



Mechanisms of bioinvasions by coastal crabs using integrative approaches – A conceptual review

Lénia D. Rato^{a,*}, Daniel Crespo^{a,b,1}, Marco F.L. Lemos^{a,*}

^a MARE – Marine and Environmental Sciences Centre, ESTM, Polytechnic of Leiria, 2520-641 Peniche, Portugal

^b CFE – Centre for Functional Ecology – Science for People & the Planet, Department of Life Sciences, University of Coimbra, Calçada Martim de Freitas, 3000-456 Coimbra, Portugal

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ABSTRACT

Crustaceans are amongst the most reported invaders of coastal habitats, and predatory brachyuran crabs one of the most successful marine invasive groups. They hold high tolerance to abiotic stress and their genetic, life-history, and behavioural adaptation mechanisms prompt their invasive conspicuousness. However, there is a generalized ambiguity on the specific processes that make these bioinvasions successful. No trait-related patterns have yet been found, mostly since traits attributed solely to non-indigenous crab species lack confirmation by comparison with their native counterparts and across each other. Therefore, this review discusses the available literature on fitness and plasticity of brachyuran crabs under global changes, and advances the increasing importance of addressing native versus non-native invasive species comparisons in the annals of brachyura invasion dynamics. Further on, integrative approaches are highlighted and proposed as innovative tools to disentangle trait-related tolerance, overall crab phenotypic plasticity and further adaptation. These indicator tools will advance the knowledge on crabs' invasive potential, which ultimately affects upcoming population dynamics and ecosystem services, adding value to an effective management of coastal bioinvasions.

1. Introduction

Biological invasions, known as the geographical expansion of a species into a previously unoccupied area (Vermeij, 1996), are an increasing consequence of species' accessory transport, along with goods, services and people, across long distances (Crowley et al., 2017; Galil et al., 2007; Ros et al., 2014). Besides human-mediated transport as a global-scale introduction vector, the success of biological invasions is influenced by anthropogenic ecosystem disturbances such as climate change, the introduction of pollutants into the biosphere, or the physical modification of habitats (Dehnen-Schmutz et al., 2018; Kenworthy et al., 2018; Rahel and Olden, 2008; Simberloff et al., 2013). These dynamics are responsible for changes in species abundance and evenness as consequence of local and regional extinctions, emptying niches that can be occupied by non-native species (Byers, 2002; Sakai et al., 2001). While widely variable, some of the effects described for non-native invasive species (NIS) are the disruption of native communities due to introduction of diseases and parasites with propagating impacts through the ecological web (Boussellaa et al., 2018; Goedknecht et al., 2017;

Torchin et al., 2001), predation and competition (Olden et al., 2004), shifts in the abiotic conditions due to strong ecosystem engineering (Groszholz and Ruiz, 2009; Katsanevakis et al., 2016, 2014; Sousa et al., 2009; Zenetos et al., 2012), or global biodiversity reduction due to biological homogenization (Olden et al., 2004; Rahel, 2007; Stachowicz et al., 2002). In fact, they can negatively affect habitat nourishment, recreation and tourism, and lifecycle maintenance but, on the other hand, bring positive effects such as cognitive benefits, water purification, climate regulation, ecosystem engineering activities (Katsanevakis et al., 2014; Novais et al., 2015), and new food sources ultimately leading to cultural adjustments (Vermeij, 1996). Some authors estimate that invasive species impact could reach as much as 5% of the global economy (Pimentel et al., 2007). The associated costs include both loss of ecological services and expenses in managing and mitigating invasions (Jardine and Sanchirico, 2018).

There is still a generalized knowledge gap on the processes that allow successful invasions to occur (Lejeusne et al., 2014), namely in marine ecosystems, where abiotic and biotic factors interact, and complex synergistic and/or antagonist processes are often hard to assess. The

* Corresponding authors at: MARE – Marine and Environmental Sciences Centre, ESTM, Polytechnic of Leiria, 2520-641 Peniche, Portugal.

E-mail addresses: lenia.rato@ipleiria.pt (L.D. Rato), marco.lemos@ipleiria.pt (M.F.L. Lemos).

¹ Equal contribution to this review.

dispersal of coastal and marine species is only limited by distance, currents, and eventually by environmental gradients such as temperature or salinity. Therefore, connectivity of *meta*-populations in these open aquatic systems represents a major issue to biological invasions management when these barriers are surpassed. Estimations refer that over 7000 species may be moving globally through ships' ballast waters (Rilov and Crooks, 2009), or as fouling communities (Carlton, 1992; Karatayev et al., 2009), which means that distance and currents are no longer effective natural barriers. While environmental gradients are still a limitation, environmental changes such as the current global warming tendency will allow several species to expand their vital range to higher latitudes (e.g. Elliott et al., 2015; Raitos et al., 2010; Stachowicz et al., 2002). The creation of artificial links between water bodies intensify this nuisance: in the Mediterranean Sea, 11% of the species introduced through the Suez Canal reached invasive status and more than 50% became established (Zenetos et al., 2012).

