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Contribution to the Supplement: '*Lobsters in a Changing Climate*'

Review

European lobster stocking requires comprehensive impact assessment to determine fishery benefits

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Historically, hatcheries in Europe and North America attempted to contribute to the conservation and enhancement of clawed lobster stocks, but lacked monitoring programmes capable of assessing success. In the 1990s, this perspective was changed by the results of restocking and stock enhancement experiments that inserted microwire tags into hatchery-reared juvenile European lobsters (*Homarus gammarus*) before release. This allowed recapture in sufficient numbers to prove that lobsters had survived and recruited to the mature fishable stock. However, evidence of recruitment still failed to answer key questions about the ultimate ecological and economic benefits. As a result, a growing number of lobster stocking ventures remain hindered by a lack of clear evidence of the effects of their stocking schemes. This review evaluates these experiments and related studies on other fished species, summarizes key findings, and identifies data and knowledge gaps. Although studies of fitness in cultured lobsters provide some of the most encouraging results from the wider field of hatchery-based stocking, the limitations of physical tagging technology have significantly hindered appraisals of stocking impacts. We lack basic knowledge of lobster ecology and population dynamics, especially among prerecruits, and of the impact of stocking on wild lobster population genetics. We advocate the use of genetic methods to further our understanding of population structure, rearing processes, and stocking success. We also recommend that more focused and comprehensive impact assessments are required to provide a robust endorsement or rejection of stocking as a viable tool for the sustainable management of lobster fisheries.

Keywords: crustacea, genetics, hatchery, *Homarus gammarus*, mark–recapture, population structure, restocking, stock enhancement, tagging.

Introduction

Capture fisheries make crucial contributions to the world's well-being and prosperity. The global value of fisheries was estimated at over €65 billion per annum in 2010, ca. 10% of the world's population are dependent on fish-related jobs, and seafood products are a vital source of protein and micronutrients for 3 billion people (Fisheries and Aquaculture Department, 2014). Commonly, however, conventional management fails to prevent the overexploitation of stocks. Interventions that use hatchery technology to improve or re-establish the productivity and sustainability of capture fisheries, which can be categorized as "stocking", are, therefore, worth considering. For many aquatic species, the survival of juveniles in aquaculture facilities is several orders of magnitude higher than in the wild, allowing increased recruitment above natural levels (Lorenzen, 2005). Stocking schemes aim to improve and sustain capture fisheries and are categorized as either "restocking" (the release of cultured juveniles to restore spawning biomass) or "stock enhancement" (the recurrent release of cultured juveniles to overcome recruitment limitations) (Bell et al., 2006). Lorenzen

(2008) advocates that aquaculture-based enhancement of stocks ranks alongside regulation of fishing effort and restoration of key habitats as a principal means by which wild fisheries can be sustained and improved.

With many capture fisheries under intense pressure, aquaculture technologies have become an increasingly important means of seafood production, largely through the full grow out of marketable fish, but also by restocking and stock enhancement of wild populations. Hatchery stocking is undertaken worldwide and has been most successful in large-scale schemes coordinated and funded by government or industry. For example, the government-financed programme in Japan alone involves the enhancement of >80 marine species (Kitada, 1999) and is estimated to account for 90% of the chum salmon (*Oncorhynchus keta*) fishery, 50% of the kuruma prawn (*Penaeus japonicus*) and red sea bream (*Pagrus major*) catch, 30% of the flounder (*Paralichthys olivaceus*), and almost all the scallop harvest (Kitada *et al.*, 1992; Kitada and Kishino, 2006). However, the contribution of stock enhancement to global fisheries production has remained small (~2%), and few case studies have been declared outright successes (Lorenzen, 2008). Overall, the available literature appraising the impact of stocking is heavily biased towards certain finfish; Araki and Schmid (2010) found that 62% of genetic-based stocking impact studies evidenced salmonids, flatfish, and bream, despite these groups accounting for only 5% of the catch tonnage of enhanced fisheries.

For many years, the progress of stocking enterprises was hindered by a lack of appropriate research into wild life histories and by a lack of effective methods for distinguishing released individuals from wild conspecifics. As a result, robust evaluation of the economic and ecological benefits of stocking has been impeded, restricting impetus within the industry. Extensive knowledge of the ecosystem, species biology, and population-specific data is required for the design of successful stocking programmes. For example, of eight species across a variety of taxa cultured in Japan reviewed by Kitada (1999), six showed significant variation in the effectiveness of stocking with differing release locations and/or release densities. The method, timing, and recipient habitat of releases and the density, size, and conditioning of released animals can all have significant effects on survivability (van der Meeren, 2000; Ball *et al.*, 2001; Stunz and Minello, 2001; Svåsand *et al.*, 2004; Leber *et al.*, 2005; Hamasaki and Kitada, 2008a; Ochwada-Doyle *et al.*, 2010).

The focus on this review is the European lobster (*Homarus gammarus* L.), an ecologically and economically important decapod crustacean ranging from northern Norway to Morocco and the eastern Mediterranean (Triantafyllidis *et al.*, 2005). Global catches of the European lobster have been increasing since the 1980s, with recent recorded pot-caught landings reaching 5913 t in 2011 (Fisheries and Aquaculture Department, 2014). Compared with many finfish or the recent very large landings of the American lobster (*Homarus americanus*) in North America [e.g. 50 000 t in Maine (Steneck and Wahle, 2013)], European lobster landings are small and come from sparse stocks. The species is of very high value, however, fetching an average market price of €12.50 kg^{-1} at the time of writing (Fish Information and Services, 2014). Therefore, lobster populations are disproportionately important to local fishing communities and regional economies as well as fulfilling key roles in the maintenance of healthy and diverse marine ecosystems (Mann and Breen, 1972; Breen and Mann, 1976). Aquaculture-based augmentation of wild Homarid lobster populations has been attempted on both sides of the North Atlantic for over 150 years using many release strategies and life history stages (Nicosia and Lavalli, 1999). Because enhancement of existing populations was difficult to identify, few of these experiments have been assessed in terms of benefits to fisheries (Addison and Bannister, 1994; Nicosia and Lavalli, 1999). Lobster hatcheries have provided most of the recorded information on clawed lobster life history (Nicosia and Lavalli, 1999), but significant voids still exist in our understanding of the species' basic ecology.

The basic technology to rear lobsters through the planktonic phases has long been available. This lifestage is presumed to be an important recruitment bottleneck due to predation in the wild (Richards and Wickins, 1979; Bannister and Addison, 1998). However, efforts to trial the stocking of lobsters were renewed in Europe throughout the 1980s–1990s in response to three key drivers. First was a severe collapse of the fishery throughout Scandinavia from 1930 to 1970 due to overexploitation and inadequate management, which saw landings decline 99% in Denmark, 92% in Norway, and 90% in Sweden, all but wiping out a once-thriving export commodity (Dow, 1980; Agnalt *et al.*, 1999; Fisheries and Aquaculture Department, 2014). This led to aspirations to restock depleted populations as well as to enhance stocks where uncapped potting effort rose in response to new continental export opportunities, such as the United Kingdom (Bannister, 1986). Second, it was demonstrated that hatchery-reared lobsters acquired benthic, shelter-seeking behaviours (Cobb, 1971; Cooper and Uzmann, 1980; Botero and Atema, 1982) that might decrease their vulnerability to wild predators and hence improve survival (Howard, 1980, 1988). Third, the development of coded microwire tagging (CWT) technology (Jefferts *et al.*, 1983) allowed cultured juvenile lobsters to be distinguished from wild conspecifics after release (Wickins *et al.*, 1986; Bannister and Addison, 1998).

