1. **The physiology of climate change: how potentials for acclimatization and genetic adaptation will determine ‘winners’ and ‘losers’ (Somero 2010)**

Tropical species are uniformly more heat tolerant than temperate species and, within each latitudinal group, species occurring highest in the intertidal zone have the highest LT50 values. 1

the most warm-adapted congeners of porcelain crabs are further disadvantaged by possessing a relatively small ability to increase LT50 during acclimation (Stillman, 2003) 1.

Congeners found highest in the intertidal zone are most heat tolerant, yet, because of the similarity of LT50 and MHT, they face greater threats from warming than less heat-tolerant subtidal species that rarely, if ever, encounter temperatures near their LT50. 1.

The conjecture that the most warm-adapted species within a genus of marine intertidal invertebrates are likely to be most threatened by climate warming agrees with broad conclusions reached in recent analyses of terrestrial ectotherms from different latitudes (Deutsch et al., 2008; Tewksbury et al., 2008) 1.

Tropical ectotherms are more threatened by climate change than species from mid-latitudes because tropical species live closer to their upper thermal tolerance limits and, in some cases, live at temperatures above those at which physiological processes exhibit their thermal optima. These authors also emphasize that the range of temperatures experienced by an ectotherm may strongly determine its capacity for coping with rising temperatures (Tewksbury et al., 2008). 1.

Many of these species have evolved for over 15 million years under conditions of extreme and stable cold temperatures. As a consequence of their evolutionary histories – and for the mechanistic factors discussed in the final section of this review – animals of the Southern Ocean are remarkably stenothermal. Many endemic species of the Southern Ocean die of acute heat death at temperatures only a few degrees above their normal habitat temperatures. 1.

Moreover, many of these species have extraordinarily narrow ranges over which acclimation can occur (Peck et al., 2009). A study of 13 marine invertebrates from the Antarctic Peninsula found the highest temperatures of acclimation that could be tolerated over periods of months were 1°C to 6°C (Peck et al., 2009). 1.

If these upper temperature limits reflect the genetically fixed abilities of these animals to tolerate high temperatures, some species could be in jeopardy from climate change over the next one or two centuries. 1.

Because different species of fishes and invertebrates exhibit differences in thermal tolerance and capacities to acclimatize, food webs are likely to be impacted because of differential fitness and, thus, mortality in different groups of animals. Furthermore, size and activity level also have a significant effect on thermal tolerance, with smaller individuals of a species having greater heat tolerance than larger individuals, and more active species having higher tolerance than less active or sessile species. Thus, extinctions from warming may lead to altered ecosystem function due to shifts in size and activity levels of the surviving species (Peck et al., 2009). 1.

Although many studies have examined differences in thermal tolerance among conspecifics from different latitudes or altitudes, e.g. the killifish Fundulus (Fangue et al., 2006), kelp crabs (Storch et al., 2009), Drosophila (Hoffmann et al., 2003) and whelks (Kuo and Sanford, 2009). 1.

This patterning of thermal tolerance is a clear illustration of how heat stress varies across latitude as a consequence of interactions between temperature per se and the timing of the tidal cycle (Helmuth et al., 2002; Helmuth et al., 2006; Helmuth, 2009). 1.

The likelihood that these inter-population differences in N. canaliculata were genetically based, rather than consequences of acclimatization, is high because the animals studied were second generation (F2) individuals bred and raised under common garden conditions in the laboratory. The warm-adapted mid-latitude whelks would appear to offer a potential for replenishment or replacement of lower latitude populations that face local extinction from rising temperatures. 1.

The development of these locally adapted populations may be related to the life history of this species, specifically its direct development and limited dispersal capability. In contrast to whelks and other species whose larvae or juveniles have restricted dispersal, species whose larvae spend long periods in the plankton and are distributed over broad ranges of latitude may be less prone to developing locally adapted populations. 1.

Although a number of physiological systems might be instrumental in causing acute thermal death, any physiological system that collapses rapidly at an organism’s lethal temperature is clearly a sufficient cause of death, whether or not other systems are collapsing simultaneously at these same high temperatures. An obvious candidate for a cause of acute thermal death is cardiac function, which for a number of animals has been shown to decrease precipitously as acutely lethal body temperatures are reached (Hochachka and Somero, 2002). 1.

That cardiac function is an important determinant of thermal tolerance and warm-adapted species live nearer their thermal limits than cold-adapted species. Thermal tolerance of Tegula snails found highest in the intertidal zone, e.g. T. funebralis, is several degrees higher than that of lower-occurring congeners (Tomanek and Somero, 1999). 1.

Proteins are a highly temperature-sensitive component of organisms and clear patterns of adaptive variation have been discovered in structural and functional properties of proteins from species adapted to different temperatures (Somero, 2004). 1.

