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Original Research Article

Effects of environmental factors on reproductive potential of the Gulf of Maine northern shrimp (*Pandalus borealis*)Hsiao-Yun Chang^{a,*},¹, R. Anne Richards^b, Yong Chen^{a,1}^a School of Marine Sciences, University of Maine, Orono, Maine 04469, USA^b 124 West Falmouth Highway, Falmouth, MA 02540, USA

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ABSTRACT

The northern shrimp (*Pandalus borealis*) once supported a significant winter fishery in the Gulf of Maine (GOM). However, the population collapsed in 2012 and a fishery moratorium has been in effect since 2014 due to record low levels of spawning stock biomass and persistent recruitment failure. An important parameter in determining population dynamics, fecundity, has not been evaluated for more than 30 years, during which time the GOM has warmed significantly. In this study, we quantified three reproductive characteristics related to fecundity: potential fecundity (PF, number of viable eggs), relative fecundity (RF, number of viable eggs per gram of body weight), and egg size (ES) for GOM northern shrimp. The results showed that PF was strongly related to body size, while RF was independent of body size. Egg size declined with increasing body size for larger females. Egg size is related to size at larval hatch, suggesting that although larger females produced more eggs, those eggs may produce smaller larvae. In contrast with previous studies, PF and RF were positively correlated with bottom temperature in the relatively warm years of our study. We hypothesize that the positive temperature-fecundity relationship we observed may not reflect a direct effect, but possibly a compensatory response relating to decreased population density during the time period of our study. In addition, the environmental effects we observed may to some extent reflect progression of the inshore migration of females. The information derived in this study can help us have a better understanding of environmental effects on reproductive potential for climatically vulnerable species such as the GOM northern shrimp.

1. Introduction

Northern shrimp once supported a significant winter fishery in the Gulf of Maine (GOM) (Clark et al., 2000). However, landings have fluctuated widely and the fishery has collapsed three times since its inception in the 1930s (Clark et al., 2000; ASMFC NSTC, 2018). The most recent collapse occurred in 2012, and a moratorium has been imposed on the shrimp fishery since 2014 due to low stock size and recruitment failure for several successive years (ASMFC NSTC, 2018). Recent recruitment failures have been associated with unfavorably warm water temperatures in the GOM (ASMFC NSTC, 2018), which has been warming faster than 99% of the global oceans (Pershing et al., 2015). The intense warming rates have shifted hatch timing of northern shrimp (Richards, 2012), driven

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distributional (Nye, 2010; Kleisner et al., 2017) and phenological shifts (Staples et al., 2019; Staudinger et al., 2019) of various marine species, and impacted fisheries in the GOM (Mills et al., 2013; Pershing et al., 2015; Mazur et al., 2018).

Northern shrimp are sequential hermaphrodites (Shumway et al., 1985). They hatch as males in near-shore areas in GOM during winter-spring. During their second year of life, they migrate to offshore areas where they mature as males and remain until they transform to mature females at presumed age 3. They then reproduce for 2 years as females. Following molting and mating, females extrude eggs that are fertilized externally and attached to their pleopods. The eggs are carried for several months before the females move to near-shore areas to release the offspring (Shumway et al., 1985; Richards, 2012). Unlike many fish species, most crustacean species' egg development is synchronous and fecundity is determinant (Parsons and Tucker, 1986). This means that all fertilized eggs develop at the same pace and no new eggs are extruded during incubation, thus the number of eggs (reproductive potential) can be estimated at the onset of spawning.

A well-defined stock-recruitment relationship is highly beneficial to fisheries management because it facilitates the estimation of exploitation levels that ensure future recruitment and sustainable fisheries (Hannah et al., 1995). Stock can be represented by several measures, including parental stock biomass, mature female stock biomass, or egg production (Hilborn and Walters, 1992). Of these, egg production estimated from size-specific (or age-specific) fecundity is considered the best measure of spawning stock (Morgan et al., 2012). An advanced understanding of reproductive potential and its relationship with environmental variables could help elucidate the causes of recruitment failure of northern shrimp in the GOM.

Direct and indirect effects of climatic factors are important for determining species' vulnerability to climate change (de los Ríos et al., 2018). GOM northern shrimp are perceived to be particularly susceptible to environmental variability as they are at the southernmost limit of their distribution in the North Atlantic Ocean (Shumway et al., 1985). A few studies have estimated size-fecundity relationships for GOM northern shrimp (Apollonio and Dunton, 1969; Haynes and Wigley, 1969; Apollonio et al., 1986) and one of these examined possible temperature effects on fecundity, but found no correlation between spatial variation in bottom temperature and fecundity (Apollonio et al., 1986). However, these studies were conducted more than fifty years ago, before the steep warming trend began (Richards et al., 2012; Pershing et al., 2015). In the current study, we provide a contemporary estimate of the size-fecundity relationship for GOM northern shrimp and examine possible effects of environmental variability on potential fecundity (PF), relative fecundity (RF) and egg size (ES) in order to better understand environmental effects on reproductive potential of northern shrimp, and their possible relations to recruitment failures.

2. Materials and methods

2.1. Biological samples and environmental data

Samples of female shrimp were collected during bottom trawl surveys conducted in the GOM by the Northeast Fisheries Science Center (NEFSC) during October and November, 2012–2016 (Fig. 1 and Table 1). The NEFSC bottom trawl surveys are designed to capture a broad range of species across the northeast continental shelf of the United States. The survey uses a stratified random

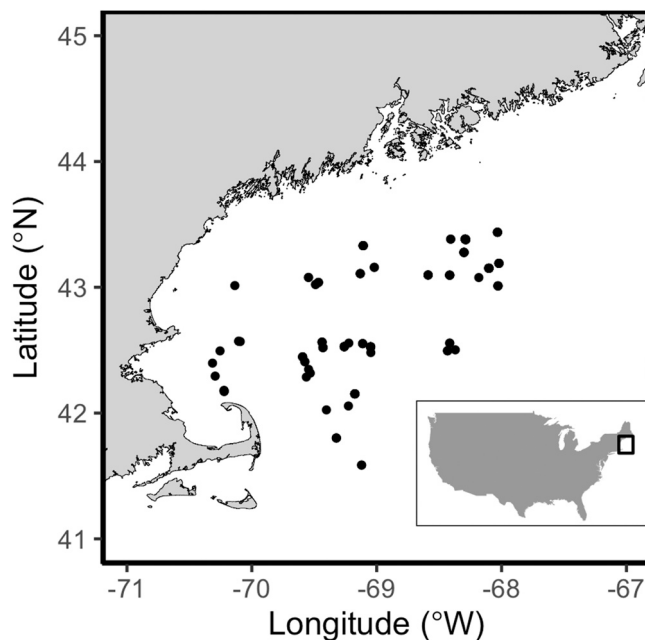


Fig. 1. Sampling locations of the Northeast Fisheries Science Center fall bottom trawl surveys where northern shrimp (*Pandalus borealis*) were collected in the Gulf of Maine during 2012–2016.

sampling design in which sampling locations are randomly selected within strata that are defined by bathymetry and latitude (Politis et al., 2014). The number of stations within a stratum is generally proportional to the area of the stratum and the overall variation of multispecies distribution among strata (Politis et al., 2014). At each sampling station, bottom temperature and bottom salinity data were measured with electronic profiling conductivity/temperature/depth sensors (Politis et al., 2014). Samples of the shrimp catch were frozen at sea, then thawed and processed at NEFSC for collecting size and life stage data, then refrozen for later laboratory processing for fecundity data collection. A total of 143 samples collected from 46 sampling locations in October and November 2012–2016 were used for estimating PF, RF, and ES (Table 1).

