

Contribution to the Themed Section: 'Marine aquaculture in the Anthropocene' Food for Thought

Moulding the ideal crab: implications of phenotypic plasticity for crustacean stock enhancement

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Numerous examples of behavioural and morphological differences between hatchery-cultured and wild individuals exist for a range of crustacean species; however, we submit that these variances are not deficiencies, but rather are adaptive responses to an unnatural rearing environment that may be detrimental in the natural environment. This phenotypic plasticity could be beneficial for stock enhancement because such plasticity suggests potential for change with adjustments to rearing protocols to achieve improved ecological competence. We examine how specific plastic responses can affect crustacean ecology through effects on predation, foraging, competition, and reproduction. For developing stock enhancement programmes, we recommend consideration of plastic phenotypic patterns before large-scale releases are initiated. Researchers can identify environmental factors that cue plasticity during hatchery rearing, determine if induced responses are ecologically influential after release into the wild, and examine the temporal scale on which phenotypic plasticity operates. Communal hatchery rearing at low-to-medium stocking densities with predator cues and natural substrates along with *in situ* conditioning, releases during periods of low predation risk, and coupled laboratory-field studies can contribute to improved ecological performance during stock enhancement. Finally, presentation of non-significant research results is needed to avoid bias towards hatchery–wild differences and help guide future conditioning programmes.

Keywords: conditioning, ecological competence, phenotypic plasticity, release strategy, stock enhancement

The need for aquaculture and stock enhancement

The expanding global human population has increased pressure on wild fish stocks (Pauly *et al.*, 1998; Pauly *et al.*, 2002): ~33% of marine fish stocks are over-exploited (FAO, 2018). Aquaculture could help meet future global fish demand in the face of constraints to capture fisheries expansion. Although a

large proportion of aquaculture is used for direct food production (i.e. farming), improved culture technology has enabled the expansion of fisheries enhancement through the release of cultured juveniles to augment wild populations (see Leber *et al.*, 2004; Bell *et al.*, 2005; Bell *et al.*, 2006; Leber, 2013 for a review), including cold water crustaceans (Nicosia and Lavalli, 1999;

Stevens *et al.*, 2014). Wild releases of cultured juveniles have occurred worldwide for a range of species and purposes with mixed degrees of success. Generally, the goal of release efforts is to (i) replace locally extinct populations (restocking), (ii) augment a natural population where released individuals are harvested at a larger size (“put and take” fisheries or sea ranching), or (iii) rebuild natural populations by overcoming recruitment limitation and bolstering the spawning stock (stock enhancement) (Leber, 2013).

The basis for stock enhancement for recruitment-limited stocks

Stock enhancement works to bolster the spawning stock if the natural supply of juveniles is limited (Blankenship and Leber, 1995), either from high natural mortality during the larval stages or inadequate reproductive success (Bartley and Bell, 2008). However, if substantial natural recruitment is present, density-dependent mortality may negate any benefits of stock enhancement, especially if released individuals are too small to surpass conspecific predation bottlenecks (Lorenzen, 2005). In some cases, releases of cultured individuals can reduce the abundance of natural recruits through density-dependent processes resulting in displacement of the natural population (Lorenzen *et al.*, 2012). Furthermore, if factors such as limited habitat, food availability, high predation pressure, or suboptimal adult or juvenile environmental conditions are the primary causes of low population abundances, then mortality in later juvenile or adult stages can preclude successful stock enhancement. In the case of most harvested crustaceans, a spawner–recruit relationship is typically very poor or non-existent, whereas, the juvenile–recruit relationship is often much more robust (Wahle, 2003). This suggests that mortality during the larval and settling stages is both high and variable, whereas post-settling mortality is more predictable. This general pattern further suggests that crustaceans may be, in general, good candidates for stock enhancement when stocks are depleted.

Stock enhancement could be a powerful fishery management or restoration tool to increase recruitment and smooth out highly stochastic recruitment trends and thereby increase either depressed populations or predictability in fisheries yields. Yet, the science behind stock enhancement is largely in its infancy (Molony *et al.*, 2003; Leber, 2013), especially for marine invertebrates (but see Bell *et al.*, 2005 for a review). Most marine fish and invertebrate stocks display dramatic recruitment fluctuations, likely caused by complex interactions among environmental conditions and shifts in local population demographics operating at varying temporal and spatial scales (Sissenwine, 1984; Fogarty *et al.*, 1991), which makes predicting recruitment strength difficult. Optimizing stock enhancement efforts requires identifying recruitment-limited populations.

Marine crustaceans as candidates for enhancement

In this article, we focus on marine decapod crustaceans, specifically crabs and lobsters, which are good candidates for stock enhancement because they have high commercial value and are often recruitment limited. Marine decapod crustaceans are especially susceptible to fishery overexploitation because they have variable recruitment and are in high demand. In addition, many species are slow-moving, aggregated, and/or have shallow distributions, which makes them accessible to harvest. Although

marine crustaceans currently represent a relatively small proportion of global aquaculture production (<1% by weight), they comprise a significant proportion of economic value (2.3 billion USD in 2017; FAO Global Aquaculture Production dataset). Advances in aquaculture technology have allowed for an increase in the number of cultured crustacean species from 0 species/groups in 1980 to 41 species/groups in 2017 (FAO Global Aquaculture Production dataset); however, stock enhancement is not a new concept for marine crustaceans. Clawed lobsters were cultivated in Europe (*Homarus gammarus*) and North America (*Homarus americanus*) since the late 1800s (Beard *et al.*, 1985; Dannevig, 1885; Rathbun, 1886; Addison and Bannister, 1994; Aiken and Waddy, 1995; Bannister and Addison, 1998; Nicosia and Lavalli, 1999), and crab enhancement programmes have emerged worldwide in recent decades (Ut, 2002; Obata *et al.*, 2006; Cheng *et al.*, 2008; Zohar *et al.*, 2008; Lebata *et al.*, 2009; Stevens *et al.*, 2014). Still, marine invertebrate stock enhancement has received less attention than finfish (Kitada and Kishino, 2006). Many crab and lobster wild capture fisheries have declined over the past three decades (e.g. red king crab *Paralithodes camtschaticus*, blue crab *Callinectes sapidus*, Australian spiny lobster *Panulirus cygnus*, Cape rock lobster *Jasus lalandii*). Small-scale enhancement efforts have been explored during times of localized recruitment failure, even for species that experience high commercial landings (e.g. American lobsters; Maine, USA; Beal and Chapman, 2001; Beal, 2012 and references therein).

