathrm{E}(Y_i)$ is the expected value of Y_i, $s(X_i)$ is a cubic spline function of the environmental variable (temperature or depth), $\log(\gamma_i)$ is an offset term to account for the tow distance of tow i, and k is the dispersion parameter of the NB distribution. We specified the degree of smoothing for the environmental term by setting its degrees of freedom to a maximum of 5, although the optimal degree of smoothing was estimated by generalized crossed-validation. The maximum was chosen to avoid model over-fitting following preliminary analyses. Model residuals were examined for each species and survey to ensure model adequacy. The GAM analysis was performed using the gam() function in the mgcv package for R (R Core Team 2015).

RESULTS

Long-term trends in shrimp biomasses

The biomass of shrimp in the nGSL survey increased 4-fold from 1991 to 2004, before declining to a level comparable to biomass values in the early 2000s (Fig. 2). Three species comprised over 98% of this biomass in any given year: *Pandalus borealis*, *P. montagui*, and *Pasiphaea multidentata* (Fig. 3). *P. borealis* dominated the total shrimp biomass and was the only one of the 3 species to increase in biomass during the 1990s and early 2000s. The apparently low and uncalibrated catchability prior to 2004 of all other shrimp species in the nGSL survey (Supplement S1) precluded us from determining how their abundances changed during the period of increase for *P. borealis*. The decline in biomass after 2010 involves a number of species in addition to *P. borealis*, including *Argis dentata*, *Lebbeus groenlandicus*, *L. polaris*, *Sclerocrangon boreas*, *Spirontocaris phippsii*, and *S. spinus* (Fig. S1 in Supplement S1).

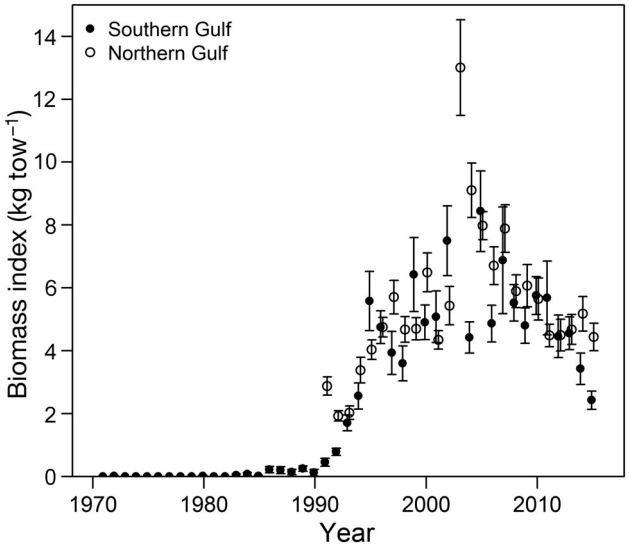


Fig. 2. Biomass indices (mean ± SE) for shrimp (all species combined) in the southern (1971–2015) and northern (1991–2015) Gulf of St. Lawrence bottom-trawl surveys

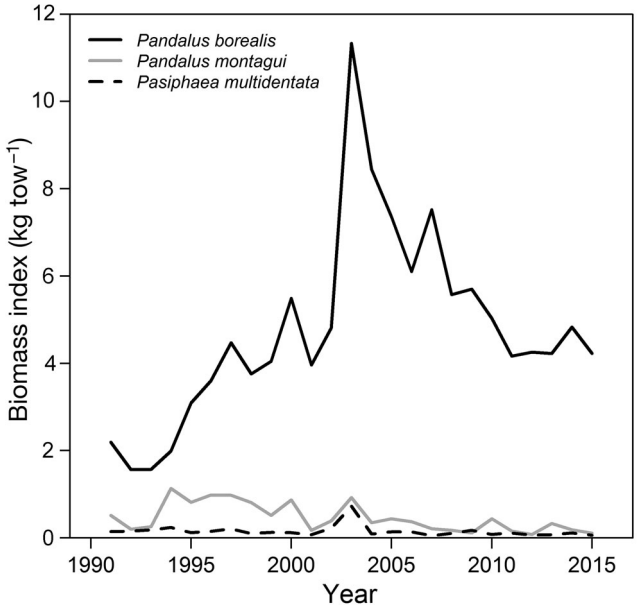


Fig. 3. Biomass indices for the 3 most abundant shrimp species in the northern Gulf of St. Lawrence (nGSL) bottom-trawl survey. These are also the only shrimp species in the nGSL survey for which conversion factors are available to adjust for a change in catchability beginning in 2004 resulting from a change in the survey trawl and vessel

The biomass of shrimp in the sGSL survey was very low until the mid-1980s, increased by 2 orders of magnitude through the 1990s, reached an asymptote in the 2000s, and slightly declined after 2010 (Fig. 2). The increase in shrimp biomass occurred throughout the sGSL, which indicates that it did not only involve the commercially harvested *P. borealis*, whose distribution is largely limited to the Laurentian Channel (Fig. 4). Indeed, the average biomass index values over the period 2004–2015 for *A. dentata*, *Eualus macilentus*, and *P. montagui* were all above the average total shrimp biomass index for 1985–1990, with no overlap in the respective confidence intervals, indicating that the biomass of these species must have increased from the late 1980s to the 2000s (Table 1).

