From the Adriatic to Northern Norway—geographic differences in moult increment and moult probability of the European lobster (*Homarus gammarus*), across the natural range

Matthew T. Coleman ⓘ [1,2]*, Anne-Lisbeth Agnalt[3], Jack Emmerson[4], Martial Laurens[5], Joanne S. Porter[1], Michael C. Bell[1]

[1]*International Centre for Island Technology, Heriot Watt University, Stromness, Orkney, UK*
[2]*Orkney Sustainable Fisheries Ltd, Stromness, Orkney, UK*
[3]*Institute of Marine Research, Nordnes, Bergen, Norway*
[4]*School of Ocean Sciences, Bangor University, Menai Bridge, Anglesey, UK*
[5]*Laboratoire de Biologie Halieutique, Centre Bretange, Ifremer, Brest, France*

Corresponding author: tel: + 44 (0)1856850605; e-mail: mtc2@hw.ac.uk.

This study collated existing data on lobster moult increment from studies across the range of *Homarus gammarus*, together with new tagging data from Orkney, United Kingdom. Generalized additive models were used to investigate geographical differences in absolute moult increment and moult probability. Absolute moult increment was seen to differ significantly between regions and between sexes and showed a non-linear relationship with pre-moult size. Smaller absolute moult increments were observed at southern and northern latitudes with larger increments observed in the centre of the species range. Temperature was identified as a significant factor explaining differences in absolute moult increment between regions, consistent with there being a thermal optimum for growth for in *H. gammarus*. Moult and double moult probabilities decline with pre-moult size, with greatest probability of moulting occurring around day 250. Probability of double moulting increased with mean annual sea surface temperature. Regionally variable growth patterns, and localized adaptation to abiotic variables such as temperature, should therefore be taken into account when defining lobster stock assessment and fishery management areas.

Keywords: climate change, growth, Homarus, lobster, moult, tag recapture, temperature, thermal preferendum

Introduction

The geographic distribution of European lobster, *Homarus gammarus*, spans the Mediterranean to northern Norway. Annual landings across this range total up to 5600 tonnes (FAO, 2019) and the best harvest rates being around the British Isles. The high market price means that this relatively low abundance species supports socio-economically valuable fisheries, predominantly consisting of small inshore vessels. Despite this socio-economic importance, we lack data on such fundamental population dynamic topics as the temporal–spatial variations in growth rates, which are the topic of this paper.

In the case of crustaceans, growth is achieved through a process of ecdysis and growth rates are described by a combination of moult frequency (inter-moult period) and the size of each moult increment (growth factor). Observations of growth across several populations suggest that environmental factors, temperature in particular, can explain at least some of the variation in the size-at-age relationship, where greater inter-moult periods and

smaller growth factors (i.e. growth rate) are observed at the thermal boundaries of a species (Hartnoll, 2001; Green *et al.*, 2014). In *Homarus americanus*, Waddy *et al.* (1995) showed that moulting is inhibited <5°C, whilst temperatures <25°C are physiologically stressful or lethal. Between 8 and 25°C, however, growth rates are positively correlated with temperature. This is evident in the observed faster growth rates in warmer southern summer temperatures of Southern Gulf of St. Lawrence and Southern New England *H. americanus* populations, whilst slower growth is exhibited by northern population in Bay of Fundy and Eastern Gulf of Maine, which experience colder regimes (Wahle and Fogarty, 2006). Similarly, differences in growth rates are observed in other Crustacea; southern rock lobster *Jasus edwardsii* exhibits localized site specific adaptation in response to thermal regimes in Southern Australia (Mcgarvey *et al.*, 1999), whilst Norwegian brown crab *Cancer pagurus* populations (Bakke *et al.*, 2018) exhibit decreasing moult frequency with lower temperatures at higher latitudes.

Growth, and its relationship with other vital processes such as maturation and natural mortality, is a key component of the biomass dynamics of a population and its resilience to exploitation. Growth rates define the scale of productivity, and the intervals between size-related life events such as recruitment to a fishery and attainment of sexual maturity, and these growth relationships are intimately tied up with localized environmental factors such as temperature (Hartnoll, 2001; Wahle and Fogarty, 2006). Setting size-selective harvesting regimes, with minimum landing size appropriate to the size-at-maturity, is generally regarded as a basic principle of good management in crustacean fisheries (Bannister, 1999).

The role of temperature and its subsequent effect on stock dynamics is becoming increasingly important for managing the impact of climate change on fisheries (Steneck and Wahle, 2013; ICES, 2019). Observed shifts in size at maturity in *H. americanus* have been observed in American fisheries (Waller *et al.*, 2019), where size at maturity has decreased over the last 50 years, coinciding with increased water temperature ranges that have altered ovary maturation over the same period (Waddy *et al.*, 1995), alongside the size-selective evolutionary effects of fishing (Haarr *et al.*, 2017). The effect of environmental variation on growth is complex and species-specific relationships between growth, moult frequency, and temperature require careful investigation (Hartnoll, 2001).

In the case of *H. gammarus*, relatively little research has been conducted to investigate the full range of spatial differences in growth and moult frequency and to identify any of the underlying changes or drivers over time. Existing studies describe differences that are regional (Thomas, 1958; Simpson, 1961; Hepper, 1967; Gibson, 1969; Shelton *et al.*, 1981; Sheehy *et al.*, 1999; Agnalt *et al.*, 2007; Schmalenbach *et al.*, 2011) or spatially more localized (Agnalt *et al.*, 2009). These are all individual studies that address specific regional questions relating to growth or stock definition whereas the overall aim of this study is to provide the first systematic study of differences in *H. gammarus* growth patterns across the entire geographic range. This is achieved using two approaches: first, geographic differences in absolute moult increment in length are examined by compiling existing lobster growth increment data and combining it with new lobster growth date from Orkney, United Kingdom, and previously unpublished data from Norway and France. Second, differences in the probability and timing of moult were investigated, first using Orkney data,

and moulting patterns explored using data from five distinct regions (Le Croisic, France; Cornwall, United Kingdom; Norfolk, United Kingdom; Yorkshire/Holderness Coast, United Kingdom; and Orkney, United Kingdom) selected because of the high number of recapture events recorded in these regions.

Material and methods
New growth data from Orkney
Legal [>90-mm carapace length (CL)] and sub legal lobsters (<90-mm CL) were caught in the commercial fishery by a mixture of traditional and parlour pots during normal days of fishing activity around the Island of Hoy, Orkney in August and September 2017. All captured individuals prior to release were sexed and CL measured to the nearest millimetre below using Vernier callipers, from the eye socket to the base of the carapace. Individuals were tagged using sequentially numbered streamer tag FTSL-73 (http://www.floytag.com). Streamer tags were inserted into the adductor muscle on the dorsal side of the individual between the cephalothorax and abdomen in the abductor muscle. Following tagging individuals were released and the global positioning system coordinates of the releases positions recorded. Lobsters that were subsequently recaptured were recorded by either on-board observers or the participating fisher. Growth was calculated as size at recapture minus the size when tagged at their previous recapture. The total number of lobsters released was 640 from a total of 4 potting days.

