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Original Article

Recent declines in American lobster fecundity in southern New England: drivers and implications

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Lobsters in southern New England (SNE) have experienced decades of environmental stressors along with a suite of emerging diseases. We hypothesized that the sublethal effects of physiological stress resulting from increased temperatures have contributed to a decline in reproductive investment in SNE lobsters. Using the presence of epizootic shell disease (ESD) as a proxy for stress, we examined lobster potential fecundity through the number of recently extruded, early-stage eggs and their nutritional quality; realized fecundity based on counts of late-stage eggs nearing hatch; and compared realized fecundity to historical data (1980s) from the region. Generalized linear modeling revealed that female size was a significant predictor of both potential and realized fecundity as expected, but that ESD status did not result in differences in fecundity. Dry weight was the only difference in nutritional content egg^{-1} between non-diseased and diseased females. There was also no relationship detected between potential fecundity and any nutritional metric from non-diseased females. However, both dry weight and protein were negatively correlated with potential fecundity in diseased females. Most importantly, realized fecundity of recent-day females was significantly reduced compared to the fecundity of historical females, characterized as a 23% decrease predicted by our model. Stressful environmental conditions, particularly temperature, may have contributed to decreased fecundity over a 30-year period in SNE. Our data demonstrate that expectations around the potential for the SNE stock to rebuild need to be adjusted to this new regime of decreased reproductive output and can no longer rely on past estimates of egg production and recruitment.

Keywords: egg quality, epizootic shell disease, fecundity, female reproductive investment, *Homarus americanus*, southern New England, thermal stress

Introduction

The health and stability of populations is affected by the life-history strategies that organisms adopt toward increasing their fitness. Such strategies impact life expectancy, growth rate, size at maturity, larval duration, and the allocation of resources that contribute to reproductive performance. For most invertebrates with brooding modes, reproductive output consists of the number of eggs (fecundity) as a trade-off to the size of those eggs (quality), optimized over time to maximize reproductive success (reviewed in Ramirez Llodra, 2002). The ability to assess and describe fecundity provides a powerful and informative tool by which to gauge population dynamics, and enhance our understanding of change over time, as well as the drivers that contribute to that change (Hadfield and Strathmann, 1996). This is particularly important for many decapod crustaceans (crabs and lobsters), where estimates of fecundity have been used in evaluating and modelling biological reference points (e.g. egg-per-recruit, spawning stock biomass) in the valuable fisheries that they support (Green *et al.*, 2014; Swiney and Long, 2015; Gardner *et al.*, 2020). Appraising fecundity is especially crucial for the American lobster (*Homarus americanus*), the single largest and most valuable single-species fishery in North America (NMFS, 2019; ASMFC, 2020), as well as within the context of climate vulnerability and change in other areas of the fishery (e.g. Mazur *et al.*, 2020).

The maintenance of egg production has been a cornerstone of management for the US lobster fishery, and many tools intended to conserve broodstock have been implemented over time (e.g. protection of ovigerous females, v-notching; Miller, 1995; Le Bris *et al.*, 2018; ASMFC, 2020). Fecundity data supporting this management strategy have been available for over 100 years, dating back to the seminal work by Herrick (1896), and have since included estimates over most of the fished range for lobsters from Newfoundland to southern New England (SNE) (reviewed in Fogarty, 1995; Cobb and Castro, 2006). Some overarching patterns from previous studies suggest that (1) fecundity is directly scaled with lobster size (Waddy *et al.*, 1995); (2) fecundity changes over a large spatial scale, such that geographically based differences in overall brood sizes are apparent (Cobb and Castro, 2006; Currie and Schneider, 2010); and more recently, (3) declines in fecundity and increases in egg loss have been reported in some areas, raising concern for future recruitment success and health in these stocks (Koopman *et al.*, 2015; Tang *et al.*, 2018). American lobsters follow an investment strategy of producing few, but larger eggs relative to other lobsters (Waddy *et al.*, 1995), with a prolonged egg incubation period (9–11 months) governed primarily by temperature (Aiken and Waddy, 1980). In general, mature females produce egg broods once every 2 years and can have a reproductive lifespan of decades in the absence of harvest (Waddy *et al.*, 1995).

The suite of factors that may impact fecundity in Homarid lobsters is wide ranging and includes maternal history, nutrition, size at maturity, environmental conditions (e.g. temperature and salinity), and stress (Waddy *et al.*, 1995; Ellis *et al.*, 2015; Koopman *et al.*, 2015; Goldstein and Shields, 2018; Tang *et al.*, 2018). We view "stress" in this case as a product "from conditions where an environmental demand exceeds the natural regulatory capacity of an organism" (Koolhaas *et*

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al., 2011), while a "stress response" is assumed to imply a deleterious response that may include reduced reproductive output (Stoner, 2012). Thermal stress is probably one of the most widely known stress factors in American lobsters that directly and negatively impacts many physiological responses, including gas exchange, immune response, acid–base regulation, and cardiac performance (Whiteley *et al.*, 1997; Jury and Watson, 2000; Dove *et al.*, 2005; Worden *et al.*, 2006; Qadri *et al.*, 2007). Temperature also modulates most aspects of lobster reproductive physiology (reviewed in Quackenbush, 1994), including vitellogenesis (Dehn *et al.*, 1983), egg development, and hatching (Perkins, 1972; Haarr *et al.*, 2020), causing pernicious effects on these energy-demanding processes under sustained and elevated thermal conditions (Aiken and Waddy, 1986; Sasaki *et al.*, 1986; Goldstein and Watson, 2019).

One longer-term outcome of thermal stress appears to be the increased incidence of emerging diseases and syndromes in the southern New England stock (Shields, 2013, 2019). Epizootic shell disease (ESD) is the most prominent of these diseases, primarily characterized as an external condition caused by bacterial degradation of the shell, leaving erosions and pits that in severe cases penetrate the endocuticle (Chistoserdov *et al.*, 2005; Smolowitz *et al.*, 2005; Meres *et al.*, 2012; Feinman *et al.*, 2017). This disease is easily identifiable, even leaving scars on newly molted lobsters that had severe cases of ESD prior to molting (Stevens, 2009). The amount of the shell affected, and the degree of degradation worsen over time, and temperature is linked to the rate of ESD progression, although other unknown factors also appear to play a role (Tlusty *et al.*, 2014; Barris *et al.*, 2018). Severe cases with extensive penetration into the endocuticle can result in mortality during molting, as the lobster fails to extract itself from the old shell (Stevens, 2009). Several studies have proposed that the presence of shell disease is an external symptom of internal physiological distress in an individual lobster (Sindermann, 1989; Castro *et al.*, 2006; Tlusty *et al.*, 2007; Shields *et al.*, 2012).

