

Morphometric variability in UK populations of the European lobster

Valerie J. Debuse*[†], Julian T. Addison*[†] and John D. Reynolds[†]

*The Centre for Environment, Fisheries and Aquaculture Science, Lowestoft Laboratory, Pakefield Road, Lowestoft, Suffolk, NR33 0HT and [†]School of Biological Sciences, University of East Anglia, Norwich, NR4 7TJ.

[†]Corresponding author, e-mail: j.t.addison@cefas.co.uk

European lobsters (*Homarus gammarus*) were sampled from nine sites around the UK coast to determine whether populations could be differentiated on the basis of morphometric variability, and to relate this to depth and indices of population size at each site. Discriminant analysis indicated that exoskeleton damage was the only characteristic that could distinguish males between sites. In contrast, females were distinguished between sites on the basis of variation in exoskeleton damage, claw spines and rostrum teeth, which tended to be positively correlated to indices of population density. This study suggests that female morphology may respond more strongly than male morphology to local selection pressures, albeit in a limited capacity.

INTRODUCTION

Differences in morphometric traits among populations of species typically stem from a combination of genetic variation and differing environmental conditions (Pianka, 1988; Hoffman & Merilä, 1999). If morphological variation within populations is heritable, populations may diverge due to responses to local selection pressures (Schluter, 2000). Divergence may be constrained by high gene flow (Árnason et al., 1992), opposing selection pressures (Schluter et al., 1992), and the degree to which heritability is expressed under different environmental conditions (Hoffman and Merilä, 1999).

In terrestrial and freshwater species there is strong evidence for local adaptation being the predominant mechanism of population divergence (e.g. Schluter et al., 1992; Adams et al., 1998). In marine species, there are numerous cases of divergence for which local selection pressures are proposed as the predominant mechanism (reviewed by Hilbish, 1996), despite there being few barriers to gene flow (Ward et al., 1994). Local adaptation may be mediated by competition within populations. Clawed lobsters (*Homarus* spp.) are aggressive and highly competitive (Atema & Voigt, 1995; Debuse et al., 1999). Morphological characteristics, such as claws and elongated rostra, may be used as weapons during aggressive encounters, and other traits, such as claw spines and rostrum teeth, may function as protective armour (Hyatt, 1983; Sneddon et al., 1997). Thus, if population differentiation is predominantly driven by local conditions, spatially varying selection pressures due to competition for mates or resources should explain differences in functionally important traits.

Homarus spp. have the potential for high gene flow since the larvae are planktonic, and their distribution is strongly influenced by factors such as ocean currents and wind strength and direction (Aiken & Waddy, 1986). Nevertheless, there is conflicting evidence for long distance adult

dispersal and the potential for high gene flow. American lobsters (*Homarus americanus*) in offshore areas disperse extensively (Haakonsen & Anoruo, 1994), whereas tagging studies of the European lobster (*Homarus gammarus*) in UK waters show that the majority of individuals remain close to their release location (J.T. Addison, unpublished data; Smith et al., 1998).

In this paper we aim to determine whether European lobsters sampled in nine UK locations could be differentiated on the basis of morphometric variability, and whether patterns of divergence could be predicted by differences in depth, geographical distance or by an index of population density.

METHODS

Samples of lobsters were taken from five distinct lobster fisheries around the south, east and west coasts of England between July and October in 1997 and 1998 (Figure 1). Within the Yorkshire (sites 1 and 2), Norfolk (sites 3 and 4) and South Coast fisheries (sites 5 and 6), we took samples from both inshore waters (within five miles of the coast), and deeper offshore waters. In Devon, only offshore lobsters were measured because there were insufficient numbers of inshore lobsters caught (site 7). In Cornwall, the majority of lobsters were from inshore areas, so we sampled individuals caught within five miles of the mainland (site 8) and those caught in shallow coastal waters around the Scilly Isles (site 9). All samples were collected in September, with the exception of ~1/4 of Norfolk and Yorkshire samples, which were measured in July and October, respectively.