Geographic samples and analysis
To investigate large-scale geographic drivers in growth variability of *H. gammarus* around the Mediterranean, Western Europe and Scandinavia data were collated from nine different studies plus unpublished data from Norway (A-LA, unpublished data) and France (ML, unpublished data), equating to 991 individuals from a total 18 regions (female—16; male—17; Figure 1; Table 1). Each regional sample location was assigned the latitudinal and longitudinal coordinates from the approximate centre of the spatial range of sampling as ascertained from the individual studies. Mean annual sea surface temperature (MASST) data were obtained for each location during the year(s) of the study using a variety of resources in order to achieve full coverage of the studies used. Primary SST data were obtained where possible from national hydrographical stations (United Kingdom—www.cefas.co.uk; Norway—www.imr.no) and through EMODnet Physics portal (www.emodnet-physics.eu/Portal). EMODnet provides access to data collected by moorings and oceanographic buoys across the EU member states. In cases when hydrographical station data were not available, SST data were in the first instance sourced from the ICES data portal (https://www.ices.dk/marine-data) and second from the HadISST data base (Rayner *et al.*, 2003). Sea bottom temperature (SBT) would be a preferred metric due to the benthic nature of the lobster, but SST was used as it is more widely available and is significantly correlated with SBT (Ellis *et al.*, 2015). Prior to statistical analysis, cross correlation of exploratory variables was investigated, indicating that MASST and latitude were highly negatively correlated ($R^2 = -0.73$) (Raper and Schneider, 2013), resulting in the dropping of latitude as separate exploratory variable.
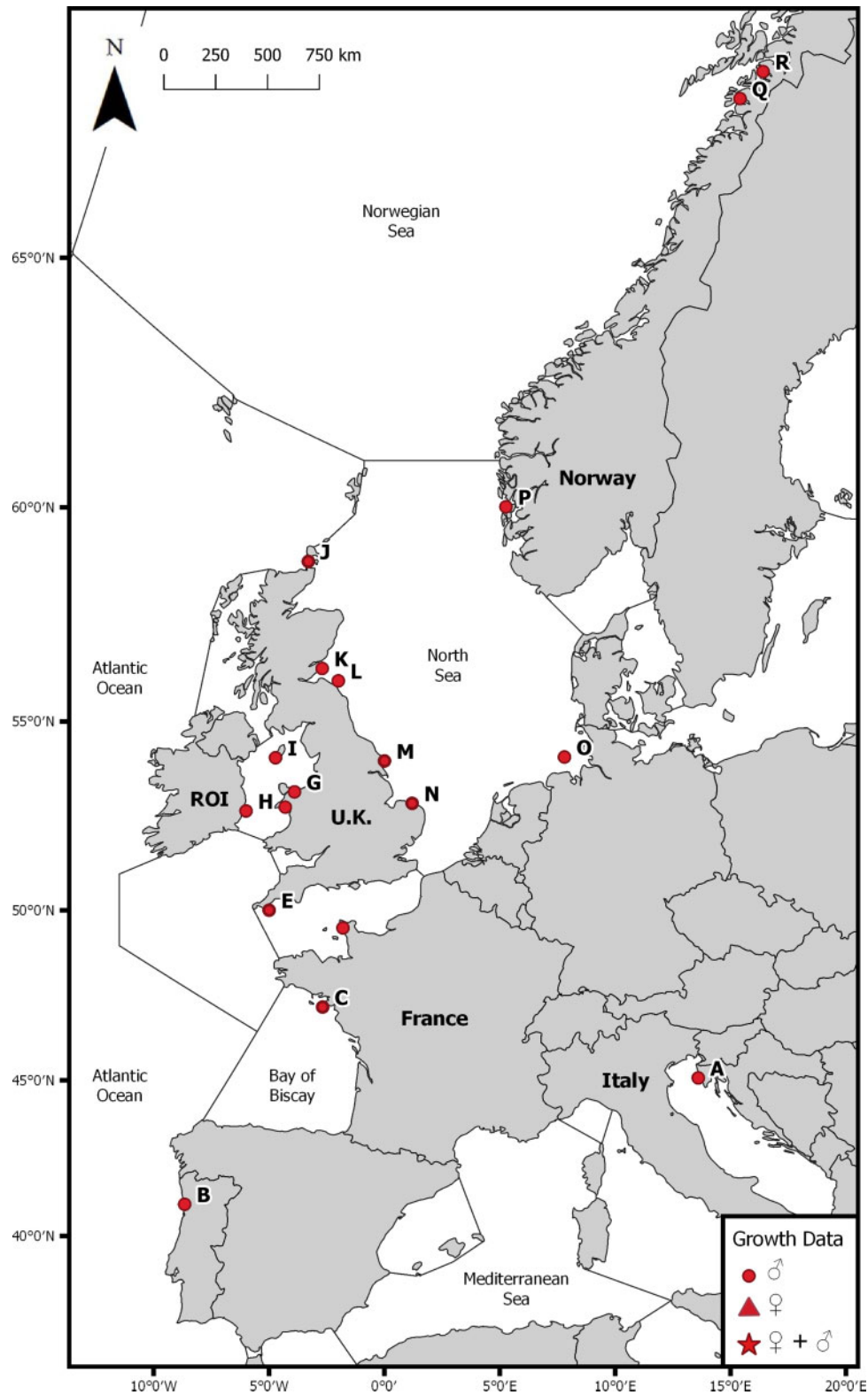
Figure 1. Geographic extent of sample locations used in estimating geographic differences in moult increment of European lobster *Homarus gammarus*. Sample locations: (a) Rovinj, Croatia (Devescovi and Lucu, 2000); (b) Porto, Portugal (Couto de Jesus, 2016); (c) Le Croisic, France (ML, unpublished data); (d) Flamanville, France (ML, unpublished data); (e) Cornwall, United Kingdom (Hepper, 1967); (f) Pwllheli, United Kingdom (Simpson, 1961); (g) Menai, United Kingdom (Simpson, 1961); (h) Ireland (Gibson, 1969); (i) Isle of Man; (j) Orkney, United Kingdom; (k) St. Andrews, United Kingdom (Shelton et al., 1981); (l) Eyemouth, United Kingdom (Thomas, 1958); (m) York/Holderness Coast, United Kingdom (Hepper, 1967); (n) Norfolk, United Kingdom (Bennett et al., 1978); (o) Heligoland, Germany (Mehrtens, 2008; Schmalenbach et al., 2011); (p) Vinnes, Norway (A-LA, unpublished data); (q) Nordfolda, Norway (A-LA, unpublished data); and (r) Stefjord, Norway (A-LA, unpublished data).