ESD has been widely observed and documented in the SNE lobster stock since the late 1990s (Castro and Angell, 2000; Glenn and Pugh, 2006; Castro and Somers, 2012), affecting >50% of the catch for several inshore portions of the region (Castro and Angell, 2000; Groner *et al.*, 2018; Pugh and Glenn, 2020). Ovigerous females have the highest prevalence of ESD symptoms due to their prolonged intermolt period associated with brooding egg clutches (Glenn and Pugh, 2006; Castro and Somers, 2012). The increasing prevalence of ESD is tied with warming waters in the nearshore SNE environment, particularly temperatures >20°C (Glenn and Pugh, 2006; Groner *et al.*, 2018; ASMFC, 2020). Declines in the SNE stock abundance have also been linked to this period of increasing water temperature and strong positive temperature anomalies (Oviatt, 2004; Nixon *et al.*, 2004; LeBris *et al.*, 2018; ASMFC, 2020), and work has linked increasing shell disease prevalence to decreases in recruitment in SNE (Wahle *et al.*, 2009), due in part to the associated mortality (average of 70% mortality in moderate to severe ESD) in ovigerous females (Hoenig *et al.*, 2017).

As thermal stress likely plays a role in ESD and other associated diseases (e.g. excretory calcinosis, Dove *et al.*, 2004) in the SNE lobster stock, stress may also affect a female lobster's ability to produce eggs or reduce the quality (energy content) of those eggs (Sasaki *et al.*, 1986; Attard and Hudon, 1987; Ouellet and Plante, 2004; Miller *et al.*, 2013; Koopman *et al.*, 2015; Goldstein and Watson, 2019). The influence of environmental and disease stress has been documented in several marine invertebrates, and can negatively affect offspring fitness (Marshall and Keough, 2004, 2008). Because of the documented linkage between ESD and thermally-stressful water temperatures, here we use the presence of ESD as an easily detectable symptom to indicate physiological deficiency (stress) in an individual lobster; this assumes that a lobster acquires ESD due to an underlying compromised health status, which is consistent with the host-susceptibility hypothesis (Tlusty *et al.*, 2007). Thus, the overall objective of this work was to use ESD as a stress indicator to examine lobster reproductive capabilities with regard to the presence or absence of this factor. We used potential fecundity and egg quality to examine initial reproductive investment (number and quality of early-stage eggs), as well as realized fecundity (number of late-stage eggs) in female lobsters with and without ESD collected from the nearshore waters of southern Massachusetts within the SNE stock. We explored the hypothesis that diseased females produce fewer eggs, and that those eggs would be of lower quality compared to non-diseased females. Complementary to this, we also tested the hypothesis that lobster fecundity has decreased over time by using a historical fecundity dataset for lobsters sampled in the same area to explore whether fecundity has changed over a 30-year period.

Methods

Fecundity definitions

Here, we describe fecundity as the total number of eggs produced within a single clutch/brood, and have further categorized fecundity into two distinct events: (1) potential fecundity, or the total investment to eggs, counted as the number of recently spawned or extruded eggs attached to the female's abdomen; and (2) realized fecundity, or the total number of late-stage eggs attached to the female's abdomen that are nearing hatch (Ramirez Llodra, 2002). Thus, females with early-stage (newly extruded) eggs are designated as potential fecundity females; females with late-stage (nearing hatch) eggs are described as realized fecundity females. Females from data collected in 1987–1988 (Estrella and Cadrin, 1995), are referred to as historical females, and were obtained at a similar time of year and egg stage, to our realized fecundity (late-stage) females collected in 2017–2018. As the historical data were collected prior to the onset of ESD (Castro and Somers, 2012), and before the inception of documented stressful environmental conditions (Estrella and Cadrin, 1995; ASMFC, 2020), we assumed these data were representative of lobsters experiencing substantially less environmental stress, and therefore serve as a reference sample for "healthy" lobsters in the SNE stock.

Lobster collection and assessment

Ovigerous female lobsters were collected by Massachusetts Division of Marine Fisheries (MADMF) biologists aboard commercial lobster vessels from the study area in the nearshore waters off southern Massachusetts (within an 8-km region roughly surrounding 41°18′44″N 70°57′48″W) under a National Marine Fisheries Service (NMFS) Experimental Fishing Permit (EFP permit # 16077; sample sizes in Table 1). Females were obtained over temporal windows corresponding with the timing of egg development, specifically targeting two distinct groups: (1) females with recently spawned, early-stage eggs collected in early fall 2016 for determination

Table 1. The total number of ovigerous females from our sampling and historical data.

Female type	Analysis type	ESD status	Total	Non-cull	Cull	CL range (mm)
Potential fecundity	Fecundity	Non-diseased	32	23	9	73–94
Potential fecundity	Fecundity	Diseased	144	118	26	72–99
Potential fecundity	Egg quality	Non-diseased	19	12	7	77–93
Potential fecundity	Egg quality	Diseased	35	29	6	75–87
Realized fecundity	Fecundity	Non-diseased	16	10	6	77–95
Realized fecundity	Fecundity	Diseased	91	78	13	74–102
Historical (1980s)	Fecundity	Non-diseased	152	–	–	71–102

The above table shows the number of individuals who were non-diseased (no active ESD), diseased (active ESD), and culled (missing or regrowing chelae), with carapace length (CL).

of initial clutch sizes (potential fecundity) and egg quality; and (2) females bearing late-stage eggs collected in late spring/early summer 2017–2018, just prior to hatching, to determine how many eggs were fully developed and should successfully hatch (realized fecundity). In addition to gross egg condition, individuals were selected based on size to obtain a sufficient number of samples per size bin and by prioritizing non-cull lobsters (i.e. both major chelae intact). However, due to the limitations of sampling within critical temporal egg staging windows, lobsters at various stages of claw regrowth from absent to regenerated were sampled. Upon removal from traps, each ovigerous female was immediately wrapped securely in cheesecloth (to avoid tail-flipping behaviour and subsequent egg loss; Aiken and Waddy, 1982), placed in insulated totes under damp burlap, and kept cool.

After each collection trip, all lobsters were immediately transported to the University of Massachusetts Amherst Gloucester Marine Station (Gloucester, MA, USA), and placed in individual holding containers in a flow-through seawater tank; females were then processed within 24–48 h. Descriptive information was collected for each ovigerous lobster including carapace length (CL, to the nearest mm), gross egg stage, and cull status. Each female was closely examined to determine the presence or absence of ESD. Severity of ESD was not considered for this work because linking the onset and progression of disease to the timing of available resources for reproductive investment was not practical with our field-based study design. All lobsters were individually tagged with a cinch-up knuckle band and egg masses were preserved in one of three ways: (1) keeping lobsters cold until further processing (for potential fecundity); (2) severing tails (with eggs intact) and storing these in a 95% ethanol solution; and (3) stripping eggs by hand and storing all eggs in a 95% ethanol solution. All egg samples were held in glass storage jars, then transported in temperature-controlled coolers to the Wells National Estuarine Research Reserve (Wells, ME, USA) laboratory for egg processing.