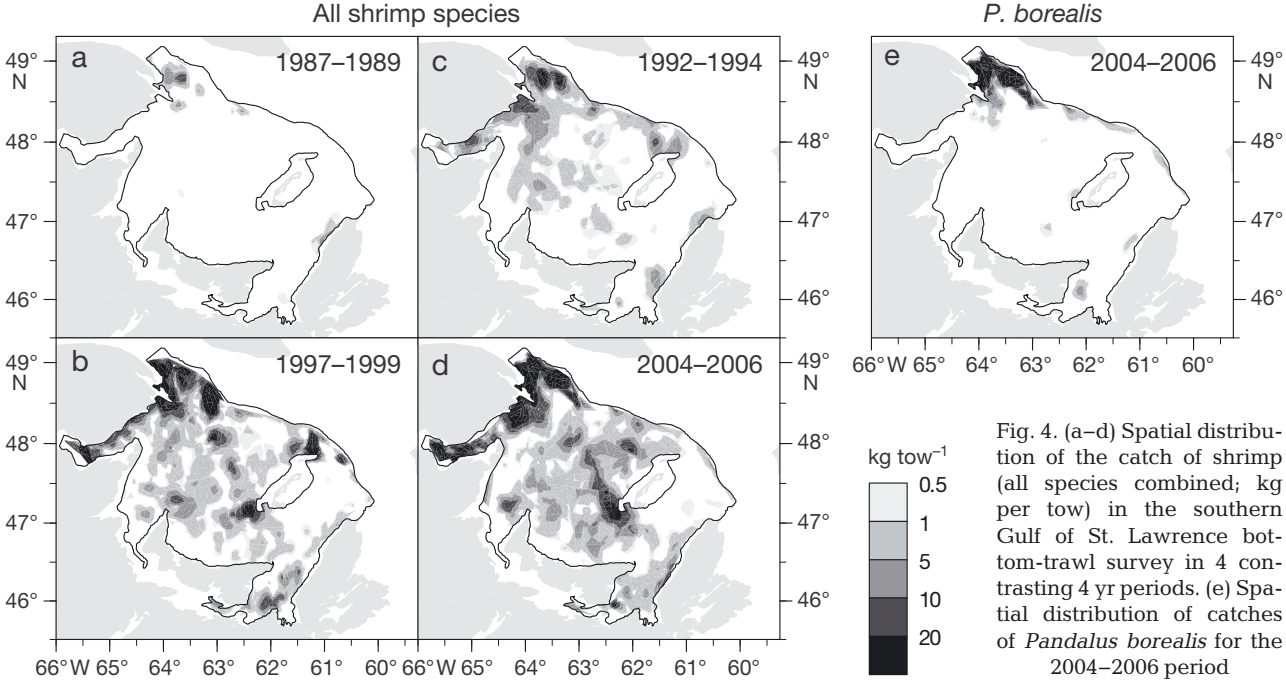


Fig. 4. (a–d) Spatial distribution of the catch of shrimp (all species combined; kg per tow) in the southern Gulf of St. Lawrence bottom-trawl survey in 4 contrasting 4 yr periods. (e) Spatial distribution of catches of *Pandalus borealis* for the 2004–2006 period

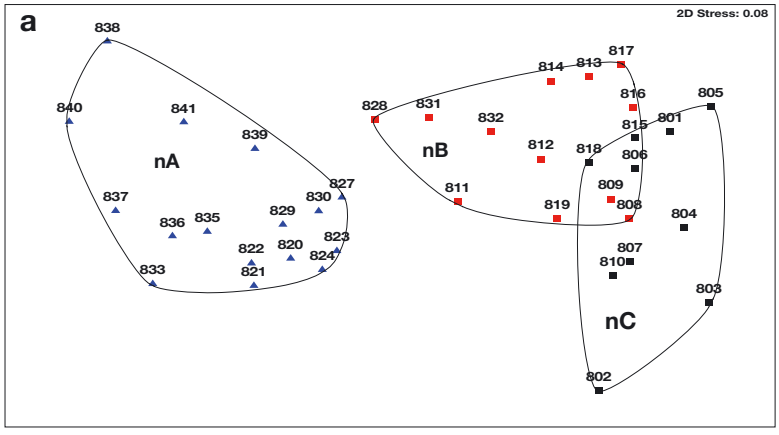
Table 1. The 2004–2015 mean (with 95% confidence intervals) annual biomass indices for each shrimp species in the southern Gulf of St. Lawrence survey. Values in **bold** are those that are above the 1985–1990 average of annual total shrimp biomass indices, 0.156 kg tow^{-1} (95% confidence interval: 0.089–0.223)

Species	Mean biomass index	Confidence interval
Argis dentata	**0.971**	**0.784–1.173**
Crangon septemspinosa	0.005	0.002–0.007
Eualus fabricii	0.008	0.004–0.011
Eualus gaimardii	0.018	0.012–0.024
Eualus macilentus	**0.400**	**0.263–0.536**
Lebbeus groenlandicus	0.001	0.000–0.002
Lebbeus polaris	0.021	0.016–0.025
Pandalus borealis	**1.447**	**0.944–1.950**
Pandalus montagui	**1.894**	**1.536–2.251**
Pasiphaea multidentata	0.036	0.025–0.042
Sabinea septemcarinata	0.050	0.036–0.065
Sclerocrangon boreas	0.028	0.021–0.039
Spirontocaris liljeborgi	0.002	0.001–0.003
Spirontocaris phippsii	0.001	0.000–0.002

Shrimp assemblage structure

During 2004–2015, the nGSL survey captured 25 species, of which 6 were caught too infrequently to be included in the analyses (*Acanthephyra pelagica*, *Aristaeopsis edwardsiana*, *Hymenopenaeus debilis*, *Pasiphaea tarda*, *Plesionika martia*, and *Sergia robusta*). With the exception of *P. tarda*, catches of these rarer species were limited to the deepest waters in the Laurentian Channel (Fig. S5 in Supplement 4). Over the same period, 21 species were captured in the sGSL survey. Of these, catches of *E. pusiolus*, *L. microceros*, *Pontophilus norvegicus*, *P. tarda* and *S. robusta* were too infrequent to warrant inclusion in the analyses. The spatial distribution of each shrimp species in each survey is shown in Fig. S5 (see Supplement 4).

The ordination analyses revealed shrimp assemblages in the nGSL that were spatially structured and at least partly associated with bathymetry (Fig. 5). Three reasonably well defined groups were observed in the cluster analysis. Group nA was associated with strata <200 m deep, located in eastern and northern portions of the nGSL, along the Newfoundland coast, the Quebec lower north shore, and the northern and eastern shore of Anticosti Island. Group nB corresponded to strata 200–320 m deep and located mainly in Esquiman and Anticosti Channels and waters west of Anticosti Island. Group nC was the only group associated with strata >320 m deep and occurred almost exclusively in strata located along the Laurentian Channel and in a small area of the Esquiman Channel. The average group similarity was 42.6, 59.3, and 70.0%, respectively, and was mainly driven by 2 or 3 species (Table 2). Multivariate dispersion indices showed that Groups nA and nC were slightly more dispersed and less cohesive than Group nB. Species that contributed mainly to the