Table 1. Summary of regional samples analysed including sample size (*n*) per sex; size range of samples and study origin.

Region	n♀	n♂	Size range CL (mm)	Reference
Croatia—Rovinj (A)	–	6	89–141	Devescovi and Lucu (2000)
Portugal—Porto (B)	–	4	77–154	Couto de Jesus (2016)
France—Le Croisic (C)	23	14	70–156	ML, unpublished data
France—Flamanville (D)	34	–	78–128	ML, unpublished data
United Kingdom—Cornwall (E)	36	25	74–123	Hepper (1967)
United Kingdom—Pwllheli (F)	25	13	75–113	Simpson (1961)
United Kingdom—Menai (G)	11	16	71–109	Simpson (1961)
Ireland (H)	61	47	63–118	Gibson (1969)
Isle of Man (I)	10	13	73–87	JE, unpublished data
United Kingdom—Orkney (J)	30	50	75–129	Coleman *et al* (This study)
United Kingdom—St Andrews (K)	45	46	64–115	Shelton *et al.* (1981)
United Kingdom—Eyemouth (L)	62	50	71–89	Thomas (1958)
United Kingdom—Yorkshire/Holderness Coast (M)	65	27	64–116	Hepper (1967)
United Kingdom—Norfolk (N)	15	16	60–99	Bennett *et al.* (1978)
Germany—Heligoland (O)	25	12	40–123	Mehrtens (2008); Schmalenbach *et al.* (2011)
Norway—Vinnes (P)	71	69	51–117	A-LA, unpublished data
Norway—Nordfolda (Q)	3	11	75–118	A-LA, unpublished data
Norway—Stefjord (R)	24	31	57–97	A-LA, unpublished data

Moult increment in length

Overall variation in growth was investigated by comparing increment growth increment per moult (mm). Data obtained from Croatia (Devescovi and Lucu, 2000) and Portugal (Couto de Jesus, 2016) record moult increment relative to total length (TL) as opposed to CL. Data from these studies were therefore converted to CL using the equation CL = (0.401TL) − 10.5' obtained from Hepper (1967) as regional conversion factors are not available. Multiple moults can potentially occur over the course of a year or longer period at liberty (Hepper, 1967). To identify absolute growth increments containing multiple moults, the percentage of pre-moult size was calculated as increment divided from pre-moult size multiplied by one hundred. Based on Hepper (1967) increments, <20% of pre-moult size were considered to represent multiple moults and were excluded from further analysis. Following Agnalt *et al.* (2007), growth increments <2 mm were also excluded as likely to represent measurement errors rather than growth following a moult.

Geographical differences in growth

Differences in absolute growth increment were modelled using the explanatory variables of region and MASST. Given the relationship between growth and temperature in *H. americanus* (Waddy *et al.*, 1995) and the broad range of MASST experienced by *H. gammarus*, it was hypothesized that the interaction of MASST would have a non-linear effect on growth increment. Generalized additive mixed modelling (GAMM) was therefore used to describe the relationship between increment and smooth terms for CL and MASST, with sex treated as a factor variable and region as a random effect (Wood, 2017). The full model had the form

$$\mu = \text{intercept} + \text{sex} + s(\text{CL}) + (1|\text{region}),$$

where μ is the growth increment, sex is a factor variable s(CL) is a smooth term for CL, and (1|region) is a random intercept. Given positive-only values, increment was modelled using a log link and a gamma error distribution. This starting model included sex, region, and CL, with smooth term MASST considered as potential

simplifications of the region effect. Selection of the most parsimonious model within the full model hierarchy was by minimum value of the Akaike information criterion (AIC) (Burnham and Anderson, 2002).

All statistical analysis was conducted in R version 3.5.3 (R Development Core Team, 2011). All models were fitted using the *gam* function in the *mgcv* package in R (Wood, 2017), with the thin-plate regression splines for smoothers.

Probability of moulting

In modelling probability of moulting, only data from Orkney were used owing to the availability of complete individual recapture history and suitable sample size (*n* = 134). Moulting probability (1 = moulted, 0 = no moult) was investigated using the explanatory variables of sex treated as a factor and smooth terms for day of year (doy) and CL. doy was defined as the date of recapture. A generalized additive model (GAM) was used, and the full model had the form

$$\pi = \text{intercept} + \text{sex} + s(\text{doy}) + s(\text{CL}),$$

where π is the probability of moulting, modelled using a logit link and a binomial error distribution. The most parsimonious model within the full model hierarchy was selected by minimum value of AIC.