2.2. Laboratory procedures

Only shrimp bearing early developmental stage (non-eyed) larvae (Haynes and Wigley, 1969) were used for estimating fecundity. These could be readily identified under a microscope because the eggs were transparent and eyes had not yet formed. Non-eyed individuals comprised 99.9% of the samples collected. Fecundity (number of viable eggs of an individual female) estimated from our samples taken in the fall were considered PF rather than realized fecundity (number of eggs successfully hatched per female) due to potential egg loss during the remaining 3–4 months of incubation. RF was estimated as the number of eggs per gram of female body weight (potential fecundity/female body weight without eggs), which is a measure of individual reproductive investment (Pereira et al., 2017). Parasite-infected eggs (white eggs; Haynes and Wigley, 1969, Apollonio et al., 1986, Chang et al., 2020) were recognized under a microscope based on their appearance. The proportion of white eggs ranged from 0% to 33% with an average of 2.16% of all eggs for an individual (Chang et al., 2020). These white eggs were excluded from the analyses as they are non-viable (Chang et al., 2020).

An analysis of the optimal number of samples needed for estimating fecundity indicated that length-stratified random sampling is more cost-effective than simple random sampling assuming the fecundity of northern shrimp is size-dependent (Chang and Chen, 2020). Therefore, we used length-stratified sampling which divided the range of shrimp sizes (dorsal carapace length, DCL, mm) into 10 length intervals (approximately 1 mm per length interval) and sampled 1 shrimp from each length interval. All available samples were processed, adhering as closely as possible to the protocols developed in Chang and Chen (2020).

Shrimp were processed for fecundity estimation by thawing the specimens at room temperature and using forceps to gently tease the eggs masses off the pleopods. Biological data including DCL (mm), lateral carapace length [LCL, mm; for comparing with Apollonio et al. (1986)], wet weight of each egg mass (g), and female body weight [air-thawed wet weight (g)] without eggs were measured. Egg samples were then preserved in 10% neutral formalin (Parsons and Tucker, 1986) for later processing. Eggs were removed from formalin, stained with toluidine blue and imaged under a trinocular dissecting microscope (OMAX V434BL54P-C140U) mounted with a digital camera (OMAX A35140U3). Egg masses were gently teased apart using forceps. ObjectJ (Schneider et al., 2012) was used to count all eggs (except white eggs) in each egg mass and measure their longest diameter (μm). ES of an individual female was defined as the average diameter (μm) of viable eggs in her egg mass.

2.3. Statistical analysis

Generalized additive mixed models (GAMMs; Wood, 2017) with negative binomial, Gaussian, and lognormal distributions were used to examine the relationships between predictors and PF, RF, and ES, respectively. The distributions chosen were based on the distributions of the dependent variables (Zuur et al., 2009). A variance inflation factor (VIF) analysis was conducted to identify multicollinearity before fitting models to the data. Predictors with VIFs exceeding 3 were considered collinear with other variables, a threshold VIF of 3 was thus set for evaluating possible collinearity between predictors in the data set (Schmiing et al., 2013; Brosset et al., 2019). The form of the GAMMs was:

$$g(y) \sim \alpha + \sum_{i=1}^k f_i(x_i) + \varepsilon_y + \varepsilon_l + \varepsilon$$

where $g()$ is the link function, y is PF, RF or ES, f_i is the i^{th} smooth function based on thin plate regression splines, x_i is the i^{th} explanatory variable, ε_y and ε_l are random effects of year and sampling location, and ε is residual error. Year and sampling location were included in the models as nested random effects to account for possible spatial or temporal pseudoreplication and for variation among years and sampling locations (Hurlbert, 1984; Zuur et al., 2009; Weltz et al., 2013; Thorson and Minto, 2015).

Table 1

Number of stations where northern shrimp (*Pandalus borealis*) were collected and number of northern shrimp successfully used for estimating fecundity and egg size.

Year	Number of stations	Number of northern shrimp used	Sampling period
2012	7	14	Oct 3–Nov 10
2013	5	8	Nov 13–Nov 15
2014	12	40	Oct 31–Nov 10
2015	21	76	Oct 21–Nov 5
2016	1	5	Nov 7
Total	46	143	