Marine crustacean life history is favourable for stock enhancement efforts. High fecundity allows for large-scale hatchery production that is orders of magnitude greater than for marine finfish (Kitada, 1999). Larvae survival is the most likely population bottleneck for most crustacean species, and culturing larvae in the hatchery could bypass this by eliminating or reducing many potential sources of natural mortality. For example, natural red king crab survival from hatching to the settling post-larval stage is likely <1–2% (Shirley and Shirley, 1989) compared to 50% survival in the hatchery (Swingle *et al.*, 2013). Likewise, in the wild, blue crab larval survival was 0.16% to the settling stage (McConaughy, 1992) compared to 43% survival in a hatchery (Zmora *et al.*, 2005). The considerable improvement in hatchery survival could be enough to allow released juveniles to overcome recruitment limitation.

Ecological competence

Crustacean stock enhancement programmes require production of millions of juveniles for use in large-scale releases (Aiken and Waddy, 1995; Bannister and Addison, 1998; Secor *et al.*, 2002; Bell *et al.*, 2005; Stevens, 2006a; Zohar *et al.*, 2008; Stevens *et al.*, 2014). The numbers are irrelevant if the individuals that are produced are maladapted for life in the wild, where survival will depend on predator avoidance, successful foraging, and competition for resources. Hatchery-cultured individuals often have poorer survival rates than their wild counterparts (Munro and Bell, 1997), but if ecologically competent individuals were produced in the hatchery, then mortality rates of released individuals could be more similar to those in the wild. To achieve this goal, enhancement programmes need to balance production goals and methods to produce individuals that are ecologically competent.

Hatcheries rarely attempt to mimic natural conditions, but rather seek to maximize production by limiting the mortality and optimizing the growth, while minimizing the cost. Thus, rearing

occurs at high densities, under artificial lighting conditions, at elevated temperatures, with limited dietary variability, with absent or non-natural substrata, and with frequent human intervention. As such, the hatchery environment lacks or obscures many environmental cues present in the wild; cultured animals have no experience with seasonal cycles, predator avoidance, foraging for natural food items, or social interactions. In addition, rearing individuals in isolation, if needed to prevent cannibalism (Van Olt *et al.*, 1980; Swiney *et al.*, 2013), may impede natural brain development due to a lack of stimuli (Sandeman and Sandeman, 2000). Extending the duration of rearing to the juvenile stage for larger release size may exacerbate rearing effects. Thus, rearing duration and culture efficiency end up trading off with methods to attain juveniles that are ecologically competent.

Differences or abnormalities of hatchery individuals may be overinflated in the scientific literature. Published research often de-emphasizes non-significant comparisons, either because such results are not submitted for publication, or papers are rejected in the peer review process on the basis of their non-significance (Csada *et al.*, 1996). Highlighting traits that are statistically different between hatchery and wild individuals is important, yet statistical differences are not necessarily ecologically meaningful and may not reflect an inability to survive in the wild. The critical factor to consider for stock enhancement is the potential impact of a trait on an individual's ecological competence for survival in the wild after release. By definition, hatchery-induced deficiencies imply that the given trait is plastic and thus is likely capable of change to a more "natural" state if exposed to natural environmental cues. The first challenge in understanding ecological competence is identifying environmental factors, if any, that cue plasticity.

Behavioural plasticity

Behavioural responses to environmental cues are the fastest way for an animal to respond to environmental variation. Many crustaceans exhibit behavioural plasticity such as hermit crab shell manipulation; blue crab burial; juvenile red king crab crypsis; and American, European, and spiny lobster sheltering (Hazlett, 1995; van der Meeren, 2001; Davis *et al.*, 2004; Castro and Cobb, 2005; Oliver *et al.*, 2006; Daly *et al.*, 2012a; Long *et al.*, 2015; Lyons *et al.*, 2016). Retention of behavioural modification to external cues in the short or long term begs the question: are the animals "learning"? Although we cannot possibly review the vast amount of existing literature on animal learning, considerable scientific advancements in our understanding of invertebrate learning include the role of conditioning in behavioural modification and avoidance behaviours. Bethe (1898) believed that crustaceans could not learn by experience, but subsequent seminal research proved the contrary (Schöne, 1961). For example, green crabs (*Carcinus maenas*) are able to press levers via claw extension to obtain food and this behaviour can be learned in 2 days (Abramson and Feinman, 1990). Crayfish can be trained in 5–7 days to manipulate their large cheliped through a small access point to obtain food (Bierbower *et al.*, 2013). On the other hand, hermit crabs can both detect predation danger via olfactory cues and alter shell preference based on experience, but they cannot connect predation danger level and shell preference (Hazlett, 1995).

The mechanism of memory retention and the duration of learned adaptive behaviours are unclear for crustaceans, but some degree of cognitive retention exists. Hermit crabs display short-

term memory for shell aperture location that is not retained long term (Jackson and Elwood, 1989). Naive juvenile red king crabs immediately respond to predators by increasing levels of crypsis and retain this behaviour after a 48-h predator exposure period (Daly *et al.*, 2012a). Male American lobsters' level of aggression depends on previous interactions with conspecific opponents 24 h earlier (Karavanich and Atema, 1993). These studies show that some level of cognitive retention operates on the order of days. Examples for longer-term modifications are less common. European lobsters retain the memory of previous agonistic interactions with conspecifics from 1 to 2 weeks prior (Agnalt *et al.*, 2017). Crayfish retain olfactory associations for weeks (Hazlett, 1994), and executed behavioural patterns may depend on previous experience, but this may be a short-term experimental effect (Hazlett, 1990; Hazlett, 1995). Emergence behaviour of captive spiny lobsters (*Jasus edwardsii*) can be manipulated with predator presence, but lobsters immediately recognize and respond to predators in the wild even without prior experience (Oliver *et al.*, 2006). As with most invertebrates, retention of behavioural experience by crustaceans likely operates via short-term memory and behavioural associations likely decay unless reinforced).