Probability of double moulting

Observed differences in the number of moulting events have been recorded in *H. gammarus* previously, with increased probability of double moulting at size <90-mm CL, and a reduced moulting frequency above ∼120-mm CL (Bennett *et al.*, 1978). The probability of geographic differences in double moulting was explored across five regions (Le Croisic, France *n* = 63; Cornwall, United Kingdom *n* = 99; Norfolk, United Kingdom *n* = 98; Yorkshire/Holderness Coast, United Kingdom *n* = 110; and Orkney, United Kingdom *n* = 125; Figure 2). Recaptures were classified as double moulting if the increment was <20% of pre-moult size. A maximum threshold of 40% of pre-moult size was also used, negating
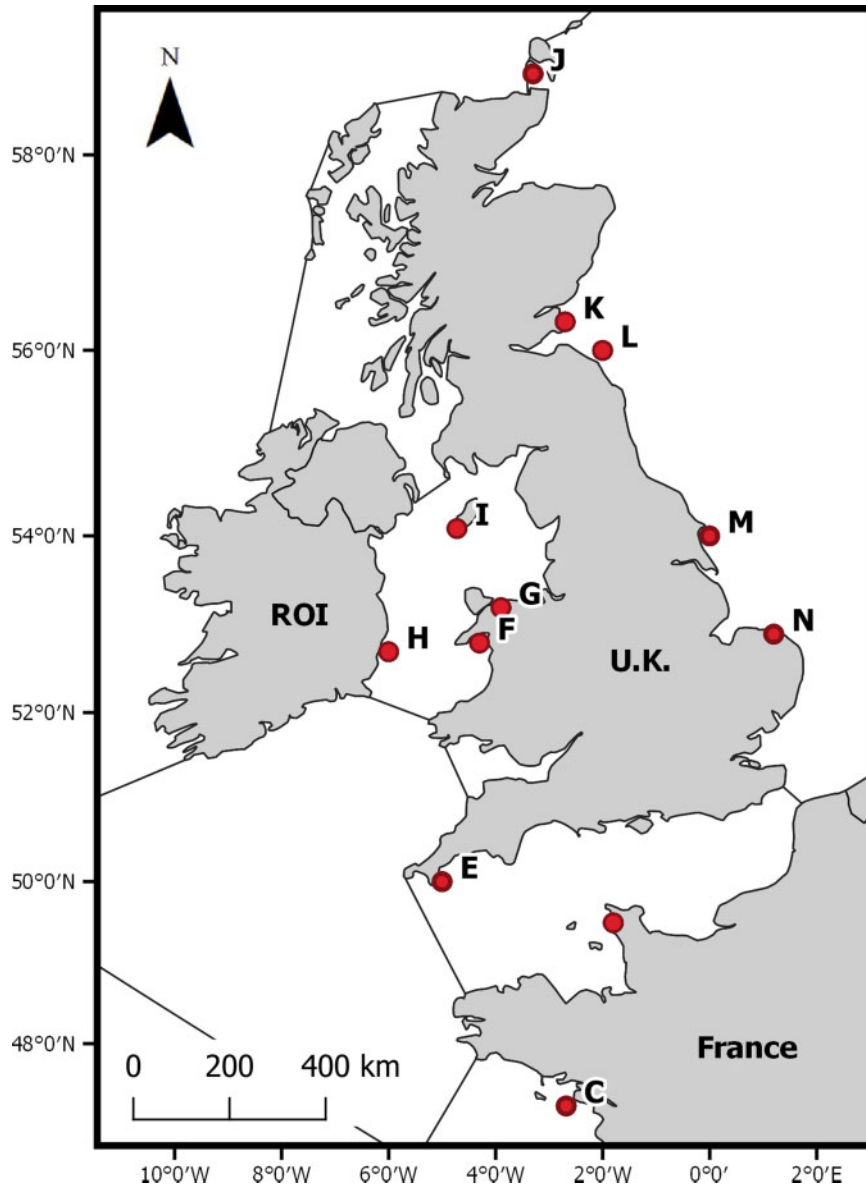
Figure 2. Geographic extent of sample locations used to estimate geographic differences in double moult probability. (C) Le Croisic, France; (E) Cornwall, United Kingdom, (N) Norfolk, United Kingdom; (M) York/Holderness Coast, United Kingdom; (J) Orkney, United Kingdom.

the inclusion of potential multiple moult events in individuals which time at liberty was >365 days or time at liberty was unknown. This threshold was derived from individuals with full recapture history >~365 days and exhibited the occurrence of double moult events.

The occurrence of double moulting (1 = moulted, 0 = no moult) was modelled using a GAM with logit link and a binomial error distribution. Smooth terms were defined for CL, MASST and longitude, with region and sex treated as a factor variable. The starting model had the form

$$\pi = \text{intercept} + \text{region} + \text{sex} + s(\text{CL}),$$

where π is the probability of double moulting. A smooth term for MASST was considered as an alternative to region as a factor. The most parsimonious model was selected by modelling the full model hierarchy, with the final model selection using AIC.

Results

Sexual and geographical differences in moult increment

Moult increment data were compiled for 991 individuals across 18 geographic regions from published, unpublished and grey literature sources. GAMM selection (by minimum AIC) identified sex-, region-, and sex-specific smoothers for CL as having a significant effect on moult increment in European lobsters. This model accounted for 39.4% of the deviance explained, with region being the most significant contributor ($p < 0.001$). Sex-specific regional variation in moult increment was also identified. Nevertheless, regional differences in moult increment
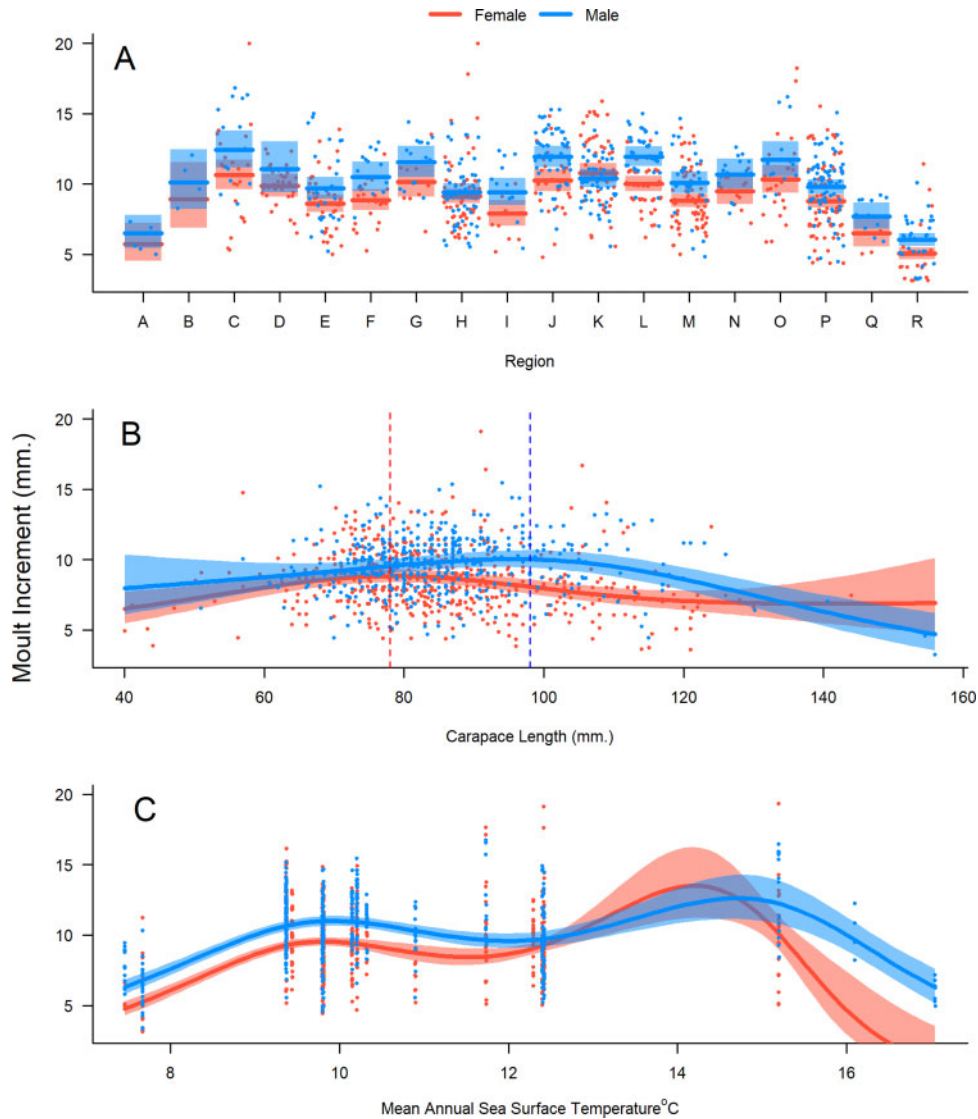
Figure 3. Estimated smoother by generalized additive modelling for the effect of (a) region, (b) carapace length, and (c) mean annual sea surface temperature on sex-specific moult increment size (mm). Dashed lines on (b) denote identified changes in morphometric growth: red—female ∼79 mm CL; blue—Male ∼ 98 mm CL (Lizarraga-Cubedo et al., 2003). Buffered lines denote 95% confidence intervals, points represent partial residuals.

demonstrate a broadly similar pattern between males and females, with significantly smaller moult increments observed in females per region compared to males (Figure 3a). Moult increments were similar between males and females and increasing with CL up to 78 mm CL, then decreasing in females at larger sizes (Figure 3b). Male moult increments continued the trend of increase up to 98 mm CL, decreasing at larger sizes (Figure 3b).