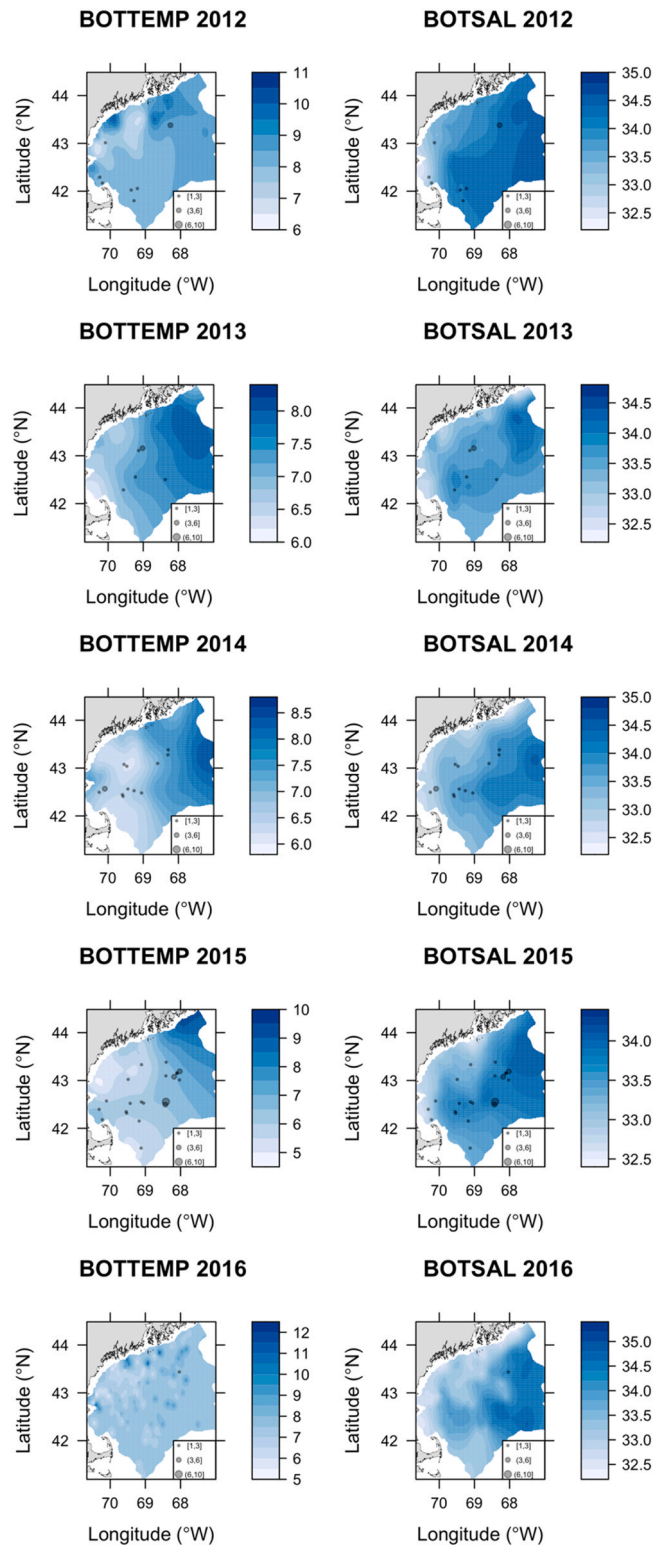


Fig. 2. Sampling locations of the Northeast Fisheries Science Center fall bottom trawl surveys where northern shrimp (*Pandalus borealis*) used in this study were collected in the Gulf of Maine during 2012–2016. Different sizes of dots denote number of shrimp used from each location. Maps of contours of interpolated bottom temperature and bottom salinity were overlaid on the bottom.

Table 2

Observed ranges, means, and standard deviations of response and explanatory variables in this study, Richards et al. (2012), and Apollonio et al. (1986). DCL = dorsal carapace length; BOTTEMP = bottom temperature; BOTSAL = bottom salinity; PF = potential fecundity; RF = relative fecundity; ES = egg size; SD = standard deviation; n = number of samples; RMSE = root mean squared error. The DCLs of Apollonio et al. (1986) were converted from lateral dorsal carapace length (LCL) based on the equation: $LCL = 1.464 + 1.086 \times DCL$ ($n = 653$, $r^2 = 0.92$) which was developed using data collected in this study.

Study	DCL (mm)			BOTTEMP (°C)			BOTSAL (‰)			PF (number of eggs)			RF (number of eggs/g)			ES (µm)			n	RMSE
	range	mean	SD	range	mean	SD	range	mean	SD	range	mean	SD	range	mean	SD	range	mean	SD		
This study	18.15–30.84	25	2.56	5.67–11.01	7.6	1.19	32.42–34.63	33.83	0.43	124–3557	1442.2	620.7	15.0–289.3	161.9	52.3	891.8–1335.9	1091.6	69.2	143	417
Richards et al. (2012)	22.24–30.82	27	2.4	NA	NA	NA	NA	NA	NA	882–3396	2425.9	628.2	NA	NA	NA	NA	NA	NA	47	288.8
Apollonio et al. (1986)	21.93–30.78	25.65	1.66	NA	NA	NA	NA	NA	NA	734–2775	1616.4	344.2	NA	NA	NA	NA	NA	NA	202	221.6

Table 3

Model statistics of the best models within 2 Δ AICc for potential fecundity (PF), relative fecundity (RF), and egg size (ES) of northern shrimp (*Pandalus borealis*). DE=deviance explained, EDF=estimated degrees of freedom, LOOCV RMSE=leave-one-out cross validation root mean squared error, ω AICc=AICc weights, ω BIC=BIC weights, DCL=dorsal carapace length, TEMP=bottom temperature, SAL=bottom salinity. σ_y and σ_1 =random effects of year and sampling location. The DCL in the PF model is in parentheses as DCL was included in the null model.

Models										DE	EDF	LOOCV RMSE	Δ AICc	Δ BIC	ω AICc	ω BIC
PF	~	(DCL)	+	TEMP	+	SAL	+	σ_y		0.484	7.155	476.494	0	1.236	0.977	0.334
RF	~			TEMP	+	SAL	+	σ_y	+	0.569	28.031	52.075	0	0	0.456	0.782
RF	~					SAL	+	σ_y	+	0.582	29.792	51.433	1.821	4.569	0.183	0.08
ES	~	DCL			+	SAL			+	0.59	30.81	65.376	0	3.356	0.388	0.133
ES	~					SAL			+	0.564	29.203	67.431	0.387	0	0.32	0.713
ES	~			TEMP					+	0.573	30.624	69.667	1.841	3.414	0.154	0.129

The VIF analysis indicated that multicollinearity was not an issue as all explanatory variables (DCL, bottom temperature, and bottom salinity) had VIFs < 3. Therefore, models of all combinations of the three explanatory variables were built (Fisher et al., 2018). Model selection was based on full-subsets information theoretic approaches (Anderson and Burnham, 2002; Fisher et al., 2018), using Akaike’s information criterion corrected for small sample sizes (AICc; Akaike, 1973; Hurvich and Tsai, 1989), Bayesian information criterion (BIC; Wit et al., 2012), AICc weights (ωAICc) and BIC weights (ωBIC, Fisher et al., 2018), deviance explained by the model, and graphical inspection. Root mean squared error (RMSE) estimated with leave-one-out cross-validation (LOOCV) was used to evaluate predictive performance of models (Zuur et al., 2009; Arlot and Celisse, 2010). The random structure was first assessed by AICc with all the smooth terms included in the models (Zuur et al., 2009) using restricted maximum likelihood (REML) methods. The random effects included in the model that had the lowest AICc were considered the optimal random structure.

After the random components were determined, models with different combinations of predictors were developed and compared using maximum likelihood methods. The base model for estimating PF included DCL based on previous studies (Haynes and Wigley, 1969; Apollonio et al., 1986). Little is known about the effect of DCL on RF and ES for northern shrimp, so the effect of DCL was not included in the null model for RF and ES.

