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1 **Advancing our understanding of the connectivity, evolution and**  
2 **management of marine lobsters through genetics**

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16  
17  
18 **ABSTRACT**  
19

20       The genomic revolution has provided powerful insights into the biology and ecology  
21 of many non-model organisms. Genetic tools have been increasingly applied to marine  
22 lobster research in recent years and have improved our understanding of species delimitation  
23 and population connectivity. High resolution genomic markers are just beginning to be  
24 applied to lobsters and are now starting to revolutionise our understanding of fine spatial and  
25 temporal scales of population connectivity and adaptation to environmental conditions.  
26 Lobsters play an important role in the ecosystem and many species are commercially  
27 exploited but many aspects of their biology is still largely unknown. Genetics is a powerful  
28 tool that can further contribute to our understanding of their ecology and evolution and assist  
29 management. Here we illustrate how recent genetic advancements are (1) leading to a step  
30 change in our understanding of evolution and adaptation, (2) elucidating factors driving

31 connectivity and recruitment, (3) revealing insights into ecological processes and can (4)  
32 potentially revolutionise management of this commercially important group. We discuss how  
33 improvements in sequencing technologies and statistical methods for genetic data analyses  
34 combined with increased sampling efforts and careful sampling design have transformed our  
35 understanding of lobsters biology in recent years. We also highlight possible future directions  
36 in the application of genomic tools to lobster research that can aid management, in particular,  
37 the close-kin-mark-recapture method. Finally, we identify gaps and challenges in lobster  
38 research, such as the lack of any reference genomes and predictions on how lobsters will  
39 respond to future environmental conditions.

40

41

42 **Keywords:** adaptation, close-kin-mark-recapture, connectivity, genomics, lobster,

43 management

44 **Running title:** Genetics of marine lobsters

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46

## 47 **1. Introduction**

48

49 Lobsters are a morphological and ecologically diverse group of decapod crustaceans  
50 that include four infraorders (Achelata, Astacidea, Glypheidea and Polychelida; Bracken-  
51 Grissom et al. 2014). Many marine lobster species are bottom-dwelling decapods with  
52 greenish, dark grey or red exoskeletons, long antennae, compound eyes, and a first pair of  
53 legs that in some groups are modified into large, powerful pincers. Lobsters inhabit a wide  
54 range of habitats from tropics to high latitudes, deep to shallow and freshwater to marine  
55 ecosystems. As some lobsters are keystone species, they are crucial for ecosystem dynamics  
56 and function, therefore variation in their abundance can have important impacts at the  
57 ecosystem level (e.g. Eddy *et al.* 2014). Lobsters also support valuable fisheries and  
58 aquaculture industries worldwide with important commercial species within the Astacidea  
59 and Achelata (Bracken-Grissom et al. 2014). However, many aspects of lobsters biology  
60 remain unclear such as how the marine environment affects larval dispersal and therefore  
61 genetic structure, the influence of historical events and past demographic changes on  
62 speciation and the scale of local adaptation. Efficient tools that can fill in these gaps in  
63 knowledge are imperative for improved management.

64 Genetics is a powerful tool for understanding a range of ecological and evolutionary  
65 questions. The recent development of new and affordable genetic techniques (e.g. restriction-  
66 site associated DNA sequencing [RAD-Seq]) has contributed to a marked increase in our  
67 understanding of lobster biology, providing important insights on deep evolutionary  
68 relationships, species delimitation (e.g. Groeneveld et al. 2007; Palero et al. 2008),  
69 population connectivity (e.g. Benestan et al. 2015; Truelove et al. 2015b; Woodings et al.  
70 2018) and adaptation (e.g. Benestan et al. 2016; Al-Breiki et al. 2018).

71 Here, we critically review insights into lobster biology gained through the use of  
72 genetic tools. We first explore evolutionary aspects including phylogenetic relationships and  
73 adaptation, and then expand on factors affecting connectivity and recruitment. Finally, we  
74 identify gaps in the application of genomic tools for lobster research and fisheries  
75 management and highlight future research areas that can benefit from genomic tools.

76

### 77 **1.1. Trends in study species and genetic tools**

78 Using the ‘Web of Science’ (www.isiknowledge.com), we searched up to June 2019  
79 using the search phrase TS =(lobster\* AND (genetic\* OR genomic\* OR transcriptomic\*)),  
80 which generated 493 results. We then retained original articles that specifically employed  
81 genetic markers to the lobster infraorders we are focusing on this review (Achelata,  
82 Astacidea, Glypheidea and Polychelida), resulting in a total of 149 articles (Table S1). The  
83 articles were published between 1975 and 2019 mainly in the areas of population genetics,  
84 phylogenetics and species delimitation. Most of the studies were conducted on *Panulirus* spp.  
85 (35%) and *Homarus* spp. (22%) (Fig. 1). The extensive research on *Panulirus* spp. and  
86 *Homarus* spp. likely reflects their economic importance as they are the basis of important  
87 fisheries worldwide (FAO 2017). Most studies focused on Northern and Central Atlantic  
88 species *Homarus gammarus*, *Homarus americanus* and *Panulirus argus*.

89 Of the total articles published between 1975 and 2018, 38% used mitochondrial DNA  
90 (mtDNA), 33% used microsatellites, 9% used allozymes and 5% used single nucleotide  
91 polymorphisms (SNPs). The remaining studies (11%) used other types of markers such as  
92 random amplified polymorphic DNA (RAPD) and restriction fragment length polymorphism  
93 (RFLP). Allozymes were initially applied to lobster research in the 1970s but plateaued  
94 throughout the 2000s as a result of advances in microsatellites development in the 1990s and

95 SNPs in the 2000s (Allendorf 2017). The use of both microsatellites and mtDNA commenced  
96 in the 1990s and then increased rapidly in the early 2000s (Fig. 2).

97         The main forces that have driven the recent rapid growth of SNPs applied to lobsters  
98 were technological improvements in methods and decreasing costs (e.g. RAD-Seq), which  
99 have allowed the collection of genetic data from large numbers of individuals (Davey et al.  
100 2011). The genotyping of many more SNPs with a higher consistency than, for example,  
101 microsatellites means that a larger proportion of the genetic variation within the genome is  
102 represented. Consequently, connectivity can be assessed at finer geographic scales for non-  
103 model organisms (Baird *et al.* 2008; Sansaloni *et al.* 2011; Peterson *et al.* 2012). Although  
104 SNPs are just beginning to be applied to lobsters (Fig. 2), these high resolution markers are  
105 revolutionising our understanding of lobster biology. Recently SNPs have yielded significant  
106 insights in detecting fine scale population structure (Benestan et al. 2015), thermal adaptation  
107 (Benestan et al. 2016) and detecting chaotic genetic patchiness and evidence of post-  
108 settlement selection (Villacorta-Rath et al. 2018). Following trends in other non-model taxa  
109 (Helyar et al. 2011), we expect to see an increasing number of studies using SNPs in lobsters  
110 providing greater insights into the processes driving fine scale population genetic structure.

111

## 112         **1.2. Marker resolution**

113

114         Molecular markers are important tools for generating information on ecology and  
115 evolution of lobsters. There is a variety of genetic markers with different characteristics  
116 therefore, the correct tools need to be chosen according to the research question(s). Among  
117 the most recently used markers is mtDNA which is relatively easy to use, has fast rates of  
118 base substitution and low recombination (e.g. Brasher et al. 1992b; Stamatis et al. 2004;  
119 Tolley et al. 2005; Tsoi et al. 2011). However, due to its maternal inheritance, studies using

120 only this marker may be biased to female-mediated processes (Zhang and Hewitt 2003).  
121 Microsatellites are widely distributed throughout the genome, are highly polymorphic,  
122 apparently evolve under neutral processes, and biparentally inherited. As a result, they have  
123 improved the assessment of genetic diversity, parentage and relatedness, fine-scale  
124 population structure, and recent population history (e.g. Selkoe et al. 2010; Kennington et al.  
125 2013a; Thomas and Bell 2013). However, the results obtained with microsatellites by  
126 different laboratories are not always comparable because of inconsistencies in allele calling  
127 and size determination. SNPs are more abundant in the genome, have a simpler nomenclature  
128 and suitability to automated analysis and data interpretation (Zhang and Hewitt 2003). Recent  
129 advances in high-throughput sequencing and bioinformatics have facilitated the use of SNPs  
130 that are expected to become more popular in lobster research.