If MASST is included in the model as an alternative to region, this also had a significant, sex-specific effect on absolute moult increment size ($p < 0.001$; Figure 3c). This model only explained 29.4% of the deviance.
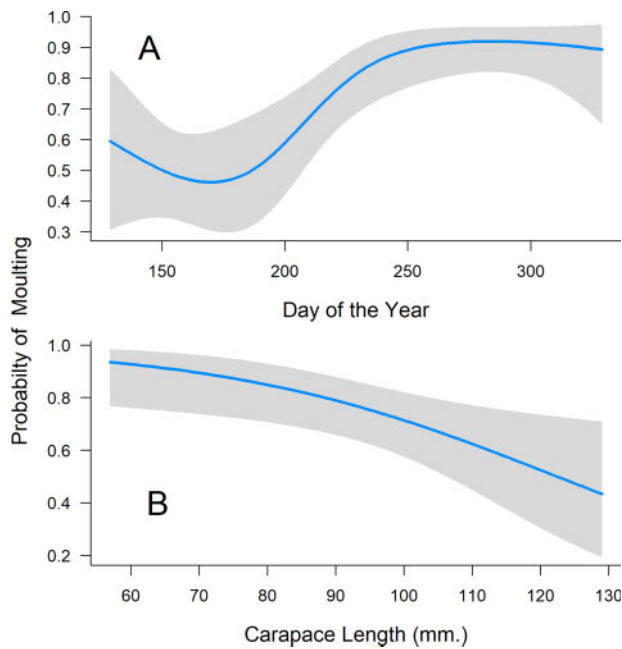
Probability of moulting and double moulting

Moulting

The GAM identified CL ($p = 0.01$) and doy ($p < 0.001$) as having significant non-linear effects on the probability of moulting. This

accounted for 16.4% of the deviance, with day of the year the most significant contributor. Low proportion of deviance accounted for indicates the influence of other external factors affecting the timing and probability of moulting. Sex had no significant effect on the probability of moulting and was not retained in the minimum AIC model. Day of the year had a significant effect on the probability of moulting, with lower probability (∼0.5) in late spring/early summer (days 130–200) contrasted with higher probability (∼0.9) in early autumn and winter (days 250–325) (Figure 4a). CL had a significant effect on the probability of moulting, estimated to be <90% at 60-mm CL and decreasing to ≈40% by ≈130-mm CL (Figure 4b).

Double moulting

The GAM selection (by minimum AIC) identified region-specific CL as having a significant effect on the probability of double

Figure 4. Estimated effect of smoothers (a) day of year and (b) carapace length (mm) on the probability of moulting for European lobsters *Homarus gammarus* in Orkney, United Kingdom. Dashed lines denote 95% confidence intervals.

moult, sex being dropped from the final model. This model accounted for 37.9% of the deviance explained. Probability of double moult decreases with size in all regions, but with differences in the rate of decline: fastest in Yorkshire lobsters, for which the probability of a double moult is effectively zero by 85-mm CL; slowest for Le Croisic, for which zero probability of double moult is expected to occur at ≈130-mm CL (Figure 5a). Orkney, the most northerly site, is intermediate. Large confidence intervals are observed in Yorkshire samples, this is attributed to the lack of samples >90-mm CL comparative to the other regions analysed in the model.

If MASST is included in the model as an alternative to region, this also shows a significant effect on double moult probability ($p < 0.001$). The relationship is positive but non-linear (Figure 5b). This model accounted for 36.1% of the deviance, only slightly less than the full regional model. The probability of double moult increases rapidly with temperature up to ≈11°C, with probability plateauing >11°C.

Discussion

This is the first reported study to compile and compare data on the absolute moult increment and moult frequency of *H. gammarus* across the entire geographic range. This includes data based on new tag-recapture results for Orkney. The main analysis has identified for the first time statistically significant differences in growth between regions. Growth increments appear broadly similar across the central distribution of *H. gammarus* from 50 to 59°N. This could in part be attributed to genetic similarity of populations, owing to genetic connectivity or stepping-stone dispersal (Ellis *et al.*, 2017). In contrast, lower growth increments apparent at both northern and southern range limits could be evidence of reduced gene flow and localized recruitment at

boundary extremes resulting in localized adaptation of attributes such as growth (Agnalt *et al.*, 2009).

Regional variation in absolute growth increment driven by localized differences in abiotic factors is frequently reported in crustaceans, with temperature most often identified as the most significant influence (e.g. Whiteley *et al.*, 1997; Brylawski and Miller, 2006; Kuhn and Darnell, 2019)). A statistically significant effect of MASST on moult increment was estimated, which differed between the sexes. Moreover, MASST only partially accounts for regional differences, indicating that local differences are more important over at least parts of the overall range. Newman and Pollock (1974) identified benthic productivity, and hence food availability, as a source of variation in growth patterns in the rock lobster *Jasus lalandii*. Other factors that have been implicated as drivers of regional growth variability in crustaceans include salinity (Jury *et al.*, 1994), depth (Chandrapavan *et al.*, 2010), and population density (Marks *et al.*, 2020). Size-selective exploitation can exert selection pressure towards populations dominated by smaller, faster-growing individuals (Swain *et al.*, 2007), which can be evident in terms of moult increments (Parma and Deriso, 1990). McGarvey *et al.* (1999) noted a negative relationship between male moult increment and catch rates in the southern rock lobster *J. edwardsii*. Direct evidence is lacking, but such patterns could exist in *H. gammarus*, which experiences localized exploitation of varying intensity across its range.