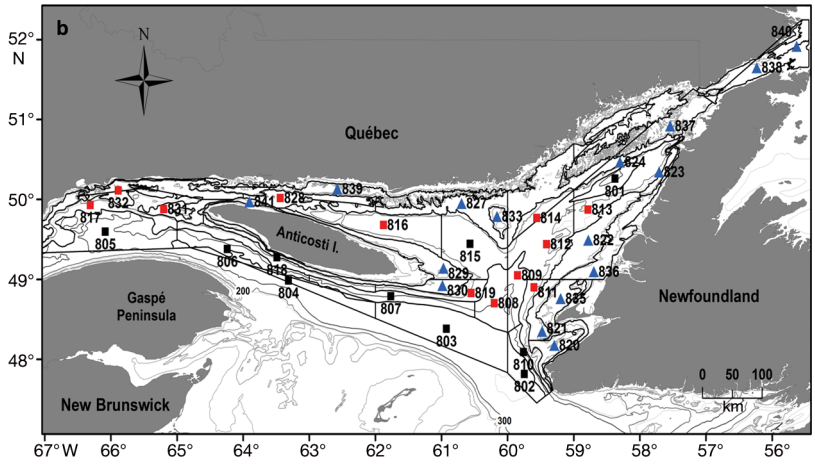


Fig. 5. Spatial structure of shrimp assemblages in the northern Gulf of St. Lawrence. (a) Nonmetric multidimensional scaling ordination plot of survey strata; the solid lines represent a distance level of 0.95 among strata, and strata from the same cluster (labeled in **bold** letters: nA, nB, nC) are plotted with a common symbol. (b) Geographical location of strata; black lines indicate the strata boundaries, and symbols for strata clusters are the same as in (a)

Table 2. Percentage contributions of species to the average similarity of assemblages, identified by SIMPER analysis for the northern Gulf of St. Lawrence. Ranks of principally contributing species are in parentheses

Shrimp species	Code	Midshore assemblage Group nA (<200 m)	Deep assemblage Group nB (200–320 m)	Deepest assemblage Group nC (>320 m)
Argis dentata	AD	13.33 (2)	0.07	–
Sabinea septemcarinata	Sse	7.61 (3)	0.01	–
Pandalus borealis	PB	7.38 (4)	87.58[a] (1)	61.04[a] (1)
Pandalus montagui	PM	52.1[a] (1)	3.3 (3)	–
Pontophilus norvegicus	PN	0.20	2.69 (4)	4.28 (3)
Atlantopandalus propinqvus	Atp	–	0.01	0.14
Eualus macilentus	EM	2.21 (8)	0.12	–
Eualus gaimardii	EG	0.26	0.01	–
Eualus fabricii	EF	1.33	–	–
Eusergestes arcticus	EA	–	–	0.2
Sclerocrangon boreas	SB	2.35 (7)	–	–
Sabinea sarsii	Ssa	0.56	0.03	–
Pasiphaea multidentata	Pmu	–	5.13 (2)	33.9[a] (2)
Pasiphaea tarda	PT	–	–	0.01
Lebbeus polaris	LP	7.25 (5)	0.83	0.21
Lebbeus groenlandicus	LG	0.89	–	–
Spirontocaris spinus	SS	3.89 (6)	0.01	–
Spirontocaris liljeborgi	SL	0.42	0.22	0.12
Average similarity by group (%)		41.57	59.34	70.05
Multivariate dispersion index		1.033	0.930	1.015

[a]Species characterizing the groups (i.e. ratios of average similarity to standard deviation, Sim:SD > 1.5)

shallow assemblage (Group nA) were: *P. montagui*, with 52.1% of total contribution; *A. dentata* (13.3%); and *Sabinea septemcarinata*, *P. borealis*, and *L. polaris*, each with a contribution of around 7% (Table 2). *P. borealis* contributed most to the total percentage of similarity in the deep assemblage (Group nB), with 87.58%. *P. borealis* and *P. multidentata* contributed most to the similarity in Group nC, with 61.0 and 33.9%, respectively. More than 60% of dissimilarities between the 3 groups can be attributed to 5 species: *P. borealis*, *P. montagui*, *P. multidentata*, *A. dentata*, and *P. norvegicus*.

The ordination analyses revealed a somewhat similar spatial structure in the sGSL. Five groups were distinguished in the cluster analysis at a distance of 0.6 (Fig. 6). Group sA

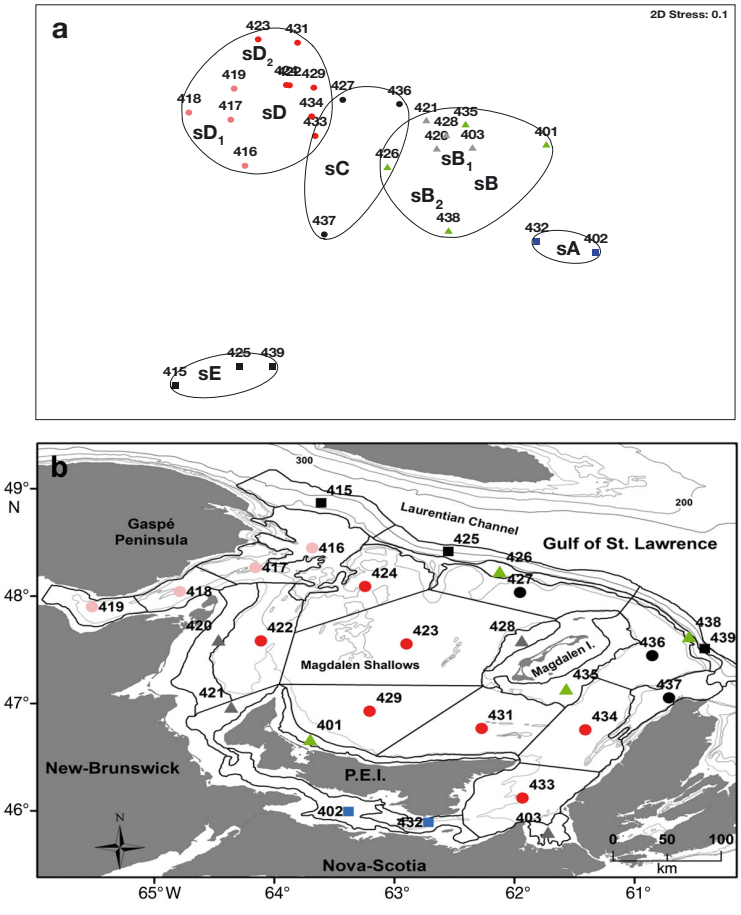


Fig. 6. Spatial structure of shrimp assemblages in the southern Gulf of St. Lawrence. (a) Non-metric multidimensional scaling ordination plot of survey strata; the solid lines represent a distance level of 0.6 among strata, and strata from the same cluster (labeled in **bold** letters: sA–sE) are plotted with a common symbol. (b) Geographical location of strata; black lines indicate the strata boundaries, and symbols for strata are the same as in (a)

Table 3. Percentage contributions of species to the average similarity of assemblages identified by SIMPER analysis for the southern Gulf of St. Lawrence. Ranks of principally contributing species are in parentheses. The numbers directly under the column headers indicate the strata that comprise each group (see Fig. 6)