131         The increased resolving power of molecular markers in detecting fine scale structure  
132 is illustrated in the most widely studied lobster, the American lobster, *H. americanus*. Early  
133 studies employing allozymes (Tracey et al. 1975) and RAPDs (Harding *et al.* 1997) detected  
134 little to no evidence of genetic differentiation, suggesting that *H. americanus* was essentially  
135 a well-connected homogeneous genetic stock. In contrast, using microsatellite markers,  
136 Crivello *et al.* (2005) detected statistically significant genetic differentiation between *H.*  
137 *americanus* populations located <50 km apart. More recently Kenchington *et al.* (2009)  
138 detected fine scale genetic differentiation between locations situated ~50 km to ~20 km apart.  
139 Improvements in marker resolution have enabled studies to detect finer scale structure with  
140 reduced numbers of individuals. For example, within the Gulf of St Lawrence Benestan *et al.*  
141 (2015) genotyped 306 *H. americanus* individuals and found 6 genetically distinct populations  
142 using SNPs, while Kenchington *et al.* (2009) genotyped 2,555 individuals in the same  
143 geographic region and could only detect 2 genetically diverse populations using  
144 microsatellites (Table 1).

145 This general trend of less genetic differentiation detected by allozymes, RFLPs and  
146 mtDNA than microsatellites and SNPs has also been observed in *Panulirus argus* and *Jasus*  
147 *edwardsii*. No genetic differentiation was detected in studies employing either RFLP's  
148 (Silberman et al. 1994) or mtDNA (Naro-Maciel *et al.*, 2011) between Caribbean *P. argus*  
149 populations, while microsatellite loci were used to detect genetic differentiation both within  
150 and between Caribbean regions (Truelove et al. 2017). For *J. edwardsii*, analyses employing  
151 RFLPs detected no genetic differentiation between Australian and New Zealand populations  
152 (Ovenden et al. 1992). However, more recent studies employing microsatellite loci detected  
153 genetic differentiation between some Australian and New Zealand populations (Thomas and  
154 Bell 2013) and between populations within Australia (Morgan et al. 2013), while analyses  
155 using SNP data detected significant differences between Australian and New Zealand  
156 populations (Villacorta-Rath et al. 2016, 2018). These examples illustrate the sensitivity of  
157 different molecular marker and the importance of applying higher sensitivity markers and a  
158 large number of samples for a comprehensive understanding of fine scale connectivity.

159

## 160 **2. Lobster evolution**

161

### 162 **2.1. Phylogenetics**

163 Over the past 20 years phylogenetic relationships between higher level lobster taxa  
164 have been subject of considerable debate. It is clear that the infraorders comprising 'lobsters'  
165 (i.e. Astacidea, Achelata, Polychelida and Glypheidea) have close phylogenetic relationships  
166 with several 'non-lobster' infraorders including Brachyura (crabs), Anomura (including  
167 hermit crabs and king crabs), Gebiidea and Axiidea (the latter two clades contain mud  
168 shrimps previously contained together within Thalassinidea). Relationships between these  
169 taxa have been unstable however, and 'lobsters' have been recently found to be both



170 monophyletic (Toon et al. 2009; Tsang et al. 2009) and non-monophyletic (Crandall et al.  
171 2000; Ahyong and O’Meally 2004; Porter et al. 2005; Bracken et al. 2009) depending on  
172 taxonomic sampling, phylogenetic analysis methods and the genes and morphological  
173 characters included.

174         The most recent molecular studies have found ‘lobsters’ to be a non-monophyletic  
175 group but have found contrasting and unstable phylogenetic relationships. In a study based on  
176 50 decapod mitochondrial genomes, Shen, Braband, & Scholtz (2013) reported that the  
177 lobster infraorders Astacidea and Polychelida were sister taxa in phylogenies resulting from  
178 the majority of their analyses and that together these taxa formed a monophyletic group with  
179 a clade containing several non-lobster taxa (i.e. Gebiidea, Axiidea, Anomura and Brachyura).  
180 These authors found that in the majority of their analyses this broader clade was the sister  
181 taxon to the lobster infraorder Achelata. However, these authors did not include  
182 representatives of the lobster infraorder Glypheidea in their analyses. Subsequently Bracken-  
183 Grissom *et al.* (2014) included representatives of all known lobster families (173 species),  
184 and their close non-lobster relatives in an analysis of fragments of mitochondrial (12 rRNA,  
185 16S rRNA, cytochrome c oxidase subunit I) and nuclear markers (histone H3, 18S rRNA,  
186 28S rRNA), in conjunction with 190 morphological characters. They found the lobster  
187 infraorders Astacidea and Glypheidea were sister taxa in phylogenies resulting from analyses  
188 of both a combined molecular and morphological dataset and also a dataset containing  
189 molecular markers only. Together this clade was sister taxa to a clade containing several  
190 non-lobster taxa (Gebiidea, Axiidea, Anomura and Brachyura) in phylogenies resulting from  
191 analyses of molecular and morphological data (Fig. 3). In contrast, analysis of molecular data  
192 only resulted in a sister taxon relationship between Glypheidea+Astacidea and Achelata.  
193 Short branch lengths between several infraorders were evident in phylogenies presented in  
194 both studies by Shen, Braband, & Scholtz (2013) and Bracken-Grissom *et al.* (2014) and this

195 potentially reflects a lack of resolving power in the datasets employed and a rapid radiation.  
196 Divergence time estimates suggest that the lobster infraorders were already present by the  
197 Carboniferous (~339 Mya, Bracken-Grissom *et al.* 2014) and thus saturation of molecular  
198 data may be obscuring deeper evolutionary relationships.

199         There is a general consensus on broader phylogenetic relationships within the  
200 infraorder Achelata in studies employing molecular data. A sister taxon relationship between  
201 Scyllaridae and Palinuridae is well-supported (Shen *et al.* 2013; Bracken-Grissom *et al.*  
202 2014). Furthermore, it is well-accepted that Palinuridae is comprised of two reciprocally  
203 monophyletic clades; the Stridentes (which possess a sound-producing stridulating organ)  
204 and the Silentes (Chu *et al.* 2009; Bracken-Grissom *et al.* 2014).

205         Similarly, relationships within Astacidea are less contentious than those at deeper  
206 phylogenetic levels. The Southern hemisphere crayfish (Parastacoidea) and Northern  
207 hemisphere crayfish (Astacoidea), both freshwater groups, are well-supported sister taxa as  
208 are the reef lobsters (Enoplometopidae) and Nephropidae (the latter family containing the  
209 Thaumatochlidae) (Tsang *et al.* 2008; Bracken-Grissom *et al.* 2014). Focusing specifically on  
210 the Astacidea, Shen *et al.* (2015) investigated mitochondrial gene order rearrangements and  
211 showed convergent evolution in mitochondrial gene order in several instances. This indicates  
212 that mitochondrial gene order is not a useful phylogenetic character within this infraorder and  
213 will likely be limited in its utility at a deeper phylogenetic level.

214         Transcriptomic methods will provide much larger genetic datasets for investigating  
215 evolutionary relationships within lobsters and may provide resolution within deeper  
216 phylogenetic levels (as it has been the case for other taxa e.g. Tanner *et al.* 2017) – but there  
217 has been little progress in this area to date. Recently, target capture sequencing (based on  
218 probes developed from double digest restriction site-associated DNA sequencing  
219 [ddRADseq]) was demonstrated to be successful in capturing sequence data across all *Jasus*

220 species and *Sagmariasus* (Souza et al. 2017). Such targeted capture methods do not  
221 necessarily require samples with high quality DNA and will therefore likely enable  
222 sequencing of rare and difficult to obtain taxa held within museum collections.

223

## 224 **2.2. Species divergence and adaptation**

225         Given the potential for long distance dispersal in many marine lobsters, population  
226 divergence leading to reproductive isolation and subsequent speciation is generally difficult  
227 to detect. Radiations of some marine lobsters appear to have occurred despite a lack of  
228 obvious physical barriers to population connectivity (e.g. Palero *et al.* 2009). Allopatric  
229 speciation is the norm in freshwater species (e.g. Pedraza-Lara *et al.* 2012) as separate  
230 populations are generally spatially isolated. However, most of the hypotheses around  
231 speciation in marine lobsters, are reliant on changing circulation systems (e.g. Pollock 1993),  
232 and are generally based upon allopatric isolation of populations due to currents preventing  
233 gene flow.