Egg staging

We verified that egg clutches for each ovigerous female were early- or late-stage by manually removing ~20 eggs from the center of each clutch using forceps. The eggs were stored cold in vials with 4% sterile seawater and buffered formalin solution (Goldstein and Watson, 2015). Each egg was examined microscopically to determine Perkins eye index (PEI; Perkins, 1972) and developmental progress, using well-documented egg staging methods (Helluy and Beltz, 1991). Only females with egg clutches where eggs contained eyespots <18% developed (50–70 μm PEI), were retained for analyses of potential fecundity and egg nutritional quality, as we were specifically aiming to examine eggs that contained a full complement of nutritional investment (Sasaki *et al.*, 1986). Conversely, egg clutches that yielded 80–85% development (450–500 μm PEI) were considered close to hatching (i.e. late stage; Helluy and Beltz, 1991) and therefore suitable for realized fecundity analyses.

Egg clutch preparation

Each female's egg clutch was removed by dipping and gently agitating the entire abdomen for 2–3 min in an 18:1 seawater-sodium hypochlorite (bleach) solution bath and then straining the dropped eggs from the liquid through a mesh sieve to remove the cement matrix holding the eggs together (Johnson *et al.*, 2011). Eggs from each clutch were then washed and rinsed multiple times with cold seawater (32–35 psu). For purposes of retaining and stabilizing all potential egg nutritional constituents for egg clutches associated with potential fecundity, once these eggs were stripped, the clutches were immediately frozen at −80°C for ~1 week after which they were freeze-dried at −40°C for 24 h (Labconco Freeze Dryer 5, Kansas City, MO, USA), and dry weights then calculated to the nearest 0.0001 g. For realized fecundity egg clutches, rinsed eggs were dried in an oven for 24 h at 60°C. Dried eggs were cleaned over coarse metal mesh sieves (850 and 500 μm) to remove additional cementin filaments, setae, and debris. Total egg clutches were weighed to the nearest 0.0001 g to obtain the dry weight of each clutch, and then divided by fecundity to determine dry weight egg^{-1}.

Fecundity estimates

Fecundity estimates (both potential and realized fecundity) were determined following the general methodology of Estrella and Cadrin (1995) for purposes of historical comparison. A total of three 1-g subsamples from each clutch were weighed to the nearest 0.0001 g then counted, and the average count scaled up to total clutch weight to estimate total clutch size (number of eggs) for each lobster. As a check of our methods, we also employed two cross validation exercises to confirm that our estimates were within an acceptable margin of error. First, a total of three 200-egg samples were weighed for a subset of lobsters ($n = 12$) and then scaled to our subsample weights, giving us an overall error of 0.43%, which was within range of the Estrella and Cadrin (1995) study. Second, we blindly selected one clutch (76-mm CL lobster) and hand counted the entire clutch, then compared the result with the subsampling-generated estimate, yielding a 20-egg difference.

We used generalized linear models (GLM) to examine the effect of ESD on potential and realized fecundity in female lobsters. Fecundity was modeled with a gamma error dis-

tribution (exponential family) and log link function as data were positive, right skewed, and variance tended to increase with the mean. Covariates included in the global model were lobster size (CL; continuous variable), ESD status (categorical with two levels: non-diseased and diseased), and cull status (categorical with two levels: non-culled and culled) using all possible interactions due to the potential combined influence of the covariates on fecundity. Culled is defined as either or both claws missing or regenerating. Cull status was included because we assumed claw regrowth could affect resources available for investment in reproduction. Model selection, including evaluation of the null model, was accomplished using the Akaike information criterion, corrected (AICc), with models ≤4 ΔAICc considered to have similarly strong support (Burnham and Anderson, 2004). Fit of the top candidate models was evaluated based on examination of the residuals. Differences between the top model candidates were tested using Analysis of variance (ANOVA), with non-significant *p*-values indicating no difference between competing models in explaining variation in the data. Nagelkerke's pseudo-R^2 were also reported to indicate how well the models fit the data (Nagelkerke, 1991).

Realized fecundity from the current study for females (n = 107; CL range = 74–102 mm) were also compared to results from a previous fecundity study using late-stage eggs from lobsters in the nearshore waters off southern Massachusetts (Buzzards Bay) in 1987–1988 (n = 152; CL range = 71–102 mm; Estrella and Cadrin, 1995). GLMs (gamma error distribution and log link function) were fit to examine the effect of time period, with CL and time period (categorical with two levels: historical and recent) as covariates. The most parsimonious model was selected based on AICc, as described above.

We also examined differences between potential fecundity (early-stage clutches) and realized fecundity (late-stage clutches) at any given female size to represent an estimate of egg loss, which were compared to previous estimates of egg loss rates (Perkins, 1971). Mean egg loss between early- and late-stage clutches was calculated based on differences between potential fecundity (in 2016) and realized fecundity (in 2017–2018) by 5-mm-CL size bins to control for the size-fecundity relationship (Waddy *et al.*, 1995).

Egg quality

To examine the effect of ESD on initial egg quality, we quantified the nutritional condition for a subset of the potential fecundity female clutches (n = 54) using a series of common biochemical assays (e.g. Attard and Hudon, 1987; Koopman *et al.*, 2015) comparing eggs from non-diseased and diseased females. Total lipids were quantified gravimetrically using protocols detailed in Bligh and Dyer (1959). This procedure consisted of using a modified ratio of 1:2:2.5 chloroform–methanol–water extraction, respectively. Triplicate samples from each clutch (60 eggs sample^{-1}) were dried for 24 h at 37°C and stored in a glass desiccator before being weighed. Total protein levels were determined with a modified Lowry method (Lowry *et al.*, 1951), using Coomassie Brilliant Blue G-250 reagent (Bio Rad protein assay kit) and bovine serum albumin as a standard (Bio-Rad Laboratories, Hercules, CA, USA). In brief, six replicate samples (60 eggs sample^{-1}) were digested in 1N NaOH, filtered, and read on a clinical spectrophotometer (Beckman DU-250; λ = 595). Detailed protocols for both total lipids and proteins can be found in Goldstein (2012). Dry ash content was evaluated by weighing out two replicates of 200 dried eggs and using a modified method for determining total inorganic ash (AOAC, 2000). We burned each sample in pre-weighed, aluminum dishes in an Isotemp Programmable Muffle Furnace (Fischer Scientific, Pittsburgh, PA, USA) at 550°C for a total of 5 h, after which all samples were cooled and then re-weighed.

To evaluate differences in nutritional metrics between lobsters with either no active ESD (non-diseased) or active ESD (diseased), two-way *t*-tests with equal variances or Mann–Whitney *U*-tests (α = 0.05) were used after testing for normality. Extreme outliers, defined as the first quartile minus- and the third quartile plus-three times the interquartile range, were excluded from analyses due to their influence on the result using the *rstatix* package in R (Kassambara, 2021), but are not assumed to be observation error as they fall within reported ranges (n = 2; 479.72 and 253.50 μg lipids egg^{-1}). Mean ± standard deviation is reported. Comparisons of means and medians for egg nutrition are representative of the sampling unit (ash: 200 eggs; lipids and proteins: 60 eggs), and we also calculated per egg values as part of our overall results. Relationships between female size or fecundity and nutritional metrics were examined with Pearson's r correlation test, or Spearman's *rho* when normality assumptions were violated. All statistical analyses were performed in R (R Core Team, 2020).