Our study showed large-scale patterns in growth in *H. gammarus* that were similar between male and females, but males showed larger increments, consistent with previous observations for this species (Thomas, 1958) and for *H. americanus* (e.g. Tremblay and Eagles, 1997; Comeau and Savoie, 2001). In addition, the results documented for the first time clear observed differences in absolute moult increment with pre-moult size, which at larger sizes was also shown to differ between the sexes. Such differences may be associated with reproductive aspects of life-history, notably greater energy requirements for gamete production in females (Templeman, 1933; Ennis, 1972), and size-selective mating preferences (Sørdalen *et al.*, 2018). It is notable that the peak moult increment in males at 98-mm CL (Figure 3b) corresponds with size at male morphometric maturity estimated by Lizarraga-Cubedo *et al.* (2003). Divergence of growth between males and females at 80-mm CL (Figure 3b) could be attributed to increased allocation of energy to reproduction at the onset of maturity in females (Templeman, 1933; Free *et al.*, 1992; Tremblay and Eagles, 1997; Lizarraga-Cubedo *et al.*, 2003; Wood, 2018) as well as increased inter-moult period owing to spawning periodicity.

Although this study found only weak evidence for the role of temperature in determining growth increment, further study of the influence of this factor is warranted. Previous studies have documented the importance of temperature in regulating growth and associated life-history processes [see review by Hartnoll (2001)]. There is at least some evidence (Figure 3c) of a thermal optimum at ≈10°C, with possible declines in moult increment at the thermal extremes, consistent with patterns noted for *H. americanus* (Waddy *et al.*, 1995). Understanding the relationship of growth with temperature may provide an avenue for improved fishery management by providing regionally appropriate growth parameters to support stock assessment [c.f. general growth model for *H. americanus* by Raper and Schneider (2013)]. Stock assessments for *H. gammarus* are commonly limited by the availability of regionally appropriate growth (and other) parameters, with single values applied across populations separated at scales
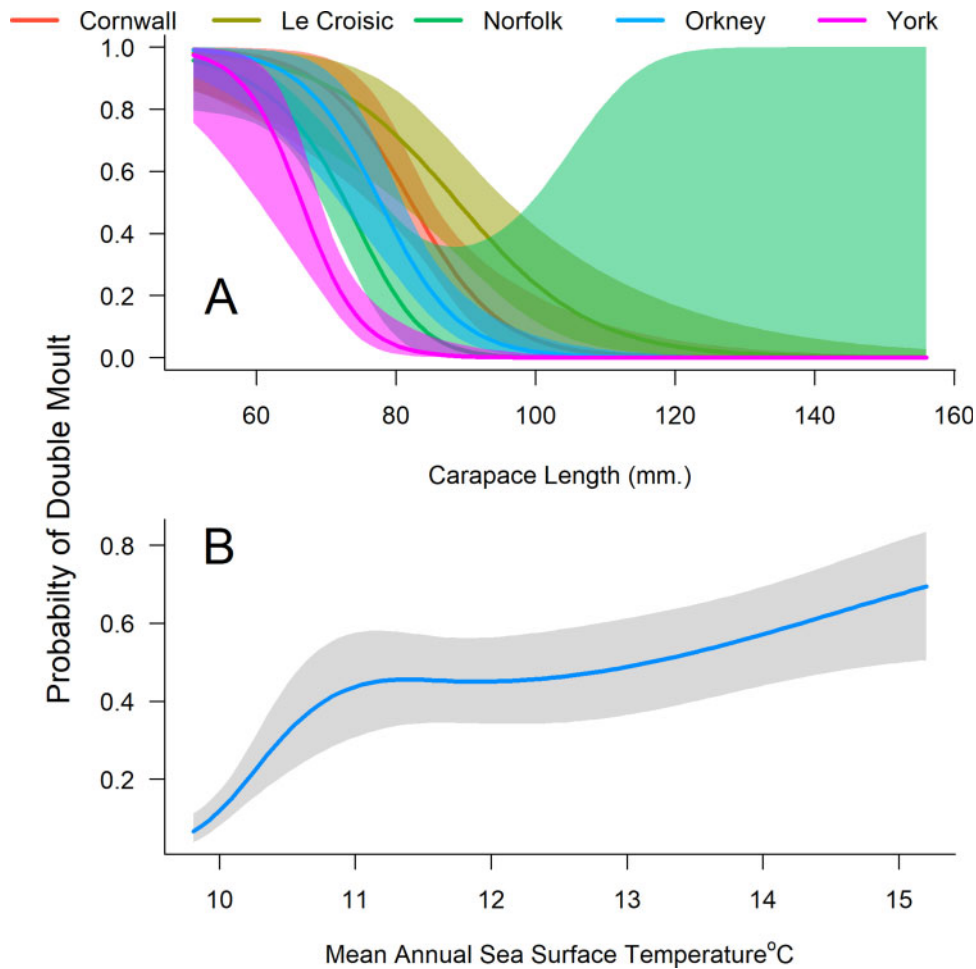
Figure 5. Estimates of (a) region-specific smoothers of carapace length (mm) and (b) MASST (°C) on the probability of double moult event occurring in European lobster *Homarus gammarus*. Buffers denote 95% confidence intervals.

of 100 km and greater (Mesquita *et al.*, 2017; McIntyre *et al.*, 2017).

Potential alterations in productivity driven by climate change provide further context for considering the role of temperature in determining growth patterns in *H. gammarus*, but this needs careful consideration in relation to other factors. Climatic impacts are evident in *H. americanus*, whose Gulf of Maine stock and fishery have surged owing to reduced predation by groundfish (Steneck and Wahle, 2013) but are potentially threatened by recent increases in sea temperature close to or above the thermal limit for this species (Le bris *et al.*, 2018). Evidence is emerging of ecosystem responses to climatic shifts in the North Sea. Recent declines in stock biomass of Atlantic cod *Gadus morhua* are attributed to a combination of fishing pressure and climate change (ICES, 2019). *Homarus gammarus* could potentially benefit from reduced predation of cod on pre-recruits, as happened in the Gulf of Maine (Steneck and Wahle, 2013), but warming could also impact upon populations at the southern end of the range.

Similar to moult increment, the low explanatory power of our models for moult probability indicates that drivers are complex, similar to what has been found for the brown crab *C. pagurus* (Bakke *et al.*, 2018). Our observed moult probabilities for *H. gammarus* are in line with those for *H. americanus* (Tremblay and Eagles, 1997), showing strong declines

with increasing size. Limited availability of data on moult timing in *H. gammarus* restricts comparisons between regions, but regional variation is known to occur owing to localized variation in seasonal temperature regimes [see review by Green *et al.* (2014)]. Such patterns are also evident in other species such as *C. pagurus* (Bakke *et al.*, 2018). Moulting in Orkney lobsters was seen to increase around early summer, peaking from early autumn onwards, corresponding with water temperatures increasing from 7 to 13°C (Coleman, 2017). Timing of moult to coincide with peak water temperature is thought to facilitate time and condition for calcification of new exoskeleton, with metabolic rates accelerating over the temperature range 8–25°C in *H. americanus* (Aiken, 1977).

