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

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ABSTRACT

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

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

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

Running title: Genetics of marine lobsters

1. Introduction

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

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

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

1.1. Trends in study species and genetic tools

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

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

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

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

1.2. Marker resolution

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

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

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

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

2. Lobster evolution

2.1. Phylogenetics

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

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

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

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

Transcriptomic methods will provide much larger genetic datasets for investigating evolutionary relationships within lobsters and may provide resolution within deeper phylogenetic levels (as it has been the case for other taxa e.g. Tanner *et al.* 2017) – but there has been little progress in this area to date. Recently, target capture sequencing (based on probes developed from double digest restriction site-associated DNA sequencing [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

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

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

3. Genetics of connectivity and recruitment

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

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

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

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

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

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

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

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

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

3.2. Stochasticity in connectivity patterns

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

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

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

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

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

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

4. Gaps and future directions

4.1. Integration of genetics with stock assessment strategies

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

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

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

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

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

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

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

4.2. The pursuit of a reference genome

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

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

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

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

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

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

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

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

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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_{ST} Ranges
Tracey *et al.* (1975)	Allozymes	44	290	43 loci exhibited genetic homogeneity; 1 loci detected 3 populations	-
Harding *et al.* (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 *et al.* (2005)	Microsatellites	9	507	2 populations; slight evidence of genetic differentiation between an additional 3 locations	0.0033-0.2
Kenchington *et al.* (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 *et al.* (2015)	SNPs	10,156	586	Gulf of St Lawrence-Gulf of Maine genetic divide; 11 populations	0.00002-0.00374

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Figures legends

Fig. 1. Number of original articles indexed on the 'Web of Science', between 1975 and 2019 with the keywords "lobster", "genetic", "genomic", and "transcriptomic" in the topic, employing genetic markers. 'Others' include genus *Chelarctus* (Achelata), *Galearcturs* (Achelata), *Linuparus* (Achelata), *Palinurellus* (Achelata), *Palinustus* (Achelata), *Petrarctus* (Achelata), *Polycheles* (Polychelida), *Puerulus* (Achelata), *Sagmariasus* (Achelata), *Scyllarides* (Achelata), *Scyllarus* (Achelata), *Stereomastis* (Polychelida), *Thaumastocheles* (Astacidea) and *Thenus* (Achelata).

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

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

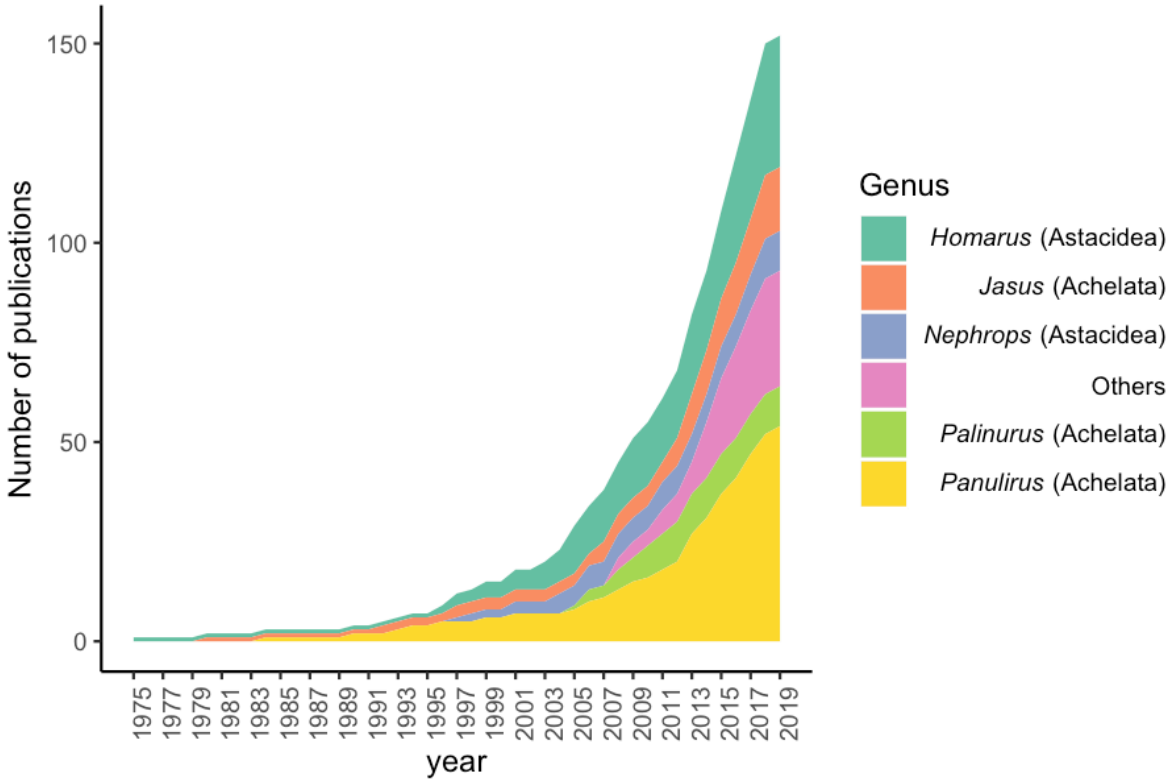
Fig. 4. Approximate distribution range of *Jasus* spp. (adapted from Booth, 2006). More recently, Groeneveld et al. (2012) suggested that species *J. tristani* and *J. paulensis* should be synonymized as *J. paulensis*.

