



Contribution to the Supplement: 'Lobsters in a Changing Climate' Original Article

Geographic and environmental drivers of fecundity in the European lobster (*Homarus gammarus*)

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Fecundity in the European lobster (*Homarus gammarus*) has been shown to exhibit extensive spatial variation across northern Europe. Previously, this has been attributed to a lack of methodological standardization among samples. Instead, we show significant correlations between fecundity and both geographical and environmental drivers. We use linear mixed-effect models to assess the contribution of latitude, longitude, and measures of sea surface temperatures on the size–fecundity relationships of 1058 ovigerous females from 11 locations in the UK, Ireland, and Norway. We include new data for 52 lobsters from Falmouth, UK, the southwest limit of existing samples. Fecundity at mean female size correlated positively with eastings and greater annual ranges in sea surface temperature, but not with mean temperature or latitude. This contradicts the established latitudinal and mean temperature dependence reported for the closely related *H. americanus*. We postulate that proximity to stable Atlantic currents is the most likely driver of the relationship between fecundity and longitude. Mechanisms are discussed by which egg production or retention may be influenced by temperature range rather than by mean temperature. With further validation, we propose that temperature-correlated fecundity predictions will provide a valuable tool in ensuring that management thresholds are appropriate for the reproductive characteristics of lobster populations.

Keywords: crustacea, egg production, environmental driver, fishery management, general linear model, reproductive ecology, reproductive variation.

Introduction

Measures of egg production are vital parameters for estimating the reproductive capacity of marine populations, the maintenance of which is a key objective of fishery management. Knowledge of reproductive capacity is critical for informed management of exploited populations because it is required for models of stock and recruitment dynamics and can be used to define the maximum threshold for fishing mortality (Laurans *et al.*, 2009). It is also important to determine the geographic scales over which the reproductive characteristics of managed species vary to apply commensurate stock conservation measures to each region (Tully *et al.*, 2001; MacCormack and DeMont, 2003; Currie and Schneider, 2011).

A size-specific fecundity factor is well documented in populations of the European lobster (*Homarus gammarus*, L.), a prized

decapod crustacean fished extensively throughout its range (e.g. Hepper and Gough, 1978; Bennett and Howard, 1987; Tully *et al.*, 2001; Lizarraga-Cubedo *et al.*, 2003; Agnalt *et al.*, 2007; Agnalt, 2008). However, published estimates of mean fecundity have varied considerably among putative populations throughout north-west Europe (Agnalt, 2008), ranging from ~5200 eggs per oviposition in southeast Scotland (Lizarraga-Cubedo *et al.*, 2003) to ~12 500 in southern England (Roberts, 1992) and southwest Norway (Agnalt, 2008), among females of 100 mm carapace length (CL).

Environmental determinants of fecundity variation have been identified in many marine species (Wright, 2013), including seawater parameters such as temperature, salinity (e.g. Gomez *et al.*, 2013), and dissolved oxygen (e.g. Wu *et al.*, 2003). Temperature

(or latitude, as a proxy) has been found to correlate tightly with the exponent of size-specific fecundity variation in American lobster (*Homarus americanus*; Currie and Schneider, 2011). It also aligns with reproductive traits in other lobsters, including Southern rock lobster (*Jasus edwardsii*; Annala et al., 1980; Gardner et al., 2006), and in fish inhabiting a similar range throughout the Northeast Atlantic, such as Atlantic cod (*Gadus morhua*; Thorsen et al., 2010; Wright et al., 2011a; Hansen et al., 2012) and Dover sole (*Solea solea*; Witthames et al., 1995; Mollet et al., 2013). We aimed to test associations between *H. gammarus* fecundity and geographical and environmental factors, to assess whether they may contribute to the observed spatial variation in fecundity. Management has failed to prevent extensive and enduring stock collapses in the recent past (e.g. throughout Scandinavia in the mid-20th century; Dow, 1980; Agnalt et al., 1999), and where stock thresholds fail to reflect regional differences in fecundity, the management of pressured fisheries can be seriously undermined (Lambert, 2008; Morgan, 2008). Therefore, the identification of drivers that explain reproductive variation may be important in conserving lobster populations (Green et al., 2014).

Despite the established influence of ecological drivers in reproductive variation across a range of taxa, whether regional differences in *H. gammarus* fecundity may be driven by environmental factors has not been assessed. Observed variation in clutch size among clawed lobsters has been attributed to differences in the success of attaching the externally incubated eggs (Currie and Schneider, 2011), the rate of egg loss over a lengthy incubation of 9–10 months (Wahle et al., 2013), and the retention of eggs during capture and subsequent handling and storage (Agnalt, 2008). Agnalt (2008) hypothesized that a lack of methodological standardization among studies may prevent the detection of population-level variations, but we aimed to assess whether the influence of thermal environment might be detectable within the observed variation of *H. gammarus* fecundity.

We hypothesized that a relationship would exist between temperature and fecundity among putative populations of *H. gammarus*. To test this hypothesis, egg counts of ovigerous females were collated from existing studies of fecundity in northern Europe. A new fecundity measurement was also made for females from the Atlantic peninsula of Cornwall, UK, an unassessed region at the southwest edge of the range of available data where the lobster fishery is vital in supporting 370 commercial potting vessels (S. Davies, pers. comm.; Cornwall IFCA, 2014). Parameters of the size-specific fecundity relationships of these samples were regressed against geographical and environmental covariates. We find longitudinal and environmental predictors of fecundity at mean size and discuss our findings in relation to lobster physiology, evolutionary ecology, and fishery management.