The effects of temperature on growth in *H. gammarus* are evident in the increase in probability of double moulting between 10 and 15°C (Figure 5b). Warmer temperatures provide protracted moulting seasons that may compensate in some degree for smaller increment sizes (Serfling and Ford, 1975; Hartnoll, 2001). This would similarly have effects on other life-history traits, such as prevalence of double egg clutches, as seen in French populations in Le Croisic (Laurans *et al.*, 2017) and increased recruitment in Flamanville, France (Sleben and Addison, 2019). Multiple moult events have been recorded in pre-recruits from previous tagging studies (Hepper, 1967).

Conclusion

This study demonstrates for the first time geographical differences in growth of *H. gammarus*, spanning the distribution of the species. The study also highlights the difficulty in attributing regional growth patterns to a simple abiotic variable. The evidence points to the influence of regional factors on growth pattern, of which temperature is a significant but by no means the sole component. Understanding these patterns is crucial for effective fishery management underpinned by stock assessment and criteria for sustainability defined at a regionally appropriate level.

The data underlying this article were provided by A-L Agnalt, ML, and JE by permission. Data will be shared on reasonable request to the corresponding author with permission of co-authors where required.

References

Agnalt, A. L., Farestveit, E., Gundersen, K., Jørstad, K. E., and Kristiansen, T. S. 2009. Population characteristics of the world's northernmost stocks of European lobster (*Homarus gammarus*) in Tysfjord and Nordfolda, northern Norway. New Zealand Journal of Marine and Freshwater Research, 43: 47–57.

Agnalt, A.-L., Kristiansen, T. S., and Jørstad, K. E. 2007. Growth, reproductive cycle, and movement of berried European lobsters (*Homarus gammarus*) in a local stock off southwestern Norway. ICES Journal of Marine Science, 64: 288–297.

Aiken, D. 1977. Molting and growth in decapod crustaceans with particular reference to the lobster Homarus americanus. Division of Fisheries and Oceanography Circulation. (Australia. CSIRO), 7: 41

Bakke, S., Larssen, W. E., Woll, A. K., Søvik, G., Gundersen, A. C., Hvingel, C., and Nilssen, E. M. 2018. Size at maturity and molting probability across latitude in female *Cancer pagurus*. Fisheries Research, 205: 43–51.

Bannister, R. 1999. Crab and lobster: have we reached the critical point. *Based on an article first published in Fishing News, 10.*

Bennett, D., Brown, C., Howard, A., and Lovewell, S. 1978. Comparison of Lobster (*Homarus gammarus*) Growth Rates in Norfolk and Yorkshire, England. ICES Document CM 1978/K:6. 8 pp.

Brylawski, B. J., and Miller, T. J. 2006. Temperature-dependent growth of the blue crab (Callinectes sapidus): a molt process approach. Canadian Journal of Fisheries and Aquatic Sciences, 63: 1298–1308.

Burnham, K. P., and Anderson, D. R. 2002. A Practical Information-Theoretic Approach. Model Selection and Multimodel Inference, 2nd edn. Springer, New York.

Chandrapavan, A., Gardner, C., and Green, B. S. 2010. Growth rate of adult rock lobsters *Jasus edwardsii* increased through translocation. Fisheries Research, 105: 244–247.

Coleman, M. 2017. Orkney Sea Bottom Temperature Monitoring: Project Update May 2017. Orkney Sustainable Fisheries Ltd.

Comeau, M., and Savoie, F. 2001. Growth increment and molt frequency of the American lobster (*Homarus americanus*) in the Southwestern Gulf of St. Lawrence. Journal of Crustacean Biology, 21: 923–936.

Couto de Jesus, S. A. 2016. Projeto de Marcação e Recaptura do Lavagante Europeu, Homarus gammarus, na Praia da Aguda. Master's degree, Universidade do Porto.

Devescovi, M., and Lucu, C. 2000. Growth patterns of the lobster *Homarus gammarus* in the North Adriatic. Periodicum Biologorum, 102: 189–193.

Ellis, C., Hodgson, D., Daniels, C., Collins, M., and Griffiths, A. 2017. Population genetic structure in European lobsters: implications for connectivity, diversity and hatchery stocking. Marine Ecology Progress Series, 563: 123–137.

Ellis, C. D., Knott, H., Daniels, C. L., Witt, M. J., and Hodgson, D. J. 2015. Geographic and environmental drivers of fecundity in the European lobster (*Homarus gammarus*). ICES Journal of Marine Science, 72: i91–i100.

Ennis, G. 1972. Growth per moult of tagged lobsters (*Homarus americanus*) in Bonavista Bay, Newfoundland. Journal of the Fisheries Board of Canada, 29: 143–148.

Free, E., Tyler, P., and Addison, J. 1992. Lobster (*Homarus gammarus*) Fecundity and Maturity in England and Wales. ICES Document CM 1992/K43.

Gibson, A. F. 1969. Age, Growth and Maturity of Irish lobsters.

Green, B. S., Gardner, C., Hochmuth, J. D., and Linnane, A. 2014. Environmental effects on fished lobsters and crabs. Reviews in Fish Biology and Fisheries, 24: 613–638.

Haarr, M., Sainte-Marie, B., Comeau, M., Tremblay, M., and Rochette, R. 2017. Female American lobster (*Homarus americanus*) size-at-maturity declined in Canada during the 20th and early 21st century. Canadian Journal of Fisheries and Aquatic Sciences, 75: 908–924.

Hartnoll, R. G. 2001 Growth in Crustacea—Twenty Years on. Springer Netherlands, Dordrecht. 111–122.

Hepper, B. T. 1967. On the growth at moulting of lobsters (Homarus Vulgaris) in Cornwall and Yorkshire. Journal of the Marine Biological Association of the United Kingdom, 47: 629–643.

ICES. 2019. Cod (*Gadus morhua*) in Subarea 4, Division 7.d, and Subdivision 20 (North Sea, eastern English Channel, Skagerrak). *Report of the ICES Advisory Committee*. ICES Advice 2019.

Jury, S. H., Kinnison, T., Huntting Howell, M., W., and Watson, W. H. 1994. The effects of reduced salinity on lobster (*Homarus americanus* Milne-Edwards) metabolism: implications for estuarine populations. Journal of Experimental Marine Biology and Ecology, 176: 167–185.

Kuhn, A. A., and Darnell, M. Z. 2019. Elevated temperature induces a decrease in intermolt period and growth per molt in the lesser blue crab Callinectes similis Williams, 1966 (Decapoda: Brachyura: Portunidae). Journal of Crustacean Biology, 39: 22–27.