Shrimp species	Code	Group sA 402; 432	Group sB 401; 403; 421–421; 426; 428; 435; 438	Group sC 427; 436–437	Group sD 416–419; 422–424; 429; 431; 433–434	Group sE 415; 425; 439
Argis dentata	AD	0.13	21.58 (2)	25.62 (2)	34.32[a] (1)	0.34
Sabinea septemcarinata	SSe	0.03	3.84 (4)	12.92 (3)	10.55 (3)	1.9
Pandalus borealis	PB	0.02	2.44 (5)	9.37 (4)	3.94 (5)	60.93[a] (1)
Pandalus montagui	PM	59.72[a] (1)	59.59[a] (1)	35.99[a] (1)	30.36[a] (2)	5.23 (3)
Pontophilus norvegicus	PN	–	–	–	–	0.11
Eualus macilentus	EM	–	0.98	0.73	9.7	0.06
Eualus gaimardii	EG	0.03	1.52	4.98 (5)	5.04 (4)	0.01
Eualus fabricii	EF	0.01	0.19	0.58	0.34	–
Sclerocrangon boreas	SB	–	4.4 (3)	0.03	0.25	–
Crangon septemspinosa	CS	40.06[a] (2)	0.52	–	0.04	–
Spirontocaris spinus	SS	–	1.36	4.2 (6)	2.38 (7)	0.08
Spirontocaris phippsi	SP	–	0.05	0.61	0.24	0.01
Spirontocaris lilljeborgi	SL	–	0.54	2.12 (8)	0.2	0.47
Pasiphaea multidentata	Pmu	–	–	–	–	29.93[a] (2)
Lebbeus polaris	LP	–	2.26 (6)	2.85 (7)	2.6 (6)	0.74
Lebbeus groenlandicus	LG	–	0.7	–	0.03	–
Pasiphea spp.	Psp	–	–	–	–	0.17
Average similarity by group (%)		61.16	39.97	44.03	55.03	59.95
Multivariate dispersion indices		0.783	1.458	1.310	0.981	0.803

[a]Species characterizing the groups of strata (ratios of average similarity to standard deviation, Sim:SD > 1.5)

was associated with strata in the Northumberland Strait, characterized by shallow depth. Group sB was associated with strata located in nearshore environments in the Shediac Valley, northern Prince Edward Island, and the Magdalen Islands. Group sC was associated with the strata located near the slope of the southeastern portion of the Laurentian Channel. Group sD was associated with strata located in Chaleur Bay and on the Magdalen Shallows. Finally, group sE was associated with the strata located along the slope of the Laurentian Channel, which are deeper than 200 m and contiguous with nC in the nGSL. The average group similarity ranged from 40.0 to 61.2%, while the multivariate dispersion indices showed that Groups sB and sC were more dispersed and less cohesive than Groups sA, sD, and sE (Table 3). However, the small differences between average group similarities suggested that a few species defined those groups (Table 3). Two species contributed almost exclusively to group sA: *P. montagui* and *Crangon septemspinosa*. For group sB, *P. montagui* and *A. dentata* (another crangonid shrimp) were the dominant species. Species that contributed most to the total percentage of similarity in group sC were *P. montagui*, *A. dentata*, *S. septemcarinata* (another crangonid shrimp), and *P. borealis*. Species that contributed mainly to Group sD were *P. montagui*, *A. dentata*, and *S. septemcarinata*. Groups sC and sD had almost identical species makeup. The deeper group sE was characterized by 2 species, *P. borealis* and *P. multidentata*. Discrimination between groups of strata (>70% average dissimilarity) could be attributed to only a few species: *P. borealis*, *P. montagui*, *P. multidentata*, *A. dentata*, *C. septemspinosa*, and *E. macilentus*.

At a threshold distance of 0.5, Groups sB and sD were further divided into subsets (Fig. 6). For Group sB, the strata located in nearshore Shediac Valley and west shore of Magdalen Island (Subgroup sB_1) clustered separately from those located in the eastern part of sGSL (Subgroup sB_2). For Group sD, the strata located in Chaleur Bay (Subgroup sD_1) clustered separately from those on the Magdalen Shallows (Subgroup sD_2). Species that discriminated the 2 Subgroups sB_1 and sB_2 were *A. dentata*, *P. montagui*, *Sclerocrangon boreas*, and *S. septemcarinata*, with more than a 50% contribution to dissimilarity. *S. septemcarinata* was more abundant in Subgroup sB_2, while the others were more abundant in Subgroup sB_1. For Subgroups sD_1 and sD_2, the discriminating species were *E. macilentus*, *P. borealis*, *P. montagui*, and *A. dentata*, with ~65% contribution to dissimilarity. The first 3 species were more abundant in Subgroup sD_1, whereas the abundance of *A. dentata* was quite similar between the subgroups.

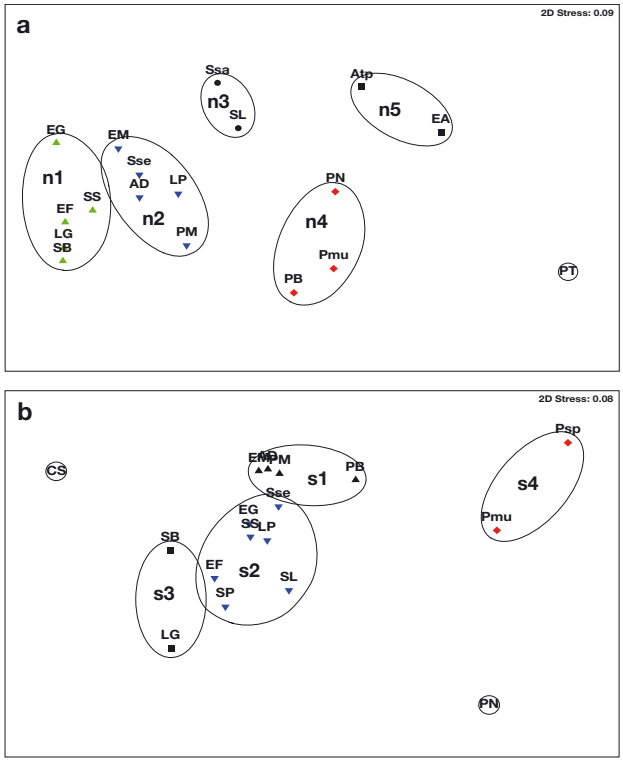


Fig. 7. Non-metric multidimensional scaling plot of shrimp species communities (species groups) in the (a) northern and (b) southern Gulf of St. Lawrence. Solid lines delineate groupings at the 10% similarity level which were found to be significant at $\alpha < 0.05$ using SIMPROF profile analysis, and species within clusters are plotted with common symbols. For species codes see Tables 2 & 3. Note that the symbols are used to distinguish the clusters in each panel of the figure and do not correspond to the symbols in Figs. 5 or 6, nor is there a link between the symbols used in a and b