Material and methods

New samples

Animal acquisition and storage

Ovigerous female lobsters ($n = 52$) were caught in baited pots and collected directly from inshore fishers working in Falmouth Bay, southwest UK in January–March 2013. This was carried out with permission from the local authority, as the landing of ovigerous females within inshore waters is normally prohibited (Cornwall IFCA, 2014). A large and evenly distributed range in female sizes was requested because this improves the accuracy of estimates of size–fecundity relationships (Estrella and Cadrin, 1995). A broad size range was achieved, although legal landing restrictions meant

that no females could be obtained less than the 90-mm CL jurisdictional minimum landing size. Most females were sampled immediately upon collection; where this was not possible, females were stored for a maximum of 3 d in a modern ~2000 l recirculation system, where chilled temperatures (5–6°C), shelter provisions, and low stocking density (maximum 3 m⁻²) ensured egg loss was negligible (daily net cleaning revealed that egg loss equated to <10 eggs lobster⁻¹ d⁻¹).

Physical fecundity estimation

CL was measured using Vernier calipers, rounding down to the nearest whole millimetre, and the egg mass was collected by hand, as per Agnalt (2008). A subsample of the eggs was separated and counted manually, ranging from 517 to 708 individual eggs (mean = 606, ± 3.45). No repeat subsamples were taken because Agnalt (2008) showed that the correlation between two counts was >0.99 using even smaller subsamples [wet weights of 1–1.5 g, compared with 2.2–3.9 g (mean = 2.97 g, ± 0.05 g) in this study]. Egg development was similar among all females, with most clutches being partially “eyed”, although no formal measurements of development stage were taken.

Individual fecundity estimates were made by calculating the dry weight of the egg mass against that of the counted subsample; dry weight was preferred so that any variation in the amount of seawater incidentally gathered with the egg mass would not bias the measurement. All egg samples were dried in a drying oven (UT6200, Thermo Electron LED, Germany) at 105°C for 24 h (± 1 h). Samples were moved into a sealed desiccating cabinet to cool before mass was measured to the nearest 1 mg by electronic balance (AE240 Balance, Mettler, UK). After an additional hour in the drying oven, sample mass was remeasured to check that it was stable and that drying had completed; all samples were deemed fully dried after this check because the difference in mass between the measurements was <1% of the total sample mass. The dry mass of the subsample of known egg count was used to determine the mean dry mass per egg as:

$$\text{Dry mass per egg (mg)} = \frac{\text{Subsample dry mass (mg)}}{\text{Subsample size (}n\text{ eggs)}} \quad (1)$$

Fecundity estimates for each individual were then obtained from the total dry mass of eggs as:

$$\text{Fecundity (}n\text{ eggs)} = \frac{\text{Subsample dry mass (mg)} + \text{Remaining sample dry mass (mg)}}{\text{Dry mass per egg (mg)}} \quad (2)$$

Geographical survey

Data collection and statistical modelling

To test potential geographic and environmental drivers of fecundity variability in *H. gammarus*, data were collected from five studies assessing fecundity among 1009 individuals in 10 areas around the UK, Ireland, and Norway, plus the 52 individuals from Falmouth, southwest UK (Figure 1), measured by this study. Each regional sample location was assigned latitudinal and longitudinal coordinates from the approximate centre of the spatial range of sampling, as could be best deduced from study methodologies. The mean sea surface temperature (SST) data were obtained for each location the first day of each month during the year(s) of the study and one preceding year, since the majority of Homarid lobsters spawn in