Reliance on shorter-term (days or weeks) memory could be advantageous in a heterogeneous ecosystem, where environmental variables such as predator/prey composition and microhabitat type can fluctuate seasonally. Long-term retention of behaviours or over-specialization could be suboptimal in a changing environment. Predators with different foraging techniques may induce different anti-predator mechanisms. For crabs, burial or crypsis reduces detection by visual ambush predators, whereas a flight response is required for avoiding non-visual predators such as seastars. Thus, the ability to shift behavioural responses is likely advantageous in a changing environment and may reflect a reliance on shorter-term cognitive retention.

Within the context of stock enhancement, the short-term nature of behavioural changes in crustaceans is both a cause for concern and a mechanism for the alleviation of that concern. The hatchery environment may induce behaviours that are maladaptive in the natural environment. This short-term plasticity in behaviour means that individuals can alter their behaviours after release or that conditioning pre-release may induce such behaviours that continue for a short time after release. Below we review pertinent behaviours that are of concern for stock enhancement.

Habitat selection and predator avoidance

Refuge from predators is essential for crustacean survival, especially for small, early benthic phase juvenile stages that are released after hatchery rearing. This predator avoidance is probably the single most important behaviour for survival after release. Crypsis, the primary predator avoidance behaviour of marine crustaceans, involves burial or hiding in complex structures to reduce predator encounter rates via physical concealment or camouflage. Recently settled American lobsters seek cobble habitat where the crevice spaces are the ideal size for hiding (Cobb, 1971; Wahle and Steneck, 1991). Similarly, juvenile red king crabs associate with complex habitats such as cobble, shell, or structural invertebrates (McMurray *et al.*, 1984; Dew, 1991; Loher and Armstrong, 2000; Pirtle *et al.*, 2012), and small blue crabs bury and use seagrass and coarse wood debris in nearshore waters as structural refugia (Hovel and Lipcius, 2001; Long *et al.*, 2013). Although predator avoidance behaviour is innate for some

species, cultured individuals can fail to seek and use complex habitats, increasing their susceptibility to predators. Hatchery-reared juveniles can adapt quickly to the natural environment or be conditioned prior to release. For example, European lobsters have increased shelter occupancy and survival when cultured communally with natural structures compared to individuals without prior shelter experience (Agnalt *et al.*, 2017). Initial burial rates of hatchery-cultured blue crabs are lower than wild crabs but are similar to wild crabs after 2–4 days of exposure to sediment (Davis *et al.*, 2004). The maladapted behaviour of increased daytime activity of captive spiny lobsters is reduced with the presence of a predator or modified feeding schedules; yet individuals display normal sheltering behaviour once released in the wild regardless of experience with predators (Oliver *et al.*, 2006) and have similar survival rates (Mills *et al.*, 2004). On the other hand, hatchery-cultured juvenile red king crabs increase crypsis with prior predator exposure (Daly *et al.*, 2012a) and individuals without predator exposure experience high mortality in the first day after release but thereafter survive, as well as wild crabs (Long *et al.*, 2018), suggesting that behavioural deficiencies can have a short-term effect that is easily overcome.

Mechanisms of predator exposure can matter in the hatchery setting. Predator visual or chemical cues alone may initiate a response in some species, in which case a physical barrier or effluent from separate holding tanks may be an efficient conditioning strategy. Other species may require physical contact with a predator, which has obvious risks. Exposure to small or benign predators could allow direct physical contact without compromising hatchery production.

Foraging

Most decapod crustaceans are opportunistic omnivores that consume a broad range of food items. Nutritional requirements are unknown for many crustacean species, and although hatchery individuals are typically fed to satiation, commercial feeds are not typically species specific. In the wild, individuals must actively forage for prey items under the risk of predation; therefore, predator avoidance behaviour may reduce foraging opportunities and ultimately growth (Relyea and Auld, 2004). Juvenile blue king crabs reduce foraging behaviour in complex habitats, which may be an adaptive behaviour to balance foraging efficiency and predator avoidance (Daly and Long, 2014a).

Hatcheries feed animals in excess, and individuals rarely encounter natural prey. Such inexperience might hinder an animal's ability to identify, select, and capture food items, thus depressing growth and survival. Yet, to date no study indicates that this is a problem for crustaceans. Cultured blue crabs adapt quickly to natural prey items without prior experience feeding on a similar breadth of prey as wild crabs (Davis *et al.*, 2004; Young *et al.*, 2008). Released hatchery blue crabs aggregate on bivalve patches in the wild, just as wild crabs do (Young *et al.*, 2008). Spiny lobsters released into the wild adapt to wild food sources after being fed a homogenous diet of mussels and commercial feed pellets in captivity for 12 months (Mills *et al.*, 2004). The opportunistic nature of crustacean feeding likely means that they are well adapted to switching between different food types and foraging strategies, thus explaining why they acclimate to natural prey in the wild soon after exposure, suggesting that differences in foraging behaviour are not a concern. Incorporating food items into the diet that are expected to be encountered at release sites could build

experience identifying and handling a range of prey types encountered in the wild, but there is no evidence that this helps to improve crustacean post-release survival. Given this and the economic and logistical challenges of administering a diversity of natural food items on a large scale, it is unlikely to be worthwhile in most cases.