In coastal and marine systems, crustaceans are conspicuous invaders (e.g. Brockerhoff and McLay, 2011; Hammock et al., 2016; Ros et al., 2014). Found from hydrothermal vents to coastal and estuarine areas, decapod crustaceans display remarkable endurance through complex processes such as moulting regulation (e.g. Chang and Mykles, 2011; Chen and Chen, 2003; Díaz et al., 2003; Gong et al., 2015; Yuan et al., 2017) or interspecific competitive behaviour (Haarr and Rochette, 2012; Hobbs et al., 2017; van den Brink et al., 2012). They are also considered one of the most tolerant taxonomic groups to global change scenarios such as warming (Giomi and Pörtner, 2013) and ocean acidification (IPCC, 2014; Wittmann and Pörtner, 2013). Within decapod crustaceans, the infraorder brachyura (crabs) – as high profile invaders – encompass active predators, hitchhikers, or stowaways (Caldwell et al., 2007). Brockerhoff and McLay (2011) report 73 species of brachyuran and crab-like anomuran decapods known as alien species worldwide (65.8% became established) while, recently, Swart et al. (2018) identified 56 species of predatory brachyuran crabs spreading outside their native ranges. Their mobility leads to high avoidance, distribution and dispersal abilities, which are advantages when exposed to local environmental stress. Connectivity, and life-history traits such as reproductive strategies and behaviour, are thoughtfully proposed as vectors for brachyurans invasive success and further analysed in this review. Plasticity can be shaped adaptively in populations that evolve in a variable environment (Huang and Agrawal, 2016), by allowing differential genotype expression and increased tolerance to wider ranges of environmental conditions. Therefore, plasticity is also advanced as a hypothesis for invasive capacity in these highly mobile species. Adaptative plasticity, as alterations in behaviour, morphology, or physiology in response to a distinctive environment (Price et al., 2003), highlights the importance of understanding the adapting mechanisms and traits that allow introduced crab populations to become truly invasive.

In fact, most traits attributed to invasive crab species lack confirmation by comparison with their native counterparts and have been poorly studied regarding “native *versus* NIS” integrative scenarios. The two available *meta*-analysis on crab bioinvasions and traits (Brockerhoff and McLay, 2011; Swart et al., 2018) encountered several bottlenecks (further discussed in Section 5). Since some of the traits that so often characterize efficient invaders can also be found in native species, this review compiled applied examples on crab plasticity, identifies key gaps in our knowledge, and highlight future research priorities towards holistic, integrative approaches as multi-level and multi-stressor methods addressing life-history, functional or physiological traits at several levels of biological organisation. These comprehensive approaches will potentially allow a mechanistic understanding of invasive success since, as mentioned by Donelson et al. (2019), compartmentalization of responses is an oversimplification that probably doesn't meet reality.

2. Methods

An extensive amount of literature providing a background on the

mechanisms that influence bioinvasions in coastal and marine organisms was analysed throughout this review, including brachyuran traits such as reproductive biology, connectivity, behaviour, tolerance and plasticity, and responses under environmental stress. There is an effort to understand crabs' ecophysiology through research lines such as global warming, ocean acidification, salinity shifts, or pollution, and, therefore, the traits allowing them to become conspicuous invaders are directly or indirectly addressed. Nevertheless, knowledge is still lacking regarding integrative scenarios and native *versus* NIS dynamics. Not intending to be a *meta*-analysis, a brief survey was carried to gauge the latest research efforts on native and non-native invasive crabs and pinpoint the current application of integrative approaches or the need to do so. This analysis was focused in research articles published between 2000 and 2019 in major scientific databases (Science Direct and Web of Science) dealing with environmental tolerance within brachyuran crabs.

A conceptualization was developed where integrative approaches are proposed as indicative tools of more realistic ecological scenarios, and significant solutions to forward knowledge on plasticity contribution to invasive success, further facilitating environmental management and policy making.

3. Mechanisms and life-history traits in invasive brachyuran crabs

Brachyuran crabs share several mechanisms with most invasive aquatic species: high reproductive rates associated with *r*-strategies, opportunistic behaviour such as eurytopy and polyphagy (Gothland et al., 2014; Kenworthy et al., 2018; Varó et al., 2015), early maturation (Kolar and Lodge, 2001), and synergistic association with humans (Hufbauer and Torchin, 2007; Sakai et al., 2001). They also have planktonic dispersal and the ability to survive in wide ranges of biotic and abiotic conditions (habitat, feed, and environmental conditions). The highly invasive Asian shore crab *Hemigrapsus takanoi*, for instance, exhibits a short life-cycle through fast growth, early sexual maturity, and high adult mortality: these features, combined with high fecundity and high dispersal ability, are coincident with *r*-selected strategy which would explain its success (Gothland et al., 2014). However, some of these traits are shared by native or underperforming introduced species. Therefore, the potential to attain a successful invasion also lays on other factors, such as the features of the invaded habitat (Byers, 2002), abundance of suitable prey (Karlsson et al., 2019), and propagule pressure - which is the power of continuous inoculation, i.e. the amount of individuals that are introduced (Blackburn et al., 2011; Kolar and Lodge, 2001; Simberloff, 2009). These factors are included in several proposed theories and hypothesis (Table 1) focusing on the mechanisms that allow species to become invasive. These hypotheses are not mutually exclusive neither universally valid, as the mechanisms that they describe can occur simultaneously.

The diversity and multiplicity of these hypothesis provide further insights on the influence of environmental context and how NIS success may be determined by biological characteristics (Cardeccia et al., 2018), acclimatization capacity and phenotypic plasticity (Tepolt and Somero, 2014), the typology of the introduction vector and recipient area (Brockerhoff and McLay, 2011), or the relationship with the surroundings (e.g. native and human communities). When considering crab species, three main life history traits seem to play important roles on invasive potential: reproductive strategies, early-life stages and connectivity, and behaviour.

3.1. Reproductive strategies

One of the most efficient strategies to warrant NIS dominance in invaded areas is the investment in reproduction and recruitment, especially at the range edge (Wassick et al., 2017). Even if survival rates are low, invaders will deliver relevant amounts of new individuals to the habitat - a clear example of *r*-strategy, presenting several recruitment

Table 1
Proposed theories/hypothesis on invasion mechanisms.