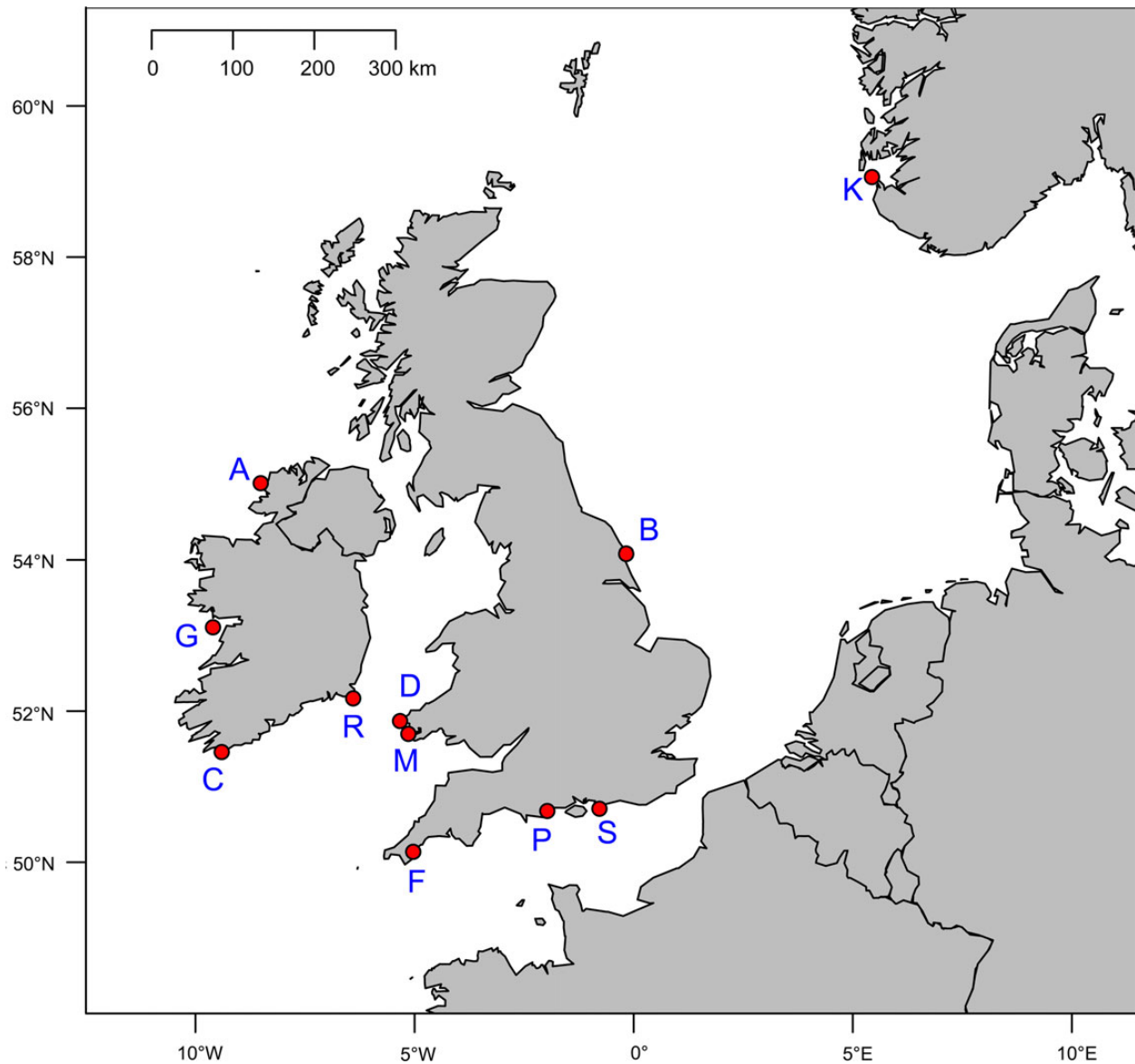


Figure 1. Map of the UK and Ireland, with continental Europe around the North Sea, showing the locations of regional fecundity samples. Fecundity in Falmouth (F) was assessed in this study, while other samples used to model correlations with temperature were: Arranmore (A), Galway (G), Cork (C), and Rosslare (R) from Tully *et al.* (2001); St Davids (D) from Bennett and Howard (1987); Milford Haven (M), Selsey (S), and Bridlington (B) from Free (1994); Poole (P) from Roberts (1992); and Kvitvøy (K) from Agnalt (2008). See Table 1 for further information on regional samples.

a biennial cycle (Tully *et al.*, 2001; Comeau and Savoie, 2002; Agnalt *et al.*, 2007). Using SST data, the mean temperature (mean SST of all months in all years) and temperature range (the mean difference between the mean SST of the three coldest months and the mean SST of the three coldest months of each year) were calculated for each location. SST data were obtained via AVHRR Oceans Pathfinder from the Physical Oceanography Distributed Active Archive Center (PO.DAAC, 2014) for all locations except Falmouth, UK, for which SST data were only available via MODIS Aqua EOS-PM from the Goddard Space Flight Center (OceanColor, 2014) due to the recentness of the sampling.

SST was utilized instead of seabed temperature (SBT) because SBT was unavailable at the spatial and temporal resolutions required. While SBT may present a more biologically relevant parameter for benthic lobsters, the use of SST was supported by a

regression of 80 surface (mean = 1.8 m below surface) and bottom (mean = 3.3 m above seabed) temperature measurements obtained by depth casts (ICES Data Centre, 2014) taken between 1998 and 2008 at fishable locations (within 15 km of the coast and < 85 m depth) across the geographic range of the study. The relationship showed a highly significant correlation between surface and bottom temperatures (Pearson's product-moment correlation, $r^2 = 0.96$, $p < 0.01$).

General linear models (GLMs) were constructed using R (R Core Team, 2012) to apply power (log-log), log-linear, and linear fits to the global relationship between fecundity (F) and female size (CL) across all 1061 individuals. Analysis of the distribution of residuals and comparisons of the log-likelihood ratio statistic and Akaike information criterion (AIC) of each model confirmed that the power fit, $\log(F) = \log(aCL)^b$, best described this relationship (see

Table 1. Summary of regional samples analysed including: study origin; sample region; sample size (n); central coordinates used for sample SST data and geographic factors in modelling, SST-derived mean temperature, and temperature range; a and b (F_{slope}) of the power-fitted relationship between fecundity and CL ($F = a\text{CL}^b$), with r^2 and associated p -values; and F_{mean} .