Aggression

Aggressive behaviours, involving competition for mates, food, shelter, and defence against predators, are important for an animal's survival. Rearing conditions (excess feed, no predators) can eliminate the pressure to compete for food or defend against predators. Cannibalism is one of the largest challenges in decapod crustacean culture, as these animals are most vulnerable at the time of moulting (reviewed in Romano and Zeng, 2017). To address this concern in the hatchery setting, individuals can be reared in individual containers to improve survival, but whether this strategy will increase survival after release is unclear. Hyper-aggression in American lobster can occur when individuals are reared in isolation (Dunham, 1972; Hoffman *et al.*, 1975), which could be in part due to inexperience with visual signals from conspecifics, as observed for crayfish (Bruski and Dunham, 1987). Research into the hormones associated with aggression may provide solutions to reduce cannibalism in the future (Romano and Zeng, 2017). Cultured blue crabs do not displace wild crabs, suggesting little evidence of hatchery-induced aggression after release in this species (Davis *et al.*, 2005b; Young *et al.*, 2008). Hyper-aggressive, naive European lobsters decrease aggression when predators are present (van der Meeren, 1993), and hyper-aggression of cultured spiny lobsters does not impede anti-predator responses in the wild (Oliver *et al.*, 2008). Culturing conditions can alter social interactions, but hyper-aggression is likely plastic and can decrease with experience.

While the role of social cues is unclear for crustaceans, communal rearing could provide interaction experience that is helpful later. Early development of other social behaviours such as mate detection may also benefit from communal rearing. For these reasons, we suggest avoiding rearing in isolation whenever possible. In addition to being cost and labour intensive, individual holding can impede growth and obscure conspecific social cues, among other issues. Thus, we suggest communal holding at moderate-to-low stocking densities with shelters where individuals can experience social cues from conspecifics but can avoid excessive agonistic interactions to meet a balance between hatchery production and juvenile quality.

Reproduction

Released individuals need to survive to maturity and contribute to the natural spawning stock to successfully enhance a depressed stock. Reproductive success will depend on specific breeding behaviours, including spatial overlap with mates, mate identification, competition for mates, and maternal care. Any reproductive behavioural incompetence may prevent cultured individuals from contributing to the reproductive output of a population, rendering releases useless, even if individuals survive to maturity. Although very limited, the available evidence suggests that hatchery-reared crustaceans can mate successfully in the wild (Agnalt, 2008; Young *et al.*, 2008). Specific behaviours such as mate detection, reproductive displays, and copulatory embrace are likely not acquired by social experience in early life (i.e. early benthic

phase), but either inherited or acquired through conspecific interactions as later juveniles or adults. For crustaceans, it is unknown how larger-scale behaviours such as spatial overlap with mates are affected by hatchery origin. Additional research is needed on the effect of artificial culture on mating behaviours in crustaceans.

Migration

Small- and large-scale spatial migrations are important behaviours relevant to all aspects for crustacean life history. In particular, the ability for hatchery-cultured individuals to integrate into the wild breeding population should not be overlooked. Individuals must spatially overlap with mates for successful reproduction, which can involve migration to spawning grounds. Thus, the timing and extent of migration behaviours (e.g. site fidelity, homing, large-scale seasonal movement) of cultured individuals must match the rhythms of the wild population. This may be especially critical for species with complex reproductive strategies. For example, female blue crabs have a unidirectional long-distance seasonal migration from low salinity mating areas to higher salinity spawning areas to release her clutch (Aguilar *et al.*, 2008).

Juvenile crustaceans generally have low dispersal rates and long residence times in nursery habitats compared to other species groups, such as finfish. However, as adults, some species undergo large-scale migrations (e.g. blue crab spawning migration). It is unclear if and how hatchery culture will affect behaviour later in life, and it probably varies by species. Small-scale behavioural movements differ between hatchery and wild individuals, but broad-scale ecological rhythms may be innate. For example, captive-reared spiny lobsters and transplanted European lobsters have higher rates of inter- and intra-site movement than their wild (Mills *et al.*, 2005) or native counterparts (van der Meeren, 1997), but cultured European lobsters have strong site fidelity over several years (Bannister *et al.*, 1994). Given that effects of artificial culture on longer-term behavioural processes such as migrations are ambiguous, the entire life cycle must be considered when developing stock enhancement strategies. For example, migration corridors or spawning sanctuaries may be needed as part of an enhancement initiative (Aguilar *et al.*, 2008).

Morphological plasticity

Morphological plasticity can be adaptive or not but in either case influences how individuals interact with their environment. Morphological changes generally operate on longer temporal scales than behavioural responses, and the rate of plasticity depends on the timing of the induced phenotype and the duration of environmental change (Miner *et al.*, 2005). Below we describe the growth and morphological characteristics affected by artificial rearing conditions that could affect survival in the wild after release. The examples focus on morphological features that are plastic and could affect survival after release, either by having effects on an individual's ability to defend against predators (avoidance and defence), ability to capture food, and/or ability to compete for resources.

Spination

Spination is an important crustacean predator defence that can be plastic and likely improves survival by impeding the predator's ability to ingest the organism. Crab larvae develop spines to deter gape-limited fishes, which can detect and learn to avoid prey based on spine length (Morgan, 1989; Morgan, 1990). In juveniles

and adults, lateral spines increase the required predator mouth gape, while spines covering the carapace and pereopods impede or deter ingestion (Figure 1; Lyons *et al.*, 2016). Shorter spines occur in cultured compared to wild blue and mud crabs (Figure 2; Davis *et al.*, 2004; Davis *et al.*, 2005a; Young *et al.*, 2008; Parkes *et al.*, 2011). In some cases, the mechanism for spine induction is understood. Predator presence can influence spine development. Cultured blue crabs develop longer spines when exposed to chemical and visual cues of fish predators for several weeks in the laboratory, and after several weeks in the wild (Davis *et al.*, 2004; Davis *et al.*, 2005a; Young *et al.*, 2008). The morphological response may be predator specific; conspecific predators do not induce a morphological response for blue or mud crabs, but fish predators do (Young *et al.*, 2008; Parkes *et al.*, 2011). Conversely, laboratory-reared juvenile red king crabs have longer carapace spines than their wild counterparts during parts of the year (Westphal *et al.*, 2014). The ecological significance of shorter spine length likely varies by species. Longer spines increase survival in the field for blue crab (Davis *et al.*, 2005a), yet the effect of reduced spine length on *in situ* survival is unknown for other species. Statistical differences between spine lengths of hatchery and wild individuals do not necessarily imply reduced survival in the field, and this needs to be considered for each species.