Name	Description	Focused in	References
<i>Preadaptation</i>	NIS are already equipped with the features that allow them to thrive in the new environment	Species	Hufbauer and Torchin, 2007
<i>Novel weapons hypothesis</i>	NIS introduce new biochemical compounds for which native species have not evolved adaptations and therefore are defenceless against	Species	Callaway and Ridenour, 2004
<i>Invasional meltdown</i>	New invaders are aided by the NIS already present in the system, in a process of mutualistic invasion	Species/habitat	Hufbauer and Torchin, 2007
<i>Empty niche</i>	NIS capitalize resources (including space) that native species abandon or use deficiently	Species/habitat	González-Ortegón et al., 2010; Hufbauer and Torchin, 2007
<i>Enemy release</i>	NIS abandon their native regulators (predators, parasites, and competitors) and the pressures of the native range are reduced when they arrive into the new habitat	Species/habitat	Hufbauer and Torchin, 2007; Schultheis and MacGuigan, 2018
<i>Increased competitive hypothesis</i>	In the absence of the selective pressures from their native range, NIS route their energetic demands into growth and reproduction in the invaded areas, and are more efficient than their native counterparts	Species	Blossey and Notzold, 1995

every year or a continuous spawning activity (Forsström et al., 2018; Gothland et al., 2014; McMahan, 2002). Consequently, propagule pressure is the most prevailing life-history trait in successful invaders (Sakai et al., 2001; Simberloff, 2009). It is the case of *Hemigrapsus takanoi*, which takes advantage over *Carcinus maenas* through less conspecific cannibalism and an extended recruitment period (Geburzi et al., 2018). *Hemigrapsus* spp can generate 5 to 6 recruitment events per year and as much as 10,000 eggs per brood (Gothland et al., 2014), while *Callinectes sapidus* may produce up to 7 clutches over 1 to 2 spawning seasons (Darnell et al., 2009). The European green crab, *C. maenas*, can show a highly variable regional output, ranging from two recruitment events per year to a less common continuous presence of ovigerous females (Best et al., 2017). High propagule pressure also allows invaders to reach higher densities, even if underperforming (McMahon, 2002), or to occupy emptied niches after catastrophic events such as floods or hurricanes (González-Ortegón et al., 2010), as described in the empty niche theory (Table 1). There are hints that reproductive output may be enhanced in invaded areas as observed in the invasion of southeastern USA by the green porcelain crab *Petrolisthes armatus* (native from South America, Wassick et al., 2017). In the same study, another advantageous NIS trait was described – smaller size at maturity, i.e. early maturity. This trait is shared by the conspicuous invasive *Hemigrapsus takanoi*, which reaches maturity with a carapace length as small as 5.1 mm (Miyajima and Wada, 2017). Some brachyurans also feature the ability to store male spermatophores in a morphological apparatus named spermatheca: *Carcinus maenas* were shown to do it for 4 1/2 months or longer (Broekhuysen, 1936). Also, *Hemigrapsus sanguineus* and *Callinectes sapidus* females are able to store sperm and produce up to two and seven broods (respectively) from a single copulation (Anderson and Epifanio, 2010; Darnell et al., 2009). These features may result in enhanced fecundity or reproductive

advantage through faster establishment of the invading population, thus contributing to propagule pressure.

Flexibility in the timing of the reproductive events is also described for invading decapod crabs such as *C. maenas* and *P. armatus* (Best et al., 2017; Wassick et al., 2017). It enables NIS to better adapt to new habitat dynamics such as environmental pressure or intra- and inter-specific interactions (Lee et al., 2018), for instance, by shifting reproductive events along the year and, therefore, avoiding synchronous recruitment events with native species and competition over resources and predation pressure on early life stages. The aforementioned flexibility in *C. maenas* reproductive timings allows this species' recruitment events to occur during the most favourable season, with larvae facing less stressful conditions than adults along the year (DeRivera et al., 2007). Despite the paramount importance of this reproductive plasticity, i.e. the species ability species to shift between reproductive methods and strategies, it is often a disregarded trait in literature, at least for marine invertebrates. Thus, it should be consistently studied in the future in order to assess the extension of the effect of differential reproductive strategies in the overall success of NIS.

3.2. Early life-cycle stages and connectivity

The release of pelagic offspring into the water column, which is subjected to further dispersal and recruitment, is part of the life-history of many marine organisms, including benthic species (Brickman, 2014) such as brachyuran crabs. This process carries advantages and disadvantages to organismal life dynamics, as carefully revised by Pechenik (1999). It seems that species with shorter or even absent larval phases may show a faster invasion rate, mainly due to consecutive population establishment and adaptation at regional scales (Brickman, 2014). Also, it is acknowledged that the vast majority of produced eggs and larvae do not recruit after the drift process due to extrinsic pressures such as advection, predation, and starvation (McEdward, 1995). Larvae tend to exhibit narrower physiological tolerances than adults (DeRivera et al., 2007), reinforcing the idea that abiotic control can occur in early life stages (also applying to NIS). Nevertheless, crustacean early life-stages mortality may be lower than once hypothesized (White et al., 2014) as they seem to display several adaptation mechanisms (Brown et al., 2018; Epifanio and Cohen, 2016). They may reduce the instar sequence and produce larvae with hyper regulatory capacity (Paula et al., 2001), or adjust to abrupt transitions and stressful conditions of the receiving waters by extending the time in plankton until suitable settlement sites are found (Grosholz and Ruiz, 2009). In fact, the invasive *Hemigrapsus takanoi* and *Hemigrapsus sanguineus* larvae have shown remarkable tolerance to wide salinity and temperature ranges (Araujo et al., 2017; Cohen et al., 2015). Also, as observed by Cohen et al. (2015), larvae from *H. sanguineus* had similar swimming behaviour as those observed in successful native species under similar environmental conditions, being consistent with transport out of the estuary, growth in coastal areas through dispersal, and then return to the adult coastal/estuarine habitat, a clear example of the preadaptation theory (Table 1, Hufbauer and Torchin, 2007). Given the ability to control horizontal and vertical transport, further predictive studies on recruitment modelling should be considered, also regarding NIS.