Study	Sample region	n	Lat.	Long.	SST mean (°C)	SST range (°C)	a	b (F_{slope})	r^2	p -value	F_{mean} (n eggs)
Ellis <i>et al.</i> (this study)	Falmouth, SW England	52	50°8'24"N	5°1'48"W	11.85	6.76	0.0066	3.08	0.68	<0.001	11 011
Tully <i>et al.</i> (2001)	Arranmore, NW Ireland	73	55°0'36"N	8°30'36"W	11.64	4.63	0.0042	3.18	0.81	<0.001	9559
Tully <i>et al.</i> (2001)	Galway, W Ireland	144	53°6'36"N	9°35'60"W	12.41	5.31	0.0017	3.29	0.73	<0.001	9353
Tully <i>et al.</i> (2001)	Cork, SW Ireland	70	51°27'36"N	9°24'0"W	12.87	5.98	0.0031	3.18	0.57	<0.001	8947
Tully <i>et al.</i> (2001)	Rosslare, SE Ireland	111	52°10'12"N	6°24'0"W	12.13	7.40	0.0164	3.01	0.49	<0.001	10 105
Bennett and Howard (1987)	St Davids, SW Wales	80	51°52'12"N	5°19'48"W	11.10	7.13	0.0003	3.42	0.73	<0.001	9466
Free (1994)	Milford Haven, SW Wales	8	51°42'0"N	5°8'24"W	11.75	7.19	0.0000	3.14	0.48	0.02	10 293
Free (1994)	Selsey, S England	76	50°42'36"N	0°46'48"W	12.94	7.81	0.1827	2.85	0.26	<0.001	11 622
Free (1994)	Bridlington, NE England	177	54°4'48"N	0°10'12"W	10.06	8.68	0.0344	2.84	0.59	<0.001	11 776
Roberts (1992)	Poole, S England	50	50°40'48"N	1°58'12"W	12.49	7.05	0.0114	3.03	0.53	<0.001	11 208
Agnalt (2008)	Kvitsøy, SW Norway	217	59°3'36"N	5°26'24"E	9.84	9.38	0.0047	3.11	0.85	<0.001	12 920

Supplementary material). Power law models have been favoured in other recent studies (e.g. Tully *et al.*, 2001; Lizarraga-Cubedo *et al.*, 2003; Agnalt, 2008) because they account for the volumetric nature by which the brooding capacity of the abdomen increases in length and width with increasing CL. The outlying data of three individuals for which fecundity estimates lay beyond 4 s.e. of the allometric relationship were removed from the analysis.

A linear mixed-effects model was constructed using the R package lme4 (Bates *et al.*, 2014) to test the effect of the sizes of potential geographical and environmental drivers on lobster fecundity. Geographical factors assessed were latitude, longitude, and the interaction between the two, while environmental factors (analysed separately) were mean temperature, temperature range, and the interaction between the two. The relative strength of all geographical and environmental covariates was standardized via an adjustment to similar scales (mean = 0; s.d. = 1). From these models, coefficients of log(fecundity) at the mean size of all sampled females (F_{mean}) and the exponent of the size-specific fecundity power relationship (F_{slope} ; b value) were extracted for each regional sample and then regressed in GLMs against the scaled geographical or environmental covariates. All combinations of models containing the effects of geographical or environmental factors on F_{mean} and F_{slope} in each regional sample were compared using multimodel inference and model averaging in the R package MuMIn (Barton, 2013). Model-averaged effect sizes and AIC weights (the proportion of weight accumulated by all models containing the assessed variable) were extracted to evaluate the relative importance of each variable on F_{mean} and F_{slope} . Correlation between geographical and environmental factors was tested by linear regressions. The GLMs used to regress F_{mean} and F_{slope} against geographical and environmental parameters were weighted by the sample sizes studied in each lobster population to limit the influence of imprecise estimates on global relationships.

Some existing fecundity samples within the spatial range investigated were not analysed because raw data were unavailable (e.g. eastern and western Scotland; Lizarraga-Cubedo *et al.*, 2003) or were collected before the backdated availability of SST measurements (e.g. northwest France; Latrouite *et al.*, 1984). Data from another sample taken near Whitby in northeast England by

Bennett and Howard (1987) were omitted because it was deemed likely that they were biased by considerable egg loss before fecundity estimation. The data included extremely low egg counts (e.g. <750 eggs) and yielded a very low correlation for the power-fitted size–fecundity relationship ($r^2 = 0.12$). A sample from Milford Haven, Wales (Free, 1994), was included despite the sample size being very small ($n = 8$) because the data exhibited a reasonable correlation for a power-fitted size–fecundity slope ($r^2 = 0.62$).

Results

Physical fecundity estimation

Among females collected from Falmouth, UK, CL ranged from 90 to 155 mm (mean = 110 mm, ± 1.9 mm), and estimated egg production ranged from 3712 to 35 241 eggs ind.⁻¹. The relationship between fecundity (F) and female size (CL) was described by $F = 0.0066 \text{ CL}^{3.10}$ using a power-fitted model ($r^2 = 0.68$, $p < 0.001$; Table 1), or by $F = 406.92 \text{ CL} - 29 749$ using a linear-fitted model ($r^2 = 0.77$, $p < 0.001$). The mean dry mass egg⁻¹ ranged from 1.53 to 2.24 mg among females, but demonstrated no relationship with overall fecundity (linear fit; $r^2 = 0.14$, $p < 0.01$). Mass egg⁻¹ appeared to fit a natural logarithm relationship with female size, as described by Agnalt (2008), although overall correlation of this model fit was weak ($r^2 = 0.29$, $p < 0.001$; see Supplementary material). Compared with the sample from Kvitsøy (K) and pooled Irish samples (I), the mean dry mass egg⁻¹ (mg) at Falmouth (F) was slightly higher at the lower distribution of female sizes (90 mm CL: $K = 1.3$; $I = 1.4$; $F = 1.6$), but was comparable at upper size limits (150 mm CL: $K = 1.9$; $I = 1.9$; $F = 2.0$; Tully *et al.*, 2001; Agnalt, 2008). Estimates suggest that fecundity among lobsters from Falmouth is fairly central within the range recorded for the species across northern Europe, despite the location lying at the southwest geographical extremity of all samples.