Laurans, M. M., Fifas, S. S., Weiss, J. J., Sclaich, I. I., Robigo, L. L., Legrand, V. V., and Pengrech, A. A. 2017. Can the French lobster female (*Homarus gammarus*) be considered a super female? 11th International Confere and Workshop on Lobster Biology & Management, Portland, Maine.

Le bris, A., Mills, K. E., Wahle, R. A., Chen, Y., Alexander, M. A., Allyn, A. J., Schuetz, J. G. *et al.* 2018. Climate vulnerability and resilience in the most valuable North American fishery. Proceedings of the National Academy of Sciences of the United States of America, 115: 1831–1836.

Lizarraga-Cubedo, H. A., Tuck, I., Bailey, N., Pierce, G. J., and Kinnear, J. 2003. Comparisons of size at maturity and fecundity of two Scottish populations of the European lobster, *Homarus gammarus*. Fisheries Research, 65: 137–152.

Marks, R., Hesp, S. A., Johnston, D., Denham, A., and Loneragan, N. 2020. Temporal changes in the growth of a crustacean species,

Portunus armatus, in a temperate marine embayment: evidence of density dependence. ICES Journal of Marine Science, 77: 773–790.

Mcgarvey, R., Ferguson, G. J., and Prescott, J. H. 1999. Spatial variation in mean growth rates at size of southern rock lobster, <emph type="2">Jasus edwardsii</emph>, in South Australian waters. Marine and Freshwater Research, 50: 333–342.

Mcintyre, R., and Masefield, R., and Bell, E. 2017. Cefas Stock Status report 2017: Lobster (Homarus gammarus).

Mehrtens, F. 2008. Untersuchungen zu den Entwicklungsbedingungen des Europäischen Hummers (Homarus gammarus) bei Helgoland in Freiland und Labor. PhD thesis, University of Hamburgh.

Mesquita, C., Miethe, T., Dobby, H., and Mclay, A. 2017. Crab and lobster fisheries in Scotland: results of stock assessments 2013-2015. Scottish Marine and Freshwater Science.

Newman, G. G., and Pollock, D. E. 1974. Growth of the rock lobster Jasus lalandii and its relationship to benthos. Marine Biology, 24: 339–346.

Parma, A. M., and Deriso, R. B. 1990. Dynamics of age and size composition in a population subject to size-selective mortality: effects of phenotypic variability in growth. Canadian Journal of Fisheries and Aquatic Sciences, 47: 274–289.

R Development Core Team. 2011. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing Vienna, Austria.

Raper, J. L. D., and Schneider, D. C. 2013. Spatial scaling from latitudinal gradients: growth rates in the American lobster Homarus americanus. Marine Ecology Progress Series, 483: 231–243.

Rayner, N. A., Parker, D. E., Horton, E. B., Folland, C. K., Alexander, L. V., Rowell, D. P., Kent, E. C. et al. 2003. Global analyses of sea surface temperature, sea ice, and night marine air temperature since the late nineteenth century. Journal of Geophysical Research: Atmospheres, 108(D14).

Schmalenbach, I., Mehrtens, F., Janke, M., and Buchholz, F. 2011. A mark-recapture study of hatchery-reared juvenile European lobsters, Homarus gammarus, released at the rocky island of Helgoland (German Bight, North Sea) from 2000 to 2009. Fisheries Research, 108: 22–30.

Serfling, S. A., and Ford, R. F. 1975. Laboratory culture of juvenile stages of the California spiny lobster Panulirus interruptus (Randall) at elevated temperatures. Aquaculture, 6: 377–387.

Sheehy, M. R. J., Bannister, R. C. A., Wickins, J. F., and Shelton, P. M. J. 1999. New perspectives on the growth and longevity of the European lobster (Homarus gammarus). Canadian Journal of Fisheries and Aquatic Sciences, 56: 1904–1915.

Shelton, R. G. J., Angus, I., and KinneaR, J. A. M. 1981. Preliminary results of a lobster tagging experiment in St. Andrews Bay—Scotland. ICES Journal of Marine Science, K20: 1–16.

Simpson, A. C. 1961. A Contribution to the Bionomics of the Lobster (Homarus vulgaris Edw) on the Coast of North Wales. HM Stationery Office.

Sleben, C., and Addison, J. 2019. Marine Stewardship Council (MSC) Year 2 Surveillance Report—Normandie and Jersey Lobster Fishery. Control Union Pesca Ltd.

Sørdalen, T. K., Halvorsen, K. T., Harrison, H. B., Ellis, C. D., Vøllestad, L. A., Knutsen, H., Moland, E. et al. 2018. Harvesting changes mating behaviour in European lobster. Evolutionary Applications, 11: 963–977.

Steneck, R. S., and Wahle, R. A. 2013. American lobster dynamics in a brave new ocean. Canadian Journal of Fisheries and Aquatic Sciences, 70: 1612–1624.

Swain, D. P., Sinclair, A. F., and Mark hanson, J. 2007. Evolutionary response to size-selective mortality in an exploited fish population. Proceedings. Biological Sciences, 274: 1015–1022.

Templeman, W. 1933. Female lobsters handicapped in growth by spawning. Fisheries Research Board of Canada Atlantic Progress Report, 6: 6.

Thomas, H. J. 1958. Observations on the increase in size at moulting in the lobster (Homarus vulgaris M.-Edw). Journal of the Marine Biological Association of the United Kingdom, 37: 603–606.

Tremblay, M., and Eagles, M. D. 1997. Molt timing and growth of the lobster, Homarus americanus, off northeastern Cape Breton Island, Nova Scotia. Journal of Shellfish Research, 16: 383–394.

Waddy, S., Aiken, D., and De Kleijn, D. 1995. Control of growth and reproduction. Biology of the Lobster Homarus americanus, 217–266.

Wahle, R. A., and Fogarty, M. J. 2006. Growth and development: understanding and modelling growth variability in lobsters. In Lobsters: Biology, Management, Aquaculture and Fisheries, pp. 1–44.

Waller, J. D., Reardon, K. M., Caron, S. E., Masters, H. M., Summers, E. L., and Wilson, C. J. 2019. Decrease in size at maturity of female American lobsters Homarus americanus (H. Milne Edwards, 1837) (Decapoda: Astacidea: Nephropidae) over a 50-year period in Maine, USA. Journal of Crustacean Biology, 39: 509–515.

Whiteley, N. M., Taylor, E. W., and El Haj, A. J. 1997. Seasonal and latitudinal adaptation to temperature in crustaceans. Journal of Thermal Biology, 22: 419–-427.

Wood, J. M. 2018. New estimates and complications in the assessment of female functional maturity for the European lobster (Homarus gammarus) on the Yorkshire Coast (UK). Journal of Fisheries, 6: 635–638.

Wood, S. N. 2017. Generalized Additive Models: An Introduction with R. CRC press.

Handling editor: Anna Kuparinen