Experimental lobster stock enhancement programmes were launched to release large numbers of juvenile lobsters onto known lobster grounds at a range of sites in France (Henocque, 1983; Latrouite and Lorec, 1991), the United Kingdom (Burton, 1992; Bannister *et al.*, 1994; Cook, 1995), and Norway (Agnalt *et al.*, 1999, 2004; Agnalt, 2008). Coded microwire tags were inserted into late-stage juveniles before release, and their recapture provided the first definitive evidence that cultured lobsters were able to survive in the wild. In both UK stock enhancement and Norwegian restocking trials, cultured lobsters were shown to attain adult sizes (Bannister *et al.*, 1994; Agnalt *et al.*, 1999) and add to spawning–stock biomass (Bannister *et al.*, 1994; Agnalt, 2008). Restocking also showed that released lobsters could augment rather than simply displace natural stocks (Agnalt *et al.*, 1999, 2004). Although most of these studies declared the renewed lobster stocking efforts as tentatively successful, it was also proposed that production costs and lobster market values did not make the observed recapture rates economically viable (Whitmarsh, 1994; Moksness *et al.*, 1998).

In this review, we summarize current practices in lobster stocking, and reappraise the measurement of stocking success and the practices of monitored stocking trials. We then highlight critical issues for lobster stocking, including hatchery production methods, understanding the ecology of lobsters in the wild to optimize success of released lobsters, and genetic considerations. Finally, we address the problem of comparing stocking with alternative management strategies and conclude by suggesting future research directions and hatchery protocols.

Hatchery rearing of European lobsters

The rationale for current European lobster cultivation is typical of hatchery enterprises. Fishery stakeholders are attracted to stocking where other management options are limited or unappealing. Intensive developments in husbandry, infrastructure, and stakeholder engagement are required to establish a lobster hatchery, and significant gaps remain in our understanding of aspects of the biology and ecology of *H. gammarus*. Nevertheless, severe stock depletions, high market value, and well-functioning rearing technology continue to encourage new lobster stocking efforts in Europe (Svåsand *et al.*, 2004).

Female lobsters, bearing eggs fertilized naturally in the wild, are typically bought or loaned from fishers or merchants and are held until the larvae have hatched. Larvae are normally reared communally through the planktonic lifestages (Zoea larval stages I–III and post-larval stage IV) in tapered hoppers or Hughes/Kreisel cones in which upwelling air and/or water reduces settling and cannibalization (Richards and Wickins, 1979; Beard *et al.*, 1985; Grimsen *et al.*, 1987; Beard and Wickins, 1992; Burton, 1992; Cook, 1995; Nicosia and Lavalli, 1999; Daniels *et al.*, 2010). Survival of the planktonic phase is highly sensitive and variable even in the captive environment, and although individual batches may attain survival >50%, typically 10–15% of stage I larvae reach the onset of benthic behaviours a few days after moulting to stage IV (Burton, 1992; Nicosia and Lavalli, 1999; Daniels *et al.*, 2010). The absence of interspecific predation suggests that cultured larval survival is likely to far exceed that of wild larvae, although the scarcity with which wild conspecifics are found (Nichols and Lovewell, 1987) means that no reliable estimates of natural survival exist for comparison. Once they attain stage IV, post-larvae have a much greater swimming ability and are generally then separated into individual holding compartments for on-growing before being released into wild environments at an early benthic juvenile phase.

Over 1.4 million cultured juvenile European lobsters have been released by known stocking programmes between 1983 and 2013. Of these releases, 90% can be classified as stock enhancement of existing commercial fisheries around the United Kingdom, Ireland, and France, and 10% as restocking heavily depleted populations in Norway, Germany, and Italy (Table 1). Approximately 255 000 released lobsters (mostly in Norway and the United Kingdom) were grown on to late juvenile stages [12–21 mm carapace length (CL), Latrouite and Lorec, 1991; Burton, 1992; Cook, 1995; Bannister and Addison, 1998; Agnalt *et al.*, 1999; Schmalenbach *et al.*, 2011] and tagged to allow wild survival to be monitored. More recently, stock enhancement programmes in Orkney, Scotland, and Cornwall, England, and restocking trials in Lazio, Italy, have released some 900 000 untagged juveniles at earlier lifestages (stage V+, >5 mm CL; D. Shearer and G. Nascetti, pers. comm.).

Assessments of lobster stocking success

Monitored stocking trials

Long after the development of the requisite technology to rear lobsters through the larval phases for release as juveniles, the success of early stocking programmes still could not be formally evaluated (Addison and Bannister, 1994). Ecdysis (exoskeletal moulting) precludes the use of externally fixed markers in lobsters, particularly juveniles which moult frequently. As a result, there was no lasting method to discriminate between hatchery-reared and wild individuals. Whether released animals survived and actually enhanced natural stocks (instead of displacing them) were unproven, proponents of stocking were unable to demonstrate whether the method provided any benefits to fisheries (Addison and Bannister, 1994).

Flawed attempts to recognize recaptured hatchery-reared individuals led to the trial release of 1300 *H. gammarus* × *H. americanus* hybrid juveniles in France during the 1970s (Latrouite and Lorec, 1991), despite no evidence of their ecological suitability and the

Table 1. Summary of major and/or widely reported stock enhancement projects for European lobsters 1972–2013.

Location (hatchery—area)	Release years	Monitoring years	Release age/stage	Number released	Number recapture	Recapture ratio (% recaptured)	Source reference
France (Ile de Sein; Ile d'Yeu; Ile de Houat)	1972–1977	–	Stage 5–1 year	~265 000	–	–	Henocque (1983)
France (Ile de Sein; Ile d'Yeu; Ile de Houat)	1978–1983	1980–1983	~1 year	1300[b]	0	–	Latrouite and Lorec (1991)
United Kingdom (MAFF—Bridlington; NWSFC—Aberystwyth; SFIA—Ardtoe; Orkney)	1983–1990	1985–1994	~1 year	90 925[a]	1471	1 : 62 (1.6%)	Bannister *et al.* (1994); Cook (1995); Burton (1993); Bannister and Addison (1998)
France (Ile de Sein; Ile d'Yeu; Ile de Houat)	1984–1987	1987–1989	~1 year	25 480[a]	22	1 : 1 158 (0.1%)	Latrouite and Lorec (1991)
Norway (Kvitsøy)	1990–1994	1992–2001	~1 year	127 945[a]	7950	1 : 16 (6.2%)	Agnalt *et al.* (2004)
Ireland (Galway; Wexford)	1993–1997	–	Stages 4–5	~292 000	–	–	Browne and Mercer (1998)
Germany (Helgoland)	2000–2005	2001–2009	~1 year	~5400[a]	487	1 : 11 (9.0%)	Schmalenbach *et al.* (2011)
United Kingdom (OSFH—Orkney)	2000–2013	–	Stages 4–10	~747 000	–	–	D. Shearer, pers. comm.
United Kingdom (NLH—Cornwall)	2002–2013	–	Stages 5–10	~150 000	–	–	This paper
Italy (CISMAR—Viterbo)	2010–2013	–	Stage 4+	~10 000	–	–	G. Nascetti, pers. comm.
Total	1983–2013	1985–2009	Stage 4–~1 year	~1 714 947 (249 750 tagged)	9930	1 : 25 (4.0%)	–