Drivers of fecundity variation

Table 1 shows SST and fecundity relationship results for each regional sample. North Sea sites at Kvitsøy and Bridlington had both the lowest mean temperatures (9.84 and 10.06°C, respectively) and highest temperature ranges (9.38 and 8.68°C). The mean

temperature was highest at sites in the English Channel at Selsey (12.94°C) and Poole (12.49°C) and in the Northeast Atlantic off western Ireland at Cork (12.87°C) and Galway (12.41°C). Western Ireland also experienced the smallest temperature ranges, decreasing northwards from Cork (5.98°C) to Galway (5.31°C) and being lowest at Arranmore (4.63°C). Across all samples, F_{mean} corresponded to a female size of 102.8 mm CL. For the log power-fitted relationship, $\log(F) = \log(a\text{CL})^b$, b (F_{slope}) was lowest for the samples from Bridlington (2.84) and Selsey (2.85), and was highest for the St Davids sample (3.42). F_{mean} ranged from 8947 eggs female⁻¹ in Cork to 12 920 in Kvitsoy. For all North Sea and English Channel samples, F_{mean} exceeded 11 000 eggs female⁻¹, whereas it was below 10 300 eggs for all samples from the Irish Sea and western Ireland.

We found that increases in F_{mean} were strongly associated with increases in both (easterly) longitude and mean annual temperature

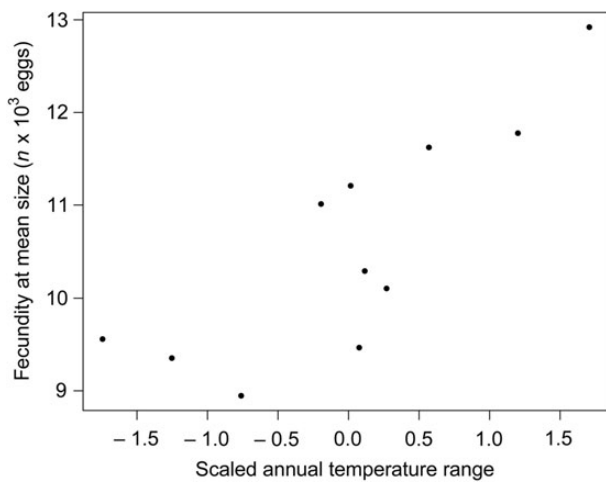


Figure 2. Plot of the relationship between F_{mean} and scaled temperature range, showing that increased F_{mean} was positively associated with increased range in annual temperature ($r^2 = 0.83$, $p < 0.002$).

range (Figure 2). Each variable had a high cumulative AIC weight (temperature range = 0.92; longitude = 0.89; Table 2), and a model-averaged effect size identifiably >0 , with 95% confidence intervals not overlapping zero (Figure 3). The influence of longitude and temperature range on fecundity also extends to females in other size classes. These variables also yielded identifiable positive effect sizes in linear mixed-effect models of fecundity at the current European Commission minimum landing size of 87 mm CL (data not presented). Latitude and mean temperature variables, and interactions of these factors, had no influence on fecundity variation, however. Modelled with F_{mean} , these variables had low cumulative model weightings (AIC weights <0.1) and 95% confidence intervals that spanned an effect-size of zero (Figure 3). We also demonstrated that variation in F_{slope} could not be attributed to any of the geographical or environmental variables investigated (Figure 3). No variable had an identifiable effect upon F_{slope} , with confidence intervals spanning zero effect-sizes and low cumulative weighting (AIC weights <0.4) for all model factors. Linear regressions between variables showed a significant positive correlation between mean annual temperature range and longitude (Pearson's coefficient: $r^2 = 0.90$, $p < 0.001$; Figure 4), and a significant negative relationship between latitude and mean temperature among regional fecundity samples ($r^2 = -0.74$, $p < 0.01$).

Discussion

Knowledge of factors contributing to fecundity variation is vital to ensure that fishery management strategies are suitable for exploited species throughout their range (Lambert, 2008; Morgan, 2008). We have demonstrated geographical and environmental factors that correlate with fecundity variation in *H. gammarus* across a portion of its range which has accounted for over 75% of the species' recorded landings in recent years (FAO, 2014). Our results are an important indication that the observed spatial variation may reflect differences between the fecundity of putative populations, not simply study-level differences in investigative approach, and that environmental temperature is a driver contributing to variation in the production and/or retention of eggs in *H. gammarus*. In isolation, the new fecundity sample taken from Falmouth,

Table 2. Summary of candidate linear mixed models with measures of model likelihood and weighting to show the effect of geographical and environmental covariates on F_{mean} .

F parameter	Factors	Model variables	d.f.	logLik	AICc	Δ AIC	AIC weight
F_{mean}	Geographical	Longitude ^a	3	20.966	-32.5	0.00	0.894
		Latitude + longitude	4	21.406	-28.1	4.36	0.101
		Latitude + longitude + latitude:longitude	5	22.075	-22.2	10.35	0.005
		Latitude	3	8.444	-7.5	25.04	0.000
	Environmental	Temperature range ^a	3	14.687	-19.9	0.00	0.915
		Mean temperature + temperature range	4	14.816	-15.0	4.98	0.076
		Mean temperature	3	9.712	-10.0	9.95	0.006
		Mean temperature + temperature range + mean temperature:temperature range	5	14.948	-7.9	12.05	0.002
F_{slope}	Geographical	Longitude	3	3.454	2.5	1.64	0.251
		Latitude + longitude	4	5.147	4.4	3.49	0.099
		Latitude	4	2.313	4.8	3.92	0.080
		Latitude + longitude + latitude:longitude	5	7.036	7.9	7.05	0.017
	Environmental	Temperature range	3	4.060	1.3	0.43	0.384
		Mean temperature	3	2.565	4.3	3.42	0.086
		Mean temperature + temperature range	4	4.680	5.3	4.43	0.052
		Mean temperature + temperature range + mean temperature:temperature range	5	4.997	12.0	11.13	0.002

Factors denoted ^a were deemed identifiable effects by model-averaging.