Results

Despite our efforts to collect similar numbers of non-diseased and diseased ovigerous females, most of the ovigerous females collected had active ESD (Table 1). For all potential fecundity females, 149 of 185 individuals had active ESD (80.5%). Prevalence of females with active ESD was slightly higher for realized fecundity females at 85.0% (91 of the 107 individuals sampled).

Fecundity

Regardless of ESD status, potential fecundity was 10580 ± 3751 eggs for lobsters with a mean CL of 84 ± 4 mm; realized fecundity was 7527 ± 3945 eggs for lobsters with a mean CL of 86 ± 6 mm. Estimates of egg loss within 5-mm-CL size bins ranged from 21.7 to 40.9% with the lowest losses observed in the smallest (71–75 mm CL) and the largest (91–100 mm CL) size classes of diseased females. Low sample sizes made egg loss comparison difficult in some size bins; for example, two non-diseased realized fecundity females 91–95 mm CL had larger clutches compared to the two similarly sized non-diseased potential fecundity females (Table 2).

The most parsimonious GLM for both potential and realized fecundity included CL only (Table 3). The addition of more variables (either ESD and/or cull status, additive or interacting) resulted in slight increases in AIC (≤4 ΔAIC; Table 3), showing that several models for potential or realized fecundity were similarly supported. Yet, all the top models indicated that only female size had a significant effect on fecundity, with non-significant variation between groups with differing ESD or cull status (see Supplementary Appendix for coefficients of the similarly-supported models). ANOVA tests further showed that there were no significant differences in the top, reduced model (fecundity ~ CL) compared to more com-

Table 2. Mean fecundity and summary statistics of females, split by potential fecundity and realized fecundity in 5-mm-CL size ranges and by ESD status.

CL range	ESD status	*n*	Minimum	Maximum	Mean	*SD*	% Egg loss
Potential fecundity							
71–75	Non-diseased	1	–	–	7 915	–	–
76–80	Non-diseased	6	4 156	12 465	8 491	3 089	–
81–85	Non-diseased	23	3 963	16 056	10 896	3 285	–
91–95	Non-diseased	2	7 422	15 447	11 435	5 675	–
71–75	Diseased	7	4 951	9 299	7 430	1 924	–
76–80	Diseased	15	999	15 557	8 858	3 647	–
81–85	Diseased	77	214	16 435	10 304	3 493	–
86–90	Diseased	33	5 666	19 761	11 797	3 303	–
91–95	Diseased	11	372	20 918	12 791	5 304	–
96–100	Diseased	1	–	–	21 500	–	–
Realized fecundity							
76–80	Non-diseased	5	4 295	7 384	5 248	1 232	38.2
81–85	Non-diseased	7	2 799	10 071	6 486	3 016	40.5
86–90	Non-diseased	2	7 306	11 180	9 243	2 739	–
91–95	Non-diseased	2	8 050	16 517	12 284	5 987	−7.4
71–75	Diseased	3	3 778	9 655	5 782	3 355	22.2
76–80	Diseased	13	1 532	11 830	5 906	3 125	33.3
81–85	Diseased	32	1 935	12 632	6 480	2 948	37.1
86–90	Diseased	22	2 537	12 936	6 969	3 046	40.9
91–95	Diseased	16	3 265	17 560	9 912	4 427	22.5
96–100	Diseased	3	12 862	22 355	16 831	4 934	21.7
101–105	Diseased	2	11 271	15 565	13 418	3 036	–

Egg loss is the difference in mean potential fecundity and realized fecundity, as a percentage, with negative values indicating increased clutch sizes.

Table 3. Selection table of the top candidate GLM of fecundity.

Model	ΔAICc	ω_i	DF	pseudo-R^2
Recent-day potential fecundity ~				
CL	0.00	0.43	3	0.10
CL + ESD	1.98	0.16	4	0.10
CL + Cull	2.09	0.15	4	0.10
CL * Cull	3.90	0.06	5	0.10
Recent-day realized fecundity ~				
CL	0.00	0.36	3	0.28
CL + Cull	1.45	0.18	4	0.28
CL + ESD	2.12	0.13	4	0.28
CL * Cull	2.83	0.09	5	0.29
CL + ESD + Cull	3.50	0.06	5	0.28
CL * ESD	3.50	0.06	5	0.28
Historical comparison realized fecundity ~				
CL + Time	0.00	0.71	4	0.43
CL * Time	1.83	0.29	5	0.43

plex models that included ESD or cull status (all $p > 0.05$). The size-fecundity relationship was observed for both potential and realized fecundity females (Figure 1). Potential fecundity was predicted to be 11222 eggs (10645–11830 eggs; 95% confidence interval [CI]) for females at minimum legal size (86 mm CL). For lobsters at the maximum size in our dataset (99 mm CL), potential fecundity was predicted to be 17294 eggs (14595–20493 eggs; 95% CI). Similarly, realized fecundity was predicted to be 7390 eggs (6793–8039 eggs; 95% CI) for 86-mm CL females and 14764 eggs (11487–18975; 95% CI) for 102-mm-CL females.

We also compared historical and recent-day realized fecundity using GLMs (Figure 2). After model selection and validation, the most parsimonious model was

$$Fecundity_i = \beta_0 + \beta_1 CL_i + \beta_2 Timeperiod_i + gamma(\varepsilon)_i. \quad (1)$$

The only other model with ΔAICc ≤ 4 compared to model (1) included CL and time period as multiplicative covariates (Table 3). However, this model was not selected as it had a higher AICc, ANOVA indicated that it was not significantly different from the additive model, and it was more complex hindering interpretability. Model (1) results show that CL had a significant positive effect on fecundity ($\beta_1 = 0.05 \pm 0.003$ standard error (SE) , $p < 0.001$), and recent-day fecundity was significantly lower compared to historical females ($\beta_2 = -0.26 \pm 0.05$ SE, $p < 0.001$). The exponentiated coefficient (i.e. coefficient on the response scale) for CL is 1.05, and is a multiplier on fecundity unit^{-1} increase in CL when holding time period constant. The exponentiated coefficient is 0.77 for a change from historical to recent-day fecundity when holding CL constant. Hence, model (1) predicts a realized fecundity of 9601 eggs (9028–10211 eggs; 95% CI) for 86 mm CL historical females, and 7398 eggs (6888–7947 eggs; 95% CI) for recent-day females of the same size, representing a 23% decrease.

Egg quality

All measures of egg nutritional content that we evaluated demonstrated no significant correlation with the size of females, given a range of 75–93 mm CL [dry weight egg^{-1}: Pearson's $r(43) = 0.03$, $p = 0.83$; ash: Pearson's $r(45) = -0.05$, $p = 0.73$; lipids: Spearman's $r(47) = -0.003$, $p = 0.98$; proteins: Pearson's $r(28) = 0.11$, $p = 0.57$]. Thus, we did not include CL as a covariate in further analyses of egg quality.