Models with differences in AICc (ΔAICc) < 2 were considered candidate models that were well supported by the data (Anderson and Burnham, 2002). Models with the lowest AICc scores were refit with REML (Zuur et al., 2009; Wood, 2017) and effect plots of these models were presented. Biological relevance and the relationships between response variables and predictors were graphically examined. Relative importance of predictors was quantified as the sum of AICc weights of models in which a predictor is present (Anderson and Burnham, 2002; Fisher et al., 2018).

The residuals of the optimal model were graphically evaluated with QQ-plots and plots of Pearson residual errors against fitted values to inspect any patterns in the residual errors (Zuur et al., 2009). Semivariance of Pearson residual errors from the most optimal model was examined for the presence of spatial autocorrelation (Cressie, 1993; Pebesma, 2004; Gräler et al., 2016). Simple linear regression models were fit to bottom temperature and bottom salinity data with day of year for exploring potential effects of spawning migration on the environmental relationships with reproductive characteristics.

2.4. Population fecundity

To fully compare with Richards et al. (2012), a GAM model was built for individual PF using only DCL as the explanatory factor in the model.

$$PF_i = f(DCL_i) + \varepsilon_i$$

The size-fecundity relationship was then applied to the stratified mean population size composition estimated in Richards et al. (2012) for estimating population fecundity:

$$N_{i,y} = \sum_{s=1}^k \frac{N_{s,i,y} A_{s,y}}{\sum A_{s,y}}$$

$$Population\ fecundity_y = \sum_{i=1}^m PF_{i,y} N_{i,y}$$

where s = stratum, i = length, y = year, N_{s,i,y} = mean number of ovigerous female at length i in stratum s in year y, A_{s,y} = area of stratum s in year y.

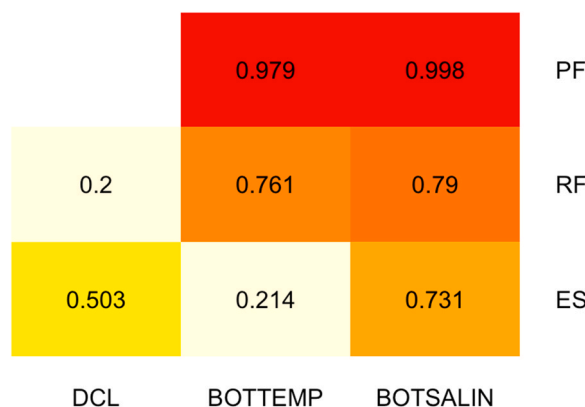


Fig. 3. A heatmap of importance scores of each variable estimated from full-subsets generalized additive mixed models with information theoretic approaches for potential fecundity (PF), relative fecundity (RF), and egg size (ES). DCL=dorsal carapace length (mm); BOTTEMP = bottom temperature; BOTSALIN = bottom salinity.

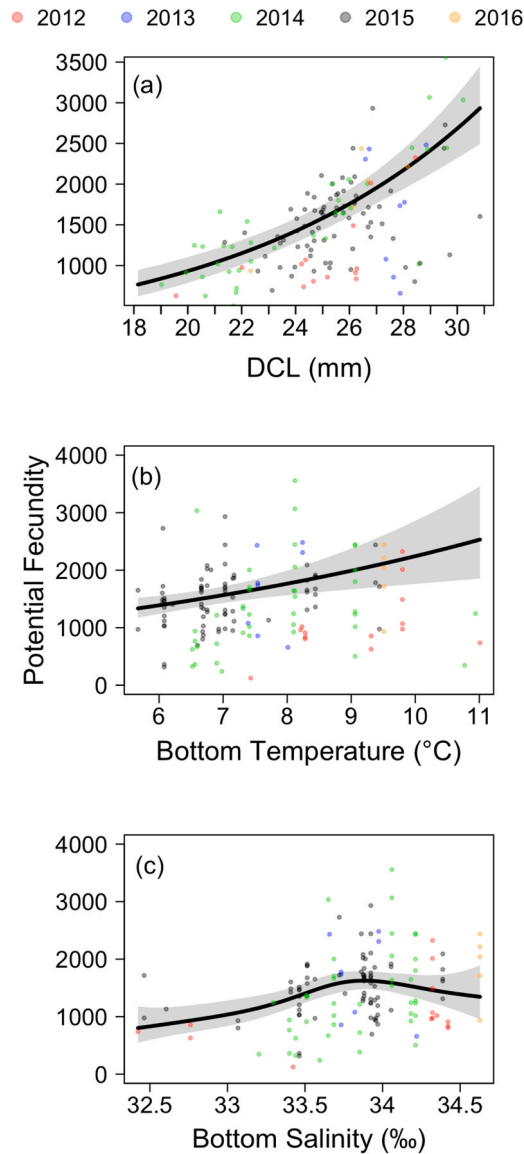


Fig. 4. Partial effects of each variable included in the best model with lowest AICc on potential fecundity (PF). The black solid lines denote the modeled relationship, the gray bands denote the 95% confidence intervals about the estimated relationship, and colored dots are observations of each year.

The same data of $N_{i,y}$ were used to estimate population fecundity based on the model developed in Richards et al. (2012):

$$Population \ fecundity_y = \sum_{i=1}^m (-0.198L_{i,y}^2 + 128.81L_{i,y} - 17821)N_{i,y}$$

where $L_{i,y}$ is the i^{th} DCL in 0.1 mm in year y .

DCLs of the full range (18.15–30.84 mm) were used for the PF model in this study, and only females ≥ 20 mm DCL were used for Richards’s et al. (2012) model.

Variability in northern shrimp PF was compared with previous studies (Haynes and Wigley, 1969; Apollonio et al., 1986). RMSEs were estimated using the data and corresponding models in each study. The DCLs of Apollonio et al. (1986) were converted from lateral dorsal carapace length (LCL) based on the equation: $LCL = 1.464 + 1.086DCL$ ($n = 653, r^2 = 0.92$) which was developed using data collected in this study (Appendix S1).

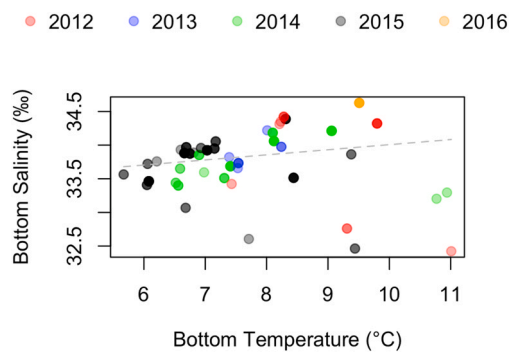


Fig. 5. Relationships between bottom temperature and bottom salinity. The gray dashed lines are linear regression lines, and colored dots are observations of each year.