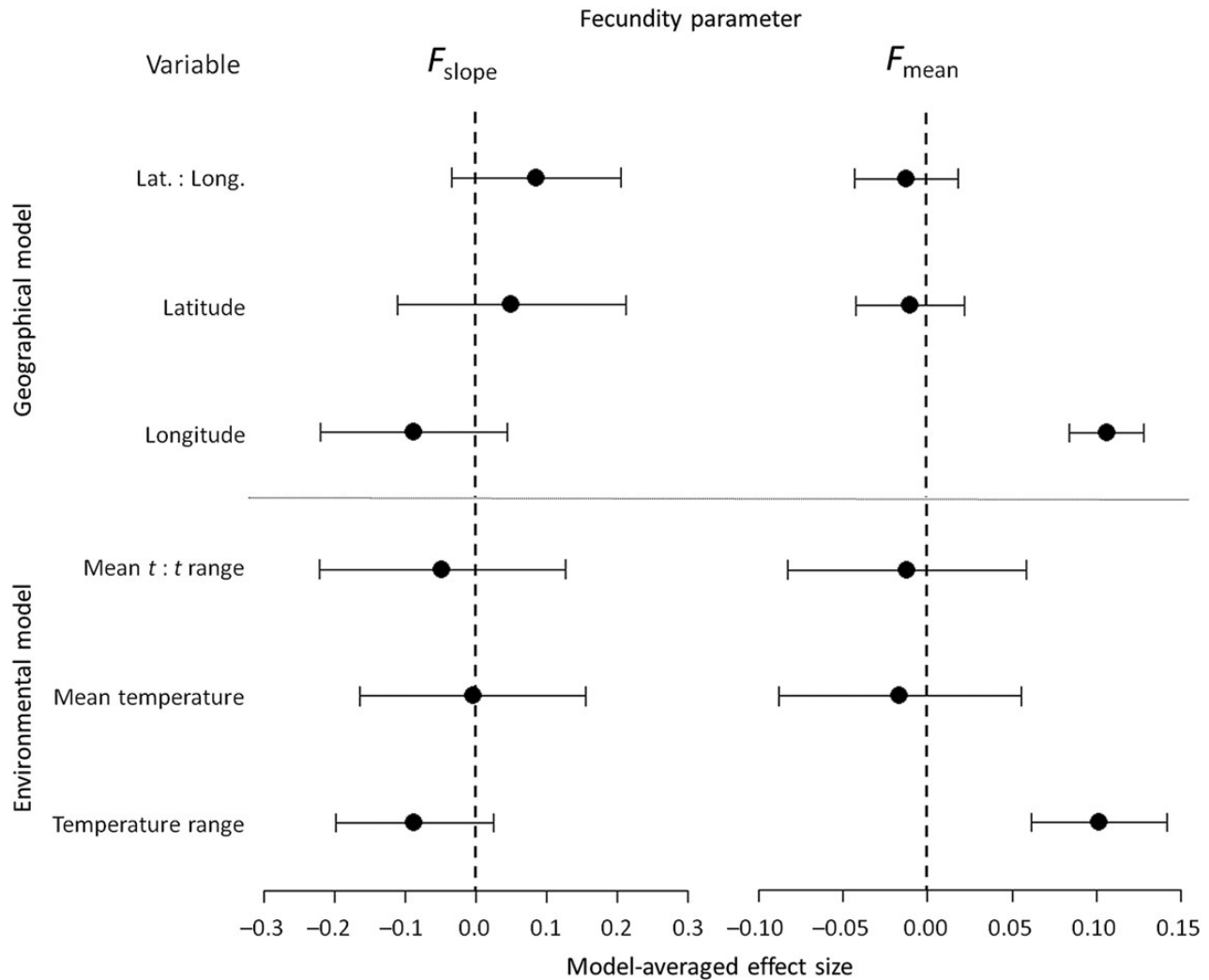


Figure 3. Model-averaged effect sizes of geographical and environmental variables modelled against the fecundity parameters F_{slope} and F_{mean} . Variables with effect-sizes that are identifiably different from zero have 95% confidence interval bars that do not overlap the model mean (dashed vertical line).

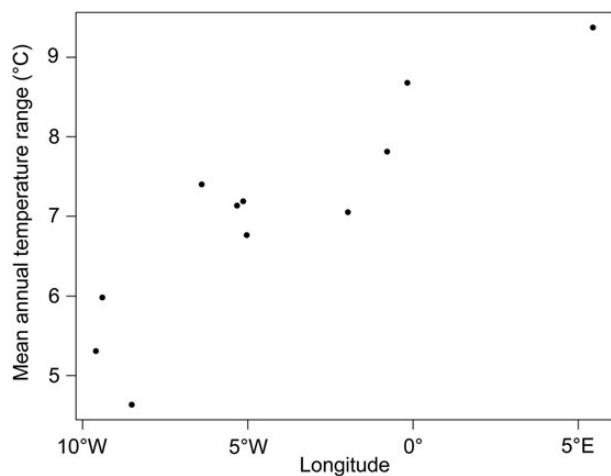


Figure 4. Plot of the relationship between longitude and mean annual temperature range among regional fecundity samples ($r^2 = 0.90, p < 0.001$).

the first such assessment in southwest England, can contribute an important parameter of the reproductive capacity of *H. gammarus* in this important regional fishery.