There were no significant differences between non-diseased (ND) and diseased (D) lobsters' egg nutritional content for: ash [$M_{ND} = 9.48$ mg, $n = 17$; $M_D = 9.40$ mg, $n = 30$; $t(45) = 1.21$, $p = 0.23$]; lipids ($Mdn_{ND} = 39.17$ mg, $n = 15$; $Mdn_D = 36.08$ mg, $n = 34$; $W = 290.5$, $p = 0.45$); and proteins [$M_{ND} = 12.86$ mg, $n = 11$; $M_D = 13.06$ mg, $n = 19$; $t(28) = -0.24$, $p = 0.81$; Figure 3]. Diseased females produced significantly heavier eggs based on dry weight egg^{-1}

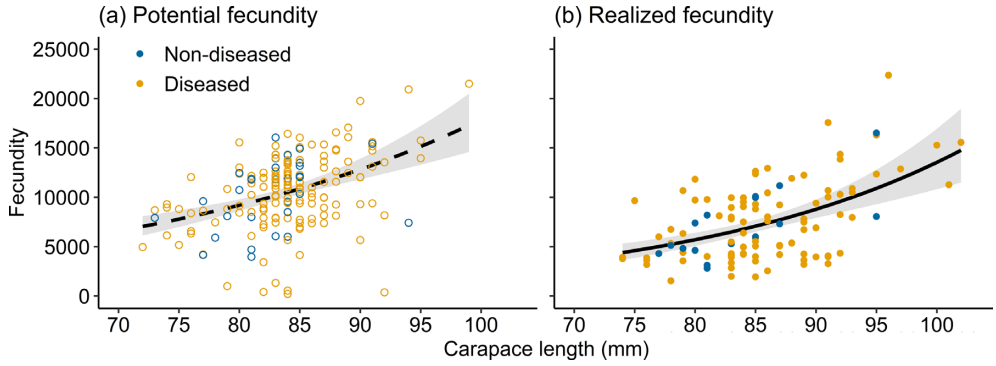

Figure 1. Potential and realized fecundity in relation to CL for females off the southern coast of Massachusetts from 2017 to 2018. Grey bands represent the 95% CI .

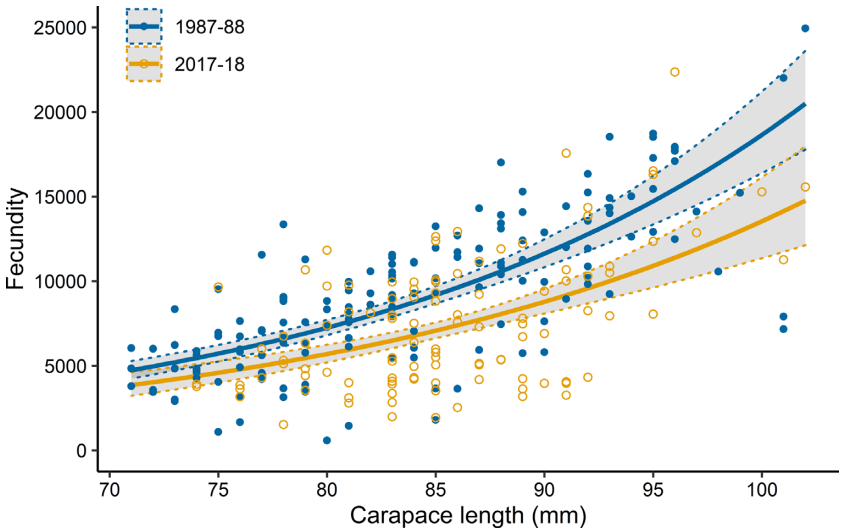

Figure 2. Realized fecundity in relation to CL for females off the southern coast of Massachusetts. Grey bands represent the 95% CI of each regression. Historical data (1987–1988) are sourced from Estrella and Cadrin (1995).

($Mdn_{ND} = 1032.02$ µg, $n = 15$; $Mdn_{D} = 1217.82$ µg, $n = 30$; $W = 116$, $p = 0.008$).

Ash and lipid content were not correlated with fecundity for either disease state [ash_{ND}: Spearman's $r(15) = -0.31$, $p = 0.26$; ash_{D}: Spearman's $r(28) = -0.06$, $p = 0.74$; $lipids_{ND}$: Spearman's $r(13) = 0.52$, $p = 0.07$; $lipids_{D}$: Spearman's $r(32) = -0.11$, $p = 0.57$; Figure 4]. However, there were differences in the relationship with fecundity for dry weight and protein content of eggs from non-diseased and diseased females. Dry weight egg^{-1} decreased with increasing fecundity in diseased females [Spearman's $r(28) = -0.64$, $p < 0.001$], but had no correlation with fecundity in non-diseased females [Spearman's $r(13) = 0.45$, $p = 0.09$]. Similarly, protein content in the eggs of diseased females significantly decreased with increasing fecundity [Pearson's $r(17) = -0.53$, $p = 0.02$], whereas there was no correlation between protein content with fecundity for non-diseased females [Pearson's $r(9) = 0.46$, $p = 0.15$].

Discussion

Overall findings

Warming waters in SNE have been linked to a downward trend in recruitment and a decline in abundance in the SNE lobster stock (Glenn and Pugh, 2006; Rheuban *et al.*, 2017; LeBris *et al.*, 2018; ASMFC, 2020), and thermal stress may be driving these population changes either directly (lethal effects) or indirectly (sublethal effects). We tested whether the sublethal physiological effects of thermal stress have reduced reproductive investment and output in female SNE lobsters, using ESD as a proxy for stress. We found a near-ubiquitous prevalence of ESD in ovigerous females, resulting in small sample sizes of non-diseased females that limited the power of our statistical tests. However, we did find a significant decline in realized fecundity compared to historical fecundity estimates (1987–1988), predicted by our model to be a 23% decrease, suggesting an overall decline in reproductive output has occurred. Another sign of compromised reproductive performance in our sampled population is the negative relationship between clutch size and both dry weight and protein content for diseased (stressed) females. Our results are consistent with findings since the late 1990s linking thermal stress to adverse changes in the physiological state and overall health of American lobsters in this region (Pearce and Balcom, 2005; Shields, 2013), substantially compromising the SNE lobster stock.