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

Supporting information

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

Table S1. List of studies compiled for this review, using the 'Web of Science' (www.isiknowledge.com), search up to June 2019 for articles with the words "lobster" and "genetic" in the topic.


Number of publications
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year
Genus
Homarus (Astacidea)
Jasus (Achelata)
Nephrops (Astacidea)
Others
Palinurus (Achelata)
Panulirus (Achelata)

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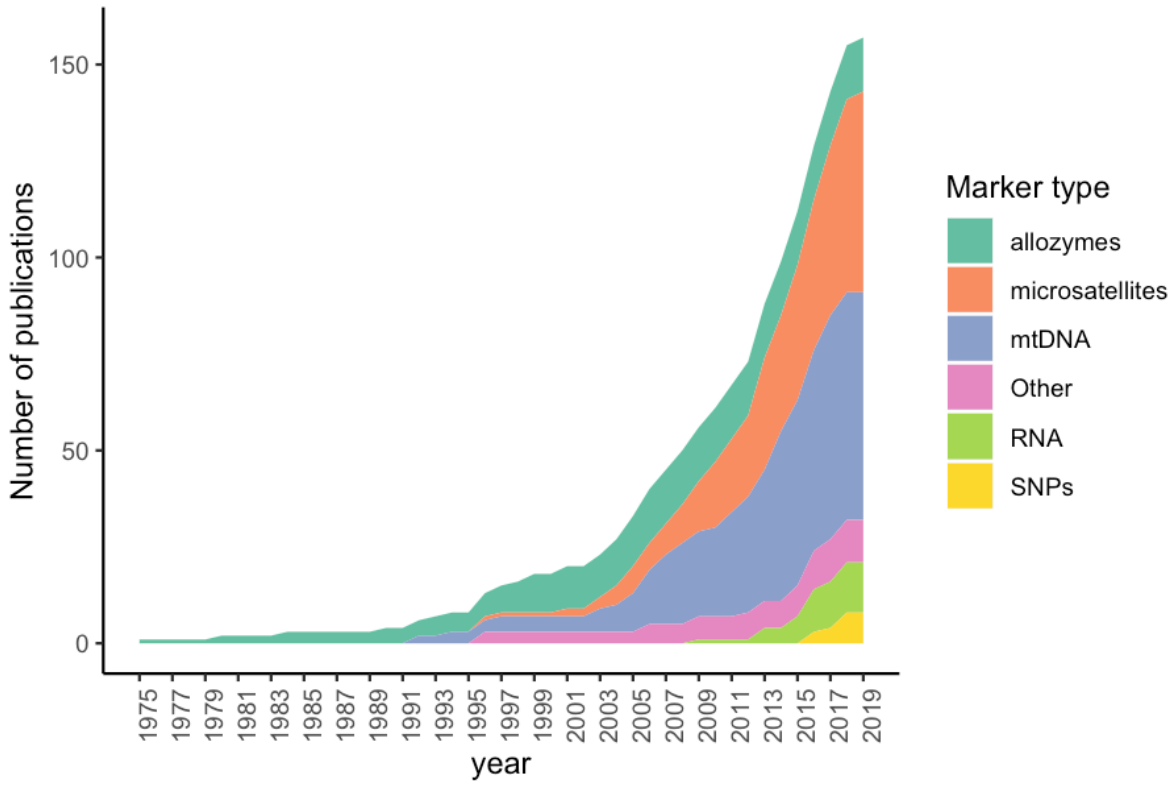
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mtDNA
Other
RNA
SNPs