Colouration

Colouration can influence camouflage effectiveness. The contrast of relatively lighter shell colour on dark substrates, or vice versa, may increase predation risk by visual predators. Colouration is influenced by background, diet, and light intensity through pathways including long-term adjustments and distribution of pigments within the exoskeleton (Robison Jr and Charlton, 1973; Rao, 1985) or a short-term physiological change via chromatophores (Ghidalia, 1985; Tlusty, 2005). In general, crustaceans that live at depth tend to be red in colour, since red wavelengths are attenuated at greater water depths, whereas shallower species exhibit colouration that resembles the surrounding benthic habitat (Ghidalia, 1985).

Cultured animals are typically reared in tanks or ponds with artificial substrate, diet, and lighting conditions, which can result in a range of colour morphs (Figure 3). Colour differences between hatchery and wild individuals occur for an array of species



Figure 1. Juvenile red king crab (*Paralithodes camtschaticus*). Note spine distribution on the carapace and pereopods. Photo by G. L. Eckert.

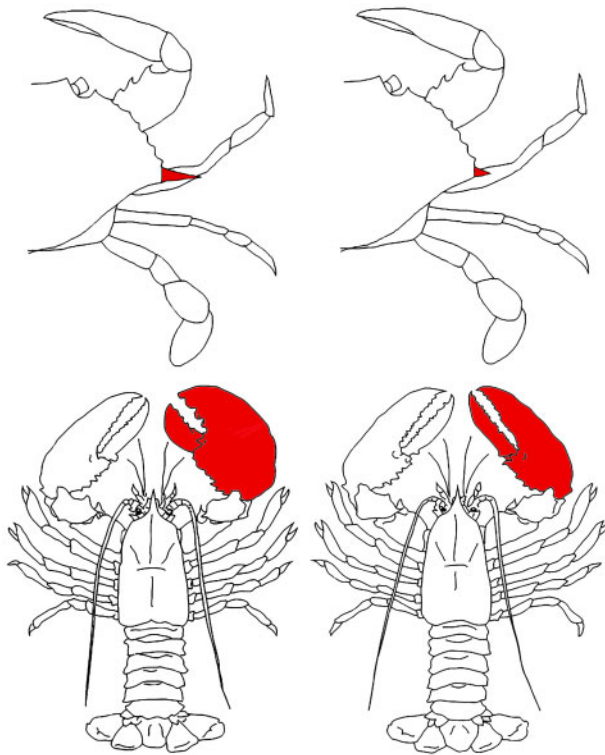


Figure 2. Top: differences in spine length (indicated by red) between wild caught (left) and cultured (right) and blue crabs [*Callinectes sapidus*; adapted from Young *et al.* (2008)]. Bottom: differences in claw morphology (indicated by red) between wild caught (left, differentiated claws) and cultured (right, symmetrical claws) American lobsters [*Homarus americanus*; adapted from Govind (1989)].

including blue crabs, red king crabs, American lobster, European lobsters, and mud crabs (Svåsand *et al.*, 1998; Davis *et al.*, 2005a; Young *et al.*, 2008; Parkes *et al.*, 2011; Daly *et al.*, 2013b). These colour differences can sometimes be reduced or eliminated by rearing with coloured tank backgrounds or with natural substrates, and these changes can occur over short time periods without moulting. For blue crabs, short-term exposure to natural sediment in the laboratory (1–2 days) and field (5 days) facilitates colour change (Davis *et al.*, 2005a). Mud crabs display colour modifications with short-term exposure to natural sediment or dark tank backgrounds for several weeks (Parkes *et al.*, 2011). Similarly, American lobsters display a morphological colour change in response to background colour and ultra-violet light after several weeks (Tlusty *et al.*, 2009). Shell pigmentation is also controlled by natural dietary carotenoids, and changes occur over several weeks (Tlusty, 2005; Tlusty and Hyland, 2005; Daly *et al.*, 2013b). Thus, changes in shell pigmentation are affected by the surrounding environment and diet and generally operate at temporal scales that range from days to weeks.

The ecological relevance of shell pigmentation varies depending on species. Colour polymorphism of rock (*Cancer irroratus*), European green, and blue king (*Paralithodes platypus*) crab is advantageous in multicoloured habitats compared to a monochromatic colour scheme (Palma and Steneck, 2001; Todd *et al.*, 2006; Daly and Long, 2014b) because individuals more closely resemble the surrounding habitat and are less likely to be detected by visual



Figure 3. Colour variation observed in hatchery-cultured red king crabs (*Paralithodes camtschaticus*). Photo by G. L. Eckert.

predators. However, colouration may be less important if organisms are located in habitats with low visibility (e.g. high turbidity, at depth) or are at the risk of predation by non-visual predators. For example, shell colour does not influence blue crab survival in the field (Davis *et al.*, 2005a), likely because the dominant predators locate prey via chemosensory perception in the turbid environment (Hines and Ruiz, 1995). The importance of shell colour for *in situ* survival is unknown for other species, including mud crabs, red king crabs, and American lobsters, and requires further examination. Regardless, colour plasticity suggests easy modification with adjusted hatchery rearing protocols including inclusion of natural substrates, holding tank colour that more closely resembles natural habitat, or dietary carotenoids, and any colour deviation may be diminished after release into the wild. The timing of colour plasticity and protocol needs further investigation on a species level in stock enhancement programmes.

Claw shape

Crustacean chelae are used for foraging, predator defence, and intra-specific agonistic interactions, such as competition for food, shelter, or mates (Vermeij, 1977; Juanes and Smith, 1995; Lee, 1995). Larger claws are presumed to be more effective, for example, in competition for mates (Conan and Comeau, 1986). Homarid lobsters have large chelae that are important for fending off predators and establishing social dominance hierarchies among conspecifics for mate selection, courtship, quality of habitat refugia, and shelter territorial defence (Elner and Campbell, 1981; Karnofsky *et al.*, 1989). Lobster claws, like many crustaceans, are naturally dimorphic: with a larger “crusher” and a smaller “cutter” or “scissor” claw. The crusher claw is stout and more robust in shape with molar-like teeth used for cracking open shells of molluscs, while the scissor claw has a more slender shape with incisor-like teeth used for tearing flesh (Govind, 1989). This asymmetry likely allows for consumption of a broader range of food items or a competitive advantage to conspecifics by dominating agonistic interactions (Goldstein and Tlusty, 2003).