Fecundity

We found no substantive evidence to conclude that fecundity was compromised by the presence of ESD in females; this was

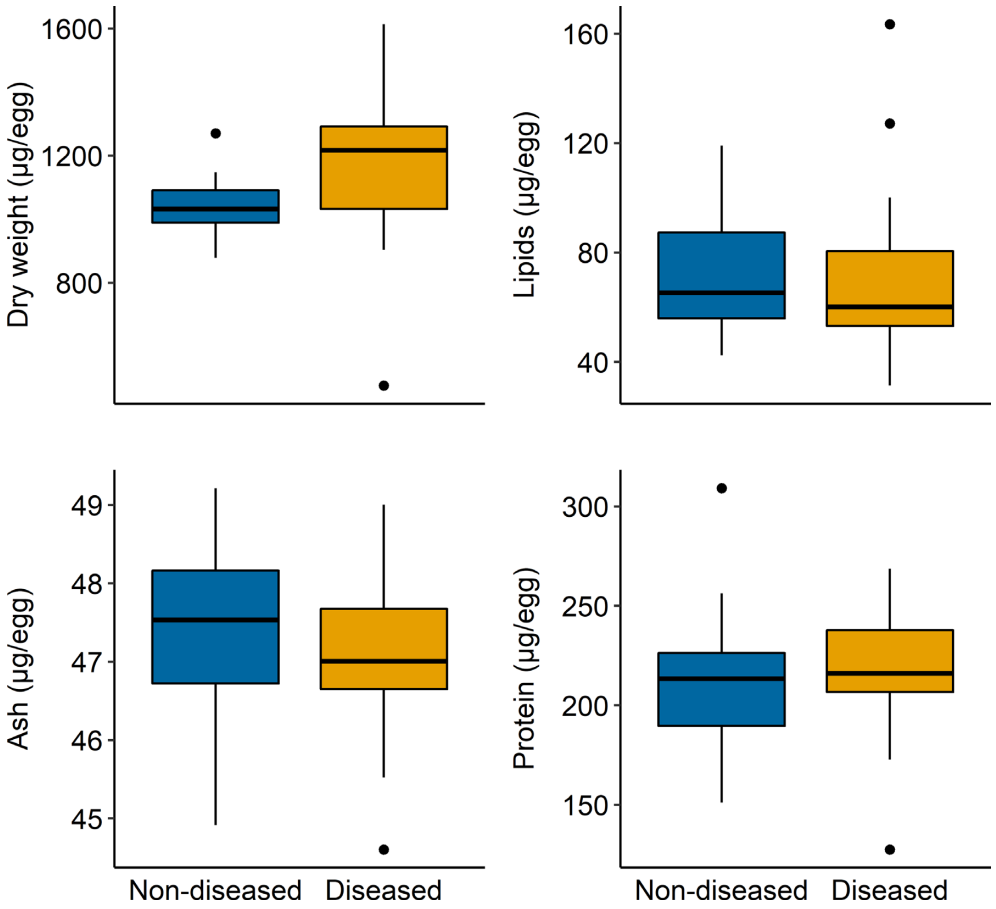

Figure 3. Nutritional content comparison in early-stage eggs for potential fecundity females with no active ESD (non-diseased) and those with active ESD (diseased). The horizontal bar in each box represents the median; the lower and upper hinges indicate the first and third quartiles respectively; the whiskers are the extent of data within 1.5 times the interquartile range.

true for potential fecundity females as well as realized fecundity females. However, we should note that our sample size of non-diseased lobsters was much lower than for diseased lobsters for both sets of females ($n = 32$ vs. 144, respectively for potential fecundity, and $n = 16$ vs. 91 for realized fecundity females), and lobsters without ESD were a challenge to procure despite multiple collection trips. Several monitoring programs have documented that the prevalence of ESD in ovigerous females is consistently much higher than in males or non-ovigerous females, with ranges from 60% to nearly 80% in some SNE inshore locations (85% for realized fecundity females in our data; Castro and Somers, 2012; DENC, 2019; Pugh and Glenn, 2020). These high occurrence rates, coupled with challenges in finding large and/or non-diseased ovigerous females during multiple days of targeted sampling are concerning given the depleted stock conditions, the comparatively reduced fecundity of smaller lobsters, and the higher mortality rates that have been associated with disease in ovigerous females (Hoenig *et al.*, 2017). The size range and disease status of lobsters we sampled are representative of those encountered by the commercial fleet in the nearshore population in SNE, indicating that larger females (>90 mm CL) present in the area are very likely to have ESD.

The size distribution of ovigerous females examined in our study was very similar to the size distribution from the historical dataset we utilized. Changes to size at maturity, which have been documented in the Gulf of Maine (GOM) lobster stock (Waller *et al.*, 2019, 2021), could influence whether females at a given size were primiparous (first-time spawners) or multiparous (spawning for at least the second time). Evidence suggests that multiparous females tend to invest more in reproductive output than primiparous females, including increases in fecundity (Oulette and Plante, 2004; Marshall, 2016). Thus, a decrease in size at maturity and subsequent increase in the proportion of females that were multiparous could have influenced the fecundity comparison between datasets, presumably increasing average fecundity in a given size range. However, females in our SNE study area do not appear to be maturing at smaller sizes; data from the late 2010s produced nearly the same estimate of size at which 50% were mature (76 mm CL), as data from the late 1980s (Estrella and McKiernan, 1989; see Appendix 1 in ASMFC, 2020). This stability over time in the maturity schedule for the area should have resulted in similar estimates for fecundity between the two datasets, but our results show that similarly sized females now show reduced realized fecundity.

The observed significant decline in realized fecundity over an ~30-year period could have been driven by several different factors, acting alone or in synergy with an observed increase in stressors in SNE. First, if potential fecundity has remained consistent through time (there are no datasets available for comparison), then egg attrition during the lengthy brooding period (9–11 months) may have increased over the past three decades. Egg attrition in American lobsters varies