The multivariate analyses aimed at identifying species associations indicated the existence of 5 groups of species at 10% of similarity in the nGSL (Fig. 7a). This low threshold for similarity likely reflects the high inter-tow variability in the data. Group n1 comprised 5 species (*E. gairmardii*, *Spirontocaris spinus*, *E. fabricii*, *L. groenlandicus*, and *S. boreas*), associated with the midshore assemblage (strata <200 m) and characterized by low relative biomass. Group n2 comprised 5 species (*A. dentata*, *E. macilentus*, *S. septemcarinata*, *P. montagui*, and *L. polaris*), also linked to the midshore assemblage, although those species were more abundant in the midshore assemblage and were characterized by broader geographic distribution in the nGSL (Fig. S5). Group n3 was also associated with the midshore assemblage and was composed of *Sabinea sarsii* and *Spirontocaris liljeborgi*. Group n4 comprised *P. borealis*, *P. multidentata*, and *P. norvegicus*. Those species dominated the 2 deeper assemblages, whilst group n5 corresponded to rare and most deeply distributed species.

Four multi-species groups were identified in the sGSL at 10% similarity (Fig. 7b). Group s1 comprised *A. dentata*, *P. montagui*, *P. borealis*, and *E. macilentus*, which were dominant species in some groups of strata observed in spatial structure (see Table 3). Group s2 comprised 7 species which were mainly associated with the strata of Magdalen Shallows (see Table 3), while group s3 comprised *S. boreas* and *L. groenlandicus* and was associated with the shallower strata. Finally, group s4 comprised *P. multidentata* and *Pasiphea* sp. and was mainly linked to deep strata. There were also 2 single-species groups: one for *C. septemspinosa* (an abundant species) in very shallow strata and one for the rare *P. norvegicus* in very deep waters.

Temperature and depth associations of assemblages

Marginal tests in stepwise distance-based linear modeling (DistLM) showed that the environmental factors temperature and depth were significant in isolation, each explaining about 38% of the variation in the nGSL and with temperature explaining 12% and depth about 21% of the variation in the sGSL (Table 4). In the nGSL, the best distance-based linear model explained 44% of the total shrimp assemblage variation and included both environmental variables (Table 4). Bottom temperature contributed much less to explained variability when modeled sequentially, which suggests that there is considerable confounding between the effects of depth and temperature in the nGSL. In the sGSL, the best distance-based linear model explained 33% of total shrimp assemblage variation (Table 4). The contribution of temperature to explained variation was similar in the marginal tests and when temperature was added as a second variable in the sequential tests. This suggests that contrary to the nGSL, the influence of temperature and depth are largely independent in the sGSL.

Temperature and depth associations of individual species

The 2 environmental variables tended to explain more of the model deviance in the nGSL analyses, with ≥25% explained deviance for most species, compared to the sGSL for which the models explained <20% for most species (Figs. 8 & 9). Notable

Table 4. Marginal and sequential results of the distance-based linear model relating shrimp assemblage and the environmental variables temperature and depth for the northern (nGSL) and southern (sGSL) Gulf of St. Lawrence. M: marginal tests, S: sequential tests for stepwise model, Res.df: residual df, Prop.: proportion of variation explained by each single variable, Cumul.: cumulative proportion of variation explained by the 2 variables. In each instance the p-value for the analysis was <0.001

Area	Variable	Tests	Res. df	Pseudo-*F*	Prop.	Cumul.
nGSL	Depth	M&S	1639	1004.9	0.380	0.380
	Temp.	M	1639	982.32	0.375	–
	Temp.	S	1638	170.84	0.059	0.439
sGSL	Depth	M&S	1785	465.69	0.207	0.207
	Temp.	M	1785	249.68	0.123	–
	Temp.	S	1784	311.36	0.118	0.325

exceptions in the sGSL analyses were *P. borealis*, *P. norvegicus*, and *P. multidentata*, 3 species that occur in the deep channels of the Gulf.

The associations between species abundance and the depth and temperature environmental variables were generally consistent between the 2 surveys despite important differences in bathymetry for the nGSL and sGSL ecosystems (Figs. 8 & 9).The peak predicted abundances of *C. septemspinosa* occurred at the most shallow depths and among the highest temperatures sampled in the sGSL survey. These depths (<40 m) are not sampled in the nGSL and therefore, it was not possible to determine whether this species occurs regularly there. Numerous species had predicted peak abundances at depths around 50 m in the sGSL survey, and generally declining abundances with depth in the nGSL due to the depth-dependent sampling constraints (e.g. *S. boreas*, *E. fabricii*, *E. gairmardii*, and *E. macilentus*; Fig. 8). These species are strongly associated with the CIL (Fig. 9), which covers most of the bottom of the sGSL but only the more coastal areas in the nGSL. The species are therefore broadly distributed in the sGSL (Fig. S5 in Supplement 4). Many of these species also have a secondary peak in predicted abundances at around 300 m in the sGSL but not the nGSL. Two factors may have contributed to this pattern. First, these species are tolerant of waters in the 4–6°C range which, during the summer and early fall when these surveys take place, occur at depths between 25 and 60 m, just above the CIL, and at depths below the CIL, i.e. <170 m. Second, the pattern may be the result of slight offshore drifting of animals in the area north of the Magdalen Islands, in Chaleur Bay and off of Cape Breton, where the depth gradient is very steep (Fig. S5 in Supplement 4). The most broadly distributed species in the nGSL were those associated with the deep water layer and had peak predicted abundances at waters of around 5°C and typical depths of 200–300 m (e.g. *P. borealis*, *P. multidentata*, and *P. norvegicus*; Figs. 8 & 9). These species were largely restricted to the northern edge of the sGSL survey, in the Laurentian Channel. Finally, 4 species had peak abundances at depths >300 m that were largely absent from the sGSL. For the most extreme case, *Eusergestes arcticus*, catches were limited to the deepest parts of the Gulf, in the Laurentian Channel near Cabot Strait (Fig. S5 in Supplement 4).