[a]Tagged.
[b]*Homarus gammarus* × *H. americanus* hybrids; "phenotypically marked", but omitted from tagged release total.

scheme relying on local fishers identifying precise morphological variations in surviving hybrids. Extensive interannual fluctuations in landings inhibited the usefulness of fishery capture statistics in quantifying stocking success (Le Gall *et al.*, 1983), but the advent of the first suitable internal tagging methods in the early 1980s encouraged three groups in France, Norway, and the United Kingdom to commit significant resources to new experimental stocking programmes (Bannister and Addison, 1998). These projects (Table 1, entries 3–5) reared and released in all 244 350 late-stage juveniles. The insertion of magnetized, batch-coded CWTs offered the prospect of detecting survivors and evaluating the contribution of stocking to fisheries. Since these experiments concluded in the late 1980s or early 1990s, only one further scientific assessment of *H. gammarus* stocking has been reported: 5400 one-year-old lobsters were tagged with visible implant elastomers (VIEs—Uglem *et al.*, 1996) and released during 2000–2005 on the German island of Helgoland (Schmalenbach *et al.*, 2011). Monitoring of these projects has enabled the identification of cultured lobsters upon recapture several years after wild release, and currently provides all the data available with which to assess the effectiveness of lobster stocking in Europe (Latrouite and Lorec, 1991; Burton, 1992; Bannister *et al.*, 1994; Cook, 1995; Bannister and Addison, 1998; Agnalt *et al.*, 1999; Agnalt *et al.*, 2004; Schmalenbach *et al.*, 2011).

There were many differences of detail in relation to release sites and methods, local fishing effort and legislations, and monitoring patterns both within and among the groups undertaking European stocking trials. However, hatchery rearing protocols were largely shared and, with little information about the habitat requirements of prerecruit lobsters, all groups released juveniles into areas populated by adults. Release numbers were maximized but dispersed in relatively small batches to reduce potential competitive interactions. Each group released a succession of annual juvenile cohorts over 4 or more years and, usually, monitored stocks and landings for at least a comparable period to estimate survival and the proportion of tagged lobsters in the fishable stock (Latrouite and Lorec, 1991; Burton, 1992; Bannister *et al.*, 1994; Cook, 1995; Bannister and Addison, 1998; Agnalt *et al.*, 1999, 2004; Schmalenbach *et al.*, 2011).

In France, Norway, and the United Kingdom, recaptured lobsters fitted with CWTs were detected using magnetic detectors on board potting vessels or at quayside landing stations (Bannister and Addison, 1998), while VIE-tagged lobsters in Germany were identified visually by fishers and divers (Schmalenbach *et al.*, 2011). The recapture profiles of release cohorts typically illustrated common sequences of growth, accumulation, and decay over the monitoring period. Annual recaptures were largely on the scale of tens to hundreds, cumulating to a total of 9930 individuals across all monitored projects, mostly recaptured 3–10 years after release as subadults or adults in the size range 50–120 mm CL (Burton, 1992; Bannister *et al.*, 1994; Cook, 1995; Bannister and Addison, 1998; Agnalt *et al.*, 1999, 2004; Schmalenbach *et al.*, 2011). Released lobsters generally showed high site fidelity (e.g. recaptured within 6 km of release sites; Bannister and Howard, 1991), and many of the adult females carried fertilized eggs, although whether these were sired by wild or cultivated males was not assessed.

Recapture rates

Monitoring of hatchery-reared European lobster recruitment has shown that releases in the order of 100 tagged juveniles have typically yielded single-figured numbers of recaptures (Table 1; Bannister and Addison, 1998; Agnalt *et al.*, 2004; Schmalenbach *et al.*, 2011). These nominal recovery rates were regarded as indicators of the potential contribution to the local fishery, but also of the potential economic rates of return (Whitmarsh, 1994).

Stocking trials in France provided the least encouraging total recapture figures (Table 1), although these results can be somewhat discounted due to deficiencies in their monitoring programmes. Although CWTs were implanted into 24 500 juveniles released around the French Atlantic coast during 1984–1987, monitoring began 2 years after the first releases, but lasted only 3 years (Latrouite and Lorec, 1991). Only 22 lobsters were recaptured, but the maximum recapture window (2–5 years for different release cohorts) appears insufficient in light of the recapture profiles of later trials elsewhere. At that same time in the United Kingdom, almost 91 000 one-year-old juveniles were tagged and released in four areas—Bridlington in England, Aberystwyth in Wales, and Ardtoe and Orkney in Scotland—where the natural stocks were depleted (though still more abundant than in Norway). Total recaptures were 1471 over the 5- to 8-year monitoring period, with the regional recovery rates ranging from 1.3 to 2.4% (Bannister and Addison, 1998).

Higher recapture results came several years later from the heavily depleted lobster stock in the Norwegian archipelago of Kvitsøy. By 2001, 6.2% of the 128 000 coded-wiretagged year-old juveniles released during 1990–1994 had been recaptured, and released lobsters outnumbered wild conspecifics among the legal-sized catch (Agnalt *et al.*, 2004). Importantly, both the proportion of hatchery-reared lobsters in the fishable stock and catch per unit effort increased over the monitoring period, suggesting that cultured lobsters had enhanced existing stocks rather than replacing them (Agnalt *et al.*, 1999; Svåsand *et al.*, 2004). Most recently, off Helgoland, >9% of the 2000–2005 release cohorts had been recaptured by 2009, when 8% of the total landings comprised hatchery-reared lobsters (Schmalenbach *et al.*, 2011). Of those lobsters released in 2001, 1 in 7 was recaptured, the highest rate recorded for any stocked *H. gammarus* cohort (Schmalenbach *et al.*, 2011).

Projections and perceptions of success

The results of European projects have produced very different perceptions about the potential worth of lobster stocking. In France, the small number of recaptures caused an abrupt and premature termination of the monitoring programme (Latrouite and Lorec, 1991). In the United Kingdom, the results were welcomed as the first definitive proof of successful survival and recruitment of cultivated lobsters in the wild (Addison and Bannister, 1994; Bannister and Addison, 1998). However, modelling showed that recovery rates were too low to generate a positive net value to the fishery, even when offsetting the costs of building a hatchery over a 25-year release period (Whitmarsh, 1994). In Norway, the large proportional contribution to the depleted stock was viewed positively (Agnalt *et al.*, 1999; Svåsand *et al.*, 2004), though production costs exceeded the value of recaptured lobsters here too (Moksness *et al.*, 1998). In a global context, lobster stocking in Norway gave more efficient fishery yields than those of prawn or crab enhancement in the Far East (Hamasaki and Kitada, 2008b).