Besides anthropogenic accountability, other human-independent dynamics such as dispersal through environmental forcing and/or rafting also influence species' colonisation and connectivity. Marine and coastal populations range from entirely closed, self-sustaining populations (e.g., endemic island species) to fully open populations (e.g. recruiting back only a relatively small proportion of offspring; Spoungle et al., 2002). The maintenance of adult populations requires replacement by recruits, and connectivity (the linkage by propagule exchange - both demographic and genetic) within marine meta-populations depend upon the spatial pattern of replenishment. Encompassing numerous possibilities of attaching to floating debris (e.g. seaweed, wood fragments, and plastic litter), rafting has also been

hypothesized as an efficient vector of dispersal, colonization, and NIS connectivity (Campbell et al., 2017; Nikula et al., 2010; Rech et al., 2018), and facilitate marine organisms' transportation, independently of life-stage or its duration. Recent observations of the crabs *Planes minutus* and *Liocarcinus navigator* rafting on floating macro-litter highlight the role of plastic and other anthropogenic debris as rafts for dispersal across marine waters, a problem that may be enhanced through time (Tutman et al., 2017). In fact, Brickman (2014) showed that this mechanism may be responsible for both short and long time-scale species dissemination, along with oceanic currents.

The conceptual invasion model is the one where propagules drift and subsequently establish themselves as population – i.e. a cycle of spawning (or rafting), settlement, establishment, and growth (Brickman, 2014) – beyond their historical range limits (DeRivera et al., 2007). Species with larger native areas have more source populations, increasing their likelihood of being transported elsewhere (Zerebecki and Sorte, 2011). As mentioned before, propagules may also provide new genotypes (Darling et al., 2014; Simberloff, 2009). Intrinsic factors such as genetic inheritance play a major part in species' adaptation capacity to wider environmental ranges. Depending on the frequency and intensity of the connectivity, local populations will display varying degrees of genetic similarity as well as records of invasive history and genetic differentiation. Tepolt et al. (2009) observed high connectivity in the invasive *Carcinus maenas* due to conservative genetic features amongst populations (bottleneck effect). Yet this low genetic diversity did not prevent *C. maenas* ability to successfully establish and spread on the west coast of North America. Evolutionary phenomena such as hybridization (Hufbauer and Torchin, 2007) or natural selection also occur, transmitting higher tolerance genotypes to further generations, and increasing invasive species potential for survival and adaptation (Kenworthy et al., 2018). There is genomic evidence for hybridization in *Carcinus* spp. invasions in Japan (Darling, 2011) and Canada (Jeffery et al., 2017), Japanese mitten crabs (*Eriocheir japonica*) in Europe (Hayer et al., 2019), and occurring naturally between two snow crab species: *Chionoecetes japonicus* and *Chionoecetes opilio* in Korea (Kim et al., 2012). At the edge of species' geographic ranges in particular, demographic factors and processes such as gene surfing and genetic stickiness may result in mean displacement of genes outpacing mean larval dispersal (Darling et al., 2014). Along with the development of molecular techniques, an increasing number of genetic studies offered important insights into connectivity and invasion histories of local populations of aquatic organisms such as *Carcinus maenas* (Darling, 2011; Tepolt et al., 2009) and other brachyuran species (e.g. Blakeslee et al., 2017; Nikula et al., 2010). Genetic confirmation would also play a key role in invasive species early life stages detection in the water column (Forsström and Vasemägi, 2016; Pie et al., 2006) – as has been shown in the Gulf of Cadiz, where Marco-Herrero et al. (2017) identified the introduction of a newly pea crab (brachyura) through DNA barcoding. Molecular approaches are also promising tools to identify donor regions, as most biological invasions history remains unsolved due to lack of detailed information (Swart et al., 2018).

3.3. Behaviour

Behaviour is becoming a prevalent explanation for invasion success, since it shapes responses to environmental stress (Nagelkerken and Munday, 2016) – e.g. linking early, sensitive responses to stress at sub-individual levels and long-term, ecologically relevant responses at the supra-individual levels in ecotoxicology (Amiard-Triquet, 2009) – and plays a part in the vast majority of invasion processes (Sol and Weis, 2019). Some species do not rely solely on tolerance to environmental factors to become invasive or mitigate biological invasions but are also territorially competitive (e.g. NIS *Carcinus maenas* over native *Cancer magister* in McDonald et al., 2001), aggressive towards other inhabitants (e.g. Hobbs et al., 2017; Hudina and Hock, 2012), or associated with high levels of boldness (e.g. Pintor et al., 2008). Other types of