For the study, 339 males and 314 females were measured (Appendix 1). However, in the case of 81 males and 92 females, the claws and rostrum were damaged, so these were excluded from the analysis. Twelve and 13 morphological characters were measured on males and females, respectively, using metal callipers to an accuracy of

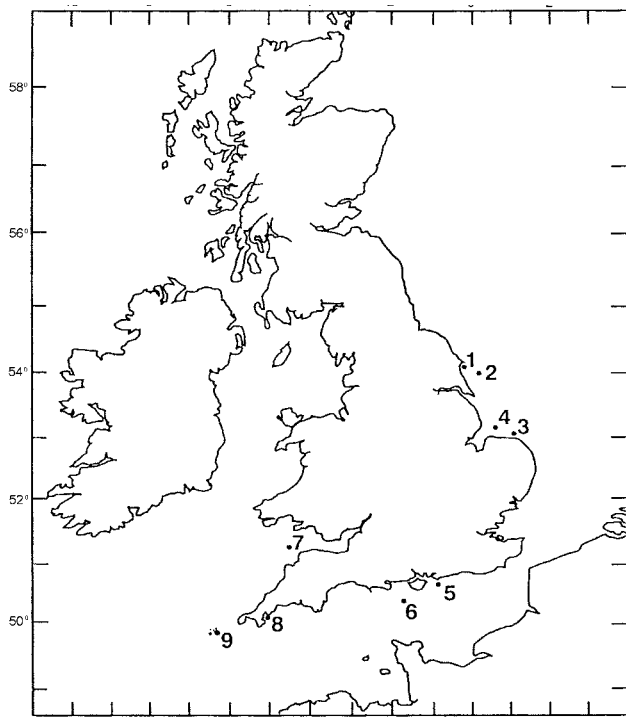


Figure 1. Locations of sampling sites: (1) Yorkshire inshore; (2) Yorkshire offshore; (3) Norfolk inshore; (4) Norfolk offshore; (5) South coast inshore; (6) South coast offshore; (7) Devon offshore; (8) Cornwall inshore (mainland); (9) Cornwall inshore (island).

0.1 mm (Figure 2). Relative fluctuating asymmetry (FA) of the rostrum teeth was measured as the difference in the number of teeth between the left and right sides of the rostrum divided by the total number of rostrum teeth. FA is thought to reflect the genetically- and environmentally-based quality of an individual by indicating its overall developmental stability (Møller & Swaddle, 1997), and is measured as small random deviations from bilateral symmetry in morphological traits. Abdomen width can be used to indicate maturity in females, so it was measured on females only. Damage was recorded as the number of marks or injuries on the exoskeleton, but recent wounds were discounted because damage can occur in traps or storage tanks. Differences in exoskeleton damage may indicate variation in the intensity of competition between sites, and thus the potential of adaptation to the local environment. Adult lobsters have few predators (Lawton & Lavalli, 1995), and so damage will arise predominantly from within-species interactions.

Measurement error was calculated for claw, rostrum and abdomen dimensions in a repeatability analysis on two repeated measures per individual using a sample of 12 individuals. The two sets of measurements were highly correlated for all traits tested (repeatability: $r_1=0.98, 0.99$; $F_{11,12}=98.073-2171.900$; $P<0.0001$ for all traits). One person made all the measurements.

All measurements met the standard assumptions of normality after log-transformation. For males, claw dimensions, claw spines and rostrum length were significantly correlated to carapace length, and in females, claw dimensions, rostrum length and abdomen width were