Although none of these monitored European stocking trials generated total recapture rates of even 10% of the number of lobsters released (Bannister and Addison, 1998; Agnalt *et al.*, 1999; Nicosia and Lavalli, 1999; Agnalt *et al.*, 2004; Schmalenbach *et al.*, 2011), some studies have estimated more encouraging survival rates from speculative calculations of capture probability. For hatchery-reared lobsters in Helgoland, the survival rate to the fishery minimum

landing size (MLS) was estimated to be 30–40% using the Lincoln–Peterson method (Schmalenbach *et al.*, 2011). When converted via an independent estimate of trap catchability, recapture numbers produced very high survival estimates of 50–84% for individual release sites in northeast England (Bannister *et al.*, 1994). Norwegian recaptures provided more tangible evidence of success by showing that cultured lobsters contributed significantly to spawning biomass. Within 4–10 years of release, cultured females were estimated to account for 27% of egg production within the Kvitsøy population and showed no difference to wild females in measures of fecundity or egg development (Agnalt *et al.*, 2007; Agnalt, 2008).

Fitness of hatchery-reared lobsters

Studies from stocked populations in Norway provide the only direct evidence of the fitness of cultured *H. gammarus* in the wild, with ecological and genetic indicators used to assess pre- and post-release fitness. Mature cultured females appear to perform as well as wild equivalents in terms of size-specific fecundity, weight of egg mass, egg size, and embryonic development (Agnalt, 2008), a crucial finding rarely achieved among other stocked species. Results have been less conclusive when rearing the offspring of wild and cultured broodstock together in competitive, "common garden" environments. The progeny of cultured females recaptured around Kvitsøy, Norway, experienced only 60% of the survival of the offspring of local wild females through both the larval and juvenile phases (Jørstad *et al.*, 2005a, 2009). While in isolation, this represents a damaging assessment of the fitness of cultured lobsters, results were confused by the performance of a second group of wild females that originated just 12 km away, but whose offspring were similarly outperformed by those of local natural females. Perhaps most tellingly though, the authors acknowledged that both wild and cultured males had access to mate with either cohort of females (Jørstad *et al.*, 2005a, 2009), which may have significantly biased the categorization of offspring as wild- or hatchery-derived, particularly within a population where natural and cultured lobsters were fairly evenly represented (Agnalt *et al.*, 2004).

Limitations of existing impact assessments

Existing assessments of lobster stocking success are susceptible to caveats and assumptions. The recapture numbers cited in Table 1 were not corrected for (i) tag loss, which would yield false negatives and underestimates of survival among tagged lobsters (Agnalt *et al.*, 2004); (ii) emigration to adjacent areas, which would reduce the number of marked lobsters available for recapture (Cook, 1995); (iii) spatial mismatch between release and resampling sites; and (iv) imperfect recapture sampling by quayside monitoring teams.

These issues have not been factored into the lobster survival estimates of any impact assessment, suggesting that the recorded recovery rates cited in Table 1 were almost certainly underestimates. As such, pessimistic assessments of the economic viability of lobster stocking by Whitmarsh (1994) and Moksness *et al.* (1998) were probably based on pessimistic estimates of the survival of cultured lobsters. More basically, these economic assessments evaluated the viability of stocking programmes to be run purely as self-financing businesses and failed to account for the long-term potential for hatchery-reared lobsters to boost or restore local recruitment. Additionally, this appraisal technique fails to account for any potential benefits of raising the profile of lobsters and sustainable fishing among the public.

Summary of stocking performance and current hatcheries

Stocking has been proved to be a potentially effective method of fisheries remediation (Bannister and Addison, 1998; Svåsand *et al.*, 2004). Despite uncertainties in the magnitude of the recovery rates, monitoring of *H. gammarus* releases have shown that hatchery-reared lobsters have survived, grown, and mated in the wild in considerable numbers and in multiple locations and ecotypes. However, there remains a considerable scope to improve our knowledge of the ecological dynamics influencing stocked lobster survival and to standardize methods of lobster stocking and assessments of its impact.

Interest in undertaking European lobster stocking has soared in recent years as a tool to conserve and improve fisheries and even to mitigate proposed offshore developments (e.g. pipe-laying, wind farms, and spoil dumping). Currently, there are two established hatcheries in the United Kingdom undertaking stock enhancement on a relatively significant scale. These programmes operate in the Orkney Islands and Cornwall (Table 1), where the continued pressure on lobster stocks and the economic importance of the fishery justify the concept of engaging in stock enhancement. They are responsible for over half of the reported releases of cultured lobsters into European waters in the past four decades, but neither programme has ever undertaken routine monitoring of their effects. This is mostly due to the prohibitive costs incurred in growing juveniles to sizes suitable for physical tagging and subsequent monitoring of the wild population for recaptures (D. Shearer, Orkney Lobster Hatchery, pers. comm.). For scientific support, they refer to the basic impact assessments already described; Orkney was one location of the 1980s mark–recapture trials, whereas Cornish enhancement endeavours are based entirely on the experimental results from outside Cornwall.

Both hatcheries have been active in undertaking research and developing technical innovations to more effectively and economically rear lobsters. They are aware that reducing expenditure per juvenile produced is a principal method of increasing their economic viability, alongside increasing the survival probability of hatchery-reared lobsters in the wild. These hatcheries also accept their obligation to validate the impact of their stocking programmes, but have been unable to self-subsidize the comprehensive ecological research and monitoring required. What follows is a summary of several aspects of marine stocking that are critical to resolve to improve or perhaps even disprove the value of releasing cultured lobsters for stock management.

Critical issues for lobster stocking

Understanding lobster ecology

Knowledge gaps regarding the ecology and population dynamics of *H. gammarus* significantly obstruct the unbiased assessment of the performance of hatchery stocking. The most serious of these is the continued absence of methodologies for locating or capturing wild post-larvae and juveniles, despite coordinated efforts (e.g. Linnane *et al.*, 2001; Mercer *et al.*, 2001). As a result, it is unknown whether recruitment is density-dependent and, therefore, limited by habitat-specific carrying capacities (as it is in *H. americanus*—Wahle and Steneck, 1991, 1992; Wahle and Incze, 1997; Steneck and Wahle, 2013), and we have no understanding of how cultured lobsters compare with wild equivalents in basic behavioural, physiological, and morphological traits. Almost all published information on the biology of early benthic phase *H. gammarus* emerges from studies based on cultured lobsters, most of which have occurred

in aquaria environments (e.g. Wickins *et al.*, 1996; Linnane *et al.*, 2000). Even when based in the wild (e.g. van der Meeren, 2000, 2005), observations of the behaviour and performance of hatchery-reared juveniles still may not accurately reflect the biology of natural juveniles in wild ecosystems.

Similarly, the planktonic larval phases are rarely collected in the wild, even in areas high in abundance of reproductively mature adults (S. Clark, Devon and Severn IFCA, pers. comm.). Light traps have proved useful for surveying wild larvae in Scandinavian fjords, which exhibit considerable water retention (Øresland and Ulmestrand, 2013), but have had limited success within the Bristol Channel in the United Kingdom due to strong tides and currents (S. Clark, Devon and Severn IFCA, pers. comm.). Elsewhere, continuous plankton recorder samples provide temporally and spatially extensive datasets of planktonic abundance, but decapod larvae are not routinely identified to species level (Richardson *et al.*, 2006). The absence of basic data on natural larvae and juveniles has inhibited the creation of demographic models that have been useful to predict the effect of stocking in other species (e.g. Lorenzen, 2005, 2006; Hervas *et al.*, 2010).