234         Despite the interest in the origins of lobster species (e.g. George, 1997, 2005; Ptacek  
235 *et al.*, 2001; Groeneveld *et al.*, 2007; Tsang *et al.*, 2009) comprehensive molecular studies of  
236 speciation are rare. The majority of published studies are based on mtDNA sequences alone,  
237 or a combination of mtDNA and a small number of nuclear loci. It is now well-established  
238 that the resolution of complex speciation generally requires genome-wide representation and  
239 coalescent-based species-tree analyses (Degnan and Rosenberg 2009). Also, a number of  
240 recent studies of lobsters suggest rapid speciation events (Machordom and Macpherson 2004;  
241 Palero et al. 2009). Interestingly, many of these divergence events may have occurred  
242 relatively recently, as evidenced by the lack of resolution of the more rapidly evolving  
243 mtDNA genes amongst some species (Palero et al. 2009; Groeneveld et al. 2012). Therefore,  
244 it is likely that lobster speciation processes may be subject to incomplete lineage sorting

245 and/or introgression and some lobster species may not be completely reproductively isolated  
246 from each other.

247         The southern hemisphere lobster *Jasus*, is a good example of the complexity of  
248 speciation processes (Fig. 4). These species have some of the longest pelagic larval duration  
249 (up to 20 months; Bradford *et al.* 2015) and despite palaeoceanographic, morphological and  
250 genetic studies (Pollock 1990; Brasher *et al.* 1992a; George 2005) there is no clear evidence  
251 of the mechanisms driving speciation within *Jasus*. Given that present day oceanic currents  
252 should allow for gene-flow amongst many of these species it is difficult to see how simple  
253 allopatric divergence can occur (Pollock 1990; Booth and Ovenden 2000).

254         Finally, it can be argued that allopatric divergence may not be the null model of  
255 evolution of marine lobsters, given the highly dispersive nature of some species, and the fact  
256 that oceanic currents are rarely stable over evolutionary time scales (van Gennip *et al.* 2017).  
257 For example, Singh *et al.* (2017) used a coalescent-based approach and found that allopatric  
258 speciation is unlikely while partial isolation and parapatric speciation is driving divergence of  
259 *Panulirus* species in eastern Africa. Population divergence may not be driven by ocean  
260 currents alone, but selection and local adaptation can play a significant role in lobster  
261 speciation. Given the mounting evidence of selection driving population differences within  
262 lobster species (Benestan *et al.* 2016; Farhadi *et al.* 2017) the role of environmental  
263 conditions driving divergence needs to be fully explored in these species.

264         Seascape genomics integrates genetic and environmental data to better understand  
265 species distribution and adaptation (Manel and Holderegger 2013). This is a very promising  
266 approach that has been widely applied in terrestrial organisms (Manel and Holderegger  
267 2013), but there has been only a few studies with lobsters combining genetic with  
268 environmental data. For example, using 21 microsatellite loci Singh *et al.* (2018) found that  
269 geographic distance and minimum sea surface temperature were significantly associated with

270 genetic differentiation in the spiny lobster *Panulirus homarus*. Benestan *et al.* (2016) used  
271 SNPs to investigate how the environment shapes adaptation of populations of the American  
272 lobster (*Homarus americanus*). The authors identified a significant association of temperature  
273 with seven SNPs and three polymorphisms located in genes previously shown to play a role  
274 in thermal adaptation. Also, Selkoe *et al.* (2010) found significant correlations in genetic  
275 patterns of microsatellite markers in the California spiny lobster *Panulirus interruptus*. Kelp  
276 cover was an important predictive variable with flow and sea surface temperature also highly  
277 ranked.

278         Increasing collection and accessibility of environmental data (e.g. by satellite  
279 imagery) combined with the decreasing costs of sequencing and improved bioinformatic  
280 pipelines are making seascape genomic studies more feasible (Selkoe *et al.* 2016). Therefore,  
281 lobsters research will further benefit from a seascape genomics approach and it will provide  
282 greater insights into the role of the environment in shaping adaptation and connectivity  
283 between populations.

284

### 285 **3. Genetics of connectivity and recruitment**

#### 286 **3.1. The role of oceanic features and larval behaviour on dispersal**

287         Lobsters have one of the longest pelagic larval durations (PLDs) and therefore have  
288 potential for long distance dispersal. However, their bipartite life cycle coupled with larval  
289 behaviour and varying patterns of ocean circulation result in differing levels of connectivity  
290 across populations (Metaxas and Saunders 2009; Incze *et al.* 2010). Direct measures of  
291 connectivity, such as tracking individual animals and physical tag-recapture studies, have  
292 successfully identified adult lobsters' movement and migration (Booth 1997; Giacalone *et al.*  
293 2015; Skerritt *et al.* 2015). Adults of some species such as *Jasus edwardsii* have very limited  
294 movement, travelling less than one kilometre per annum (Gardner *et al.* 2003; Barrett *et al.*

295 2009). Larger migrations of hundreds of kilometres have been recorded for adults of the  
296 ornate lobster *Panulirus ornatus* (Bell et al. 1987). However, the main dispersive phase for  
297 lobsters is the pelagic larval phase. Phyllosoma larvae move to the water surface shortly after  
298 hatching and are transported offshore by wind and ocean currents (Booth and Phillips 1994).  
299 Since tracking larvae using electronic devices and physical tags is unfeasible, indirect  
300 methods are often used to ascertain a measure of population connectivity. In addition,  
301 assessing larvae distribution through spatial distribution surveys is challenging because  
302 phyllosoma undergo multiple instar stages making examination of morphology and species  
303 identification very difficult. Therefore, molecular methods are a good alternative for  
304 identifying phyllosoma to species level (Chow et al. 2006; Woodings et al. 2019).

305         One approach to estimate larval dispersal indirectly involves the use of genetic  
306 markers complemented by larval dispersal modelling (Baltazar-Soares et al. 2018). Larval  
307 transport simulations can determine indicative dispersal routes, which is particularly  
308 important when dealing with species that cross jurisdictional boundaries (Truelove et al.  
309 2015a). However, these models alone can be inaccurate as circulation models perform poorly  
310 inshore, retention in local eddies is often not considered and the long pelagic phase of  
311 lobsters means further complexity needs to be added the model such as presence of food or  
312 larvae swimming behaviour (North et al. 2009). Studies combining genetic data to  
313 biophysical models can more effectively explain the physical mechanisms that may cause the  
314 observed levels of population structure in lobsters (Truelove et al. 2017).

315         In recent years it has been recognised that lobster larvae are not passive drifters, but  
316 they can alter their position in the water column, which can influence their dispersal potential  
317 (e.g. O'Rorke *et al.* 2015). Larvae exhibit diel vertical migration in response to light in the  
318 water column (Metaxas and Saunders 2009) as well as ontogenetic vertical migration (Katz et  
319 al. 1994). As larvae move through different layers in the water column they encounter masses

320 of different flow velocities and directions, altering the dispersal kernel (Metaxas and  
321 Saunders 2009). In addition to vertical migration behaviour, the settling stage of larvae  
322 (pueruli) are capable of directional swimming into settlement grounds with implications for  
323 population structure and recruitment (Incze et al. 2000). For example, a dispersal model of  
324 *Homarus americanus* that included ocean advection, wind action and directional swimming  
325 of stage IV larvae was better at explaining larval transport from offshore canyons to coastal  
326 areas in southern New England than a model that assumed passive drift. The authors  
327 concluded that directional swimming allowed connectivity of *H. americanus* populations at a  
328 regional level (Katz et al. 1994). Directional swimming occurs as a result of pueruli  
329 following settlement cues into suitable habitats. Among the most studied cues used by pueruli  
330 are reef sounds (Hinojosa et al. 2016), adult conspecifics or macroalgae odour (Boudreau et  
331 al. 1993), lunar phases (Phillips and McWilliam 1986) and water flow (Lillis and Snelgrove  
332 2010). The ability of larvae to use environmental cues for settlement can promote larval  
333 retention, genetic differentiation and eventually lead to speciation. Ovenden *et al.* (1997)  
334 suggested that speciation of *Jasus* was driven by different environmental cues as phyllosoma  
335 larvae of the common ancestor of species currently inhabiting seamount habitats (*J.*  
336 *caveorum*, *J. tristani* and *J. paulensis*) may have been able to recognize non-continental  
337 metamorphosis cues and colonized these habitats. Incorporating larval and post-larval  
338 movement into seascape genetic approaches would provide more accurate estimates of the  
339 potential and realised dispersal of lobster species.