organismal behaviour may influence the success or failure of propagules upon arrival, and in decapod crustaceans it includes predation plasticity and shifting target preys, predator recognisance and avoidance, habitat use, and learning/memory-related behaviour (Weis, 2010). In the USA, larvae of the invasive *H. sanguineus* behaved differently in response to chemical cues from potential fish predators in comparison with larvae of the native mud crab *Dyspanopeus sayi* (Araujo et al., 2017) which could give them advantage upon invasive scenarios, despite the early life stage. Interspecific competition is key to native and NIS resilience. Curiously, even species with invasive potential and a track record of detrimental effects on population dynamics around the globe have been affected in the presence of other NIS in their native range. In the Dutch Delta, for instance, the native *C. maenas* population seems to be down-regulated in areas where invasive *Hemigrapsus* spp. densities are high (van den Brink et al., 2012; van den Brink and Hutting, 2017). Despite being a smaller species, *Hemigrapsus* showed stronger competitive behaviour towards reproduction, shelter, and food. The opposite also happens since native species can mitigate or show some degree of “biotic resistance” upon NIS arrival: it was found that abundance distribution of a *C. maenas* invasive population in Chesapeake Bay (NIS) was limited by high abundances, and presumable predation and aggressiveness, of the native *Callinectes sapidus* (DeRivera et al., 2005).

Individual “personality”, an emergent proxy amongst behavioural studies, is assumed to contribute not only to competitive advantages of individual organisms but also having population and community effects at longer temporal scales (Wolf and Weissing, 2012). It encompasses aggressiveness, sociability, and willingness to explore (e.g. *Panopeus herbstii* in Belgrad and Griffen, 2018). Consequently, it is an important proxy in biological invasions (Carere and Gherardi, 2013) since the existence of individual variation in behavioural types within a population might be highly relevant to understand how animals negotiate the different stages and sequential filters of the invasion process (Wong and Candolin, 2015). Thus, generalized assumptions upon invasiveness and interspecific dynamics cannot be easily accepted. Behaviour may be determinant to NIS success or failure in a newly occupied ecological niche, in addition to specific environmental plasticity or performance.

4. Traits to plasticity: Crab responses to environmental changes

The life-history mechanisms mentioned previously, supported by the principles mentioned in Table 1, highlight that dynamics leading to success are diverse and owe to trait-related responses. As mentioned by Whiteley (2011), species likely to be more tolerant to environmental stress are those currently inhabiting fluctuating environments – which is the case of coastal and estuarine crabs.

Carcinus maenas proven ability to tolerate broad salinity, pH, and temperature ranges (Fowler et al., 2011; Hudson et al., 2018), for instance, is a shared crucial feature amongst inhabitants of extremely variable and potentially stressful intertidal and estuarine areas. This species' larval stages were able not only to survive but to successfully develop in low salinity and temperatures between 10 and 22.5 °C (DeRivera et al., 2007), which may explain their success spreading through the North American coastline (Preisler et al., 2009). Blue crab (*C. sapidus*) juveniles were able to grow and moult at temperatures ranging from 15 °C to 30 °C and salinity as low as 3 g/L (Cadman and Weinstein, 1988). The crab *Charybdis japonica*, a NIS in New Zealand, survived in a broad range of temperatures and salinities as early in its ontogeny as Stage I larvae, demonstrating its ability to endure that country's natural conditions (Fowler et al., 2011). *Hemigrapsus sanguineus* showed resilience to rapid intertidal salinity changes, and capacity of physically moving to a near optimal salinity – which enhances their competitiveness as invader (Hudson et al., 2018). In France, Piscart et al. (2011) observed that both native and non-native macroinvertebrate species from the same taxonomic group (including crustaceans) from Eurasia had very similar salinity tolerance but species from outside Eurasia (introduced by ballast or drinking water on ships) were more

salt-tolerant. This denotes the potential of non-native species to survive translocation and colonize distant habitats through preadaptation, which seems to be the case of the *trans*-Atlantic invasive success of *H. sanguineus* (Blakeslee et al., 2017).

Thus, not only tolerance but plasticity ought a significant input to invasiveness. If during pre- and post- establishment, NIS have to pass through a series of abiotic filters to become introduced, then invasive (see Blackburn et al., 2011), then one of the most powerful approaches for examining intraspecific sensitivities is invasion biology (Tepolt and Somero, 2014). The study of bioinvasions has the potential to address interspecific plasticity to environmental factors such as increasing temperature and ocean acidification, changing salinity and oxygen levels, and chemical pollution (single or in combination), even in concomitant populations. It also encompasses the mechanisms supporting current distributional patterns, where the most vulnerable species are those unable to overcome the challenges of global changes. Plasticity varies along environmental gradients, whether for native or NIS, or in the impacts of the latter in the first, which brings complexity to this study field. In fact, range width has often been suggested as a general trait of invasive success, with broad physiological tolerance and propagule pressure as main explicative variables acting together or unconnectedly. While extreme differences in environmental conditions might exceed physiological responses or environmental stressors act synergistically, plasticity should become increasingly important to survival as physical-chemical differences narrow (Smith, 2009). It is in this gap, where species with high plasticity prevail under stressful environmental conditions (Fig. 1), that invasive species seem to thrive.

As mentioned by Fox et al. (2019) it is hard to find a study that rejects plasticity as a potential source of adaptation. It has fundamental adaptive value since, while avoiding immediate extinction in new environmental conditions, allows selective pressure to act on introduced populations (e.g. López-Maury et al., 2008). Nevertheless, the proposition that invasive species tolerate a wider range of environments and, consequently, may be favoured by global changes has rarely been empirically tested (Zerebecki and Sorte, 2011). Plasticity might be either activated (costly fast response) or developmental (lower-cost but slower-acting), where the underlying mechanism determines if it is likely to be adaptive on a relevant timescale to global changes (Fox et al., 2019). Also, at the individual level, trade-offs between traits can occur (e.g. Fusi et al., 2016), and are expected to increase proportionally to the projections of multiple global change drivers (Jarrold et al., 2019). To maintain physiological homeostasis during ocean acidification (Pan et al., 2015; Rato et al., 2017), pollution (e.g. Novais and Amorim, 2013; Silva et al., 2017), or thermal stress scenarios (e.g. Kühnhold et al., 2017), energy allocation may occur and reduce adaptive potential (e.g. Diaz et al., 2018).