Lobster claw asymmetry is influenced during the early juvenile stages (Govind, 1989). At the time of settlement, the claws are identical, but differential exercise induces muscle differentiation to either fast or slow fibre types via a physiological feedback loop (Govind and Lang, 1978; Govind, 1989). As a result, typical scissor claws contain ~65% fast and 35% slow muscle fibres, while the crusher claws contain only slow muscle fibres (Costello and Lang, 1979).

Cultured American and European lobsters can lack a crusher claw (Figure 2; Wickins, 1986; Govind, 1989; van der Meeren and

Uksnøy, 2000). Because instances of two scissor claws are rare in the wild (Herrick, 1909; Addison and Bannister, 1994), this is generally recognized as a rearing artefact (Wickins, 1986). In the wild, regular foraging behaviour initiates claw development, yet the absence of natural substrates in the hatchery precludes this opportunity (Govind, 1989). As a result, cultured lobsters have longer and more slender claws, which may make them more fragile and vulnerable to damage during agonistic encounters (Scrivener, 1971; van der Meeren and Uksnøy, 2000; van der Meeren, 2005). Similar plasticity occurs in brachyuran crabs; crabs fed shelled prey grow larger and stronger claws than those fed unshelled prey (Smith and Palmer, 1994). Enabling exercise of the claws by adding natural substrate or shelled prey items such as bivalves or tubeworms during juvenile rearing promotes muscle differentiation and enhances asymmetrical claw development (Wickins, 1986; Govind, 1989; Goldstein and Tlusty, 2003) and improves overall strength in crabs (Smith and Palmer, 1994).

Growth

Variable growth rates within a cohort are ubiquitous in crustacean aquaculture and are influenced by a combination of genetic and environmental factors (e.g. temperature, food availability) (see Brett, 1979; Wickens and Lee, 2002 for a review). Typically, hatcheries optimize growth by elevating rearing temperature and feeding in excess (Hartnoll, 1982; Hartnoll, 2001; Shelley and Lovatelli, 2011). However, rearing artefacts can reduce growth or increase size variation within a cohort. High stocking densities can induce strong resource competition among individuals. Yet intra-cohort size variation can occur when individuals are reared in isolation under identical conditions (e.g. red king crab; Westphal *et al.*, 2014) suggesting a genetic predisposition for variable growth rates.

It is economically beneficial for hatcheries to maximize growth rates so that juveniles reach release size as soon as possible. In addition, hatcheries may select for faster growing individuals either from selective breeding or through competitive dominance. Generally, smaller individuals are more vulnerable to predation by larger individuals. Size grading (rearing small and large individuals separately) is commonly used in aquaculture to improve survival, growth, and feeding efficiency (Ahvenharju *et al.*, 2005; Marshall *et al.*, 2005; Zmora *et al.*, 2005; Daly *et al.*, 2012b). For example, hatchery survival of early benthic phase red king crab survival is greatly improved by removing large individuals from communal rearing tanks (Daly *et al.*, 2012b). Maintaining small individuals for wild releases may be important to conserve natural genetic variation of the target stock as the genetic contribution of those individuals would be reduced if cannibalism in the hatchery selects against individuals genetically predisposed to slow growth. Given these factors, one might expect hatchery individuals to grow faster than wild individuals, but there is little evidence of this. Growth of early benthic phase red king crabs is similar between cultured individuals and individuals sampled from the field (Westphal *et al.*, 2014). Similarly, hatchery and wild blue crabs and European lobsters grow at similar rates after release (Agnalt *et al.*, 2004; Davis *et al.*, 2004; Young *et al.*, 2008; Johnson *et al.*, 2011).

Physical damage

High-density juvenile culture exacerbates cannibalism and agonistic interactions and can result in external damage to crab (Mann *et al.*, 2007) and lobster (Van Olst *et al.*, 1975; Van Olst *et al.*, 1980) exoskeletons. On the other end of the spectrum, rearing in isolation can completely eliminate damage from

conspecifics but is labour intensive, an inefficient use of space, and could introduce a slew of other abnormalities such as hyper-aggression (Dunham, 1972; Hoffman *et al.*, 1975), reduced brain development (Sandeman and Sandeman, 2000), or reduced growth (Swiney *et al.*, 2013). Immobilization of chelipeds could reduce physical damage from conspecifics (Aiken and Waddy, 1978) but could lead to morphological abnormalities such as reduced claw size and strength or symmetrical claw shape. While low stocking densities minimize physical damage and cannibalism but yield fewer animals, higher densities could yield more animals, even with cannibalism. Moderate stocking densities, adding structures to reduce encounters, and size grading can reduce aggressive encounters to minimize injuries (Aiken and Waddy, 1978; Marshall *et al.*, 2005; Mann *et al.*, 2007) and may balance the trade-off between stocking density and survival.

Implications of plasticity for stock enhancement

The above review of how hatchery-reared individuals differ from wild individuals and the potential implications of these differences purposely does not refer to these differences as deficiencies because they may represent short-term acclimation to the hatchery environment. Some of these differences may be maladapted to the wild, but the very plasticity that causes these traits suggests that they are reversible. In many cases, hatchery-cultured individuals are reasonably fit for life in the wild and post-release plasticity adapts most species to the natural environment relatively quickly. Hatchery-cultured blue crab and red king crab experience high initial post-release mortality, but subsequent rates stabilize and are comparable to wild individuals (Davis *et al.*, 2004; Long *et al.*, 2018). Hatchery-cultured early benthic phase European lobsters can survive in the wild for up to 8 years at high rates and have been captured in commercial fisheries (Bannister *et al.*, 1994). However, for other species, hatchery-wild differences could result in high post-release mortality. Ultimately, stock enhancement programmes need to balance hatchery production and post-release survival to maximize overall programme effectiveness. Research and cost-benefit analysis is needed to identify which differences are important enough to warrant intervention at the hatchery stage. One effective strategy may be to release late-stage larvae or juveniles as soon as possible to minimize time spent in a hatchery setting. As that may not be possible, we consider how stock enhancement programmes can structure juvenile rearing and release protocols in light of biological plasticity to avoid unwanted traits (Table 1).