340 Larval transport simulations have demonstrated that larvae can encounter different  
341 oceanic features that promote or restrain their advection (Chiswell and Roemmich 1998;  
342 Chiswell et al. 2003; Bruce et al. 2007; Chiswell and Booth 2008; Incze et al. 2010). Among  
343 them, eddy systems are the main feature promoting larval retention. Larval dispersal  
344 simulations of *J. edwardsii* in New Zealand designated the east of the North Island as an area

345 of high self-recruitment due to larval entrainment in the Wairarapa Eddy (Chiswell and Booth  
346 2008). A subsequent genetic study revealed that it is likely that this oceanographic feature not  
347 only promotes recruitment on the east of the North Island of New Zealand, but also maintains  
348 genetic homogeneity in the area (Thomas and Bell 2013).

349         Conversely, strong coastal and oceanic flow can promote larval dispersal. Populations  
350 of the American lobster, *Homarus americanus*, inhabiting the north of Maine exhibited low  
351 levels of self-recruitment due to low egg production, low temperature and strong coastal flow  
352 carrying larvae southward into the Gulf of Maine (Incze et al. 2010). Similarly, microsatellite  
353 and mtDNA analyses of population structure revealed that the ornate spiny lobster, *Panulirus*  
354 *ornatus*, comprises a panmictic population throughout the Southeast Asian archipelago. A  
355 pathway map of surface currents that coupled spawning with larval dispersal explained the  
356 lack of structure across the species geographic distribution (Dao et al. 2015).

357

### 358         **3.2. Stochasticity in connectivity patterns**

359         Recent genetic studies have detected increasing evidence for chaotic genetic  
360 patchiness in lobsters (Iacchei et al. 2013; Kennington et al. 2013a; Truelove et al. 2017;  
361 Villacorta-Rath et al. 2018). This term describes a pattern of genetic heterogeneity between  
362 populations that is not consistent and forms a shifting, ephemeral genetic pattern best  
363 described as chaotic (Johnson and Black 1982). Environmental stochasticity can affect larval  
364 transport and result in ephemeral population structure at small spatial scales, giving rise to  
365 chaotic genetic patchiness in recruits (Selkoe et al. 2010). For example, a study on the  
366 Caribbean spiny lobster, *Panulirus argus*, combining a biophysical model with  
367 microsatellites detected that populations were “isolated by biophysical connectivity”. High  
368 levels of within-basin larval retention in eddies as well as stochastic long-distance dispersal



369 events were suggested to cause genetic patchiness throughout Caribbean basins (Truelove et  
370 al. 2017).

371 Ephemeral genetic structure was also found in the western rock lobster, *Panulirus*  
372 *cygnus* using allozyme and microsatellite markers (Thompson *et al.* 1996; Kennington *et al.*  
373 2013b). Additionally, microsatellite markers and mtDNA detected significant population  
374 structure and differences in levels of kinship within and between sites in the California spiny  
375 lobster, *P. interruptus* confirming the existence of chaotic genetic patchiness (Iacchei et al.  
376 2013). Sites of elevated levels of kinship were adjacent to areas of high upwelling intensity,  
377 leading to the hypothesis that upwelling promoted larval cohesiveness shortly after hatching  
378 (Iacchei et al. 2013). Studies investigating chaotic genetic patchiness should focus on newly  
379 settled recruits and sampling should be conducted over different temporal scales to  
380 incorporate different recruitment seasons. This would allow for a better understanding of  
381 interannual variability in genetic structure and diversity of recently settled individuals.

382 Chaotic genetic patchiness can also be caused by selective processes occurring prior  
383 to settlement (Johnson and Black 1984). A multiyear assessment of *J. edwardsii* pueruli  
384 recruiting into two sites separated by approximately 1,000km found genetic divergence in  
385 neutral SNP markers between consecutive years at both sites (Villacorta-Rath et al. 2018).  
386 However, the investigation of outlier SNPs only showed weak pre-settlement selection,  
387 making it difficult to attribute chaotic genetic patchiness to selective mortality of larvae  
388 (Villacorta-Rath et al. 2018). With the widespread of next-generation sequencing  
389 technologies in recent years more studies investigating the link between pre-settlement  
390 selection and chaotic genetic patchiness of lobsters are expected to be facilitated.

391 Connectivity and recruitment success are not only the result of processes affecting  
392 larvae and post-larvae, but can be highly dependent on egg production of the spawning stock  
393 (Incze et al. 2010). Environmental stochasticity can benefit reproductive success of a small

394 minority of individuals and this sweepstakes in reproductive success (SRS) can lead to year-  
395 to-year variation in the proportion of the adult population producing successful recruits. SRS  
396 generally occurs in species with high female fecundity, high dispersal potential and low to  
397 moderate levels of population genetic structure (Hedgecock and Pudovkin 2011). Under such  
398 conditions, the effective population size ( $N_e$ ) of a population is much smaller than the census  
399 size. The high reproductive output, bi-partite life cycle of lobsters and their moderate levels  
400 of population connectivity make them a good candidate for SRS. Moreover, settlement and  
401 recruitment are highly variable through time (Incze et al. 2000; Linnane et al. 2014) and  
402 although fluctuations have been attributed to environmental factors (Linnane et al. 2010;  
403 Hinojosa et al. 2017), temporal and spatial changes in egg production can also be an  
404 underlying cause (Incze et al. 2010). Studies assessing chaotic genetic patchiness in lobsters  
405 have indicated SRS as a possible cause of the ephemeral population structure (Iacchei et al.  
406 2013; Kennington et al. 2013a; Villacorta-Rath et al. 2018), however no study to date has  
407 evidenced differential reproduction in a lobster species. Future studies assessing temporal and  
408 spatial variation in egg production and its relationship to recruitment success and population  
409 structure are needed in order to inform management decisions.

410

#### 411 **4. Gaps and future directions**

##### 412 **4.1. Integration of genetics with stock assessment strategies**

413 Many of the world's marine lobster fisheries have well-supported data collection  
414 programs because of their high value. This has led to sophisticated assessment systems  
415 including the development of population models with both biological and economic elements  
416 (Gardner et al. 2013). These are used to guide management with increased use of harvest  
417 strategies that involve reference points and control rules for adjusting catch so that the stock  
418 is moved towards targets (Sloan et al. 2014). A consequence of this data-rich management in

419 many lobster fisheries is that additional biological information gained through genetic  
420 methods can have immediate relevance to management.

421 In general, one of the aims of most lobster fishery management programmes is to  
422 retain reproductive output while maintaining recruitment. In harvest strategies, sustainable  
423 reproductive output is defined as a limit reference point (FAO 1995). For example, Australian  
424 lobster fisheries are assessed as sustainable or overfished depending on whether egg  
425 production is more or less than a limit reference point set at 20% of the unfished level (Flood  
426 et al. 2016). A problem with this simplified approach can be revealed by genetic studies,  
427 which is that the spatial distribution of egg production is important to larval success. This  
428 implies that the limit reference point should be modified to give greater weighting to  
429 locations within the stock that tend to be more important as larval sources.

430 Stock assessment and harvest strategies operate at spatial scales defined by both  
431 political and biological boundaries. Genetic approaches are widely used in fisheries for  
432 defining stocks but applications are less common in lobsters where assessments usually treat  
433 the species as a single stock due to the large scale of dispersal of marine lobsters, such as  
434 reported for the California lobster *Panulirus interruptus* (García-Rodríguez and Perez-  
435 Enriquez 2006). Spatial scale is not only important for assessment but also for decisions  
436 about how to distribute the catch in application of harvest strategies. In particular, genetic  
437 approaches provide information on the appropriate geographic scale of spatial management.  
438 As explained in the context of larval connectivity, recent genetic research on *P. interruptus*  
439 (Iacchei et al. 2013) and *Jasus edwardsii* (Villacorta-Rath et al. 2018) has provided evidence  
440 of chaotic genetic patchiness. This has important implications for management as regulations  
441 that limit total catch and spatially distribute egg production are given preference over  
442 management tools that control the location of catch and concentrate egg production, such as  
443 MPAs or spatial closures.

444 Tagging data is widely used in lobster fisheries for estimating many parameters  
445 important for stock modelling such as catchability, natural mortality, fishing mortality and  
446 biomass (Frusher and Hoenig 2003). However, the collection of tag information from lobsters  
447 that are recaptured with conventional tags is often problematic (Frusher et al. 2009). Genetic  
448 tools enable the same suite of parameters to be estimated as per conventional tagging but  
449 have the important advantage of eliminating problems of tag loss and tag-induced mortality  
450 (O'Malley 2008; González-Vicente *et al.* 2012; Fig. 5).