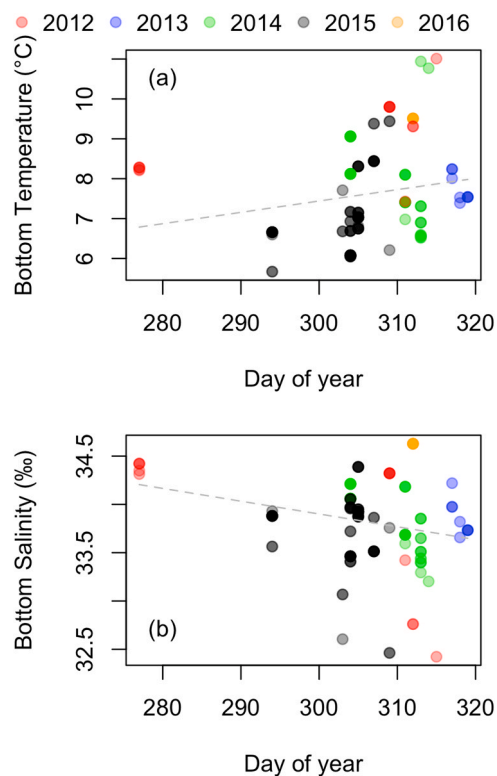


Fig. 6. Relationships between (a) bottom temperature and (b) bottom salinity with day of year. The gray dashed lines are linear regression lines, and colored dots are observations of each year.

3. Results

Maps of the sampling locations, number of samples, and contours of interpolated bottom temperature and salinity data collected by NEFSC fall bottom trawl surveys during October–November 2012–2106 are shown in Fig. 2.

3.1. Potential fecundity (PF)

The observed PF ranged 124–3557 eggs per female, and the observed DCL ranged 18.15–30.84 mm. The average PF was 1442 eggs (standard deviation, SD, 620.73) for an average sized female (25 mm DCL) (Table 2). The spatial distribution of DCL in each year is shown in Appendix S2. Spatial autocorrelation was not suggested by semivariance over the sampling area (Appendix S3).

The optimal model for PF included the random effect of year, and the smoothers of bottom temperature and bottom salinity (DCL was included in the base model, Table 3). This model had strong support from the data with an AICc weight of 0.98. The model was

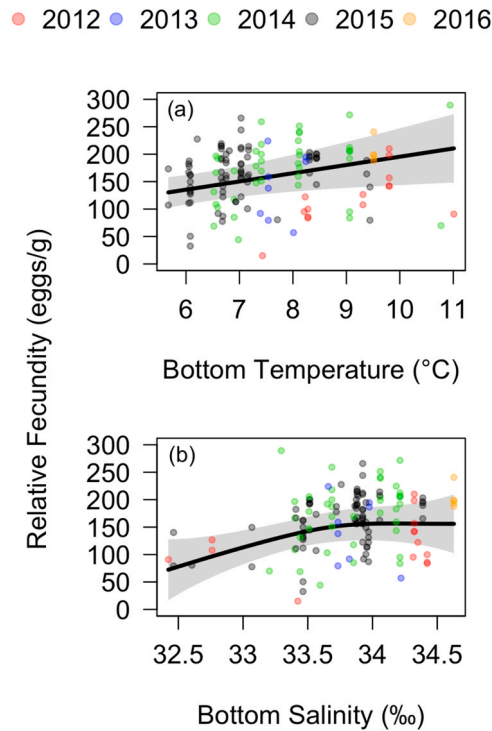


Fig. 7. Partial effects of each variable included in the best model with lowest AICc on relative fecundity (RF). The black solid lines denote the modeled relationship, the gray bands denote the 95% confidence intervals about the estimated relationship, and colored dots are observations of each year.

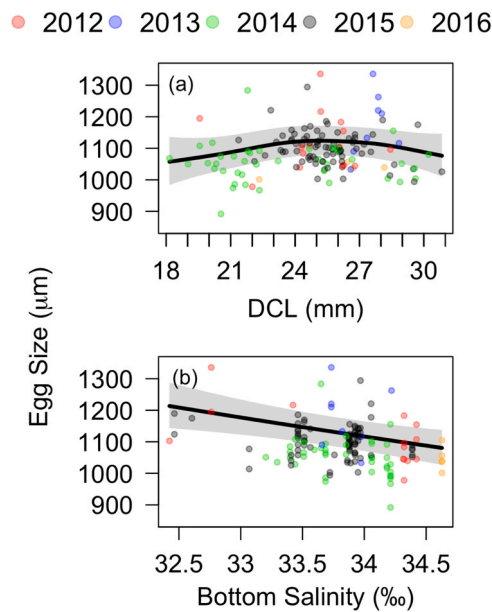


Fig. 8. Partial effects of each variable included in the best model with lowest AICc on egg size (ES). The black solid lines denote the modeled relationship, the gray bands denote the 95% confidence intervals about the estimated relationship, and colored dots are observations of each year.

able to explain 48.4% of the deviance, and the predictive error (i.e. the average bias between prediction and observation) was 476.5 eggs. Both bottom temperature and bottom salinity were significant factors explaining the variation in PF, as the best model out-competed other models (Fig. 3).

The partial effects of predictors are shown in Fig. 4. Both DCL and bottom temperature had estimated degrees of freedom of 1,

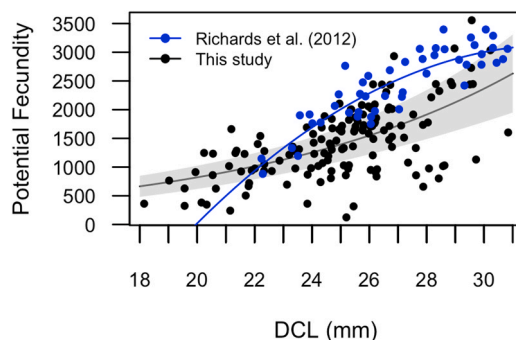


Fig. 9. Relationships between potential fecundity and dorsal carapace length (DCL) estimated by Richards et al. (2012) and this study for northern shrimp (*Pandalus borealis*). The gray shadowed area is the 95% confidence interval for the estimated size-fecundity relationship in this study.