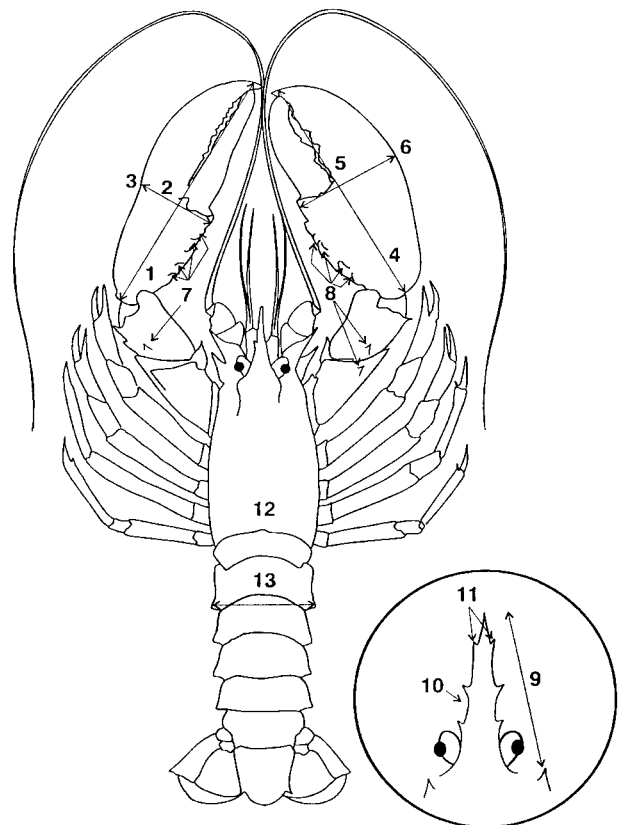


Figure 2. Morphometric traits measured: (1) cutter length; (2) cutter width; (3) cutter depth (measured at the same point as cutter width); (4) crusher width; (5) crusher length; (6) crusher depth (measured at the same point as crusher width); (7) number of cutter spines; (8) number of crusher spines; (9) rostrum length; (10) number of rostrum teeth; (11) fluctuating asymmetry of rostrum teeth; (12) exoskeleton damage; (13) abdomen width (females only).

significantly correlated to carapace length. For these traits, we reduced the correlation with body size by calculating the residuals from linear regressions between each trait and carapace length, and using these as our adjusted trait values (Reist 1985). Differences in trait means between the sexes were compared using a MANOVA, with the power calculated as $1-\beta$, where β is the probability of accepting a false null hypothesis.

Stepwise discriminant function analysis was used to compare all morphometric traits for each site to indicate which traits were most important in distinguishing sites. The reliability of these functions was determined from the percentage of individuals that were correctly classified, which was modified by a 'jackknife classification', which controls for any bias in the allocation method. The sample size was slightly smaller than in univariate statistics because cases with at least one missing trait were excluded (males, $N=233$; females, $N=209$).

Multivariate distances between pairs of sites was calculated using Mahalanobis distance D^2 , which controls for correlations between traits. Depths of the sampling sites were estimated using navigational charts and geographical distances between sites were calculated using 'Rangebear' software. For each site, an index of population density defined as the biomass of lobsters caught per unit of

fishing effort (CPUE) in kilograms per 100 pots hauled was calculated. CPUE was used as an index of population density since sites with high CPUE are likely to have higher population densities than sites with low CPUE. However, CPUE between sites may not be linearly correlated with population density due to varying effects on catchability of different gear types and environmental influences (Miller, 1990). Furthermore, fishermen vary in their efficiency, which may bias the results. To reduce this error, indices were based on averaging CPUE data for one to three regular, reliable fishermen over the period 1994–1996, except for site 9, where the data were only available for 1996–1998.

RESULTS

Morphology

Significant overall differences between mean trait size for males and females were found after standardizing for body size (MANOVA: Wilks $\gamma_{1,442}=0.421$, $P<0.0001$; $1-\beta=1.00$). Of 10 traits tested, there was significant sexual dimorphism in claw length, width and depth, with males having significantly larger cutter and crusher claws than females (one-way ANOVAs: $F_{1,442}=182.469-556.529$, $P<0.0001$ for all claw dimensions (Bonferroni-corrected $\alpha=0.005$); Appendix 1). We therefore analysed each sex separately for differences between sites.

Males

No overall difference was found in male morphology among sites (MANOVA: Wilks $\gamma_{8,224}=0.744$, $P=0.993$; $1-\beta=0.93$). The degree of exoskeleton damage was the only variable that differed significantly among sites (one-way ANOVA: $F_{8,257}=6.014$; $P=0.001$ (Bonferroni corrected $\alpha=0.004$)). For all traits pooled, only 15% of total morphometric variance was attributable to differences among sites. For nine of the 12 traits almost 100% of variation was within sites. However, there was a large amount of variation between sites in the number of rostrum teeth (>99.9%), their asymmetry (44.3%) and degree of exoskeleton damage (98.2%). Variation

between fisheries was almost negligible for all traits except for relative FA of the rostrum teeth.

Stepwise discriminant function analysis showed that only exoskeleton damage was informative when differentiating males between sites. The analysis produced one significant function, but it was unsuccessful in re-classifying individuals back to their original groups with only 17.1% (jackknife: 17.1%) of males correctly assigned to their sites. Of the misclassifications, 34.9% were assigned to sites within the same fishery. When all 12 traits were included in the analysis, it was not possible to discriminate between sites ($\chi^2_{96}=65.565$; $P=0.993$).