451 Genetic sampling potentially enables the extension of demographic parameters  
452 estimation far beyond conventional tagging when family relationships are established through  
453 “close-kin-mark-recapture” (CKMK) (Bravington et al. 2016b). For example, the  
454 identification of larval source areas and stock-recruit relationships. This method identifies  
455 parent-offspring-pairs (and other kin-relationships) from genetic sampling of a large number  
456 of individuals. It has been used to provide fishery-independent estimates of absolute  
457 abundance and survival of southern bluefin tuna *Thunnus maccoyii* from a sample of 14,000  
458 individuals (Bravington et al. 2016a).

459 CKMR is a developing area and has not been applied to lobsters yet although is of  
460 interest for both estimation of population parameters and to improve understanding of spatial  
461 differences in larval supply. The ability to determine family relationships by SNP based  
462 genotyping has reduced cost compared with traditional microsatellite approaches, which  
463 means that sampling of large numbers of individuals is now more feasible (Bravington et al.  
464 2016a). Nonetheless, CKMR involves commitment of a substantial research effort so is only  
465 suited to more valuable fisheries including many lobsters stocks.

466 CKMR has a number of assumptions for feasibility (e.g. not parthenogenetic,  
467 semelparous or super-abundant), none of which are broken with lobsters although the  
468 sampling of a large numbers of individuals is required as a result of large population sizes for

469 fished species which is a logistic and financial challenge. Estimation of population  
470 parameters is only possible once a threshold of sufficient parent-offspring-pairs is obtained,  
471 below which all sampling effort is wasted. For example, for populations of *Jasus edwardsii*  
472 in Australia this could be particularly problematic. *Jasus edwardsii* has an extended  
473 planktonic larval stage (up to two years) in a region with complex oceanic currents. The  
474 source-sink relationships remain poorly understood hence there is a danger of not including  
475 sufficient samples from critical source areas to identify a sufficient number of parent-  
476 offspring pairs. Yoshizaki *et al.* (2011) also caution that the risk of misidentification needs to  
477 be carefully managed as this potentially biases the population size estimates upwards. Further  
478 complicating the application of CKMR is the lack of accurate aging techniques which are  
479 useful for determining the age of the offspring and thus matching to the year in which the  
480 parents spawned. This can be overcome to some extent by utilising length-age curves which  
481 are available, however for some species such as *Jasus edwardsii* there is substantial spatial  
482 variability in growth rates throughout the stock. Genetic tools for aging provide a potential  
483 solution to this problem. Molecular age biomarkers are now being developed in other species  
484 and include for example methylation of three CpG sites in Humpback whale (*Megaptera*  
485 *novaeangliae*) DNA (Polanowski *et al.* 2014) and multiple mRNA markers in the mosquito  
486 *Anopheles gambiae* (Wang *et al.* 2013). These molecular age biomarkers have been applied  
487 to model and wild organisms (Jarman *et al.* 2015) and there is clear potential to apply these  
488 markers widely in lobsters.

489         Stock assessment for marine lobsters is of interest for managing fishery harvests but  
490 many freshwater lobsters have a different management issue, which is the conservation of  
491 vulnerable and threatened species. Species such as the tayatea *Astacopsis gouldi* and the  
492 Glenelg spiny freshwater crayfish *Euastacus bispinosus* have small populations and  
493 distribution so estimates of population size and survival are important for species

494 conservation (Shepherd et al. 2011). Genetic techniques have been applied and CKMR may  
495 be of value given the small population size and high catchability (Miller et al. 2014).

496

#### 497 **4.2. The pursuit of a reference genome**

498 So far, studies on lobsters have used molecular methods, such as RADseq, that do not  
499 require reference genomes (e.g. Benestan *et al.* 2015; Souza *et al.* 2017; Villacorta-Rath *et al.*  
500 2018). Recent developments in bioinformatic tools such as assembly algorithms have  
501 improved the *de novo* assembly quality and SNP calling for organisms lacking a reference  
502 genome (Davey et al. 2011; Rochette and Catchen 2017). Although these methods are cost  
503 efficient and useful, a well-assembled reference genome provides further advantages.  
504 Markers can be mapped to a reference genome and the physical positions of loci can then be  
505 used to infer haplotypes across larger chromosomal regions. This can be used for mapping  
506 traits of interest such as age of maturity (Barson et al. 2015). In addition, the number and  
507 quality of markers can be significantly improved as a reference genome assembly can be  
508 conducted to increase the statistical power to detect genomic regions of interest (Andrews et  
509 al. 2016). Reference genome(s) would also enable improved inference of population-  
510 demographic history, the detection of adaptation and identification of functional regions  
511 (Luikart et al. 2004; Fuentes-pardo and Ruzzante 2017).

512 Potential challenges that have constrained the development of a reference genome for  
513 lobsters can be related to the size of lobsters genome (e.g. *Homarus americanus* 4.75 pg,  
514 *Nephrops norvegicus* 4.90 pg, *Jasus edwardsii* 5.01 pg, *Palinurus elephas* 4.27 pg,  
515 *Scyllarides latus* 6.99 pg; Deiana *et al.* 1999). A large genome size adds significant costs for  
516 sequencing and genome assembly. Repetitive regions, commonly reported in other decapods  
517 (e.g. the whiteleg shrimp *Litopenaeus vannamei* genome has ~80% of repetitive sequences,  
518 Yu *et al.* 2015) are also particularly challenging for base-calling and assembly algorithms

519 based on short-read sequences (Hoban et al. 2016). The use of the genome sequence of  
520 closely related species is a possibility for non-model species. However even closely related  
521 species can have large differences in genomic organization such as copy number variation  
522 and structural variants which would make mapping of reads to the reference genome  
523 unfeasible (Ekblom and Wolf 2014). Therefore, a better approach is the use of long read  
524 technologies such as single molecule real time (SMRT) sequencing (PacBio long-read  
525 sequencing platform) and MinION sequencer (Oxford Nanopore Technologies). These  
526 technologies increase read length and unbiased genome coverage and have the potential to  
527 produce genome sequence with fewer gaps and longer contigs. Although there is still a high  
528 cost per nucleotide and a perceived increase in error-rate, these technologies are advancing  
529 and improving very fast (Tyler et al. 2018). In addition, new assembly algorithms such as  
530 MARVEL, which integrates a read-correction procedure that keeps long PacBio reads intact  
531 for assembly, are continuously being developed and have been successfully used for example  
532 to assemble the highly repetitive 32-Gb axolotl genome (Nowoshilow et al. 2018).

533         The development of a reference genome for lobsters would open up new opportunities  
534 for example for implementing more robust approaches such as whole genome resequencing  
535 (WGR). This method allows the most complete account of individual genomic variation to be  
536 estimated (e.g. structural rearrangements, insertion–deletion, SNPs, sequence repeats) and  
537 will likely soon become the standard for genetic studies of non-model organisms including  
538 lobsters (Ekblom and Wolf 2014; Fuentes-pardo and Ruzzante 2017).

539

### 540         **4.3. Lobsters genetics in face of environmental change**

541

542         As a result of anthropogenic impacts on the oceans there is considerable interest in  
543 how organisms will cope with environmental change. Climate-driven changes in species

544 distribution and abundance are apparent around the world (Pecl et al. 2017; FAO  
545 2018). Some lobster species are already impacted and increasingly appear in deeper and outer  
546 coastal waters (Wahle et al. 2015). Therefore it is important to understand future range shifts  
547 and genetic signatures of moving populations for predicting species persistence in new  
548 habitats, such as the recently identified range shift in gloomy octopus (Ramos et al. 2018).

549         While the ecological effects of climate change on lobsters have been well described  
550 (reviewed by Caputi *et al.*, 2013), little is known about whether lobsters will be able to  
551 genetically adapt to climate change impacts or whether there is any epigenetic basis (such as  
552 DNA methylation) to their acclimation responses to environmental change. There are a  
553 number of ways in which lobsters might be influenced directly and indirectly by climate  
554 change related effects, including increased sea surface temperature, ocean acidification and  
555 changes to weather/current patterns (reviewed by Caputi *et al.*, 2013). These impacts include  
556 changes to range distributions, alterations to size at maturity, and disruption of larval  
557 dispersal routes. For example, a number of environmental factors significantly affect puerulus  
558 settlement of the western rock lobster *Panulirus cygnus*, which occur on the west coast of  
559 Australia. Increases in water temperature, and a weakening of westerly winds in winter, have  
560 been correlated with a decrease in size at maturity and size of migrating lobsters from  
561 shallow to deep water, along with variability in settlement rates (Caputi et al. 2010).  
562 However, not all climate effects are negative. For example, Green *et al.* (2010) showed that  
563 translocated populations of *J. edwardsii* on Australia's east coast improved egg production  
564 and growth compared to residents. The authors suggested that plasticity of individuals  
565 exposed to an increase in temperature implies resilience to climate change. Further, Hinojosa  
566 *et al.* (2017) found that annual variability in local environmental factors caused more  
567 variation in recruitment than did large scale climate changes.