Although poorly addressed in crab NIS, the multi stressor projections of ocean acidification, hypoxia, shifting food-webs, global warming, and

pollution will potentially result in detrimental trade-offs in the long term. The latter are urgent to address, since realistic effects of raising temperatures and pollution on native and NIS responses can already be inferred, namely before the interference of further long-term organismal acclimation (e.g. Long et al., 2017), evolution (e.g. Reusch, 2014) or inaccurate scenario projections versus reality.

Temperature is one of the most important factors influencing the physiology, ecology, and evolution of marine ectotherms (Nguyen et al., 2011; Pinsky et al., 2019). Eurythermality, or the ability to maintain physiological function over a wide range of temperatures, for instance, has already been proposed as a trait that may be enhanced in invasive crab species. In a comparison between the native *Ovalipes catharus* and the invasive *Charybdis japonica* within New Zealand coastal areas, the latter showed greater plasticity in heart beat duration and mitochondrial membrane integrity when facing higher temperatures (Iftikar et al., 2010), theoretically closer to the “high plasticity” line on Fig. 1. If invasive species have higher physiological plasticity than natives occupying the same thermal habitat, it is likely that increased temperatures associated with climate crisis will exceed native species’ tolerance limits before those of invasive (Zerebecki and Sorte, 2011). This is especially true in intertidal species living near their temperature maxima (Stillman, 2002) - unless they disperse or adjust to the new conditions through plastic or genetic changes. By determining, for instance, which species currently live closest to these upper thermal tolerance limits (e.g. CT_{max} and LT₅₀), studies on invertebrates from thermally stressful habitats have shown that warm-adapted congeners, such as tropical marine ectotherms (Nguyen et al., 2011) are most susceptible to local extinctions. This may be explained because their acute upper thermal limits lie near current thermal maxima, therefore their ability to increase thermal tolerance through acclimation is limited (Somero, 2010). Also, Antarctic stenotherm species, when compared with species from temperate latitudes, have shown poor ability to physiologically acclimate to elevated temperatures, with similar effects to the ones from the tropics (Peck et al., 2014). For the sake of integration, future research should aim at physiological tolerance hypothesis and explore whether the effect of eurytolerance (not only eurythermality), represented in Fig. 1 by the “high plasticity” line, might be a general pattern in invasion success, and occur during NIS pre- or post-establishment (Lejeune et al., 2014).

Water pollution, a concomitant stressor to current thermal changes, impacts biological communities (Kenworthy et al., 2018). It has been hypothesized that some invasive species tend to cope better with it than natives and that, ultimately, may benefit from aquatic pollutants such as heavy metals (e.g. Varó et al., 2015; Bielen et al., 2016). These environmental stimuli may induce beneficial phenotypic alterations in organisms through epigenetic mechanisms, that can be transgenerationally inherited (Granada et al., 2018). In fact, tolerance to pollution has been perceived as heritable in species such as bryozoans (McKenzie et al., 2011) and crustaceans (Vigneron et al., 2019), which may confer adaptive advantages to NIS originally derived from polluted habitats through acquired tolerance whereas native species did not have the time to develop coping mechanisms to pollution.

5. The dichotomy native versus NIS

Despite the overviewed brachyuran plasticity and invasiveness, one can highlight that few studies have focused on the synergistic effects of several stressors on tolerance (e.g. Madeira et al., 2014), and even fewer showed what happens when species with invasive background inhabit or overlap in the same habitat (DeRivera et al., 2005; van den Brink et al., 2012; van den Brink and Hutting, 2017). In Portugal, for instance, where *Carcinus maenas* is a native species, and *Callinectes sapidus* an expanding NIS (Chainho et al., 2015), one should try to predict what would happen upon the arrival of the highly invasive *Hemigrapsus* spp. – not yet identified in Portugal but already in the vicinity of north-eastern Spain and France (Dauvin et al., 2009; Geburzi et al., 2018; Karlsson et al.,

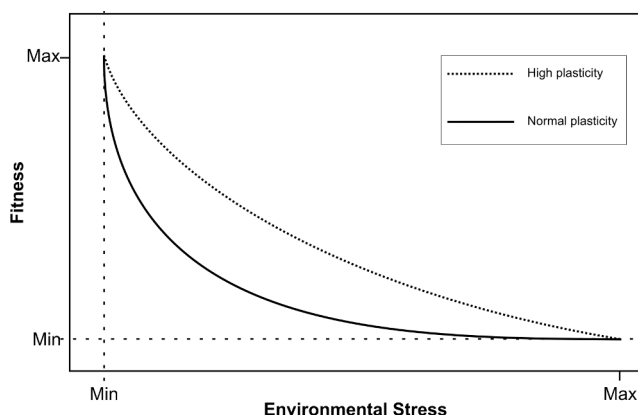


Fig. 1. Plasticity contribution to organism's fitness under environmental stress.

2019). If naturally adapted to environmental heterogeneity, which traits will translate into advantageous fitness and successful population dynamics? What will determine if they perish or thrive, and their further success?