There is a dearth of studies dedicated to operational variables and their influence on settlement success in hatchery-reared lobsters, and the lack of standardization in existing stocking trials makes their data unsuitable for analysis. Comparisons of different methodological aspects are likely to be biased by the presence of many uncontrolled covariates throughout the culture, release, and monitoring processes. Experimental features such as release methods have varied extensively within and among individual projects, with juveniles variously delivered onto benthic habitats by divers or water flume (Bannister *et al.*, 1994; Burton, 2001), released offshore at the sea surface at night (Schmalenbach *et al.*, 2011), and even released during the day into shallow waters off boats or along the intertidal shoreline (Agnalt *et al.*, 1999). In isolation, the lower recapture rates recorded in the United Kingdom compared with Norway and Germany could, therefore, be interpreted as a sign that benthic releases yield lower settlement success than surface and shore releases. However, this is counterintuitive to our expectation that delivering lobsters onto shelter-providing benthic substrates, avoiding pelagic predators, should increase settlement success. It is more likely that the lower UK recapture results arise from the higher abundance of the wild stock, as enhancing productive stocks has been less effective than restocking depleted populations in other decapod crustaceans (Hamasaki and Kitada, 2008b). However, this cannot be evaluated using existing data and should be investigated.

Improving tagging technology

Existing monitored stocking experiments have depended on the use of physical tags to detect recaptured lobsters, with first the CWT in the 1980s and later the VIE from the late 1990s. These assessments provided the first empirical evidence of the performance of hatchery-reared lobsters in the wild, but there are important limitations to the use and effectiveness of these tags. Both tag types are normally injected into ventral tissues of the upper abdomen, from where VIE tags have been shown not to alter behaviour or growth (Neenan *et al.*, 2014). VIE tags are logged visually through translucent tissues (Uglem *et al.*, 1996; Neenan *et al.*, 2014), whereas CWTs must be retrieved by dissection after initial detection by magnetometer (Burton, 1992; Bannister *et al.*, 1994). Large juveniles (7 months; 12–16 mm CL) show high tag retention (99%) and survival (97%) over 3 months when tagged with CWT and VIE and reared in aquaria (Uglem *et al.*, 1996; Linnane and Mercer, 1998). Modern hatcheries typically release younger *H. gammarus* juveniles, however (post-larval stages V–VI, 4–6 weeks old, 5–8 mm CL), which show reduced survival after tagging (83% for CWT; 68% for VIE) and significant tag migration (Uglem *et al.*, 1996; Linnane and Mercer, 1998).

The lack of a suitable tag with which to mark juveniles from the first post-larval instar has prohibited any assessment of whether the considerable investment required to grow juveniles to sizes facilitating tagging is reflected in increased recruitment. Since the founding principle of stocking is to culture vulnerable lifestages in captivity, it is conceivable that lobster survival is suitably optimized at the onset of benthic settlement behaviours (i.e. post-larval stages IV–V). This principle, plus the opportunity to maximize numerical release outputs and avoid on-growing expenses, has meant that most active European hatcheries now release early juvenile stages as standard, although the only evidence for the effectiveness of this strategy is inferred from localized increases in abundance of *H. americanus* in eastern Canada following releases of cultured post-larvae (e.g. Comeau, 2006; Côté and Cloutier, 2014). These results were obtained by the utility of before-after-control-impact (BACI) methods, where lobster abundance in release areas is compared with that, in similar, unenhanced habitats over several years. BACI methods have proved useful in implying enhancement effects where hatchery-reared lobsters are not tagged (Comeau, 2006; Côté and Cloutier, 2014), although this style of monitoring produces data that lack the definitive evidence provided by the recapture of tagged individuals. Ideally, a new physical tag is required that is cheap and easy to apply, is capable of marking lobsters from the first post-larval phase to adulthood, and is visually detectable by fishers. This would enable a large number of juveniles to be tagged as standard release procedure and facilitate assessments of optimal stocking protocols via low-cost and widespread monitoring by fishery stakeholders, who may be positively motivated by a visible tag. However, such a development is unlikely to be forthcoming, given the regular turnover of sclerotized body parts at ecdysis and the vast discrepancy in size between post-larvae and adults.

Attention is, therefore, turning to the potential for polymorphic genetic markers to assign parentage and replace or augment physical tags in future assessments of lobster stocking impact. Methods of genetic profiling can assign hatchery origin with a high degree of certainty (e.g. Jones and Arden, 2003) and have important advantages over established internal tags (Table 2). Tag loss can be effectively eliminated, individuals can be sampled sublethally on multiple occasions, and there are no restrictions on the release size of juveniles (Neenan *et al.*, 2014). Genetic profiling can allow assessments of the recruitment performance of different groups, families, or even genotypes (Sekino *et al.*, 2005; Tringali, 2006) and the extent to which wild and cultured animals integrate and interbreed in the environment. With genetic markers of sufficient quantity and variation, hatchery-derived lineages may even be tracked beyond the released generation by identifying the wild-born offspring of hatchery-reared parents, potentially enabling multigenerational assessments of stocking (Letcher and King, 2001; Blouin, 2003).

Employing genetic methods has already proved successful in the detection of hatchery-reared fish among enhanced wild populations of steelhead trout (*Oncorhynchus mykiss*; Christie *et al.*, 2012a,b) and black sea bream (*Acanthopagrus schlegelii*; Jeong *et al.*, 2007) and has been proposed as a method of establishing traceability for aquaculture-derived fish at the marketplace (Hayes *et al.*, 2005). In one of the most positive impact assessments of fishery enhancement, microsatellite-based pedigree reconstructions showed that

Table 2. Summary of the expected performance of different tag types for use in impact assessments of European lobster stock enhancement.

	Tag performance criteria								
Tag type	**Individual ID**	**No min. juvenile size**	**No tag loss**	**Sublethal sampling**	**Stakeholder independent monitoring**	**Stakeholder social impact**	**Multiple generations traceable**	**Genetic fitness impact**	**Stock integration testable**
CWT	Yes	No	No	No	No[a]	No[a]	No	No	No
VIE	No	No	No	Yes	Yes	Yes	No	No	No
Genotype	No[b]	Yes	Yes[c]	Yes	No[a]	No[a]	Yes	Yes	Yes

CWT and VIE performance is based on reported performance in previous uses, whereas genotype tag performance is based on theoretical performance and reports from other stocked species.
[a]Stakeholders may be utilized and socially impacted by monitoring, but cannot readily identify released individuals as part of routine fishing activities.
[b]Individual identification is possible, but often requires a much larger panel of genetic markers than is required to establish hatchery origin via parentage assignment, the most commonly used genotype-based method.
[c]No tag "loss", but similar error can be introduced by genotyping errors (e.g. flawed tissue collection or processing, the presence of null alleles, the interpretation of results, etc.). Repeat sample processing and analysis of data can be used to estimate and/or correct this error rate.

stocked *A. schlegelii* suffered no loss of heterozygosity, integrated with wild schools, and contributed 59% of individuals to an important fishery in Japan (Jeong *et al.*, 2007). Similarly, thorough evaluation is required to elucidate the long-term impact of stocking *H. gammarus*, although such investigations are not cheap or accomplishable without archived tissues from which the genotypes of hatchery progeny can be deduced (i.e. maternal and egg samples).