568 Lobsters may be particularly vulnerable to climate change impacts as a result of the  
569 very long larval duration found in many species (e.g. *Jasus edwardsii* between 18-23 months;  
570 Booth *et al.*, 1990) and the likely reliance of different current streams to return pueruli to  
571 suitable habitats. There is strong evidence to suggest that lobster species with long larval  
572 periods are dependent on large-scale oceanographic features for retaining larvae and enabling  
573 them to return to suitable adult habitats. For example, the larvae of the Southern rock lobster,  
574 *Jasus edwardsii*, in New Zealand are retained by the Wairarapa Eddy off the South-east coast  
575 of the North Island, which prevent the larvae from being lost to the wider Pacific Ocean  
576 (Chiswell and Booth 1999). Alterations to current flow patterns or large-scale oceanic  
577 features may have important impacts on population connectivity and population structure,  
578 and also impact the long-term persistence of fished species, but see Hinojosa *et al.* (2017).  
579 How such changes will impact lobsters are very difficult to predict as larval behaviour can be  
580 complex and there are still many uncertainties in predictive ocean circulation models.

581 Increased sea surface temperature will also have important impacts on lobsters that  
582 may influence population genetic structure. Temperature changes will impact physiological  
583 processes and also potentially cause range shifts. Some lobster species appear to have fairly  
584 wide temperature tolerances with wide geographic distributions. For example, within New  
585 Zealand the distribution of *Jasus edwardsii* spans over 15 degrees of latitude, which includes  
586 summer temperatures ranging from 10°C to 23°C (Garner 1961). This suggests wide  
587 physiological tolerance of *J. edwardsii* to temperature variation and the potential selection for  
588 different temperature tolerant genotypes. Similarly, the American lobster, *Homarus*  
589 *americanus*, occurs across a large latitudinal range on the Atlantic coasts of Canada and the  
590 United States of America, over which they experience temperatures from -1°C to 26°C  
591 (Quinn and Rochette 2015). While recent increases in temperatures appear to have supported  
592 larger populations, temperatures up to 30°C in the next 10-50 years may severely affect

593 lobster larval performance and survival (Quinn 2017). Finally, Benestan *et al.* (2016)  
594 suggested that minimum annual sea surface temperature (SST) can be a potential selective  
595 agent driving local adaptation in the American lobster and detected three candidate genes  
596 with allele frequencies exhibiting a pronounced temperature-associated cline. Although  
597 further studies on gene function are required, the identification of loci with potential effects  
598 on thermal adaptation provide important information on lobster populations responses to  
599 climate change.

600         Ocean acidification (OA) is also expected to have negative effects on lobsters,  
601 although this may be more acute on the larval stages. For example, Keppel *et al.* (2012)  
602 reported that American lobster *Homarus americanus* larvae kept in acidified (pH = 7.7)  
603 seawater had a significantly shorter carapace length than those in control seawater (pH = 8.1)  
604 after every moult. They also found that larvae in acidified seawater took significantly more  
605 time to reach each moult than control larvae and reported evidence of reduced survival in the  
606 last larval stage. However, adult lobsters may be more protected from the effects of OA as  
607 their calcium carbonate skeleton is usually covered with an epicuticle (see Ries, Cohen, &  
608 McCorkle, 2009) that may provide them greater resilience to changes in pH. If larval  
609 physiology is altered by changes to ocean pH, then this may have subsequent effects on larval  
610 duration and transport, altering connectivity patterns, gene flow and genetic structure.

611         There is increasing interest in how transgenerational exposure to stress can enhance  
612 resilience to that stress in offspring. Although there are no studies focussing on lobsters at  
613 this time, this has been demonstrated for a number of marine species, particularly with  
614 respect to ocean warming and ocean acidification. However, the molecular basis underlying  
615 such adaptive responses is still poorly known. For example, Donelson *et al.* (2012) found that  
616 the damselfish *Acanthochromis polyacanthus* was very sensitive to small (several degrees)  
617 increases in water temperature, but can rapidly acclimate over multiple generations. More

618 recently, Goncalves *et al.* (2016) investigated the genetic basis for transgenerational exposure  
619 to ocean acidification in oysters, and found that the expression of key target genes revealed  
620 that the responses of oysters appeared to be affected by population-specific genetic or  
621 phenotypic traits and by the conditions that parents had been exposed to. This clearly  
622 demonstrates the potential for organisms, including lobsters, to rapidly acclimate to changing  
623 environments, and given its ecological and economic importance this should be focus of  
624 future research in lobsters.

625         There are two potential ways that populations may persist in response to climate  
626 change either through local adaptation, whereby specific genotypes are favoured as  
627 conditions change, or phenotypic plasticity, whereby existing genetic diversity can produce  
628 new phenotypes that are equally fit in the changed environment (Stillman and Armstrong  
629 2015). The development of Whole Genome Sequences (WGS) enables genetic markers to be  
630 mapped to a specific location in the genome, and it is then possible to identify genetic  
631 markers that are associated with a particular traits (including stress resistance) and the  
632 opportunity to investigate nearby genes to potentially identify causative mutations  
633 (Hollenbeck and Johnston 2018). For marine lobsters, the development of WGS will be an  
634 important step for distinguishing between the local adaptation and phenotypic diversity  
635 effects and determining the potential for lobsters to adapt in the face of environmental  
636 change. WGS will also aid in our understanding of any potential for transgenerational  
637 acclimation to environmental change and epigenetic effects, since reference genomes are  
638 required for epigenome sequencing (Hofmann 2017). Such genetic resources may also  
639 provide potential for selective breeding of tolerant based on the genetic basis of tolerance  
640 (Hollenbeck and Johnston 2018). However, since most lobsters are harvested based on wild-  
641 capture fisheries this might not be useful for all lobster species although there are several

642 ongoing projects across the world that are trying to farm lobsters (e.g. *Homarus gammarus* in  
643 the UK).

644

## 645 **5. Conclusions**

646

647 Our review demonstrates that genetic studies on lobsters are skewed to a few species,  
648 in particular *Panulirus* spp. and *Homarus* spp. and most studies used mitochondrial DNA  
649 (mtDNA) and microsatellite markers. The extensive research on *Panulirus* spp. and *Homarus*  
650 spp. likely reflects their economic importance as they are the basis of important fisheries  
651 worldwide, while mtDNA and microsatellites have been the most economically accessible  
652 genetic markers until very recently. Overall, most studies have applied genetic tools to  
653 answer questions in the areas of population genetics and phylogenetics (including species  
654 delimitation), with a few recent studies applying high-resolution markers to investigate  
655 adaptation to local environmental conditions.

656 Speciation processes and phylogenetic relationships are often difficult to interpret and  
657 still unclear for some groups of lobsters. Despite high potential for dispersal and a lack of  
658 obvious barriers to population connectivity, a number of recent studies suggest rapid  
659 speciation events are driving lobster origins and many of these divergence events may have  
660 occurred relatively recently. Despite the interest in origins of lobster species, comprehensive  
661 molecular studies of speciation are rare. Lobster research will further benefit from seascape  
662 genomics approach which will provide insights on how the environment shapes adaptation  
663 and connectivity between populations.

664 A common pattern of population structure observed across studies is low genetic  
665 differentiation and high connectivity between populations as a result of high potential for  
666 dispersal. However, there are a few cases with substantial genetic structure at small spatial

667 scales. Settlement and recruitment are highly variable through time as a result of  
668 environmental factors and temporal-spatial changes in egg production.

669 CKMK is a genetic based approach that can aid lobsters management by providing  
670 fishery-independent estimates of absolute abundance and survival. However, CKMR is a  
671 developing area and has not been applied to lobsters yet although is of interest for both  
672 estimation of population parameters and to improve understanding of spatial differences in  
673 larval supply.