Females

For all traits pooled, no overall difference in female morphology was found among sites (MANOVA: Wilks $\gamma_{8,224}=0.563$; $P=0.257$; $1-\beta=1.00$) with variation among sites constituting only 26.8% of the total. However, we found significant differences among sites in the number of cutter spines (one-way ANOVA: $F_{8,213}=4.973$; $P=0.001$ ($\alpha=0.004$)), crusher spines (one-way ANOVA: $F_{8,216}=6.484$; $P=0.001$ ($\alpha=0.004$)) and rostrum teeth (one-way ANOVA: $F_{8,220}=3.414$; $P=0.001$ ($\alpha=0.004$)). For these traits and exoskeleton damage 99.6–99.9% of the total variance was due to variation among sites.

Discriminant analyses produced four discriminant functions, of which two discriminated significantly between sites (Function 1: $\chi^2_{32}=99.447$, $P<0.0001$; Function 2: $\chi^2_{21}=32.857$, $P=0.048$). These two functions accounted for 69.7 and 21.6% of the variation, respectively, and indicated that sites were most strongly discriminated by the number of crusher spines, cutter spines, rostrum teeth and degree of exoskeleton damage. The largest morphometric differences existed between Yorkshire and Norfolk fisheries (Table 1), but there was no clear clustering of inshore and offshore sites (Figure 3). Despite the significant discrimination between sites, the functions were fairly unsuccessful in re-assigning cases to their correct sites, with only 27.3% (jackknife: 27.3%) of individuals correctly classified. Furthermore, only 20.6% of misclassified individuals were assigned to another site within the same fishery. It was not possible to discriminate between sites when all female traits were included in the analysis

Table 1. Mahalanobis distances between females from nine sampling sites based on the number of claw spines, rostrum teeth and degree of exoskeleton damage.

Site	Yorkshire inshore	Yorkshire offshore	Norfolk inshore	Norfolk offshore	South coast inshore	South coast offshore	Devon	Cornwall inshore (mainland)
Yorkshire offshore	0.27							
Norfolk inshore	2.84*	3.73*						
Norfolk offshore	1.95*	2.30*	0.45					
South coast inshore	0.80	0.58	1.83*	0.81				
South coast offshore	0.92	1.54	0.62	0.31	0.73			
Devon	0.59	0.73	1.65*	0.81	0.33	0.47		
Cornwall inshore (mainland)	0.78	1.62	1.53	1.05	1.40	0.31	0.87	
Cornwall inshore (island)	0.30	0.78	1.69*	1.06	0.66	0.34	0.54	0.26

*, significant differences between sites after Bonferroni correction ($\alpha=0.001$).

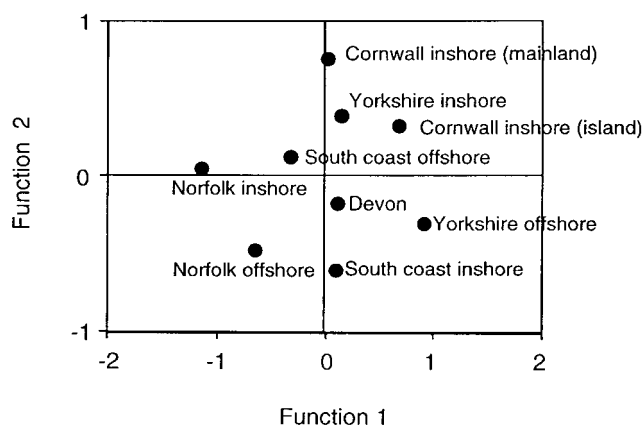


Figure 3. Distribution of female site means along discriminant function 1 and 2 axes, where large values of function 1 indicate large numbers of crusher spines and a high degree of exoskeleton damage, and large values of function 2 represent large numbers of rostrum teeth, small numbers of cutter spines and a high degree of exoskeleton damage.

(Function 1: $\chi^2_{104}=113.043$, $P=0.993$; Function 2: $\chi^2_{84}=42.729$, $P=0.999$).

Comparison of morphological, geographical and density variables

Between-site multivariate differences in female morphology tended to be correlated to differences in catch per unit effort (CPUE) (Mantel's test: $Z=325.844$; $N=81$; $P=0.066$), although cutter spines and rostrum teeth were not positively correlated with CPUE when considered alone (Kendall rank correlation: cutter spines: $Z=1.251$; $N=9$; $P=0.211$; rostrum teeth: $Z=1.043$; $N=9$; $P=0.297$). There was no relationship between CPUE and degree of exoskeleton damage in females (Kendall rank correlation: $Z=1.485$; $N=9$; $P=0.138$), but females tended to have more crusher spines at sites with high CPUE (Kendall rank correlation: $Z=1.668$; $N=9$; $P=0.095$). Overall female morphological differences between sites were not related to geographical distance between sites (Mantel's test: $Z=11897.0$; $N=81$; $P=0.294$) or differences in depth (Mantel's test: $Z=624.4$; $N=81$; $P=0.632$).