The type and quantity of markers required for parentage assignments to accurately detect hatchery-reared lobsters from large-scale surveys of wild populations would be largely dependent on the population's genetic diversity, effective size, and gene flow, the broodstock turnovers and recapture survey methods employed, and whether multiple paternity frequently exists among individual broods [as has been found in *H. americanus* (Gosselin *et al.*, 2005)]. Sampling only landed lobsters that are destined for the market may be a more practical survey method than *in situ*, on-board sampling of the catch (including undersized lobsters destined for return to the sea). The latter could be biased by the inclusion of single individuals sampled on multiple occasions, which would be indistinguishable from multiple individuals possessing genotypes that are identical by descent, although this approach does lend itself well to obtaining recapture data that could reveal the movements of stocked lobsters and the spatial impacts of stocking. Simulations and case studies have shown that parentage can be accurately assigned, even where systems boast hundreds or thousands of candidate parents, using as few as 60–100 single-nucleotide polymorphisms SNPs (Hayes *et al.*, 2005; Anderson and Garza, 2006) or 7–15 microsatellites (Bernatchez and Duchesne, 2000; Letcher and King, 2001; Hayes *et al.*, 2005; Jeong *et al.*, 2007; Christie *et al.*, 2012a), although this is also dependent on the overall power provided by the number and frequency of alleles (Bernatchez and Duchesne, 2000).

For *H. gammarus*, it may well be possible to base such parentage assignments on established and available genetic markers, such as the 12 microsatellites published by André and Knutsen (2010). However, where spatial population genetic structuring is minimal, hatchery broodstock turnovers are high, and multiple paternity occurs frequently within individual broods (all of which are possibly the case for *H. gammarus*), the number of markers required to resolve parentage may rise to become prohibitively costly. Next-generation genotyping resources, such as restriction site associated DNA (RAD) markers and larger panels of SNPs, offer the resolution to overcome such obstacles (Baird *et al.*, 2008; Hohenlohe *et al.*, 2010), and for species such as Atlantic salmon (*Salmo salar*), microarray genotyping chips featuring many thousands of SNPs are now widely available (Affymetrix, 2014). The development and widespread utilization of such technology is likely to be beyond the financial means and expertise of independent lobster hatchery ventures, however. Still, there is a significant time lag between captive rearing and potential recapture in the wild, and many universities and research facilities are now equipped with the capabilities to carry out a range of molecular genetic analyses. Therefore, even where no immediate plans exist to assess stocking, all lobster hatcheries should routinely archive tissue and several fertilized eggs from every brood female for potential future collaborative research opportunities.

Improving hatchery production

All hatcheries require the stable production of juveniles to enable release numbers to achieve stocking targets. Because facilities culturing lobster have experienced prolonged and sometimes unexplained periods of production failure, stabilizing juvenile output is required. Where cultured juveniles have no reduction in fitness, increasing both the quantity released and their chances of wild establishment can improve the effectiveness of stocking. Some significant biotechnical advances have been made in recent years that improve lobster hatchery production and cost-effectiveness. While ovigerous females are plentiful in spring and summer, the separation of some at reduced water temperatures (~6°C) slows egg development and allows the rearing season to be extended. Anecdotally, this has been more effective and reliable than the upward manipulation of egg development and raises the possibility that stable year-round production may be possible. In trials of the so-called green water technique, utilizing algal cultures and enriched live feed more than doubled survival to the first post-larval instar compared with standard rearing protocols (Browne *et al.*, 2009). The larval and post-larval stages are particularly vulnerable to the effects of nutrient limitation; therefore, nutritional enrichments improve growth and survival, even in standard culture environments (Daniels *et al.*, 2010; Schoo *et al.*, 2014). Further improvements have arisen from the long-awaited innovation of multilayered juvenile rearing systems, which increase hatchery capacity 40-fold compared with traditional single-layer vessels (Gowland, 2013). As advancements continue, hatcheries are able to increase production and the overall economic viability of lobster stocking. For example, one *H. americanus* hatchery more than doubled its production costs from 2002 to 2013, although this enabled technical advances that increased annual production

from 1500 to 417 000 juveniles, slashing the investment per juvenile from over US$33 to just US$0.26 (Haché *et al.*, 2014).

As well as ensuring they can produce the quantity of juveniles required, stocking projects must aim to ensure that the quality of cultured lobsters is sufficient to achieve long-term population enhancement. In Norway, the performance of recaptured lobsters has been promising in basic fitness traits, such as reproductive potential (Agnalt, 2008). Nevertheless, juveniles reared in captive conditions are frequently shown to have reduced suitability to the demands of life in natural ecosystems (e.g. Davis *et al.*, 2004, 2005; Castro and Cobb, 2005). Ecological naivety is evident in the higher predation vulnerability of cultured *H. americanus* juveniles compared with wild conspecifics (Castro and Cobb, 2005). For *H. gammarus*, the continued failure to locate wild juveniles has prevented comparisons of fitness to that of cultured equivalents, an approach used widely for other stocked decapods (e.g. Davis *et al.*, 2004, 2005; Castro and Cobb, 2005; Ochwada-Doyle *et al.*, 2010). Even so, studies have shown that juveniles reared in competitive communal environments grow faster than those raised in isolation (Jørstad *et al.*, 2001), while previous exposure to predator odours gives cultured juveniles a superior ability to outcompete untreated cohorts for limited shelter spaces (Trengereid, 2012).

Although some cultured decapod juveniles have matched the predator avoidance of wild conspecifics regardless of acclimation regimes (Ochwada-Doyle *et al.*, 2010), innate behaviours are likely to be complemented by targeted ecological conditioning before wild release. In hatchery-reared blue crabs (*Callinectes sapidus*), conditioning via controlled predator exposure significantly increases carapace spine length and subsequent post-release survival (Davis *et al.*, 2004, 2005). The traditional hatchery culture of *H. gammarus* juveniles is isolated and largely devoid of environmental enrichment, but in recent years, attempts have been made to on-grow juveniles in sea-based submerged containers. This semi-wild environment appears to promote traits that are likely to have a positive impact on settlement success and adaption to the natural environment and offers significant potential as an acclimation step before the release of cultured lobsters. Survival often exceeds that of hatchery-reared cohorts (Beal *et al.*, 2002; Benavente *et al.*, 2010), and container-reared lobsters typically demonstrate altered behavioural responses and improved growth and pigmentation (Figure 1). Overall, the unnatural selection pressures of culture environments are a fitness concern that remains largely unaddressed in lobster hatcheries, and significant adjustments to existing rearing and conditioning protocols may well be required to increase the viability of current lobster stocking ventures (van der Meeren, 2005; Trengereid, 2012).

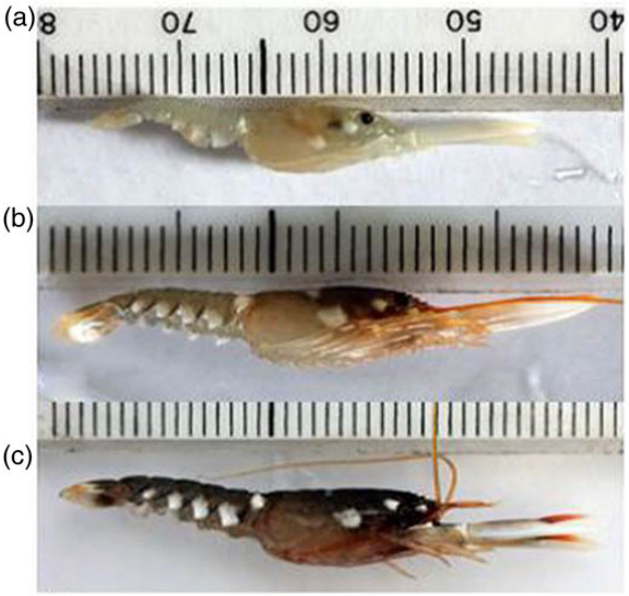

Figure 1. Cultured juvenile European lobsters on-grown in sea containers in an open bay (c) and estuary (b) show increased growth and pigmentation compared with equivalents reared only in the hatchery (a).