674 Despite its utility, no reference genome for lobster has been published to date possibly  
675 as a result of the large genome size of many lobsters and the challenges associated with  
676 sequencing, assembly and analysis. However, this has been achieved in other species with  
677 complex and larger genomes. Development of such an important resource as whole genomes  
678 will involve commitment of a substantial research effort but it will greatly benefit research of  
679 these keystone species and ultimately contribute to improved lobsters management.

680 Finally, an important unanswered question is how lobsters will respond to future  
681 environmental conditions. Some lobsters are already impacted and shifting their distribution  
682 range and little is known about whether lobsters will be able to genetically adapt to changing  
683 environmental conditions. Powerful genomic tools are already revolutionising our  
684 understanding of fine scales of population connectivity and adaptation to specific  
685 environmental conditions. These tools provide information that is unlikely to be obtained  
686 from other methods and that can be applied to fisheries, aquaculture and conservation  
687 justifying future investment in their development and application to lobsters.

688

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690

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693

694

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1078 **Tables**

1079

1080 Table 1. Summary of molecular markers and population differentiation detected in genetic  
 1081 studies of *H. americanus* over a 40 year period.

Publication	Molecular Marker	No. of markers	No. of Samples	No. Populations	F <sub>ST</sub> Ranges
Tracey <i>et al.</i> (1975)	Allozymes	44	290	43 loci exhibited genetic homogeneity; 1 loci detected 3 populations	-
Harding <i>et al.</i> (1997)	RAPD	42 primers screened; 4 primers polymorphic	110	Slight genetic differentiation between Gulf of St Lawrence and Gulf of Maine	0.000-0.073
Crivello <i>et al.</i> (2005)	Microsatellites	9	507	2 populations; slight evidence of genetic differentiation between an additional 3 locations	0.0033-0.2
Kenchington <i>et al.</i> (2009)	Microsatellites	13	2,555	Gulf of St Lawrence-Gulf of Maine genetic divide; 2 northern populations and 8 southern populations	0.000-0.02
Benestan <i>et al.</i> (2015)	SNPs	10,156	586	Gulf of St Lawrence-Gulf of Maine genetic divide; 11 populations	0.00002-0.00374

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1085 **Figures legends**

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1087 **Fig. 1.** Number of original articles indexed on the ‘Web of Science’, between 1975 and 2019  
1088 with the keywords “lobster”, “genetic”, “genomic”, and “transcriptomic” in the topic,  
1089 employing genetic markers. ‘Others’ include genus *Chelarctus* (Achelata), *Galearctus*  
1090 (Achelata), *Linuparus* (Achelata), *Palinurellus* (Achelata), *Palinustus* (Achelata), *Petrarctus*  
1091 (Achelata), *Polycheles* (Polychelida), *Puerulus* (Achelata), *Sagmariasus* (Achelata),  
1092 *Scyllarides* (Achelata), *Scyllarus* (Achelata), *Stereomastis* (Polychelida), *Thaumastocheles*  
1093 (Astacidea) and *Thenus* (Achelata).

1094 **Fig. 2.** Total number of original articles indexed on the ‘Web of Science’, between 1975 and  
1095 2019 with the keywords “lobster”, “genetic”, “genomic”, and “transcriptomic” in the topic,  
1096 employing different genetic markers to lobsters. ‘Other’ includes the following markers:  
1097 random amplified polymorphic DNA (RAPD), restriction fragment length polymorphism  
1098 (RFLP) and RNA-sequencing.

1099 **Fig. 3.** Schematics of infraorder level lobster relationships based on fragments of  
1100 mitochondrial markers (12 rRNA, 16S rRNA, cytochrome c oxidase subunit I), nuclear  
1101 markers (histone H3, 18S rRNA, 28S rRNA) and 190 morphological characters (adapted  
1102 from Bracken-Grissom *et al.* 2014).

1103 **Fig. 4.** Approximate distribution range of *Jasus* spp. (adapted from Booth, 2006). More  
1104 recently, Groeneveld *et al.* (2012) suggested that species *J. tristani* and *J. paulensis* should be  
1105 synonymized as *J. paulensis*.

1106 **Fig. 5.** Population data for lobsters is often obtained from tagging studies. This southern  
1107 rock lobster *Jasus edwardsii* has a conventional yellow T-bar tag on the underside of the  
1108 abdomen. Above this is a darker lesion which shows the lobster was previously tagged but  
1109 the tag has been lost.