DISCUSSION

This study is the first to examine the spatial structure and environmental associations of shrimp assemblages in a large ocean ecosystem, the GSL, following a period of 4-fold (nGSL) to 100-fold (sGSL) increase in shrimp abundance that coincided with the collapse of most predatory fish populations (Savenkoff et al. 2007a,b, Benoît & Swain 2008, Dufour et al. 2010). Previous studies in the GSL were limited to a small area, Chaleurs Bay, and covered a single year (Hanson & Lanteigne 1999). Here we have shown that the increase in shrimp biomass in at least the sGSL is likely to have resulted from increases in numerous species. This result is consistent, at least in part, with predation release, as it coincides with the collapse of formerly abundant fish species such as Atlantic cod and white hake (Fig. 10), which were important predators, at different points in their ontogeny, of numerous species of shrimp (Hanson & Chouinard 2002, Hanson 2011). Shrimp biomass trends in the nGSL are similarly consistent at least in part with predation release as they as they generally correspond to the early 1990s collapse and recent increase of groundish predators (Fig. 10). The increase in shrimp biomass in the sGSL also coincided with a warming of waters in the CIL from an unusually cold period in the late 1980s and early 1990s to average levels beginning in the early 2000s (Gilbert & Pettigrew 1997, Galbraith et al. 2016). Much of the increase in biomass in the sGSL occurred at intermediate depths in Chaleur Bay and on the Magdalen Shallows, areas where the bottom is covered by the CIL, and 3 of the 4 species that must have increased in abundance are associated with those waters. Bottom water temperatures in the CIL and deeper waters varied around the 30 yr average during the 2004–2015 period (Galbraith et al. 2016). The assem-

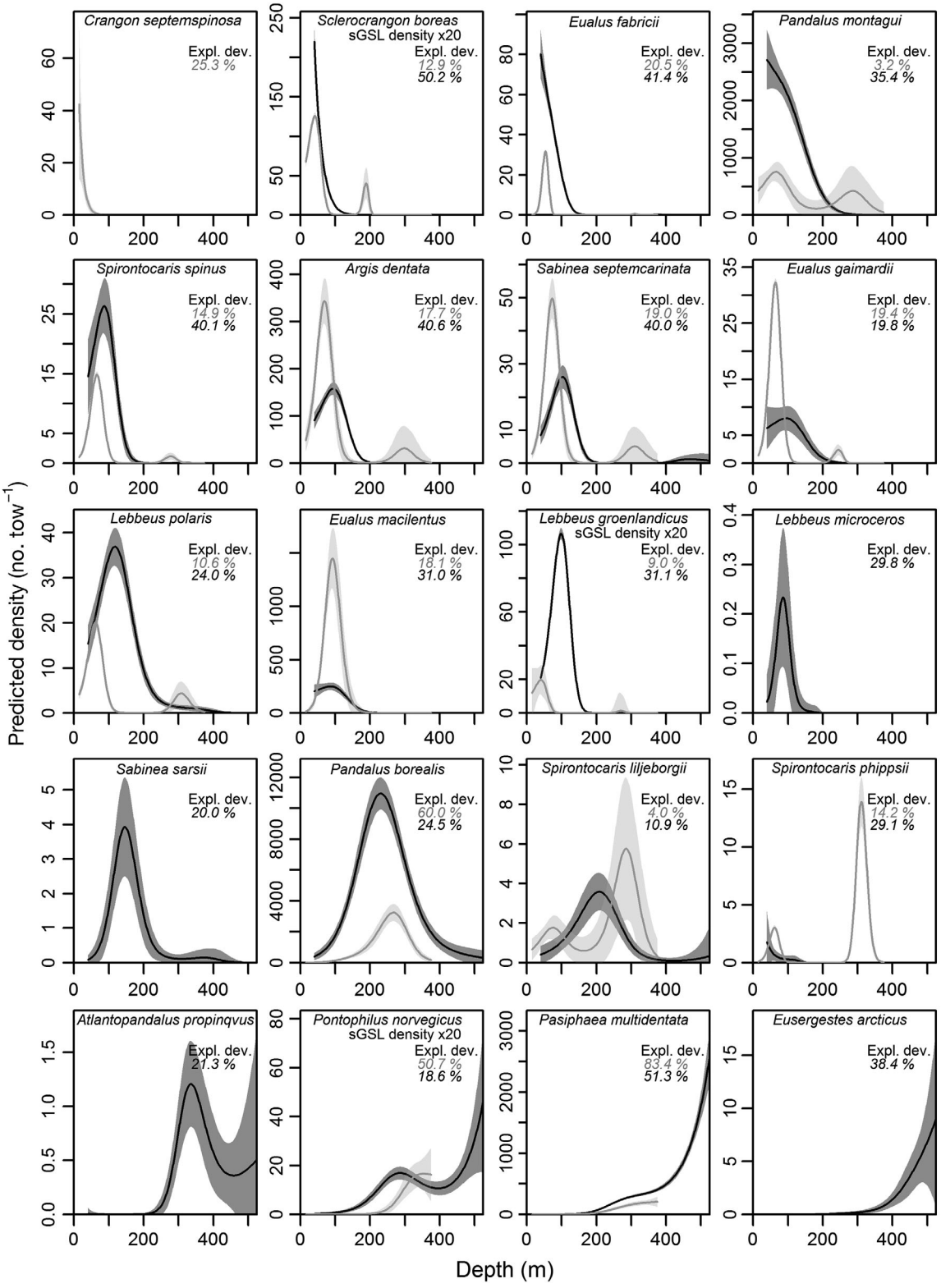


Fig. 8. Predicted abundance (numbers per tow) of each shrimp species as a function of depth from the individual generalized additive modeling analyses for data from the northern Gulf of St. Lawrence (nGSL) survey (black line and dark grey band) and the southern GSL (sGSL) survey (light grey line and band). Bands indicate the 95% confidence interval for the predictions. Panels are sorted according to the major patterns in the association with depth. Note that the differences in predicted abundance between the nGSL and sGSL may reflect differences in catchability and abundance. Predicted densities of *Sclerocrangon boreas*, *Lebbeus groenlandicus*, and *Pontophilus norvegicus* for the sGSL survey were multiplied by 20 in the plots for enhanced clarity. Values in the plots indicate the percent of deviance explained by the model for the sGSL (grey text) and nGSL (black text) analyses