It is often assumed that tolerance to a wide range of environmental factors (physiological tolerance hypothesis; Lejeusne et al., 2014) is a trait that favors the efficiency of biological invaders but has not been tested consistently to assess a clear pattern in the tolerance of successful NIS (i.e. NIS fitted closer to “high plasticity” of Fig. 1), comparing with sympatric native species. It is not clear if this tolerance is a requirement for a successful invasion in marine systems (Lejeusne et al., 2014; McMahon, 2002) since physiology is less discussed in the literature, and studies comparing physiological tolerance of native and non-native crabs that share common habitats are lacking.

Based on the present analysis of publications regarding invasive brachyuran, there is an indication of regional discrepancies in research efforts. This is congruent with the fact that the vast majority of invasive crab species originate from the North West Pacific, but the most affected areas – and therefore the most studied - are the Mediterranean Sea and North America. Simultaneously, very few articles regarding this issue were found for African and South American territories. This discrepancy does not mean that there are no invasive crabs in these less studied continents or that the issue of their physiological tolerance is ignored: this difference is most probably related with reduced funding opportunities for science that are allocated to different research priorities.

Globally, there is a clear dominance of life-history and population dynamics studies, and there seems to be some concern on the response of the invasive crabs’ populations to different stressors. The magnitude of the impacts caused by NIS are correlated with their responses to external pressures. Thus, what affects the dynamics of a NIS population affects its impacts. However, there are few research articles comparing physiological tolerance of sympatric native and non-native invasive crabs. A scaffold of scientific data is already set to impose invasion biology as an important branch of ecological sciences (Blackburn et al., 2011; Gallardo et al., 2016; Katsanevakis et al., 2014; Pejchar and Mooney, 2009; Simberloff et al., 2013) however, and despite the increasing interest about invading brachyuran, very few studies compared native and non-native species, as seen in the publishing tendency on Fig. 2. Recently, a compilation study on predatory marine crabs was undertaken (Swart et al., 2018) but no patterns were identified regarding traits of alien crabs associated with their success, although these were identified in other marine taxonomic groups such as amphipods (Grabowski et al.,

2007). The same authors referred those results as unexpected but suggested one explanation: “(...) limitations in the available literature resulted in nine traits being considered for 28 alien species. Whereas this represents the first time that the traits of crabs have been assessed in such detail, the inclusion of more species and more traits in future analyses may result in the identification of important traits that were not detected in this study (...)”. This conveys the urge to forward knowledge on these species’ plasticity, prioritizing integrative approaches, at several levels of biological organisation, which have the potential to disentangle or enlighten what makes them conspicuous invaders worldwide.

6. Integrative approaches – Indicative tools for better management

In the past decade, the multiple threats to marine ecosystems (whether derived directly or not by anthropogenic activities) have connected ecological studies to the public spotlight and raised environmental awareness, namely biological pollution through bioinvasions. In addition to this trend, ecology has evolved to further quantitative and complex modelling, and to experimental designs, where integrative studies are considered the best ecological approaches (Irschick et al., 2013). These pressing approaches derive from the diversity amongst natural biota, since many invading species share success-related traits. Nevertheless, there are few standard testing trials since researchers adapt biotic and abiotic factors, and the addressed endpoints under the scope of their investigation. Some analytic procedures and endpoints are commonly used, however, as observed by Lejeusne et al. (2014), caution is needed when comparing values between studies or species, as they clearly depend on both acclimation and experimental procedures and can also differ markedly between seasons (e.g. CTmax in *Palaemonetes varians* and *Palaemon longirostris*). Shared traits may be found among native or unsuccessful introduced species across different latitudinal ranges. Also, phenotypic plasticity, genetic diversity and selection, and their interaction with ecological processes of dispersal and migration across a species’ range seem to contribute to species’ responses in the face of environmental change (Fox et al., 2019), which brings further complexity to this study field.

While focusing on brachyuran decapods, this review described numerous study fields that should be further integrated for the sake of crab invasions’ understanding, and knowledge gaps and tools to fulfil them further enumerated. The need of filling the gap between the

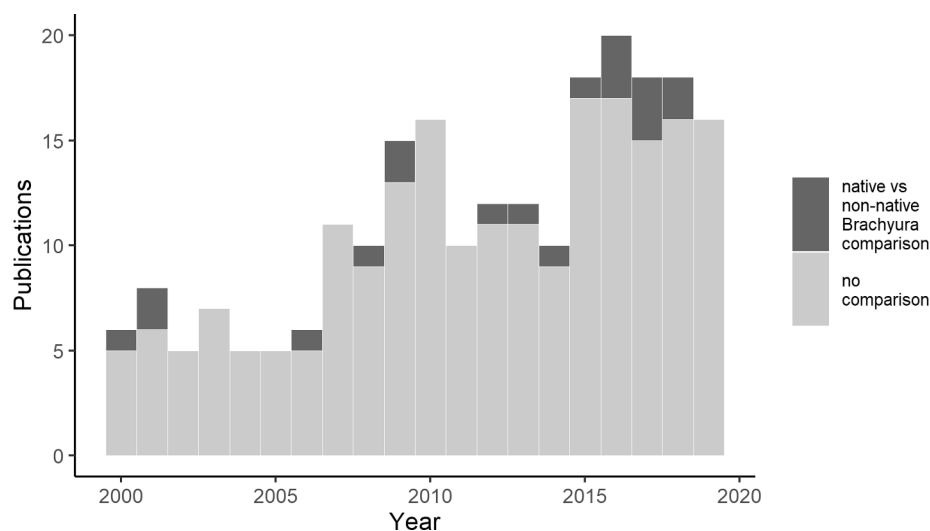


Fig. 2. Number of publications per year, between 2000 and 2019, found in the Science Direct and Web of Science databases, under the keywords “contaminant tolerance invasive brachyuran”, “introduced brachyuran”, “invasive brachyuran”, “invasive brachyuran survival”, “invasive brachyuran tolerance”, “native invasive brachyuran”, and “temperature tolerance invasive brachyuran”.