1110

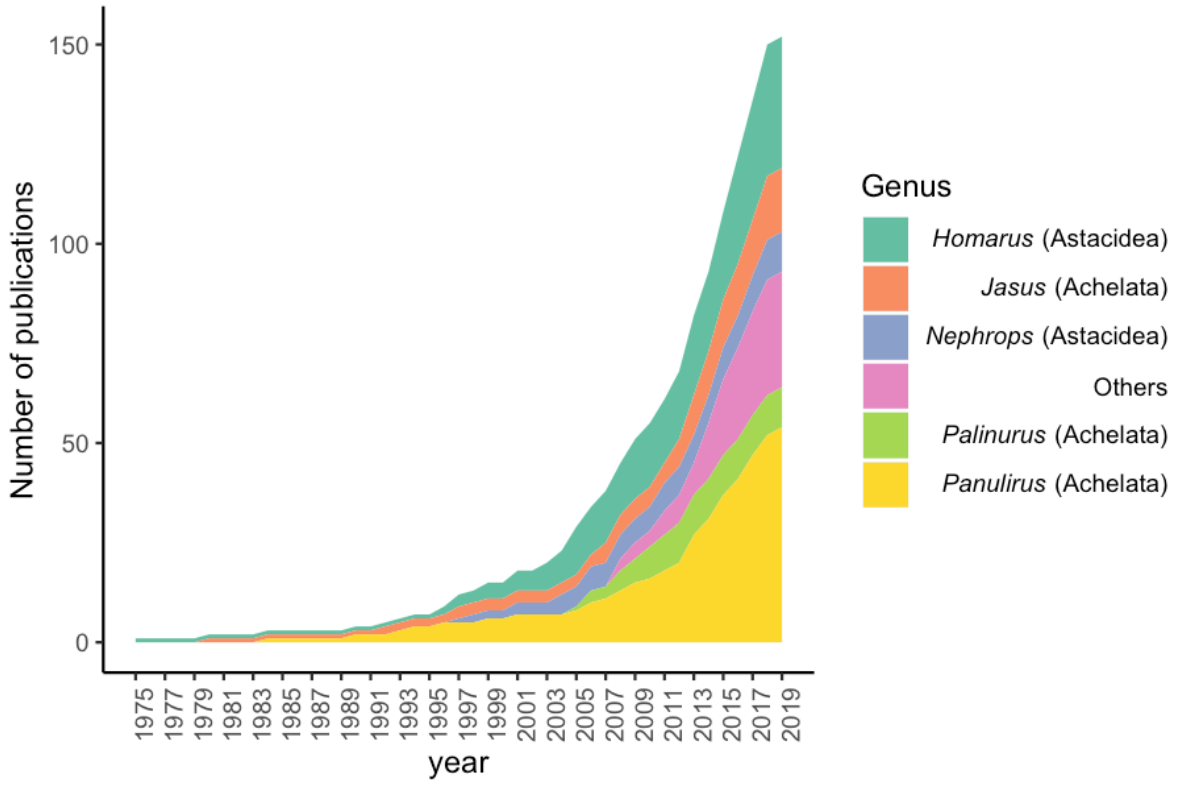
1111

1112 **Supporting information**

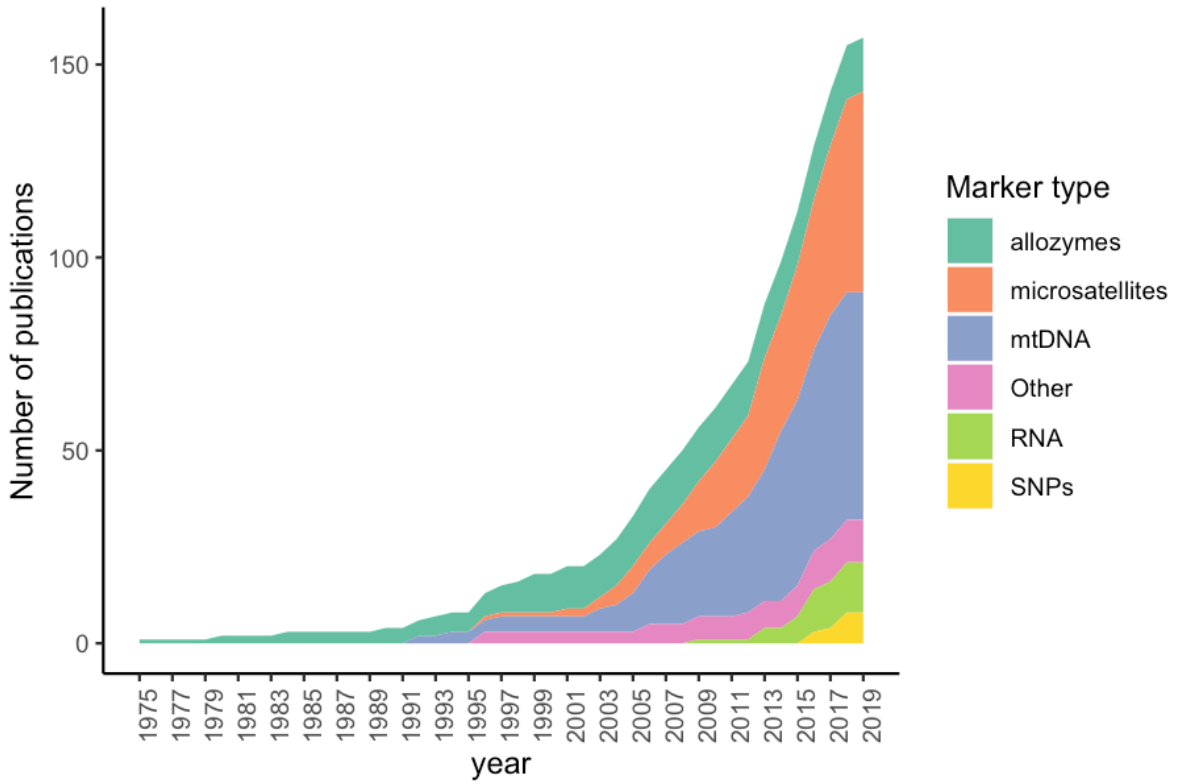
1113 Additional supporting information may be found in the online version of this article.

1114

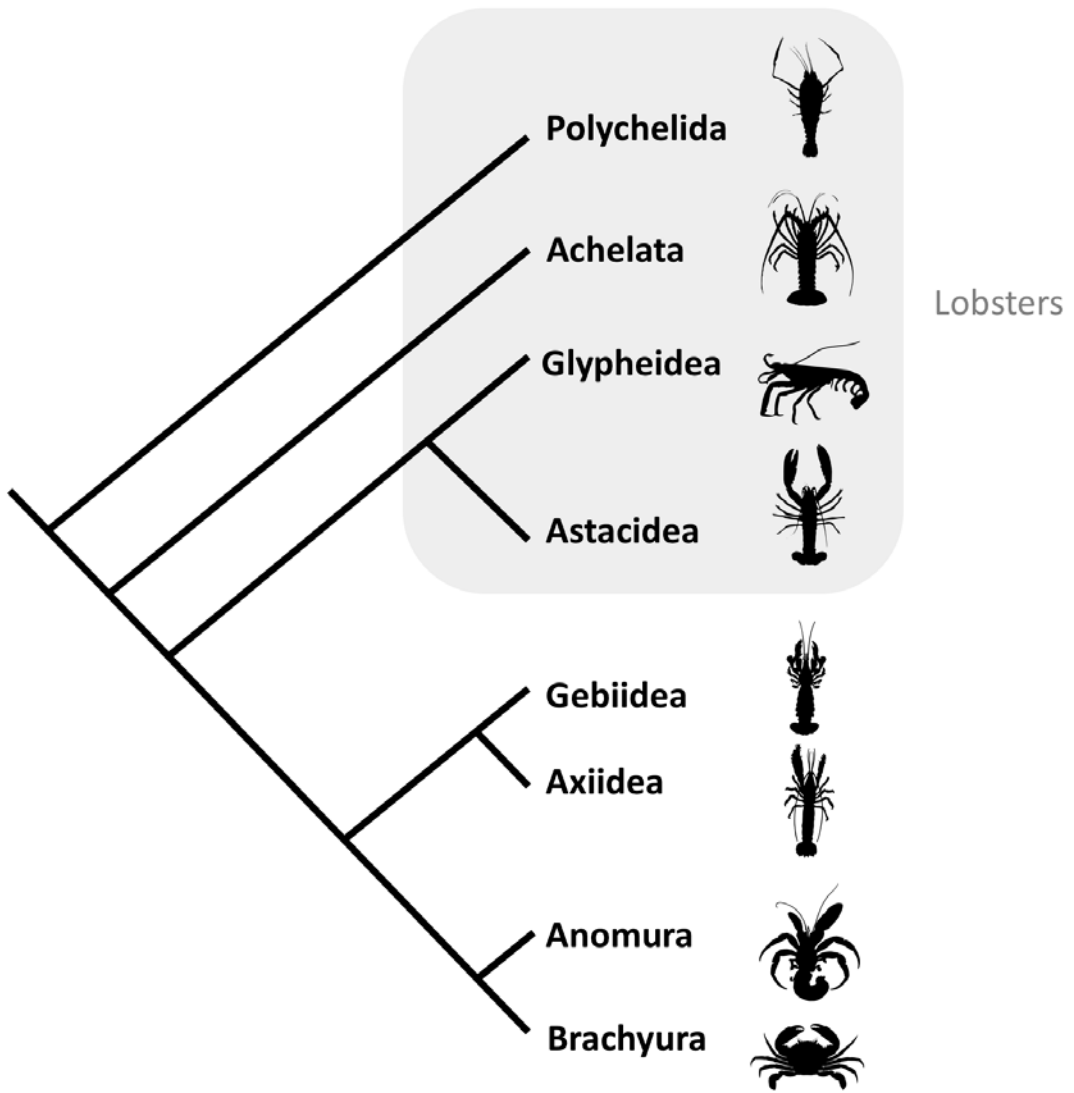
1115 **Table S1.** List of studies compiled for this review, using the ‘Web of Science’  
1116 ([www.isiknowledge.com](http://www.isiknowledge.com)), search up to June 2019 for articles with the words “lobster” and  
1117 “genetic” in the topic.  
1118



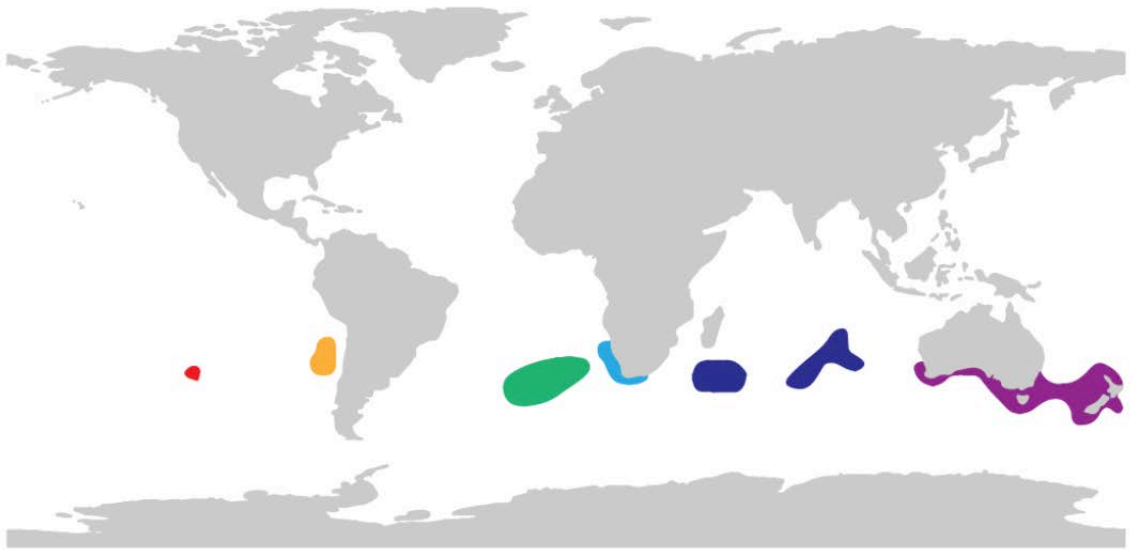
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● *J. caveorum*

● *J. tristani*

● *J. paulensis*

● *J. frontalis*

● *J. lalandii*

● *J. edwardsii*

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