Since males were discriminated between sites only on the basis of exoskeleton damage, we used univariate correlation to compare exoskeleton damage with site depth and density. There was no positive correlation between exoskeleton damage and CPUE (Kendall rank correlation: $Z=1.251$; $N=9$; $P=0.211$), but males tended to sustain more damage at deeper sites (Kendall rank correlation: $Z=1.668$; $N=9$; $P=0.095$).

DISCUSSION

Female European lobsters exhibited morphological variation among sites, but males were less differentiated. Males were only discriminated among sites by the degree of exoskeleton damage, whereas females in the nine sites were discriminated by the number of claw spines, rostrum teeth and exoskeleton damage. This lack of variation between sites was surprising given the geographical

distances between sites and the lack of evidence for large scale movements of adult lobsters.

Our results support a study on *Homarus americanus*, indicating that intraspecific variation is characterized by differences in claw spines and rostrum teeth (Tshudy & Parsons, 1998). These traits may be important in aggressive encounters, providing protection against conspecifics and our study suggested that morphological differences in females might be associated with differences in population density, perhaps due to variation in competition intensity. In sites with high CPUE, females tended to have a greater number of crusher spines than those from sites with low CPUE, although there was no difference in the amount of exoskeleton damage sustained. This supports experimental observations that crusher claws may have a more important protective function during aggressive encounters than cutter claws. Claws may have important roles in competition (e.g. Sneddon et al., 1997), mate attraction (Claxton et al., 1994) and foraging efficiency (Elner, 1980). However, we found no evidence to support selection on claws related to our index of population density. Population density also had no impact on exoskeleton damage in either sex, although males in deeper offshore waters sustained more damage than those sampled from inshore sites. Variation in exoskeleton damage was a strong trait that distinguished males and females between the nine sites, suggesting that there are differences in competitive intensity between sites.

Intensity of selection should be greater on the sex with the higher potential reproductive rate (reviewed by Reynolds, 1996). Male lobsters contribute less time to offspring production than females and so have a potentially higher rate of reproduction (Debuse et al., 1999). Thus, selection on male traits should be greater due to more intense male–male mate competition (Parker & Simmons, 1996), so we were surprised that female rather than male morphology exhibited variation among sites. The lack of male morphometric variation in our results may be due to greater overall intensity of sexual selection on males, which has left males with less scope for variation among sites. The variation in female morphology among sites suggests that the female's influence on mating patterns may be an important contributor to sexual selection (Ahnesjö et al., 1993; Berglund et al., 1993). In the European lobster, female–female competition may be as frequent as that among males (Debuse et al., 1999). Females require shelters for protection against conspecifics, particularly following their moult when they are soft-shelled (Atema & Voigt, 1995). Thus, females may compete over access to good quality shelters and males, which provide a greater level of protection. Indeed, few females are caught in the fishery at moulting time (J.T. Addison, unpublished data), suggesting that females rely strongly on shelters at this time.

Morphometric differences among sites suggest that local selection may have an influence on female morphology. The lack of male differentiation may suggest that selection on males in each site is similar due to variation in local environmental conditions, which may influence the degree to which heritable variation is expressed (Hoffman & Merilä, 1999). Another possible explanation is that phenotypic differences among populations may be constrained by opposing selection pressures that may be

driven by trade-offs between survival, growth and reproductive success (Schluter et al., 1992). Alternatively, there may be greater gene flow than tagging studies of the European lobster have previously suggested, which may partially counteract the effects of local selection, sustaining genetically relatively undifferentiated populations observed across quite large geographic areas (Jørstad & Farestveit, 1999). This would also support findings from studies on *H. americanus* and *Nephrops norvegicus*, in which no significant genetic differentiation was found among ecologically and geographically separated adult populations (Mantovani & Scali, 1992; Harding et al., 1997).