Ensuring effective genetic management

Poorly regulated fishing throughout most of the range of *H. gammarus* is likely to have seriously impacted the status of benthic ecosystems and significantly influenced the population genetics of European lobsters. Genetic management of the species has rarely been prioritized or even considered by fishery managers, and the pressures of intensive commercial fishing activities are likely to have impacted the genetics of lobster populations more profoundly than the limited activity of stocking schemes to date. However, mismanagement of lobster fisheries in general should not mean that ventures aiming to enhance and conserve these fisheries via hatchery stocking should not be expected to pursue rigorous standards of ecological accountability. While stocking is generally expected to increase short-term abundance of populations, troubling recent data in other species suggest that negative genetic impacts may arise in target stocks, undermining fishery conservation objectives (Sekino *et al.*, 2002, 2003; Bert *et al.*, 2007; Kitada *et al.*, 2009; Rourke *et al.*, 2009; Hamasaki *et al.*, 2010; Christie *et al.*, 2012a,b; Satake and Araki, 2012). It is increasingly apparent that the dual goals of short-term productivity and long-term conservation are not usually complementary and are difficult to achieve simultaneously (Satake and Araki, 2012).

Many authors have proposed ways in which stocking schemes can limit negative genetic impacts, and routinely comparing the genetic diversity and relative fitness of wild and cultured fish is commonly recommended (e.g. Blankenship and Leber, 1995; Shaklee and Bentzen, 1998; Bell *et al.*, 2006; Gaffney, 2006; Bert *et al.*, 2007; Tringali *et al.*, 2008; Laikre *et al.*, 2010; Lorenzen *et al.*, 2010). For example, Bert *et al.* (2007) suggest that stocking enterprises should study the species' regional population genetics, genotype broodstock at a resolution sufficient to distinguish their offspring, monitor the genetic variation of cultured juveniles and incoming broodstock, and use genetic assays to scan the wild population for both hatchery progeny and any flux in the larger gene pool. Many independent hatcheries are unable to fund such research or have prioritized investing in biotechnical innovations though, so genetic aspects of management have often been ignored (Bell *et al.*, 2006). This is largely the case among organizations stocking *H. gammarus* and requires rectifying to ensure that heavily exploited lobster fisheries are not subject to any deleterious effects via stocking.

Maintaining fitness and genetic diversity

Attaining long-term population growth and simultaneous conservation of the regional gene pool is unlikely where stocked animals have fitness disadvantages (Satake and Araki, 2012). Fitness disadvantages can arise in cultured individuals as a consequence of

narrow genetic make-up or via inadvertent selection processes occurring in the hatchery environment that make cultured juveniles ill-suited to their natural ecosystem. Where released animals introduce heritable reductions in fitness, stocking has the potential to have negative impacts on wild stocks. This is reported most often where target populations are small and/or show high levels of adaptation to local conditions (Lorenzen *et al.*, 2012). Released animals often have reduced fitness for the natural environment compared with wild conspecifics; Araki and Schmid (2010) reviewed 39 studies that assessed fitness effects, of which 22 found that survival, growth, or reproductive success were reduced by hatchery rearing. Given the dissimilarities between hatchery and wild environments, traits that lead to high fitness in one may reduce fitness in the other. Trout (*O. mykiss*) raised in captivity have nearly double the reproductive success of wild-born fish when spawned in a hatchery, but their offspring suffer greatly reduced performance in the wild, where survival is less than a third that of the wild-origin cohort (Christie *et al.*, 2012a).

A key principle of stocking is that offspring survival is relatively increased in the captive environment, which means that many released individuals may be closely related. Increasing the number of related individuals in a population generally decreases the overall genetic diversity and effective population size and increases the potential for inbreeding depression (Ryman and Laikre, 1991). Cultured individuals often show reduced genetic diversity (e.g. Sekino *et al.*, 2002) and have low effective population sizes, especially where broodstock are captive-reared, are used to rear multiple generations of offspring, or where competitive processes lead to highly skewed reproductive success (Sekino *et al.*, 2003; Shishidou *et al.*, 2008). Parentage assignments in hatchery-reared flounder (*P. olivaceus*) revealed that almost all the offspring were sired by one of six males, and that half of the 12 spawning females yielded no surviving juveniles at all (Sekino *et al.*, 2003). Although the influence of stocking on population genetic diversity may be trivial compared with that caused by environmental or fishing pressures (Sugaya *et al.*, 2008; Kitada *et al.*, 2009), in some cases, it can be extremely damaging; stocking doubled the number of adult trout (*O. mykiss*) on spawning grounds in Oregon, United States, but actually cut the total effective population size by two-thirds (Christie *et al.*, 2012b).

Wild-mated females have typically been utilized for *H. gammarus* stocking, with several hundred new broodstock sourced for each production season. Where broodstock are marketed for human consumption upon return to their donors, their repeated use is prevented. Whether achieved via the ease of accessing readily-mated females or by enlightened genetic practices, these methods should have contributed to ensuring relatively high genetic diversity among progeny. However, family contributions have been found to be skewed in *H. gammarus* culture (Jørstad *et al.*, 2005a), and how the genetic diversity of released lobsters compares with that within target populations requires evaluation using modern techniques.

Consideration of population structure and local adaptation

Genetic diversity is the principal origin of adaptive evolutionary potential (Frankham *et al.*, 2011), so populations are increasingly vulnerable to environmental change where genetic diversity is eroded by the release of cultured individuals (Laikre *et al.*, 2010). Where cultured animals lack hereditary adaptations to their release environment and interbreed with wild fish that are more suitably adapted, adaptive traits crucial to the species' fitness in that environment are likely to be eroded, reducing the overall fitness of the population. In recent studies on wild marine fish, molecular markers have helped reveal previously unforeseen levels of population structure and local adaptation to environmental heterogeneity (e.g. temperature and salinity), even at small geographical scales [e.g. Atlantic cod (*Gadus morhua*)—Knutsen *et al.*, 2003, 2011; Jorde *et al.*, 2007; Atlantic herring (*Clupea harengus*)—Lamichhaney *et al.*, 2012; Limborg *et al.*, 2012; Teacher *et al.*, 2013; sticklebacks (*Pungitius pungitius*, *Gasterosteus aculeatus*)—Shikano *et al.*, 2010; Shimada *et al.*, 2011; Bruneaux *et al.*, 2013; Atlantic salmon—Griffiths *et al.*, 2010)]. Although genotyping only 25 individuals per population can often provide accurate estimates of population-level differences in allele frequencies (Hale *et al.*, 2012), even relatively basic genetic studies are generally complex and expensive. As a result, population genetic data are frequently absent or outdated for stocked marine species, and such studies on *H. gammarus* provide somewhat contradictory evidence or lack peer review.