Conditioning with environmental enrichment

The notion of conditioning millions of juveniles may seem daunting, impractical, or cost-prohibitive for large-scale hatchery production for stock enhancement; however, conditioning may be needed to attain high post-release survival of hatchery-reared individuals. Incorporating cues from the natural environment does not require a broad-scale shift in culturing philosophy. The first challenge for establishing conditioning protocols is to identify environmental factors that cue plasticity, and the second is integrating these cues into hatchery production. Above, we suggest strategies to incorporate environmental cues into rearing that may provide tangible benefits. For example, including natural structures or structurally analogous artificial structures in juvenile nursery tanks has a number of potential benefits including inducing normal chelae development and shell

Table 1. Phenotypic traits that may impact ecological competence, potential remedial actions, and species studied

Trait	Maladaptive response	Remedial action	Species observed	References
Predator avoidance	No predator avoidance	Predator cues, shelters	Red king crab (<i>Paralithodes camtschaticus</i>), blue crab (<i>Callinectes sapidus</i>), spiny lobster (<i>Jasus edwardsii</i>)	Oliver et al. (2006, 2008), Daly et al. (2012a), and Davis et al. (2004)
Foraging	Reduced ability, low diversity of food items	Variety of natural prey items	Blue crab, spiny lobster	Davis et al. (2004), Young et al. (2008), and Mills et al. (2004)
Aggression	Hyper-aggression	Communal rearing, moderate density, shelters	American lobster (<i>Homarus americanus</i>), European lobster (<i>Homarus gammarus</i>), spiny lobster	Dunham (1972), Hoffman et al. (1975), van der Meeren (1993), and Oliver et al. (2008)
Reproduction	Recognition failure	Unknown	Blue crab, European lobster	Young et al. (2008) and Agnalt (2008)
Migration	Inconsistent with wild counterparts	Unknown	Spiny lobster, European lobster	Mills et al. (2005), van der Meeren (1997), and Bannister et al. (1994)
Spination	Reduced	Predator cues	Blue crab, mud crab (<i>Scylla serrata</i>)	Davis et al. (2004, 2005a), Young et al. (2008), and Parkes et al. (2011)
Colouration	Lighter, monochromatic	Dietary supplementation, background colour (tank surfaces, natural substrates), ultra-violet light	Blue crab, mud crab, red king crab, American lobster, European lobster	Davis et al. (2005a), Young et al. (2008), Parkes et al. (2011), Svåsand et al. (1998), Daly et al. (2013b), and Tlusty et al. (2009)
Claw shape	Symmetrical, smaller	Natural substrate, shelled prey	American lobster, European lobster, red rock crab (<i>Cancer productus</i>)	Wickins (1986), Goldstein and Tlusty (2003), van der Meeren and Uksnøy (2000), van der Meeren (2005), Govind (1989), and Smith and Palmer (1994)
Growth	Loss of slow growers	Size grading	Red king crab, blue crab, blue-swimmer crab (<i>Portunus pelagicus</i>)	Daly et al. (2012b), Zmora et al., 2005, and Marshall et al. (2005)
Physical damage	Injuries	Size grading, structures, moderate temperature	mud crab, American lobster	Mann et al. (2007), Aiken and Waddy (1978)

colouration, reducing physical damage from conspecifics, inspiring shelter-seeking behaviour, and reducing aggression and cannibalism. Artificial structures are attractive from a hatchery perspective because of their availability, low cost, and ease of use, but artificial structures alone may fail to achieve the desired effect. Netting structures reduce cannibalism in blue crab culture (Zmora et al., 2005) but do not promote burial behaviour as fine sediment will. Similarly, box shelters improve European lobsters' refuge-seeking behaviour (van der Meeren, 2001), but natural substrate is required to stimulate asymmetrical chelae development. Clumped gillnet and artificial seaweed are ideal for red king crab post-larvae because of ample surface area (Daly et al., 2009), yet their effect on juvenile behaviour in natural substrates such as cobble, shell, or structural invertebrates is not known. Because natural substrates are generally better at fostering sheltering behaviour, claw development, and shell colouration, a combination of natural and artificial structures is likely the best compromise between logistical feasibility in the hatchery and ecological quality.

Behavioural and morphological plasticity operate on different temporal scales, and exposure duration may impact the magnitude of the response. In general, the magnitude of

plasticity depends on the lag between the induced response and timing of the environmental change (Miner et al., 2005). Because crustacean cognitive abilities operate on short temporal scales, behavioural conditioning should focus on events or modifications that yield an immediate response. Furthermore, the desired modification will probably decay with time; thus, stochastic perturbations in the culture environment will likely not be adequate to sustain plasticity. As such, reinforcement with repetition may be needed. Conditioning duration will vary with species and depend on the specific desired behaviour. For example, sheltering behaviour may increase after short-term exposure (days), but the connection between refuge use and predator presence may take longer to establish. Conversely, morphological conditioning may operate on longer temporal scales because of the physiological mechanisms involved (i.e. assimilation of carotenoids, muscle development) and will require longer conditioning times. For these reasons, it is important to experimentally separate species-specific cues within an ecologically relevant context when examining optimal conditioning protocols and to follow survival in the field after release, as this is the most meaningful endpoint.