complexity of the natural world and simpler experimental and chemical analyses that should resemble more holistic, realistic scenarios, is conveyed or lately applied by other researchers (Donelson et al., 2019; Duarte et al., 2020; Fox et al., 2019; Osores et al., 2018; Ricciardi et al., 2010). Tools such as subcellular biomarkers evaluate differential physiological responses (e.g. respiratory and energetic metabolisms, antioxidant and detoxification mechanisms, immune responses) and, therefore, act as early-warning indicator tools of effects at higher levels of biological organisation (Lemos et al., 2010). They provide enough resolution power to detect fine differences among organisms, which may configure the marginal gains of the most fit crab species that may have been overlooked, namely under stressful conditions or living close to the edge of their vital limits. Furthermore, this would help to disclose if NIS possess intrinsic advantages over native counterparts under realistic stress scenarios. Also, molecular measurements of plasticity and “omics” are promising tools to address bioinvasions (e.g. Tait et al., 2018), adaptation capacity, and consequent spread, as lately addressed by several authors (e.g. Gong et al., 2015; Madeira et al., 2014; Storch et al., 2009). Molecular tools are precise enough to reveal how a sequence changes in order to adapt to environmental stress (e.g. temperature) and determine how genomes’ content – protein-coding genes and gene regulatory mechanisms – influence adaptive capacity to acute and long-term stress (Somero, 2010). As pointed in the same publication, a single amino acid replacement is enough to adapt a protein to a new thermal range. Also, proteins with altered expression in a Tunisian *Carcinus maenas* population were linked to moulting, oxidative stress and inflammation, innate immune response, and proteolysis (Ghedira et al., 2016). The epigenetics of marine invasions, for instance, is emerging, namely on marine invertebrates. Shifts in methylation status are associated with the process of colonization of new environments, where the maximum alteration at epigenomic level is expected to occur at the arrival and until the early expansion phase (Ardura et al., 2017). Based on common functional mechanisms to the animal kingdom, biochemical and molecular tools have already been extensively employed in *Carcinus maenas*, invasive worldwide, which was later advanced as a reliable experimental model in ecotoxicology studies (reviewed in Rodrigues and Pardal, 2014).

When applied, the integration of several levels of biological organisation (from sub-cellular to community effects) and study fields (e.g. “omics”, genetics, ecophysiology, ecotoxicology, behaviour, and state of the art ecology like population dynamics), will facilitate the understanding and prediction of the effects of global change crisis and allow better projections on its impacts on species’ fitness, and invasive potential. Also, in committed scenarios of data sharing amongst peers and resulting mechanistic data modelling, integrative studies will be key approaches to clarify the specific mechanisms allowing a specific species to invade and prosper in new geographical areas, and consequently share valuable knowledge with policymakers to the design of management measures or mitigation plans.

7. Conclusions

While biological pollution is a never-ending process that may increase globally as consequence of increasing facilitating vectors, brachyuran crabs are known agents of biodiversity homogenization, modification and engineering of habitats’ physical structure, and reduction of direct competitors (e.g. *Carcinus maenas* in Grosholz and Ruiz, 2009). Despite the possibility of being a valuable fishery resource (Mancinelli et al., 2017), they also have socio-economic impacts due to the attacks on fish, other crustaceans, or bivalves trapped in fishing and aquaculture gear (e.g. *Callinectes sapidus* and *Carcinus maenas* in Garcia et al., 2018; Grosholz and Ruiz, 2009). This raise concerns on the arising effects on stock management, and economically relevant activities such as commercial fisheries and aquaculture in Europe. It is impossible to make an exact and quantitative prediction of the next marine invaders since the answer of how successful a biological invasion will be lays in

the result of the interaction of the species with the recipient habitat. Nevertheless, establishing biological trends is important to better understand and address marine bioinvasions (Brockerhoff and McLay, 2011). Regarding their biology and dynamics, it is essential to increase the amount and quality of the generated data - and integrate it - in order to enhance the prediction ability, and to produce large scale studies easily accessible to stakeholders. This will only be achieved by the organismal study at several levels of biological organization and throughout their ontogeny. Despite predatory crabs are considered globally successful invaders, most studies have been developed through field sampling, which might overlook plasticity and interactional traits, such as specific behavioural, biochemical, or molecular responses. Research work where native and NIS were clearly studied side by side are much scarcer than desirable and are of uttermost importance. Clearly, if only a partial view of the diversity of non-native species and their interaction with native species is available, this compromises our ability to predict what type of organisms can invade, assess what environments and regions are more or less susceptible to invasions, understand invasion patterns over time and space, impair the ability to predict outcomes and interactions at population dynamics and community level as well, and truly assess the real impacts throughout. In opposition to marine, freshwater habitats are more isolated and their invasive dynamics easier to study. Studies demonstrating freshwater species’ traits to invasiveness are already available and, due to its importance, it is now time to test the verisimilitude of the traits globally attributed to NIS on marine biota, through integrative approaches. Specific grounding studies on ecophysiology could feed multi-species, higher biological organization level studies, where potentially significant traits and invasion patterns would not become unnoticed.

CRedit authorship contribution statement

Lénia D. Rato: Conceptualization, Investigation, Writing - original draft, Writing - review & editing. **Daniel Crespo:** Conceptualization, Investigation, Writing - original draft, Visualization, Writing - review & editing. **Marco F.L. Lemos:** Writing - review & editing, Supervision, Project administration, Funding acquisition.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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