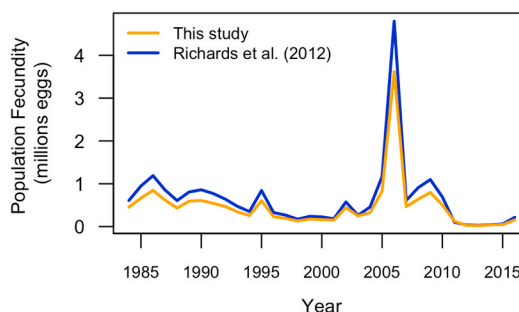


Fig. 10. Annual population fecundity of northern shrimp estimated by PF (potential fecundity) models developed in this study and Richards et al. (2012) using Atlantic States Marine Fisheries Commission (ASMFC) summer shrimp survey data during 1984–2016.

which means the relationships between PF and these two variables are linear via the link function. PF increased with DCL, showing that larger females are able to produce more eggs (Fig. 4a). Biological senescence (i.e. an asymptotic relationship) was not observed for PF. PF was also positively correlated with bottom temperature (Fig. 4b). The relationship between PF and bottom salinity was nonlinear (Fig. 4c). PF increased with bottom salinity when the bottom salinity was lower than 33.9‰, and decreased slightly when bottom salinity was higher than 33.9‰. The semivariance of the Pearson residual errors did not suggest a pattern of spatial autocorrelation (Appendix S4a). No clear patterns were found in the QQ plot and Pearson residuals against fitted values (Appendix S5a–b).

The relationship between bottom temperature and bottom salinity is shown in Fig. 5 (slope=0.076, $p < 0.05$, $r^2 = 0.04$). The observed bottom temperature where shrimp were collected increased with day of year with a slope of 0.028 (Fig. 6a, $p < 0.05$, $r^2 = 0.03$). The observed bottom salinity where shrimp were collected decreased with day of year with a slope of -0.013 (Fig. 6b, $p < 0.05$, $r^2 = 0.06$).

3.2. Relative fecundity (RF)

The observed RF ranged 15.0–289.3 eggs/g of body weight with a mean of 161.9 (SD=52.3), and the observed body weight (without eggs) ranged 3.33–15.8 g (SD=2.4) (Table 2). The optimal random structure for RF included sampling location and year in the model selected by AICc. The best model selected by both AICc and BIC included bottom temperature and bottom salinity with $\omega\text{AICc} = 0.46$ and $\omega\text{BIC} = 0.78$ (Table 3). This model explained 57% of the deviance. Both bottom salinity and bottom temperature were identified as important factors across the top models (relative importance scores of 0.79 and 0.76 respectively). RF was not driven by DCL as DCL was not found in the top models and had a relatively low importance score (Fig. 3).

RF increased linearly with bottom temperature (Fig. 7a), indicating that females with higher reproductive investment were found at higher bottom temperature. Similar to PF, RF increased with bottom salinity when bottom salinity was lower than 33.9‰, and it leveled off when bottom salinity was higher than 33.9‰ (Fig. 7b). The semivariance did not suggest a presence of spatial autocorrelation (Appendix S4b). No patterns were found in the QQ-plot and Pearson residuals against fitted values (Appendix S5c–d).

3.3. Egg size (ES)

The optimal random effect structure selected by AIC included sampling location. The model with the lowest AICc included DCL and bottom salinity with an ωAICc of 0.39 (Table 3). The second best model which included a single factor of bottom salinity was preferred by BIC with a ωBIC of 0.71 ($\omega\text{AICc} = 0.32$). The third ranking model included only bottom temperature, with $\omega\text{AICc} = 0.15$, showing

relatively lower importance of bottom temperature for explaining the variation in ES. Bottom salinity (importance score=0.73) and DCL (importance score=0.50) had higher importance for explaining ES than did bottom temperature (importance score=0.21) (Fig. 3). The top three models within $2 \Delta AICc$ had similar percentages of deviance explained and predictive errors, showing a level of model uncertainty.

The average ES increased with DCL when females were smaller than 25 mm DCL (Fig. 8a), then started decreasing with DCL when females were larger than 25 mm DCL. For the relationship between ES and bottom salinity, the average ES linearly decreased with bottom salinity, with larger eggs found in lower bottom salinity (Fig. 8b). The presence of spatial autocorrelation was not suggested by the semivariance of the Pearson residuals (Appendix S4c). No patterns were found in the plot of Pearson residuals against fitted values (Appendix S5f), although the QQ-plot right tail deviated from a normal distribution due to a few large values of ES observations (Appendix S5e).

3.4. Population fecundity comparison

The females used in Haynes and Wigley (1969) for estimating a size-fecundity relationship ranged 22.2–30.8 mm, and the observed PF ranged 881.7–3396.2 eggs. The stock assessment (ASMFC NSTC, 2018) and Richards et al. (2012) used a parabola to fit Haynes and Wigley's (1969) size-fecundity data (Fig. 9). Their estimated PF was generally higher than that estimated in this study at a given DCL. For example, the estimated PF for a 25 mm female in this study was 1394.0 eggs and was 44% higher in Richards et al. (2012) (2007 eggs). Estimated PF became negative for shrimp with DCL < 20 mm when a parabola was used [as in Richards et al. (2012)]; however, most shrimp <20 mm DCL are males. The average absolute difference between fecundity of females > 22 mm DCL estimated by Richards et al. (2012) and this study was 34.0%.

Population PF estimated in this study using Richards's et al. (2012) model is shown in Fig. 10. The population PF estimated by these two models had similar trends, although Richards's et al. (2012) population PF was almost always higher than the fecundity estimated in this study over the time series except for in 2014. The average absolute difference between population PF was 0.173 million eggs.

4. Discussion

The reproductive characteristics investigated in this study describe different aspects of reproductive investment. PF describes the potential number of eggs a female can produce, and the size-fecundity relationship is typically used to estimate egg production of populations (Hilborn and Walters, 1992). RF puts egg production into the context of energetics by taking into account the size (energy content) of individual females (Dautov et al., 2004; Pereira et al., 2017). RF can also be easily applied to the population size composition for estimating reproductive potential. ES can be an indicator of egg quality, with larger eggs generally thought to be of higher quality as larger eggs contain higher amounts of yolk (Dautov et al., 2004; Zimmermann et al., 2015). This in turn may be related to larval survival (Ramirez-Llodra et al., 2000; Dautov et al., 2004; Zimmermann et al., 2015). All these reproductive characteristics and consequently the reproductive potential of the population may be affected by environmental factors such as water temperature and salinity (Apollonio and Dunton, 1969).

4.1. Potential fecundity and relative fecundity

Relatively higher variability in northern shrimp PF was observed in this study compared to previous studies (Haynes and Wigley, 1969; Apollonio et al., 1986; Table 2). The higher RMSE could be due to sample sizes, ranges and variation in DCL, differences in spatiotemporal scales, sampling seasons, and higher natural variability. High variability in PF between years, seasons, or areas had been observed for Pandalid shrimp by several previous studies (Parsons and Tucker, 1986; Hannah et al., 1995; Jónsdóttir, 2018). Although the PF varied substantially among locations, spatial autocorrelation was not suggested by the spatial variogram for PF in this study.