Our most important findings are that fecundity at mean size improved with increasing range in annual temperature, along a gradient towards more easterly longitudes, and that longitude and temperature range were closely associated. The most obvious underlying driver linking gradients of longitude and temperature range in the area of this study is proximity to the North Atlantic Drift of the Gulf Stream. The North Atlantic Drift brings greater thermal stability to the coastal waters of the immediate Atlantic coast along western Europe than that experienced by more enclosed shelf sea areas. By example, among the three most northerly regional samples we surveyed, the mean annual range in sea temperature for the Northeast Atlantic at Arranmore was only 4.6°C, compared with 8.7°C around Bridlington and 9.4°C at Kvitsoy in the North Sea. Considering the strength of the associations we found between fecundity at mean female size and both longitude and temperature range, we propose that proximity to currents associated with the Gulf Stream contributes to the regulation of egg production

Table 3. Regional samples ranked via smallest SOM L_{P50} (the CL at which 50% of females are functionally mature), as physiologically determined by Free *et al.* (1992) and Tully *et al.* (2001), with comparison to fecundity at the global mean female size (F_{mean}) as calculated in this study using raw data from Free (1994) and Tully *et al.* (2001).

Study	Sample region	SOM (CL, mm) (rank)	F_{mean} ($n \times 10^3$ eggs) (rank)
Free <i>et al.</i> (1992), Free (1994)	Selsey, S England	82 (1)	11.6 (2)
	Bridlington, NE England	90 (2)	11.8 (1)
Tully <i>et al.</i> (2001)	Galway, W Ireland	92 (3)	9.35 (5)
	Cork, SW Ireland	94 (4)	8.95 (6)
	Rosslare, SE Ireland	95 (5)	10.1 (3)
	Arranmore, NW Ireland	96 (6)	9.56 (4)

and/or retention in *H. gammarus* across the northern part of the species' distribution.

In contrast to the relationship detected for *H. americanus* by Currie and Schneider's (2011) similar meta-analysis of spatial variation in fecundity, we found no evidence of the slope of size-specific fecundity increasing with decreased latitudinal gradient. Instead, we found that fecundity at mean size was increased among regions with high ranges in annual temperature, irrespective of mean temperature. This finding defies the expectation that mean temperature drives the reproductive investment of ectotherms (e.g. Ernsting and Isaaks, 2000; Thorsen *et al.*, 2010; Tobin and Wright, 2011; Wright *et al.*, 2011a). Currie and Schneider (2011) found that fecundity-at-size in *H. americanus* (in this case, 85 mm CL lobsters) met this expectation, as it aligned closely to latitudinal gradient. However, the direction of this relationship was unexpected, with fecundity-at-size found to increase in higher latitudes (Currie and Schneider, 2011), suggesting that clutch size does not increase with increasing temperature in either *Homarus* species.

Rather than being a function of size, Currie and Schneider (2011) propose that *H. americanus* fecundity may be age-related, with fewer growing degree-days (e.g. Neuheimer and Taggart, 2007) at higher latitudes leading to smaller size at maturity and comparatively greater clutches at equivalent body sizes. Age-at-size validation methods remain too unreliable among crustaceans (Hartnoll, 2001) to evidence this, but the proposition is not supported by Currie and Schneider's (2011) own assertion of overall increases in size-specific fecundity slopes towards southerly latitudes, nor by our finding of a disconnect between fecundity at mean size and mean temperature in *H. gammarus*. A comparable pattern to that which we revealed is shown by sole (*S. solea*) populations from colder North Sea environments, whose earlier maturity and higher reproductive investment compared with conspecifics from warmer seas to the south and west has been attributed to counter-gradient environmental adaptation. This suggests that greater fecundity can arise among populations inhabiting colder regions to compensate for high mortality caused by winter sea temperatures (Conover, 1992; Mollet *et al.*, 2013), and that similar pressures could be driving variation in egg production for *H. gammarus*. In most studies of fish, spatial and temporal trait adaptations associated with temperature variation have been attributed to phenotypic plasticity (Crozier and Hutchings, 2014), although evolutionary mechanisms are more commonly proposed to explain counter-gradient variations (Conover, 1992; Mollet *et al.*, 2013). Compared with plastic traits, locally adapted fecundity variation is less likely to be flexible to global climate change (Conover *et al.*, 2009), and evidence of such adaptation to thermal gradients has already been established among *H. americanus* populations across the Atlantic, with larval growth and planktonic duration found to be comparatively shortened under local sea temperatures (Quinn *et al.*, 2013).

Reported variation in size at the onset of maturity (SOM) also appears to support the suggestion that geographical and environmental factors may influence reproductive ecology atypically in *H. gammarus*. Female SOM has been estimated to be generally smaller in those samples farther from the mild Northeast Atlantic currents (Table 3), despite an expectation to positively align with mean temperature as a product of greater energy acquisition and growth rate (e.g. Zuo *et al.*, 2011; Green *et al.*, 2014), as has been asserted for *H. americanus* (Little and Watson, 2003, 2005; Caputi *et al.*, 2013). Physiological assessments found SOM to be smaller in Bridlington than at any location around Ireland (Free, 1994; Tully *et al.*, 2001), and morphologically determined SOM was lower in the Scottish North Sea than at the Hebridean Atlantic coast. In both scenarios, lobsters mature at smaller sizes in the area of greater temperature range, despite those areas experiencing lower overall mean temperatures. Assessing the relative contributions of environmental, demographic, and genotypic factors can be extremely challenging (Wright, 2013), but the alignment of multiple traits to gradients of temperature range is a strong indicator that reproductive variation in *H. gammarus* is driven by thermal environment.