Morphometric variation was not correlated with geographical distance in either sex, suggesting that spatial differences did not predict phenotypic variation. Since the strength of differentiation is not greater across areas of broad ecological differences, this suggests that local adaptation or genetic drift, rather than the presence of an adaptive cline, may be responsible for any observed morphometric differences between sites.

In conclusion, these results suggest that female morphology may respond more strongly to selection pressures than male morphology, perhaps in response to competition for access to good quality mates and breeding sites.

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REFERENCES

- Adams, C.E., Frasier, D., Huntingford, F.A., Greer, R.B., Askew, C.M. & Walker, A.F., 1998. Tropic polymorphism amongst Arctic charr from Loch Rannoch, Scotland. *Journal of Fish Biology*, **157**, 1259–1271.
- Ahnesjö, I., Vincent, A., Alatalo, R., Halliday, T. & Sutherland, W.J., 1993. The role of females in influencing mating patterns. *Behavioral Ecology*, **4**, 187–189.
- Aiken, D.E. & Waddy, S.L., 1986. Environmental influence on recruitment of the American lobster, *Homarus americanus*: a perspective. *Canadian Journal of Fisheries and Aquatic Sciences*, **43**, 2258–2270.
- Árnason, E., Pálsson, S. & Arason, A., 1992. Gene flow and lack of population differentiation in Atlantic cod, *Gadus morhua* L., from Iceland, and comparison of cod from Norway and Newfoundland. *Journal of Fish Biology*, **40**, 751–770.
- Atema, J. & Voigt, R., 1995. Behaviour and sensory biology. In *Biology of the lobster Homarus americanus* (ed. J.R. Factor), pp. 313–348. New York: Academic Press.
- Berglund, A., Magnhagen, C., Bisazza, A., König, B. & Huntingford, F., 1993. Female–female competition over reproduction. *Behavioral Ecology*, **4**, 184–187.
- Claxton, W.T., Govind, C.K. & Elner, R.W., 1994. Chela function, morphometric maturity, and the mating embrace in the snow crab, *Chionoecetes opilio*. *Canadian Journal of Fisheries and Aquatic Sciences*, **51**, 1110–1118.
- Debusse, V.J., Addison, J.T. & Reynolds, J.D., 1999. The effects of sex ratio on sexual competition in the European lobster. *Animal Behaviour*, **58**, 973–981.
- Elner, R.W., 1980. The influence of temperature, sex and chela size on the foraging strategy of the shore crab, *Carcinus maenas* (L.). *Marine Behaviour and Physiology*, **7**, 15–24.
- Haakonsen, H.O. & Anoruo, A.O., 1994. Tagging and migration of the American lobster *Homarus americanus*. *Reviews in Fisheries Science*, **2**, 79–93.
- Harding, G.C., Kenchington, E.L., Bird, C.J., Pezzack, D.S. & Landry, D.C., 1997. Genetic relationships among subpopulations of the American lobster (*Homarus americanus*) as revealed by random amplified polymorphic DNA. *Canadian Journal of Fisheries and Aquatic Sciences*, **54**, 1762–1771.
- Hilbish, T.J., 1996. Population genetics of marine species: the interaction of natural selection and historically differentiated populations. *Journal of Experimental Marine Biology and Ecology*, **200**, 67–83.
- Hoffman, A.A. & Merilä, J., 1999. Heritable variation and evolution under favourable and unfavourable conditions. *Trends in Ecology and Evolution*, **14**, 96–101.
- Hyatt, G.W., 1983. Qualitative and quantitative dimensions of crustacean aggression. In *Studies in adaptation: the behaviour of higher Crustacea* (ed. S. Rebach and D.W. Dunham), pp. 113–139. New York: John Wiley & Sons.
- Jørstad, K.E. & Farestveit, E., 1999. Population genetic structure of lobster (*Homarus gammarus*) in Norway, and implications for enhancement and sea-ranching operation. *Aquaculture*, **173**, 447–457.
- Lawton, P. & Lavalli, K.L., 1995. Postlarval, juvenile, adolescent, and adult ecology. In *Biology of the lobster Homarus americanus* (ed. J.R. Factor), pp. 47–88. San Diego: Academic Press.
- Mantovani, B. & Scali, V., 1992. Allozyme characterisation of the Norway lobster, *Nephrops norvegicus*, of two Adriatic trawling grounds. *Acta Adriatica*, **33**, 209–213.
- Miller, R.J., 1990. Effectiveness of crab and lobster traps. *Canadian Journal of Fisheries and Aquatic Sciences*, **47**, 1228–1251.
- Møller, A.P. & Swaddle, J.P., 1997. *Asymmetry, developmental stability, and evolution*. Oxford: Oxford University Press.
- Parker, G.A. & Simmons, L.W., 1996. Parental investment and the control of sexual selection: predicting the direction of sexual competition. *Proceedings of the Royal Society B*, **263**, 315–321.
- Pianka, E.R., 1988. *Evolutionary ecology*. New York: Harper & Row.
- Reist, J., 1985. An empirical evaluation of several univariate methods that adjust for size variation in morphometric data. *Canadian Journal of Zoology*, **63**, 1429–1439.
- Reynolds, J.D., 1996. Animal breeding systems. *Trends in Ecology and Evolution*, **11**, 68–72.
- Schluter, D., 2000. *The ecology of adaptive radiation*. Oxford: Oxford University Press.
- Schluter, D., Price, T.D. & Rowe, L., 1992. Conflicting selection pressures and life-history trade-offs. *Proceedings of the Royal Society B*, **246**, 11–17.
- Smith, I.P., Collins, K.J. & Jensen, A.C., 1998. Movement and activity patterns of the European lobster (*Homarus gammarus*) revealed by electromagnetic telemetry. *Marine Biology*, **132**, 611–623.
- Sneddon, L.U., Huntingford, F.A. & Taylor, A.C., 1997. Weapon size versus body size as a predictor of winning in fights between shore crabs, *Carcinus maenas*. *Behavioural Ecology and Sociobiology*, **41**, 237–242.
- Tshudy, D. & Parsons, G.A., 1998. Intraspecific variation in external morphology of the American lobster, *Homarus americanus*. *Proceedings of the Biological Society of Washington*, **111**, 102–109.
- Ward, R.D., Woodwark, M. & Skibinski, D.O.F., 1994. A comparison of genetic diversity levels in marine, freshwater, and anadromous fishes. *Journal of Fish Biology*, **44**, 213–232.