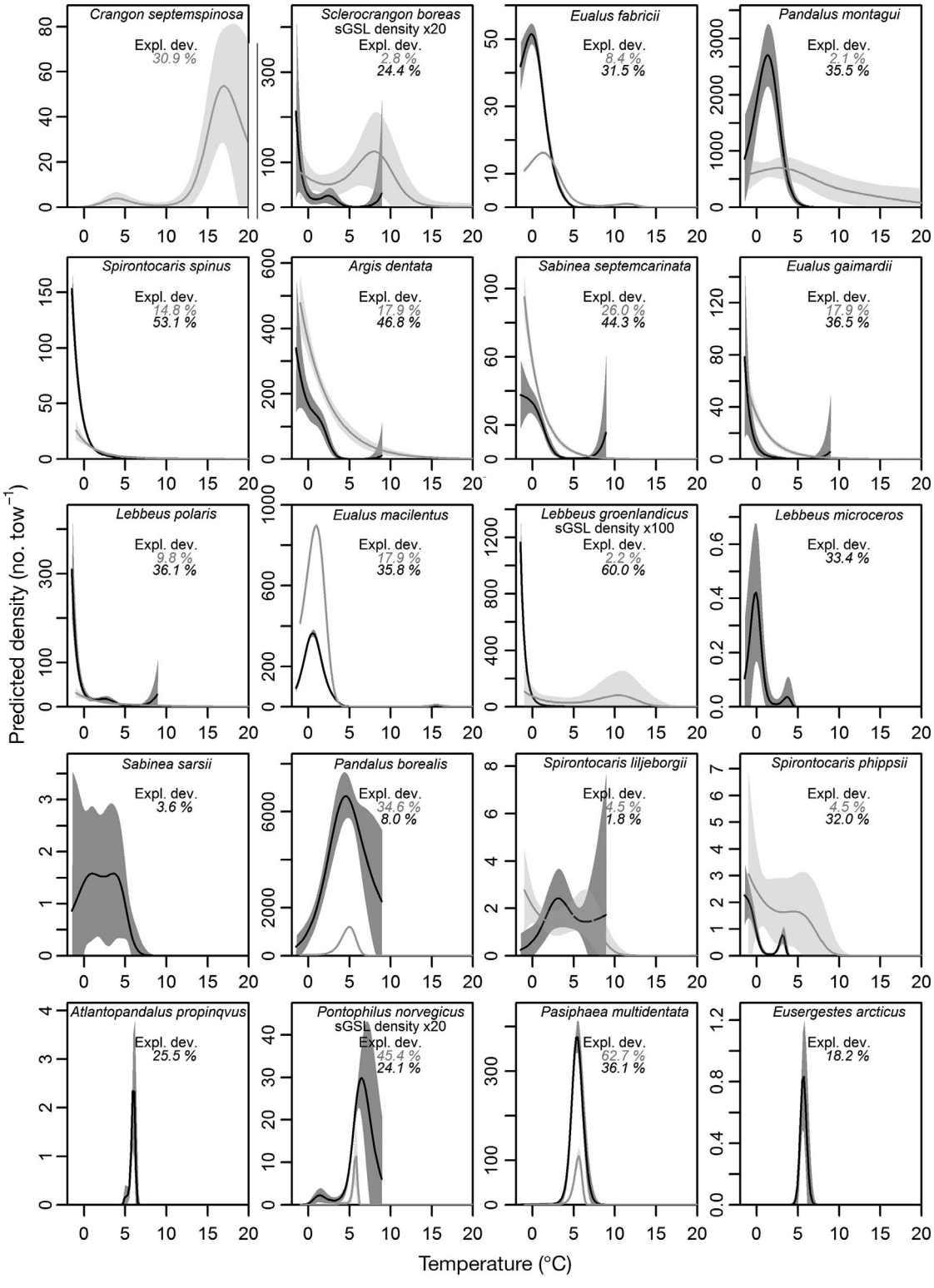


Fig. 9. As in Fig. 8, but for predicted abundance (numbers per tow) of each shrimp species as a function of temperature. Predicted abundance of *Sclerocrangon boreas*, *Lebbeus groenlandicus*, and *Pontophilus norvegicus* for the sGSL survey were multiplied by the factors indicated in the plots for enhanced clarity

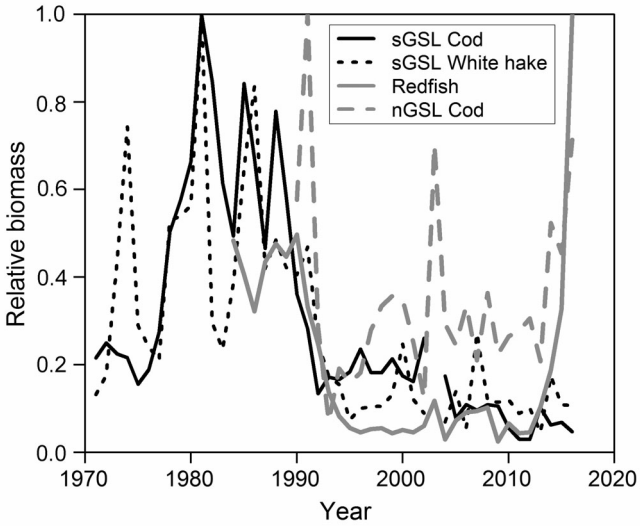


Fig. 10. Relative biomass survey indices for the major groundfish predators of the southern and northern Gulf of St. Lawrence (sGSL and nGSL). Relative biomass was calculated by dividing each biomass index series (kg tow^{-1}) by the maximum value for the series and is presented because of differences in survey catchability between populations. The standardized series begins in 1971 and excludes 2003 for sGSL cod and white hake, and begins in 1984 and 1990 for redfish and nGSL cod, respectively

blages studied here may therefore largely represent those generally present under average physical environmental conditions. Furthermore, given that the abundance of most major groundfish predators of shrimp was at or near the lowest levels in decades, possibly centuries, during most or all of the 2004–2015 period (Powles 1969, Rosenberg et al. 2005, DFO 2015a, 2016a, Swain & Benoît 2015), this study is likely reporting on shrimp assemblages during a period of particularly high abundance.

The multivariate analyses revealed comparable structuring of shrimp communities in the nGSL and sGSL despite large differences in environmental conditions. This reflects the obvious connectedness of the 2 ecosystems, similarity in patterns of temperature stratification with depth, and species–environmental associations that were generally at least of moderate strength and similar between the nGSL and sGSL. Not surprisingly, both sets of analyses identified a distinct deep-water assemblage that occurred in part in an area covered by both surveys and which was typified by *Pandalus borealis* and *Pasiphaea multidentata*. Similarly, the midshore group nA in the nGSL, which was associated with waters in the CIL, comprised a similar mix of species as the groups sB, sC, and sD in the sGSL which are entirely (sC and sD) or partly (sB) also associated with the CIL. The area where the CIL touches the bottom in the sGSL is very large, which may result in a greater potential for spatial sub-structuring in the assemblages associated with the CIL due to factors other than depth and temperature. This, combined with an associated higher sampling rate and therefore higher precision, may explain why 3 or 4 (depending on the similarity level) CIL-associated assemblages were identified in the sGSL compared to only 1 in the nGSL. Furthermore, it may partly explain why temperature and depth were weaker combined predictors of assemblage similarity and of densities for many individual species in the sGSL.