It is not possible to disentangle whether the observed spatial variation in *H. gammarus* fecundity arises as a result of differences in the production of eggs or in the retention of eggs after oviposition, or both. Agnalt (2008) measured fecundity soon after extrusion and again soon before hatch, and detected no egg loss across 7 months among lobsters from Kvitsoy, whereas Latrouite *et al.* (1984) estimated that 27% of eggs were lost during incubation off the northwest coast of France. Agnalt (2008) sourced lobsters stringently and argued that the egg loss observed by Latrouite *et al.* (1984) could have arisen from handling and inappropriate storage, factors well known to downwardly bias subsequent egg counts. Nevertheless, most studies of *H. americanus* imply that 15% or more of eggs are lost during incubation (Wahle *et al.*, 2013), and egg retention could exist as a result of thermal environment, so egg loss during incubation cannot be discounted as a mechanism of *H. gammarus* fecundity variability. Egg loss among communally captive *H. gammarus* is dramatically reduced below a thermal tipping point of $\sim 9^\circ\text{C}$ (B. Marshall, pers. comm.), with decreased metabolism and movement inhibiting behaviours and interactions which otherwise inhibit egg retention. It is also conceivable that the diversity and abundance of known fungal and nemertean pathogens of lobster eggs (e.g. Alderman and Polglase, 1986; Campbell and Bratney, 1986) is influenced by sea temperatures. However, speculative hypotheses that rate of egg loss may be improved in colder winters are tempered by the extended duration of the incubation period at lower temperatures (Charmantier and Mounet-Guillaume, 1992; Schmalenbach and Franke, 2010) and by our analysis of samples from Selsey and Poole, which also had high fecundity at mean size,

but where high temperature ranges were driven by warm summers rather than cold winters.

Although there is a tendency for mass egg⁻¹, egg and larval size, and larval robustness to increase with female size (Tully *et al.*, 2001; Agnalt, 2008; Moland *et al.*, 2010), scant evidence has been found of any trade-off between quantity and quality of egg production in *H. gammarus*. Investment per egg in terms of dry mass appears consistent between samples from Ireland, Kvitsøy, and Falmouth and showed no discernible association to clutch size in our Falmouth sample. In the geographic range of this study, it is also unlikely that fecundity variation arises as a result of regional differences in spawning frequency, as a biennial reproductive cycle has been recorded for the majority of lobsters in both Norway and Ireland (Tully *et al.*, 2001; Agnalt *et al.*, 2007), although variation in spawning strategies is apparent in the genus and is poorly understood (Gendron and Ouellet, 2009). Fishing-induced mortality is another candidate driver of spatial variation in lobster fecundity. A response to selection pressures incurred via recruitment overfishing has been proposed to explain temporal fecundity increases in North Sea populations of cod (*G. morhua*), haddock (*Melanogrammus aeglefinus*), and plaice (*Pleuronectes platessa*; Yoneda and Wright, 2004; Rijnsdorp *et al.*, 2005; Stares *et al.*, 2007; Wright *et al.*, 2011b) and was also considered as a driver of temporal SOM variation in *H. americanus* (Landers *et al.*, 2001). Among the samples we investigated, the highest fecundities at mean size were recorded from the post-collapse population at Kvitsøy (Agnalt *et al.*, 1999) and the samples from Bridlington, Selsey, and Poole, which are from stocks in the east and south of England that experience heavier fishing pressure than those of Atlantic coasts towards the southwest (Cefas, 2011). The status of stocks around Ireland and Wales are not known. The strong effects of longitude and temperature range that we identified suggest that any demographic pressure must also align closely with these gradients, although from the limited information available on current and historical fishing pressure, this does seem to be the case for *H. gammarus* in parts of northern Europe.

The confirmation and elucidation of geographical and/or environmental drivers of fecundity variation would be valuable to the management of reproductive potential in *H. gammarus* stocks, especially among unassessed regions in lieu of laborious manual quantifications (Currie and Schneider, 2011). Predictions facilitated via relationships we have demonstrated with temperature range may be a suitable method of fecundity estimation among unmeasured populations, although the associations we found between temperature and fecundity are not as categorical as those offered by Currie and Schneider (2011) for *H. americanus*. This may be an artefact of uncontrolled variation in the effective spatial ranges of the regional samples we analysed. Our findings would be strengthened by the standardized assessment of *H. gammarus* fecundity in other regions within the spatial range encompassed by this study, as well as in areas such as Subarctic Norway, the Iberian peninsula, Morocco, and the Mediterranean to determine whether temperature range may be a driver of clutch size throughout the species' range. Repeat estimations in regions previously assessed could elucidate whether fecundity varies temporally as well as spatially, and provide further evidence that the recorded variation in lobster fecundity reflects population-level differences in the production and/or retention of eggs, rather than inherent bias between samples.

Conclusions

We show that the fecundity of European lobsters at mean female size correlates positively with easterly longitude and annual range in

SSTs across the northern range of this species. Fecundity at mean size did not correlate with mean temperature or latitude, contradicting the widely assumed temperature dependence of ectotherms. We propose that the proximity of populations to stable Atlantic currents is the driver of this variation. With further validation, temperature-correlated fecundity predictions would provide a valuable tool in ensuring that conservation management is suited to the reproductive characteristics of lobster populations.

Supplementary data

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

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