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Appendix 1. Mean values (mm ±SE) for 13 morphometric traits for nine sampled sites.

Trait	Yorkshire inshore	Yorkshire offshore	Norfolk inshore	Norfolk offshore	South coast inshore	South coast offshore	Devon offshore	Cornwall inshore (mainland)	Cornwall inshore (island)
Depth (m)	13.5	30.0	8.0	15.0	3.0	50.0	42.0	18.5	2.5
CPUE	9.1	23.1	6.3	6.4	5.2	1.2	14.5	12.3	17.2
Males (N)	26	31	33	32	37	31	26	10	32
cutter length	123.5 ±1.8	143.7 ±6.0	123.8 ±2.9	156.1 ±4.3	121.3 ±1.2	149.2 ±4.8	152.1 ±5.9	180.9 ±15.0	153.2 ±6.9
cutter width	40.2 ±0.6	48.5 ±2.2	40.0 ±1.0	51.5 ±1.4	38.6 ±0.5	45.5 ±1.7	48.8 ±2.0	54.5 ±4.6	47.8 ±2.3
cutter depth	22.7 ±0.3	27.2 ±1.2	22.8 ±0.6	29.1 ±0.9	21.6 ±0.3	25.5 ±0.9	27.4 ±1.1	31.1 ±2.8	27.1 ±1.3
crusher length	121.0 ±1.9	137.4 ±5.3	122.0 ±3.0	158.3 ±4.3	118.7 ±1.4	147.1 ±5.7	153.2 ±6.9	171.7 ±14.5	151.0 ±7.7
crusher width	52.0 ±0.8	59.1 ±2.6	52.4 ±1.5	68.3 ±1.9	51.0 ±0.8	62.6 ±2.8	65.4 ±3.1	73.2 ±6.8	63.8 ±3.5
crusher depth	29.0 ±0.5	33.1 ±1.5	29.5 ±0.9	38.9 ±1.1	27.6 ±0.4	34.4 ±1.6	36.5 ±1.7	41.1 ±4.1	35.9 ±2.1
cutter spines	22.1 ±1.0	22.5 ±0.9	19.6 ±0.7	17.4 ±1.6	21.9 ±0.3	21.0 ±0.5	22.1 ±0.5	21.6 ±0.5	20.9 ±0.5
crusher spines	29.6 ±1.1	26.6 ±1.6	21.7 ±0.9	22.5 ±1.0	25.2 ±0.6	23.0 ±0.7	26.5 ±0.9	28.0 ±2.3	24.6 ±1.4
rostrum length	30.0 ±0.4	33.2 ±1.0	28.9 ±0.4	33.9 ±0.6	28.3 ±0.3	34.7 ±0.8	34.6 ±0.8	39.6 ±2.4	35.8 ±1.0
rostrum teeth	8.1 ±0.4	8.4 ±0.2	8.0 ±0.2	7.6 ±0.3	7.9 ±0.2	8.4 ±0.2	7.9 ±0.4	8.7 ±0.4	8.2 ±0.2
relative FA	-0.05 ±0.04	-0.02 ±0.02	-0.02 ±0.01	-0.01 ±0.02	0.00 ±0.01	0.01 ±0.01	0.04 ±0.04	-0.02 ±0.04	0.00 ±0.02