Plasticity and release strategies

Release strategies are a key to responsible and effective stock enhancement (Blankenship and Leber, 1995). Factors that must be considered include nursery habitat, size-at-release, release timing, ecosystem carrying capacity, and density-dependent mortality (Hines *et al.*, 2008; Seitz *et al.*, 2008), and all of these factors need to be considered for each species. The magnitude of plastic responses could be proportional to hatchery rearing duration. Thus, there is likely a trade-off between optimal release size and maladaptive traits. Release of small juveniles immediately after settlement may be optimal if conditioning of juveniles in the hatchery setting is ineffective or impractical. Some fish and mollusc stock enhancement efforts have released larvae with partial success (Arnold, 2008). Releases of larvae or post-larvae may be impractical for crustaceans if the natal population bottleneck occurs during these stages. Regardless of individual size or the extent of pre-release conditioning, hatchery-reared animals inevitably face a major transition from the hatchery to wild environments. Structuring release protocols in light of hatchery-induced maladaptive characteristics with an understanding of the timescale of the behavioural plasticity involved could help minimize negative effects. There are multiple strategies that can expose newly released individuals to both their new habitat and to predator cues while reducing the probability of predation. For example, most predation on juvenile red king crabs occurs during daylight hours by visual predators (Daly *et al.*, 2013a), suggesting that releases at dusk may be optimal. Given that predator-induced changes in behaviour can occur within 4 h (Long *et al.*, 2015), this could give the crabs enough time to find shelter before experiencing significant predation risk. Similarly, seasonal fluctuations in predator densities and assemblages could inform optimal temporal windows for release; releasing when predators are scarce would allow for plasticity to develop during low-risk periods.

In situ conditioning at release sites may be useful to either reduce immediate post-release predation or replace hatchery grow-out. Intermediate holding in field-based enclosures, or via covering habitat with netting as is frequently used in bivalve culture (e.g. Spencer *et al.*, 1992), would allow animals to adjust to ambient conditions without the risk of imminent predation. In addition, longer-term *in situ* holding could be useful if cost, time, or space limit hatchery grow-out operations (e.g. Sotelano *et al.*, 2018). Field-based enclosures have proven effective for American and European lobster enhancement programmes (Beal *et al.*, 2002; Beal, 2012). Alternatively, field conditioning in artificial habitats could be considered; red king crab in Japan were conditioned in the field in net bags, although the effectiveness of this procedure was not determined (Stevens, 2006b).

Benefits of plasticity

Phenotypic plasticity is beneficial to crustacean stock enhancement programmes. For most crustacean species, hatchery-cultured individuals are reasonably fit for life in the wild, and a dramatic shift in culturing philosophy is unnecessary. Rather, adjustments to current rearing protocols will foster traits that improve ecological competence and ultimately post-release survival. Differences between hatchery and wild crustaceans are maladaptive (*in situ*) responses induced by unnatural conditions of the culture environment that can be modified. Plasticity enables researchers to mould phenotype with consistent and reinforced cues, thus eliminating maladaptive traits and better preparing

animals for life in the wild. Because predation is likely the single biggest source of immediate mortality, hatchery conditioning programmes need to focus on dampening susceptibility to predators and integrate with a broader release strategy that considers size-at-release, optimal habitat, release timing, and *in situ* conditioning. Phenotypic plasticity provides potential for improved post-release survival and potential to expand the breadth of species for stock enhancement consideration.

The role of epigenetic mechanisms (e.g. DNA methylation) in shaping phenotypes has re-emerged in recent years with advancements in molecular biology (Eirin-Lopez and Putnam, 2019). In addition to better understanding how species adapt to climate change (Munday, 2014; Donelson *et al.*, 2018), epigenetics could have direct application in aquaculture practices by tailoring desired phenotypes (Gavery and Roberts, 2017). Environmental conditions in early life-history stages can establish developmental trajectories in preparation for such conditions later in life (Eirin-Lopez and Putnam, 2019), and some studies show transgenerational plasticity (i.e. plasticity across generations) occurs (Donelson *et al.*, 2018). For example, acidified maternal holding conditions can impact survival, morphology, and metabolic rate of Tanner crab (*Chionoecetes bairdi*) larvae (Long *et al.*, 2016). While some epigenetic research (e.g. nutritional programming) has focused on fish species (Moghadam *et al.*, 2015; Metzger and Schulte, 2016), a dearth of information exists for marine crustaceans. Research is needed to better understand species-specific environmental drivers of plasticity, thresholds that initiate the plasticity of individual traits, and the interplay of plasticity within and across generations. As the field of epigenetics advances, the aquaculture community should consider how to integrate epigenetic concepts into husbandry practices and pre-release conditioning programmes to promote desired phenotypes of cultured individuals.

Recommendations for future research

Here, we highlight the importance of ecological competence of hatchery animals, conditioning potential, and release strategies. A better understanding of epigenetics, mechanisms for induced plastic responses, and the roles of exposure duration and response magnitude on conditioning potential for a broader range of species is needed. While controlled hatchery and laboratory experiments are useful, coupled field studies are invaluable to identify interacting factors and reveal plastic traits that are ecologically important. In particular, *in situ* observational and tethering studies are useful for evaluating factors such as natal population densities, habitat use, and relative predation risk, while tagging studies are powerful for understanding spatial migrations and ecological processes that occur later in life. Because greater survival of hatchery-cultured individuals could lead to genetic swamping effects and displacement (Ryman and Laikre, 1991; Waples *et al.*, 2016), the importance of expanding genetic research to infer stock structure, reproductive biology, impacts of large-scale hatchery releases on wild stocks, and to develop tagging techniques cannot be ignored (Grant *et al.*, 2017). Furthermore, inclusion and publication of non-significant results are useful to guide conditioning programme development. Bias towards significant results in factors such as hatchery–wild differences or magnitude of plasticity can lead to incorrect or misleading conclusions. Implementing unnecessary conditioning programmes would misuse resources and may deter potential enhancement initiatives. Finally, we emphasize the need to focus research on evaluating if recruitment limitation exists in populations targeted for

enhancement. The release of cultured individuals into a stock that is over-exploited would be a wasted effort and changing environmental conditions could alter habitat quality sufficiently to preclude successful enhancement (Reum et al., 2019).

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