Investigations on genetic structure and diversity in *H. gammarus* populations using polymorphic microsatellites, allozymes, and mitochondrial DNA (e.g. Jørstad and Farestveit, 1999; Jørstad *et al.*, 2004, 2005b; Triantafyllidis *et al.*, 2005; Huserbråten *et al.*, 2013) have attempted to delineate populations and estimate gene flow within and between them. Observed restrictions in adult migration give the potential for considerable genetic isolation between *H. gammarus* subpopulations (Øresland and Ulmestrand, 2013), although the most recent research suggests that high genetic connectivity exists over relatively large spatial scales (≈400 km), even among semi-enclosed habitats (Huserbråten *et al.*, 2013). These results, obtained via microsatellite DNA analysis of heavily depleted Scandinavian Skagerrak populations, suggest that larval dispersal must be high and must be the primary origin of gene flow (Huserbråten *et al.*, 2013). Where larvae are distantly dispersed and cultured lobsters add significantly to the spawning biomass, the long-term impacts of stocking could extend far beyond the spatial boundaries over which releases occur.

Spatial heterogeneity in *H. gammarus* population genetic variation has been detected, however, particularly in regions isolated by oceanographic and topographic conditions, such as northern Norway and throughout the Mediterranean (Jørstad and Farestveit, 1999; Ulrich *et al.*, 2001; Jørstad *et al.*, 2004, 2005b; Triantafyllidis *et al.*, 2005) and even among populations from the comparatively unrestricted Atlantic coasts of Ireland, France, and Portugal (Ulrich *et al.*, 2001). There appears an overall association between geographic distance and genetic variation (Ulrich *et al.*, 2001), although considerable genetic differences can be found over modest spatial scales (e.g. 142 km between fjords, Jørstad *et al.*, 2004). Rapid recent developments in whole-genome genotyping methodologies and the field of bioinformatics now offer greater resolution and deeper insights into the extent of population structure and local adaptation. Studies utilizing these technologies throughout the range of *H. gammarus* will be critical for understanding the spatial scales that stocking may be expected to impact and for ensuring that lobster releases are non-detrimental.

Stocking vs. alternative management strategies

To date, lobster stocking in Europe has always been practiced in addition to legislative fishery management measures such as closed

seasons, closed areas, gear restrictions, and landing bans on undersized, v-notched, or ovigerous lobsters. However, assessments of the relative effectiveness of lobster stock enhancement and other alternative fishery management tools are either lacking or are too ambiguous to allow formative comparison between methods. Several conservation methods are often applied concurrently, which potentially gives a greater chance of safeguarding stocks, but it becomes difficult to appraise the relative strengths and limitations of individual components. The need for rigorous analysis of lobster stocking is particularly urgent, but so too is the analysis of other management measures to enable comparative assessments of fishery conservation tools.

Our understanding of the effects of most fishery management options is poor, but marine protected areas (MPAs) have recently demonstrated potential in sustaining exploited lobster populations. In the United Kingdom, the closure of waters off Lundy Island to all fishing activities led to a rapid increase in lobster abundance and mean body size (Hoskin *et al.*, 2011), whereas in Norway, MPA designation increased lobster cpue by 245% over 4 years, far beyond the 87% increase in control areas (Moland *et al.*, 2013). Over 95% of lobsters caught, tagged, and rereleased into both Norwegian and Swedish MPAs remained within or very near to reserve boundaries in multiannual mark–recapture analyses (Moland *et al.*, 2011; Øresland and Ulmestrand, 2013), while high genetic connectivity between these MPAs suggests that larval dispersal benefits may be extensive and far-reaching (Huserbråten *et al.*, 2013). Arguably, thoughtfully designated MPAs have offered more conclusive stock conservation benefits than hatchery stocking to date, although MPAs do have an immediate negative economic impact on displaced fishers. However, employing the two methods simultaneously (i.e. releasing cultured lobsters into MPAs) may offer a powerful stock conservation method and provide quicker enhancement of adjacent fisheries.

Conclusions

The regulation of European lobster stocking has been largely *ad hoc* and lacks alignment with the robust frameworks established for the informed management of marine stocking ventures (e.g. Blankenship and Leber, 1995; Lorenzen *et al.*, 2010). Given that recent findings from the wider field of aquatic stocking show that the successful integration of cultured individuals into dynamic wild populations is a highly complex process, this is clearly unsatisfactory. While some deviation from best practice may have been the result of insufficient and fragmented planning by regulatory managers or hatchery operators, much more has been unavoidable. The inconclusive performance of previous lobster stocking projects in providing economically viable benefits to lobster fisheries has made it hard for active hatcheries to attract significant financial backing and industry support. However, the exhaustive monitoring and technical developments required to evidence economic viability are often economically unviable in their own right; as our understanding of the potential ecological considerations mounts, the costs associated with piloting a stocking programme increase (Blankenship and Leber, 1995; Lorenzen *et al.*, 2010). In the absence of focused guidelines or coordinated investment from industry or government, active hatcheries have been largely unable to address significant gaps in our scientific understanding of lobster biology that are integral to the informed management of stocking ventures and lobster fisheries themselves. As a result, hatcheries have been forced to focus on advancing production and revenue, conducting ecological research where possible along the way.

From existing studies designed to assess the potential for stocking *H. gammarus*, a proof-of-concept has been demonstrated. Based on recaptures of hatchery-reared lobsters achieving fishery MLSs and reproductive maturity in multiple locations, conclusions have been generally positive that stocking could represent a worthwhile fishery conservation method. However, these conclusions are undermined by a lack of consistent evidence that benefits are universal and cost-effective and by a series of inconclusive or damaging reports into the effects of stocking in other marine species. Nevertheless, in the wake of increased pressures on some fisheries and the regional collapse of others, interest in stocking programmes aimed at restoring or enhancing lobster populations has only increased in recent years. The societal decision whether to pursue stocking of European lobster populations requires evidence of both positive and negative impacts of hatchery releases, so a renewed evaluation of lobster stocking, utilizing the more thorough assessment tools now available, is required to limit the ambiguity of that decision.

Impact assessments attempting to appraise the effect of European lobster stocking are significantly hindered by the elusive nature of wild juveniles and scarcity of other basic information on the ecology of natural populations and have, so far, been restricted to unfavourable juvenile tagging methods. Genetic methods should be employed to improve wider understanding of lobster biology and population ecology as well as to deliver assessments on the evolutionary fitness of cultured lobsters and the likelihood of their release to cause negative effects on natural populations. Genetic resources also require testing for their effectiveness in identifying cultured lobsters in the wild. Recent improvements in the quality and cost-efficiency of juvenile production could help make stocking a viable tool for improving the productivity and sustainability of lobster fisheries, although this requires a thorough and strategic evaluation.

Overall, our understanding of the dynamics and potential for lobster stocking remains limited, and further research using contemporary methods is required to deliver informative impact assessments. Ideally, all lobster hatcheries should implement the following initiatives: (i) archive maternal and progeny tissues from all broodstock; (ii) establish a management strategy that will limit negative impacts of releases in the presence of population structure and local adaptation; (iii) conduct controlled temporal studies of lobster abundance in release areas, both before and after stocking; and (iv) link with a research institute or university to enable collaborative research. Implementation of these procedures would help raise the ethical and ecological standards of stocking ventures, would provide basic evidence of the effect of stocking on local abundance, would lay the foundations for more comprehensive assessments of the performance of stocked lobsters, and would facilitate partnerships with organizations capable of assessing population structure and stock boundaries throughout the species' range, as well as driving efforts to locate wild juveniles to resolve associated knowledge gaps.

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