Spatial patterns in shrimp assemblage structure strongly resemble patterns previously described for demersal fishes, large decapods (such as crabs and lobster), and epibenthic communities in the GSL. Largely consistent with the results presented here for shrimp, those analyses identified coastal assemblages that occur only in the sGSL surveys, 2 or 3 shelf assemblages associated with the CIL, and 2 or 3 principal assemblages in the channels, including 1 associated with the deepest waters (Mahon et al. 1998, Chouinard & Dutil 2011, Moritz et al. 2013, Tamdrari et al. 2015). Furthermore, an analysis of data from a finer-scale survey in the Northumberland Strait distinguished fish assemblages between the western portion of the Strait (stratum 421) and in the central Strait (402, 432) (Bosman et al. 2011), as was found here for shrimp. This suggests that similar factors likely affect the distributions in shrimp, fish, and broader epibenthic communities. This is perhaps best illustrated in shrimp species that were associated with 4–6°C bottom temperature, waters which in the GSL occur in both shallower areas and in the deeper waters of the Laurentian Channel. Those species had bimodal depth distributions, something that is also observed for a number of sGSL fish species such as white hake (Benoît et al. 2003, Swain et al. 2015).

The distribution of shrimp species with respect to bathymetric gradients has been reported in numerous studies (Shumway et al. 1985, Hudon 1990, Simard & Savard 1990, Munga et al. 2013, Zimina et al. 2015). The mechanism underlying these patterns is not clear because there are numerous relevant ecological and environmental factors that co-vary with depth, such as light penetration, oxygen concentration, and sediment type (Shumway et al. 1985, Swain & Benoît 2006, Dutil et al. 2011, Majewski et al. 2013, Munga et al. 2013). Lack of sufficiently spatially resolved data for these other properties (other than temperature) precluded a closer examination of possible associations with the shrimp assemblages.

While the estimated species–environmental associations presented here reflect realized niches, which result from the influence of numerous factors (e.g. density dependence and predation) in addition to the abiotic variables, associations with bottom temperature can nonetheless indicate the existence of physiological constraints that constitute the fundamental niche (Wake et al. 2009, Shackell et al. 2014). This information has often been used as an indicator of how species distributions might change with climate warming (e.g. Cheung et al. 2009, Shackell et al. 2014). Temperature has often been identified as an important factor governing the distribution of shrimp such as *P. borealis* (e.g. Haynes & Wigley 1969, Apollonio et al. 1986, Anderson 2000, Clark et al. 2000). Consistent with those results, a number of GSL shrimp species had moderate to strong associations with a small range of bottom temperature. Those species occurred mainly in the CIL and in the deepest waters of the channels, which might make them vulnerable to the warming that is projected. Five species were associated with the coldest portions of the CIL (*Spirontocaris spinus*, *Eualus gaimardii*, *Lebbeus polaris*, and *L. groenlandicus*), and 4 species with the deeper portions of the channels, with strong peaks in predicted abundance at 6°C (*Atlantopandalus propinqvus*, *Pontophilus norvegicus*, *Pasiphaea multidentata*, and *Eusergestes arcticus*). Warming trends in the GSL have already resulted in approximately 1°C of warming on average (May–November) in surface and nearshore waters since the early 1990s and in deeper waters (>200 m) since the 1930s (Galbraith et al. 2016). Projected changes to 2069 include approximately 1°C warming of summer sea surface temperatures in parts of the nGSL and about 2°C in much of the sGSL (Long et al. 2016). The CIL volume is expected to decrease substantially, and mean temperatures in the CIL and in deeper waters are projected to increase by over 1°C. To the extent that the temperature associations for the species noted above reflect true stenothermic physiologies, their densities could decline considerably as temperatures rise and the availability of suitable thermal habitat becomes considerably reduced. In contrast, species occupying broader temperature ranges, such as *Crangon septemspinosa*, *Sclerocrangon boreas*, *P. montagui*, and *Argis dentata* in the sGSL appear to have considerably more scope for adaptation to warming and may broaden their distribution within the GSL. In particular, *C. septemspinosa* occurs well inshore of the sGSL survey area, where bottom water temperatures frequently exceed 22°C during mid-summer (Joseph et al. 2006, Debertin et al. 2017), and may have considerable scope to expand its distribution with climate warming.

The populations of almost all larger-bodied groundfishes in the sGSL remain at very low levels or continue to decline (Swain & Benoît 2015). In contrast, important shrimp predators such as Atlantic cod and, in particular, redfishes are rapidly increasing in abundance in the nGSL (Fig. 10; DFO 2015a, 2016a). Based on the most recent (2015) assessment for cod in the nGSL, projected spawning stock biomass could double to 36 000 t by 2017 if fishery catches were kept reasonably low (although this level is still low compared to historical values). More dramatically, the abundance of *Sebastes mentella* (redfish) presently recruiting to the fishery is very high and total biomass are approaching mid-1980s values. These increases, especially in redfishes, likely have increased predation pressure on shrimp populations and may explain small declines in biomass observed in recent years for the entire shrimp community (this study). Furthermore, the increased fish abundances may be contributing, along with warming of bottom waters, to declines in the biomass of commercially important northern shrimp (DFO 2017a). Fishing does not appear to be a primary driver of shrimp assemblage biomass trends because *P. borealis* is the only harvested shrimp species, and declines were observed for many species; moreover, exploitation rates on *P. borealis* since 1990 (i.e. during periods of increase and of decline) have fluctuated around average levels (DFO 2016b). Observed and projected increases in predation pressure by recovering demersal and bathydemersal fish in the GSL and off of Newfoundland, along with projected warming, have raised concerns about the future productivity of commercial shrimp stocks in Atlantic Canada (DFO 2014, 2017b). While this phenomenon is of concern given impacts on the fishery, its effects are unlikely to be limited to *P. borealis*, as other non-commercially important shrimp species also are likely to be affected. Current detailed information on the diet of predators and limited understanding of possible density-dependent changes in predator distribution preclude determining which shrimp species may be disproportionately affected.

In summary, increases in shrimp biomass in the GSL during the 1990s and early 2000s were dramatic and, at least in the sGSL, were the result of increases in numerous shrimp species. In the decade that followed, the composition of species in the shrimp communities of the nGSL and sGSL varied without trend, consistent with a high abundance period of relative stability. Shrimp assemblages during that period

were strongly structured spatially and as a function of depth and temperature, similar to structuring of demersal fish assemblages. Almost half of the shrimp species occupied a narrow range of temperatures that may indicate stenothermic adaptation and therefore vulnerability to warming, and all species are known or likely prey for fish predators. Expected changes in the short term related to important increases in predator abundance and in the longer term related to temperature change, are likely to result in considerable decreases in shrimp biomass, particularly in the nGSL, and in changes in community composition throughout the Gulf.

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