damage	3.0 ±0.3	2.8 ±0.2	2.3 ±0.2	3.0 ±0.4	2.2 ±0.1	3.1 ±0.2	5.8 ±0.9	3.2 ±0.3	3.3 ±0.4
Females (N)	26	29	31	22	26	25	21	12	30
cutter length	114.0 ±1.3	128.7 ±2.4	115.6 ±2.0	128.3 ±3.2	115.7 ±1.7	134.3 ±2.4	133.8 ±3.8	150.0 ±4.9	133.0 ±2.3
cutter width	36.3 ±0.4	40.7 ±0.7	36.5 ±0.6	41.4 ±1.4	36.1 ±0.5	40.1 ±1.0	41.0 ±1.3	44.6 ±1.5	39.5 ±0.8
cutter depth	20.3 ±0.2	22.7 ±0.4	20.3 ±0.4	23.3 ±0.8	20.0 ±0.3	22.1 ±0.5	22.8 ±0.7	25.3 ±0.8	22.2 ±0.4
crusher length	111.3 ±1.2	123.8 ±2.2	111.5 ±1.9	127.3 ±3.4	110.5 ±1.3	127.4 ±2.5	127.7 ±3.8	142.3 ±4.3	126.2 ±2.2
crusher width	45.0 ±0.5	50.4 ±0.8	45.8 ±0.7	51.4 ±1.5	45.1 ±0.5	50.8 ±1.2	51.2 ±1.6	56.7 ±1.8	50.2 ±1.0
crusher depth	24.8 ±0.3	27.5 ±0.5	25.0 ±0.4	28.2 ±0.8	24.2 ±0.3	27.3 ±0.6	28.0 ±0.8	30.6 ±1.0	27.5 ±0.6
cutter spines	21.6 ±0.4	22.6 ±0.4	19.6 ±0.4	18.6 ±1.5	22.2 ±0.4	20.5 ±0.5	20.6 ±1.1	20.4 ±0.7	19.7 ±1.1
crusher spines	25.6 ±0.6	26.4 ±0.9	21.3 ±0.6	19.6 ±1.5	24.1 ±0.6	22.8 ±0.8	24.1 ±0.6	22.8 ±1.0	23.9 ±0.7
rostrum length	29.9 ±0.3	32.7 ±0.5	29.4 ±0.5	32.6 ±0.7	29.3 ±0.3	34.3 ±0.6	33.9 ±0.9	37.2 ±1.6	35.0 ±0.6
rostrum teeth	8.7 ±0.2	8.4 ±0.2	7.8 ±0.2	7.7 ±0.2	8.0 ±0.2	8.2 ±0.2	8.0 ±0.3	8.7 ±0.3	8.8 ±0.2
relative FA	0.01 ±0.02	0.02 ±0.01	-0.01 ±0.02	0.02 ±0.02	0.02 ±0.01	0.01 ±0.02	-0.01 ±0.02	0.00 ±0.02	0.00 ±0.02
damage	2.9 ±0.2	2.8 ±0.2	2.2 ±0.2	2.6 ±0.2	2.4 ±0.2	2.6 ±0.2	2.9 ±0.3	3.4 ±0.7	2.7 ±0.2
abdomen width	56.1 ±0.9	68.3 ±1.8	57.7 ±1.5	69.4 ±2.3	52.8 ±0.9	64.8 ±2.1	65.8 ±3.0	77.8 ±4.2	65.4 ±2.0

CPUE, catch per unit effort (kg 100 pots⁻¹).