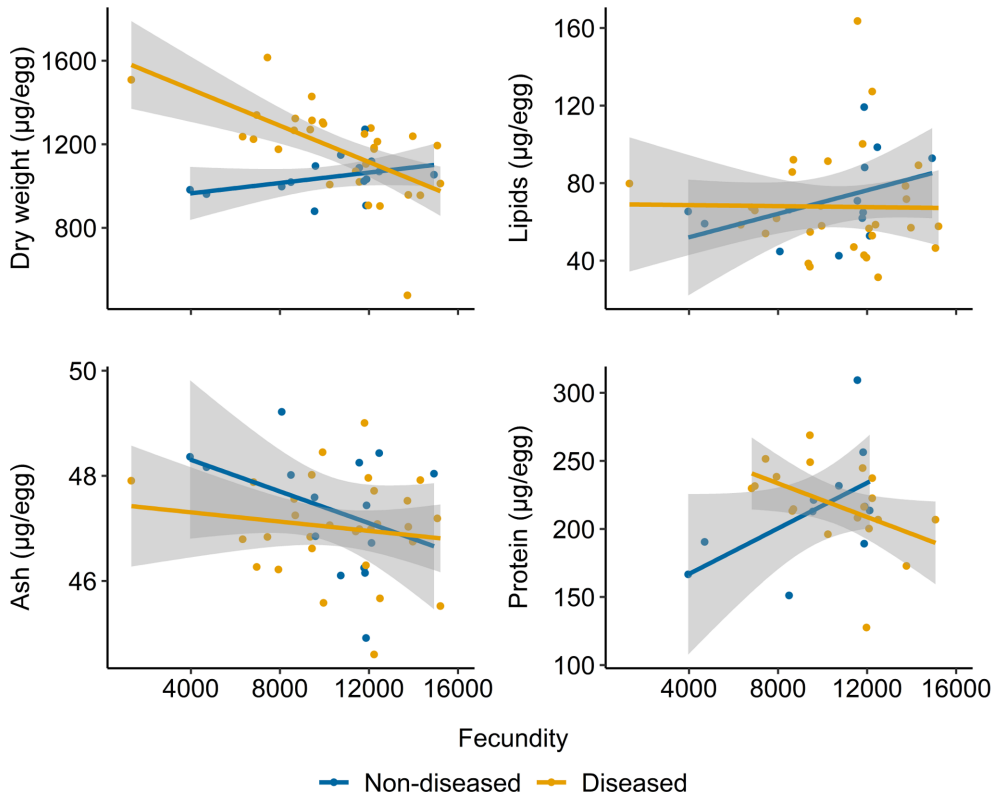

Figure 4. The relationship between fecundity and measures of egg quality for females with no active ESD (non-diseased) and active ESD (diseased). Grey bands represent the 95% CI of each regression.

widely (1–36%) by geographic area (Perkins, 1972; Waddy *et al.*, 1995; Tang *et al.*, 2018). Most of our current estimates of egg loss (22–41%) fall within this reported range, albeit at the higher end of the range, although some of our estimates have very small sample sizes. A recent assessment of lobster clutch sizes in Canadian maritime waters categorized many egg clutches as abnormally small (Tang *et al.*, 2018), and researchers suggested that a decrease in male gamete resources (i.e. sperm limitation) may be impacting brood sizes in these lobsters (Tang *et al.*, 2019). Second, infections by filamentous microorganisms (e.g. bacteria, fungi) or parasites (e.g. nemertean worms; reviewed in Kuris, 1991) may also contribute to egg mortality at varying levels in some clutches, but are not seen or reported from fishers nor from MADMF biologists working in the region (T. Pugh, pers. obs.).

Another consistent source of egg loss stems from fishing and the associated handling of ovigerous females, as they are caught and released (harvest of egg-bearing lobsters is prohibited, and they must be immediately released at sea; Aiken and Waddy, 1986; Campbell, 1986). Tail-flipping behaviour exacerbates egg loss during the handling process, and therefore contributes to some loss in clutch size over time (Aiken and Waddy, 1986; Voegtlin *et al.*, 2009). While the impact of handling-related egg loss due to the discard process is difficult to assess, overall effort and exploitation in the SNE stock have declined since the late 1980s (ASMFC, 2020). Specifically, within the Massachusetts portion of the SNE lobster stock, the number of trap hauls (representative of fishing effort) has declined from 1.8 to 2.2 million annually during the early 1990s to around 700000 in recent years (MADMF, unpublished data). This decrease in fishing effort would hypothetically reduce the amount of handling-induced egg loss over time, meaning that females in our current dataset were subject to less handling-induced egg loss than those in the historical fecundity dataset (Estrella and Cadrin, 1995). Conversely, decreased population size in SNE may increase the probability of individual ovigerous females being captured multiple times due to decreased intraspecific competition when entering traps; higher recapture rates of tagged lobsters have regularly been observed in the SNE portion of the MADMF Ventless Trap Survey compared to the GOM survey region, where the population is larger (6% of legal-sized lobsters in SNE vs. 0.6% in GOM in 2018; MADMF, unpublished data). However, because of the large overall decline in fishing effort in SNE, it seems unlikely that handling-induced egg loss is a primary driver behind diminished clutch sizes over the 30-year timespan we examined.

Environmental conditions may also influence egg loss over the brooding period. Laboratory work has demonstrated that prolonged exposure to warmer waters (>20°C) tends to exacerbate egg loss (Talbot and Harper, 1984; Waddy *et al.*, 1995), possibly related to mechanistic or physiological attributes (e.g. egg-stalk formation, chorion synthesis) associated with egg attachment and retention. The number of days bottom water temperatures have exceeded 20°C, for inshore SNE has substantially increased over the last couple decades (Rheuban *et al.*, 2017; DENC, 2019; e.g. 36 more days >20°C in the 2010s compared to the 1990s in nearby eastern Long Island Sound [ASMFC, 2020]), potentially affecting egg retention success during the brooding period and contributing to an observed decline in fecundity.

Finally, it seems most plausible given the large decline in realized fecundity, that potential fecundity has not remained constant over time, and that females are not producing the

same initial quantity of eggs as they have historically. This change in investment might be driven by environmental factors experienced by SNE females. It also may be highly likely that the absence of ESD does not necessarily equate to an unstressed lobster, and that many if not all SNE lobsters are stressed. This could explain the lack of observed differences in reproductive investment between non-ESD and ESD females. Most diseases or syndromes in lobsters from nearby Rhode Island waters, for example, occurred independent of the presence of shell disease (Shields *et al.*, 2012). Thus, those lobsters that do not have ESD may still possess other internal disease states, or be otherwise physiologically compromised, which could, in turn, influence reproductive investment. Future laboratory work observing individual females from the time of molting and mating through spawning that describes the development and progression of ESD, and the quantity and quality of resulting eggs may help to identify any direct linkages between reproductive investment and the acquisition and severity of ESD.

Egg quality

Our results did not show differences in most of the egg nutrient constituents we examined between non-diseased and diseased lobsters. We chose to examine egg quality metrics commonly reported in the literature; however, comparing results across studies is challenging because methodologies differ and values can vary with developmental stage of the clutch examined, the size range of females considered, biochemical protocols and techniques, and a lack of consistent measurement units (e.g. % weight basis or specific lipid or protein constituents). While no other comparable data were available for the SNE region, datasets from southern GOM (Goldstein and Watson, 2019) and the Gulf of St. Lawrence (Attard and Hudon, 1987) can serve as a rough proxy. In this study, lipid values were lower in our SNE lobsters than values reported from GOM, while protein values tended to trend higher in the present study compared with the Gulf of St. Lawrence. Dry weight was also higher compared to historical lobsters from the Gulf of St. Lawrence (Attard and Hudon, 1987). We did not examine which constituents are contributing to the increases in dry weight, though carbohydrates would comprise some proportion of the overall weight. Carbohydrates are essential for the synthesis of chitin but are not major contributors to egg energy reserves (García-Guerrero *et al.*, 2003a). The relatively higher levels of protein egg^{-1} in SNE lobsters was an interesting finding that could be a response to thermal stress as protein is an important energy component in eggs when lipid levels are low. Increased protein levels during embryogenesis are linked with elevated temperatures and at these increased temperatures, proteins may be catabolized after depleting lipids due to increased metabolic demands (García-Guerrero *et al.*, 2003b). Controlled laboratory studies could help to resolve the details of nutrient investment, uptake by lobster embryos, and resulting larval health due to thermal stress.