Several studies have investigated the effects of water temperature on fecundity of northern shrimp (Nunes, 1984; Apollonio et al., 1986; Parsons and Tucker, 1986). Temperature effects were not consistently detected, but when they were, the relationships were negative, i.e. fecundity was lower at higher temperatures. Apollonio et al. (1986) noted that differences in individual fecundity of northern shrimp collected from eight sampling locations in the GOM in August and September 1968 were not significant and could not be correlated with the ambient bottom temperatures. Parsons and Tucker (1986) also found no clear relationship between individual fecundity and ambient temperatures using samples collected intermittently from several locations in Canadian waters (northwest Atlantic) during 1971–1982. However, Nunes (1984) concluded that cold (3 °C) to moderate (6 °C) temperatures were more suitable than high (9 °C) temperature in laboratory studies of northern shrimp egg production in Alaska, as fecundity-at-size was higher for northern shrimp in 3 and 6 °C. Furthermore, Apollonio et al. (1986) reported a negative relationship between predicted mean fecundity of a 25 mm DCL female and annual bottom temperature (April–July) during 1968–1982 (non-consecutive years). In contrast with these previous studies, we found that potential fecundity was positively correlated with temperature. However, bottom temperatures in the GOM have changed considerably since those earlier studies, and northern shrimp population size is much smaller (ASMFC NSTC 2019). The bottom temperature observed in Apollonio et al.'s (1986) study in October–December 1967–1968 ranged ~2–6 °C, and the bottom temperature observed in Oct–Dec in this study ranged 5.7–11 °C with a mean of 7.6 °C. Bottom temperatures in NEFSC bottom trawl surveys in October and November 1967–1968 (temporal and spatial coverage comparable to our study) ranged 3.6–10.1 °C (mean 6.5).

In addition to temperature effects (see Discussion for ES), northern shrimp fecundity could also be affected by factors such as density-dependence (Shumway et al., 1985; Moraes-Valenti et al., 2010; Jónsdóttir, 2018). It has been suggested that ovigerous female GOM northern shrimp may gravitate towards the coldest water available to them when they encounter thermal gradients (Stickney and Perkins, 1977; Shumway et al., 1985). Furthermore, Chang et al. (in prep) found that the variability around the center of gravity of ovigerous northern shrimp distribution was positively correlated with population abundance and negatively correlated with bottom temperature. Therefore, we hypothesized that population density of ovigerous females may be negatively associated with bottom temperature in the GOM, and fecundity is assumed to be negatively correlated with population density due to competition for food and cannibalism of eggs of neighbor females (Elliot, 1970). More data and further analysis are needed to test this hypothesis.

The effect of bottom salinity has been rarely investigated. In our study, around 53% of the females were found in the range of 33.5–34.2‰, and bottom salinity had a very high importance score (0.998) for explaining PF. In the GOM, females undertake an extensive onshore migration to hatch their brood in relatively shallow, less saline water (Fig. 2, Haynes and Wigley, 1969, Apollonio et al., 1986). In our study, bottom salinity was negatively correlated with day of year, which likely reflects the progress of this onshore migration. Thus the high importance score of salinity may reflect changes in the ambient environment during females' inshore migration, rather than a direct association between PF and salinity. Females that have reached lower salinities presumably have been carrying their egg masses longer, so may have had greater egg loss by the time of sampling.

All three of the explanatory factors we investigated (size, bottom temperature and salinity) had high importance scores for explaining variation in fecundity; however, the correlations between PF and variables suggested by the models may not imply causal effects. Other habitat variables associated with bottom temperature or bottom salinity may be important, such as dissolved oxygen or food availability. Brillon et al. (2005) observed that females provide parental care to embryos by beating the pleopods, presumably to oxygenate the egg mass. These habitat variables can also directly or indirectly influence females' fitness, and consequently influence reproductive potential.

RF can be used as a measure of reproductive investment of an individual female. Unlike PF which increased with body size, RF was independent of DCL. Pereira et al. (2017) also found no association between reproductive investment and female body size, suggesting that individuals at all sizes make similar reproductive investment per unit of body. RF was dependent on bottom temperature and salinity and both variables had high importance scores for explaining relative fecundity. The effects of bottom temperature and salinity on RF are similar to that on PF, confirming that higher temperatures and higher salinities were correlated with higher PF and RF during incubation. Bottom temperature and salinity in our study reflected the offshore environment in October and November 2012–2016. As female shrimp migrate to inshore areas for hatching, their exposure to the environment at different stages may change as shown in the correlation between bottom temperature/salinity and day of year. These environmental effects during incubation on the final quantity and quality of eggs need further investigation.

4.2. Size-fecundity relationships

The size-fecundity relationship can be an important input in stock assessment (ASMFC NSTC, 2018). Size-fecundity relationships have been estimated for Pandalid shrimp using parabolic (Richards et al., 2012), power (Parsons and Tucker, 1986; Hannah et al., 1995), and linear regression models (Apollonio et al., 1986). In all of these, the PF was strongly correlated with female body size; however, a high level of variation may exist within sizes. Hannah et al. (1995) indicated that the curvature of the size-fecundity relationship might not be easily detected due to high variation in fecundity at a given length. Therefore, this study used a GAMM to have more flexibility to account for curvilinearity and possible biological senescence, making a biological meaningful size-fecundity relationship covering females at a wide range of sizes.

Comparison between fecundity studies is complicated by several factors in addition to different model structures. These include size range of females sampled; methods for counting number of eggs; and spatial and temporal variation. A lack of small females may result in an incomplete size-fecundity relationship and lead to biased estimates of fecundity for small females (e.g., Haynes and Wigley, 1969). Zero to five percent (mean=1%) of the ovigerous females in our study were smaller than 20 mm, and 0–16% (mean=5%) were smaller than 22 mm during 1991–2018. There could be biases in methods for counting number of eggs if eggs were subsampled and fecundity estimated by expansion. Instead of using estimated number of eggs by weight, we counted all the eggs of an egg mass for each female in this study. Our estimates of PF are thus likely more accurate than fecundity estimated from expanded subsamples. In terms of spatial and temporal variation, fecundity may differ between years and areas due to changes in environmental conditions or diseases (Parsons and Tucker, 1986; Chang et al., 2020). Assuming Haynes and Wigley's (1969) samples (collected during 1953–1966, mostly 1963–1965) were collected from similar environmental conditions as Apollonio et al. (1986) in the 1960 s, the changes in the environment could also be a reason for the differences in the size-fecundity relationships between Richards et al. (2012) and this study.

In this study, spatial patterning or significant differences between years were not observed, which is consistent with the observations of Apollonio et al. (1986). Given the fact that the GOM has been experiencing rapid warming in the past two decades (Pershing et al., 2015; Kavanaugh et al., 2017), it seems possible that the size-fecundity relationship could change due to changes in the environmental conditions. However, the sampling years in this study were mostly warm years and the time series too short to identify a pattern in temporal changes.