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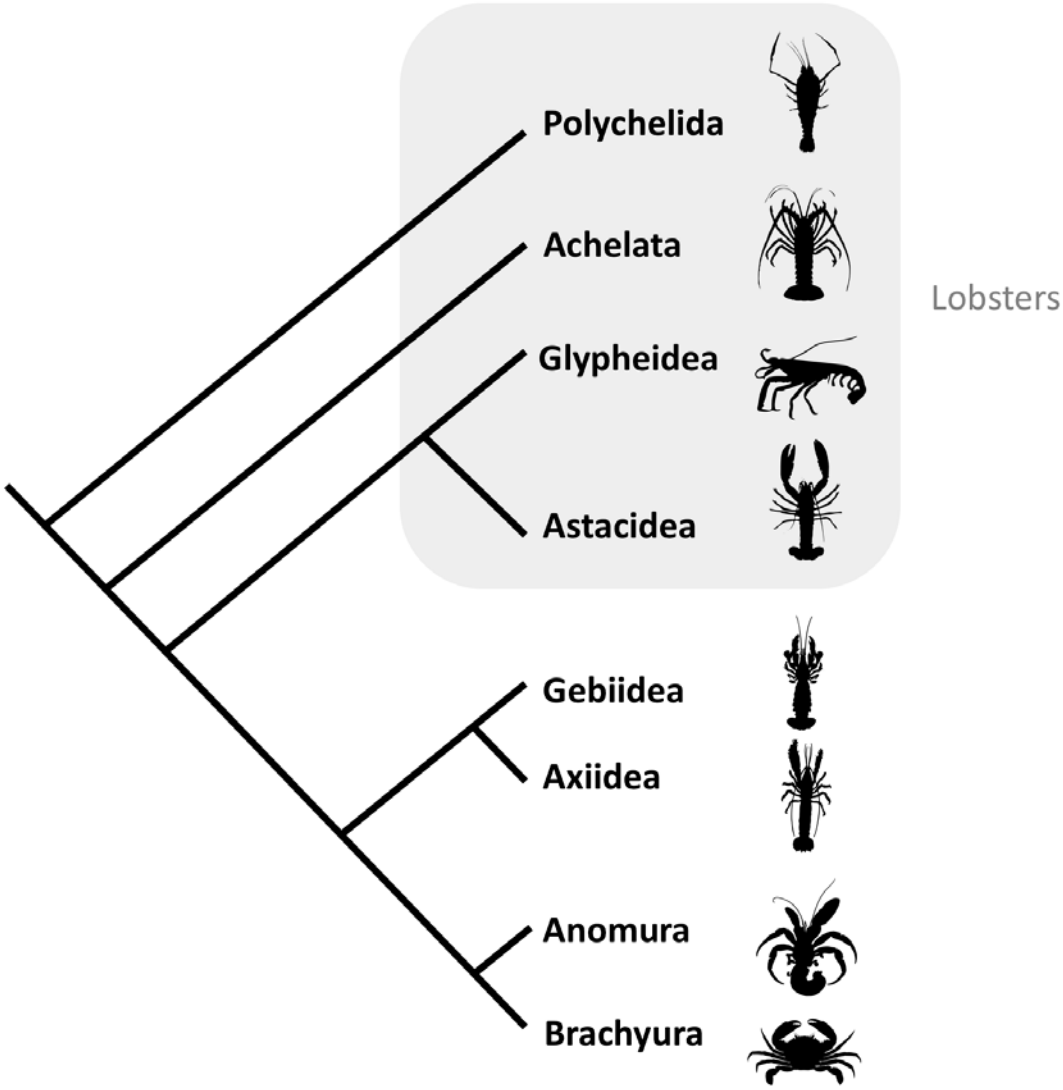
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Achelata
Glypheidea
Astacidea
Lobsters
Gebiidea
Axiidea
Anomura
Brachyura