We found no relationship between egg quality and female size, which is somewhat contradictory to previous work that has documented a positive correlation between female size and egg traits in homarid lobsters (*H. americanus* and *H. gammarus*), particularly with respect to nutritional composition (Attard and Hudon, 1987; Wickins *et al.*, 1995; Tully *et al.*, 2001; Ouellet and Plante, 2004). Larger lobsters (>100 mm CL) generally produce more eggs of higher quality (e.g. more lipids) which, in turn, likely enhance larval growth and survival of their offspring (Attard and Hudon, 1987). However, the lack of large females in our sample may have precluded detection of the quality–size relationship. Our sampled size range is representative of the size range in the SNE area, which has been extremely truncated for more than four decades now with very few lobsters of either sex >100 mm CL (see ASMFC, 2020, Figure 74, p. 300).

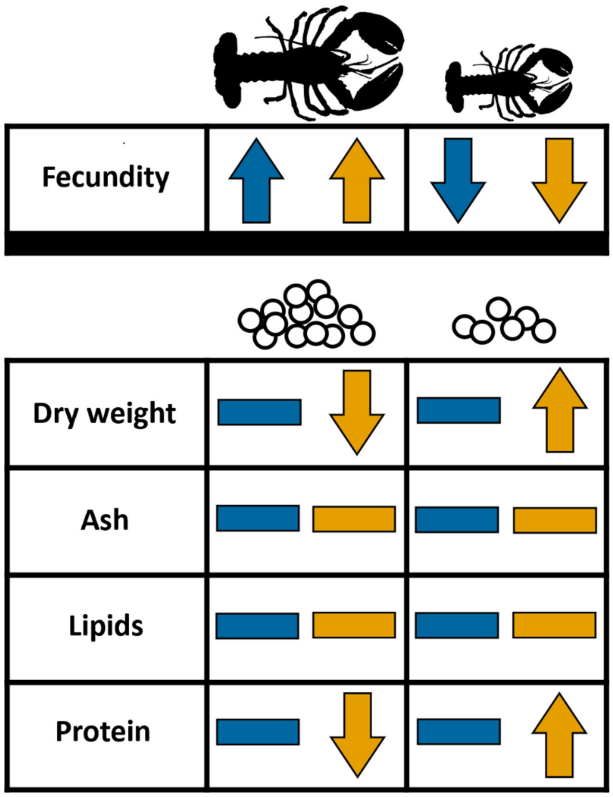

Figure 5. Graphic representation of the relationships (regressions) between lobster realized fecundity with female size (top panel) and egg quality (bottom panel) relative to disease status (blue: non-diseased, orange: diseased) (horizontal lines indicate no trend).

For non-diseased females, we found no relationship between potential fecundity and any nutritional metric, which could be related to our very small sample sizes of non-diseased females. However, we did detect a significant negative relationship between potential fecundity and both dry weight and protein content in diseased females. Data from non-diseased and diseased females overlap considerably at moderate clutch sizes for both dry weight and protein, but at smaller clutch sizes the separation of the CIs suggests that at least for these smaller clutches, investments by non-diseased vs. diseased females may differ. Our data may suggest that diseased females have to trade-off between clutch size and egg quality, only producing higher quality eggs at smaller clutch sizes (Figure 5), but why this result is evident for diseased females and not for non-diseased females is not clear. The large amount of individual variation observed in both potential fecundity and egg quality variables (e.g. energy) suggests considerable variation in female lobsters' ability to invest in reproduction. Therefore, additional work is needed to understand which egg components are most critical to larval success, and how those nutritional constituents are biologically and physiologically

coupled to both maternal condition and the environment in which oogenesis and embryogenesis occur (Giménez, 2006, 2020; Foo and Byrne, 2017; Jaglarz and Bilinski, 2020).

Implications

The overall reduction in late-stage (realized) fecundity demonstrated by our work implies that mature SNE females are no longer producing the same number of larvae per year as they have in years past. This is consistent with the overall reduction in recruits per spawner over the last two decades that has been documented in recent stock assessment work (see ASMFC, 2020, Figure 74, p. 300), and aligns with the timing of an environmental regime shift that has resulted in a substantial change to the marine thermal habitat (ASMFC, 2020). Since there appears to be no relationship between female fecundity and the presence of ESD as we have treated it here, the proximate cause of this decrease since the late 1980s remains unclear but could result from investment limitations of females, or from some decrease in male investment limiting fertilization success (Gutzler *et al.*, 2022, T. Pugh and K. Benhalima, unpublished data). While our work did not examine changes in expected lifetime egg production, coupling the observed decreased fecundity in this study with recent record lows in recruitment to the SNE population suggests a low likelihood that females are compensating for a single year of reduced fecundity with increased investment in subsequent years. The extremely truncated size structure which has persisted for decades, with few large females (or males) remaining in the population >100 mm CL, indicates that most females do not survive long enough to produce additional clutches. A stock that has been reliant on egg production from smaller size classes, with females likely spawning only once or twice, will be acutely vulnerable to reductions in the fecundity of those size classes. The additional mortality that may be experienced by ovigerous females due to shell disease would only exacerbate reductions in population size and recruitment (Hoenig *et al.*, 2017). Our data demonstrate that expectations around the potential for the SNE stock to rebuild need to be adjusted to this new regime of decreased reproductive output and can no longer rely on past estimates of egg production and recruitment. Ultimately, this reduced fecundity and uncertainty around the causal agent(s) suggest the need for a conservative management approach, focused on the goal of leaving as many mature individuals of both sexes in the population as possible to maximize the chances of reproductive success.

Factors that influence changes in reproductive output are likely complex, synergistic, and may include changes in investment strategies (or capabilities) by females and males, egg attrition, and handling stress associated with current fishing practices. However, it seems likely that thermal stress is a key underlying factor that has impacted lobster reproductive output in SNE, and a prolonged period of detrimental environmental conditions has made most female lobsters stressed in SNE (Dove *et al.*, 2005). We suspect that as changes to temperature and other environmental variables (e.g. oxygen saturation, salinity, ocean, and coastal acidification) become growing factors in modulating the health of lobsters throughout its range, "lessons learned" from SNE will add much needed value toward developing models that consider these variables in other regions to assess population-level processes and inform fisheries management.

Conflict of interest

The authors declare that they have no competing interests

Data availability statement

Data from this project are available upon written request to Dr. T. Pugh, Massachusetts Division of Marine Fisheries.

Supplementary material

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

Authors' contributions

JSG and TLP conceived of, and designed this study, collected the data, and ran preliminary analyses. KAZS contributed text to the initial draft, conducted the formal statistical analyses, and implemented the models used to interpret the results. JSG drafted the manuscript with iterative edits and revisions from both co-authors. All authors contributed to final interpretations, discussions, manuscript writing, and reviewer enquiries. Funding support for this study was provided by both TLP and JSG. This manuscript is submitted with the approval of all the authors.

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