4.3. Egg size

ES can be a measure of egg quality as larger eggs contain higher amounts of yolk and produce larger offspring which may be better prepared for competition and predator avoidance (Ramirez-Llodra et al., 2000; Dautov et al., 2004; Zimmermann et al., 2015).

Therefore, ES could be a key factor in determining the success of larval survival. Wieland (2004) observed reduced size-at-sex change of Greenlandic northern shrimp in the late 1990 s and inferred that it could have resulted from smaller eggs due to shorter incubation periods under warmer water temperatures (Wieland, 2005). This implies that temperature could have lagged effects on egg and larval sizes and consequently population productivity. In our study, DCL had a moderate importance score for explaining the variation in ES and the relationship between ES and DCL was nonlinear, which might not be detected by linear regression models (Nunes, 1984; Ahamed and Ohtomi, 2011). Larger females (DCL > 27 mm) produced more eggs but the average ES was smaller, possibly reflecting biological senescence or a tradeoff in quantity versus quality. If egg quality and offspring survival rates are positively associated with ES, then larger females do not necessarily produce offspring with higher survival rates than females at average sizes (around 25 mm DCL). However, our results could also be explained by size-dependent spawning times. If large females spawn later than small ones, larger females would have smaller eggs at an earlier developmental stage at a given sampling time. Apollonio et al. (1986) indicated that females of an older age group spawn later than the younger age group although this has not been well-documented, and the delay in spawning time between age groups was not estimated.

Although Clarke et al. (1991) suggested that factors determining reproductive output and egg size are different, in our study bottom salinity was identified as an important factor for explaining PF, RF, and ES with high importance scores across models. However, PF and RF were positively correlated with bottom salinity, while ES was negatively correlated with bottom salinity. This likely reflects progress of the inshore migration because eggs develop and ES increases over time while bottom salinity decreases as the females migrate towards the shore.

4.4. Other factors

The models we built in this study were able to explain 48–59% of the variation in PF, RF, and ES. Other factors that might explain variation in reproductive potential and fitness of female shrimp include food availability (Hannah et al., 1995), population density (Apollonio et al., 1986), disease (Chang et al., 2020), and egg loss during incubation (Elliot, 1970; Skuladottir et al., 1978; Stickney, 1981; Nunes, 1984; Apollonio et al., 1986; Brillon et al., 2005). Skuladottir et al. (1978) estimated 30–54% egg loss during seasonal migration in Iceland, and Brillon et al. (2005) observed high variation in individual egg loss (1–99%) during incubation in laboratory experiments. The ovigerous females sampled in this study were collected from an early phase of incubation (October–November), thus the fecundity estimates would not reflect total egg loss during the entire incubation period (5–6 months). Further investigations are needed for evaluating egg loss during incubation for GOM northern shrimp.

Several explanations have been observed or postulated for egg loss, including diseases (Apollonio et al., 1986), incomplete fertilization (Parsons and Tucker, 1986), cannibalism by neighboring shrimp, parental behavior (Elliot, 1970), and temperature (Brillon et al., 2005). Brillon et al. (2005) observed higher egg loss when ambient temperature of females increased, but Nunes (1984) reported highest egg loss at low temperature. Brillon et al. (2005) suggested that more intense movements of pleopods may be needed in warmer temperatures for ovigerous females to supply the higher oxygen demand of developing embryos, which might increase egg loss during incubation.

In addition to egg loss, ambient temperature during incubation could also affect size of larvae at hatching (Nunes, 1984; Brillon et al., 2005). Although the temperature effect was less important than DCL and bottom salinity on ES in this study, in laboratory studies larger larvae were observed to hatch from eggs incubated at lower temperatures with higher survival rates and growth rates in Alaskan waters (Nunes, 1984) and in the St. Lawrence estuary (Brillon et al., 2005).

A number of hypotheses have been postulated or tested for explaining the most recent collapse of the GOM northern shrimp population. Chang et al. (2020) examined the effects of bottom temperature and salinity on the incidence of parasitized eggs (white eggs) of the GOM northern shrimp, but correlations between white eggs and environmental factors were not significant. Richards (2012) observed that the hatching timing and duration of the GOM northern shrimp hatch period has shifted; however, the match-mismatch theory (Hjort, 1914; Cushing, 1990) was not able to explain variation in shrimp survival at early life stages (Richards et al., 2016). Richards and Hunter (2021) presented evidence that the sudden shrimp population collapse might have been due to a spike in predation by longfin squid (*Doryteuthis pealeii*) after a distributional shift during the 2012 heatwave. (Charleson, 2020) observed decreases in size-at-transition of northern shrimp at higher water temperatures, which could result in smaller average female size and consequent skewed population size structures, leading to decreased reproductive potential. Chang et al. (in prep) examined habitat suitability for adult GOM northern shrimp during summer and fall and found that increasing proportions of low quality habitat were correlated with a declining spawning stock biomass index at a 2-year lag. Consequently, in addition to changes in reproductive potential of the GOM northern shrimp, high predator pressure and loss of suitable habitat might be limiting population size in the GOM.

5. Conclusions

This study examined three different measures of reproductive output of GOM northern shrimp and their relationships with biotic and abiotic factors. PF quantified reproductive potential of an individual female, and the size-fecundity relationship derived from this study can be used for estimating egg production of the shrimp population. PF was most strongly correlated with female body size, yet our results showed that the ambient environmental conditions (bottom temperature and salinity) were also important for explaining the variation in PF. RF was independent of female body size, suggesting that relative reproductive output is constant across female size. RF was affected by environmental conditions similarly to PF. ES declined in large females (> 27 mm DCL), which could indicate biological senescence or may reflect differences in spawning times of large and small females. In contrast with previous studies, PF and

RF were positively correlated with bottom temperature in the relatively warm years of our study. We hypothesize that the positive temperature-fecundity relationship we observed may not reflect a direct effect, but possibly a compensatory response relating to decreased population density during the time period of our study. In addition, the environmental effects we observed may to some extent reflect progression of the inshore migration of females.

GOM northern shrimp are considered vulnerable and sensitive to environmental variability as they are at the southernmost of their distribution. Various hypotheses for the most recent collapse of the GOM northern shrimp population examined or tested in this and previous studies suggest there may be multiple factors undermining population growth and sustainability, primarily through indirect effects. Accordingly, reproductive potential should be monitored and considered in evaluating population dynamics for such vulnerable species, because it plays an important role in the process of population recovery.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at [doi:10.1016/j.gecco.2021.e01774](https://doi.org/10.1016/j.gecco.2021.e01774).

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