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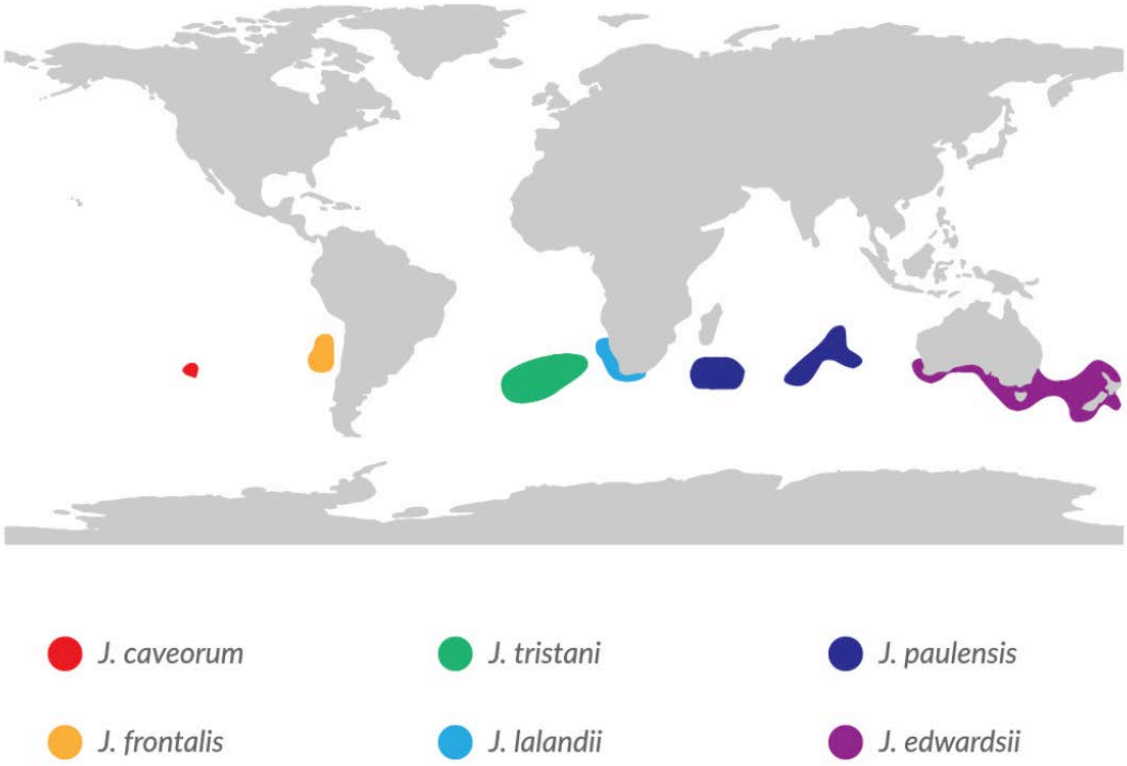
J. caveorum
J. tristani
J. paulensis
J. frontalis
J. lalandii
J. edwardsii

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