A more challenging problem in adapting to climate change arises for species that have lost genetic information required for life at increasing temperatures as a consequence of long evolutionary periods under highly stable conditions of low temperature. 1.

Three types of lesions in DNA may influence how well an ectotherm will be able to respond to rising temperatures. 1.

* First, when protein-coding genes are partially or wholly lost from the genome, the proteome of the organism is correspondingly reduced in complexity. 1.
* Second, mutations that disrupt open reading frames in protein-encoding DNA (pseudogene generation) cause loss of the corresponding proteins from the organism’s proteome. 1.
* Third, lesions in gene regulatory regions, whether through loss of DNA or mutations in sequence, that eliminate the capacity to regulate gene expression in response to thermal stress could truncate the ability of organisms to adequately modify the phenotype during acclimatization. 1.

1. **Adaptation to a latitudinal thermal gradient within a widespread copepod species: the contributions of genetic divergence and phenotypic plasticity (Pereira *et al* 2017)**

Understanding how populations adapt to heterogeneous thermal regimes is essential for comprehending how latitudinal gradients in species diversification are formed, and how taxa will respond to ongoing climate change. 2.

Adaptation can occur by innate genetic factors, by phenotypic plasticity, or by a combination of both mechanisms. Yet, the relative contribution of such mechanisms to large-scale latitudinal gradients of thermal tolerance across conspecific populations remains unclear. 2.

Although genetic divergence in heat tolerance strongly correlates with latitude and temperature, differences in the plastic response do not. In the context of climate warming, our results confirm the general prediction that low-latitude populations are most susceptible to local extinction because genetic adaptation has placed physiological limits closer to current environmental maxima, but our results also contradict the prediction that phenotypic plasticity is constrained at lower latitudes. 2.

Latitudinal gradients in abiotic factors strongly determine species distributions. Of these factors, temperature is arguably the most important, as its effects are pervasive across all levels of biological organization, from biochemistry of molecular processes to physiology of the whole organism [1–3]. As such, it is expected that organisms adapt to latitudinal gradients by matching their physiological tolerances to the local thermal environment experienced along their range [4]. 2.

Understanding the mechanisms underlying the evolution of thermal tolerance is critical not only for explaining contemporary biogeographic patterning, but also for predicting how climate change and evolutionary adaptation will affect future species distributions [5,6]. 2.

Adaptation is generally defined as a genetically-based change caused by natural selection [7,8]. 2.

Comparative physiology studies involving populations of one species or congeneric species spanning a wide latitudinal gradient have most clearly identified two non-mutually exclusive mechanisms underlying thermal adaptation: innate genetic divergence and phenotypic plasticity [6]. 2.

Divergence of genomic regions involved in thermal tolerance can alter protein expression structure and performance in different environments, affecting individual fitness by natural selection and ultimately leading to fixation of advantageous mutations in populations. This clear link between mutation, gene, function and phenotype, has made studies of genetic divergence appealing and prominent in the adaptation literature [9]. 2.

Although the genetic basis of plasticity remains debated [8,14], it is now clear that plasticity can be under genetic control, specific to certain functions, altered by natural selection [14–16], and hence provide an underappreciated mechanism for adaptation [17]. Common garden experiments have shown that the contribution of plastic responses to thermal tolerance can be equal to or even greater than that of innate genetic divergence [18]. these two mechanisms may interact to impede or promote phenotypic evolution [15,19], or even ecological speciation [20–22]. 2.

Innate genetic responses should correlate with mean environmental temperature [23], while phenotypic plasticity (or performance breadth) should correlate with the amplitude of thermal variability [24] (following the climatic variability hypothesis [25]). Studies of porcelain crabs [26,27] and tropical lizards [28] have shown some support for these hypotheses. Those results imply that warm-adapted taxa from lower latitudes, particularly ectotherms, are most threatened by further increases in temperature because (i) their innate acute thermal limits (LD50 values) lie close to current environmental thermal maxima, and (ii) they have only limited ability to modify heat tolerance through plasticity [6]. 2.

Common garden experiments with populations spanning up to 178 of latitude have shown that survivorship to acute thermal limit decreases with increasing latitude, suggesting that copepod populations are genetically adapted to a latitudinal thermal gradient [32,33]. Transcriptome analysis has shown that expression of orthologous heat-shock proteins strongly differs between a warm- and a cold-adapted population raised in common garden [34], indicating that high inter-population differentiation might facilitate genetic adaptation, via both structural changes in proteins and changes in gene expression. 2.

Previous common garden experiments have shown that populations of T. californicus have evolved genetic differences in their tolerance to acute heat-stress [32,33]. 2.

Across all heat-stress temperatures, northern populations have a lower survivorship than southern populations. 2.

That even relatively mild heat-stress (33 and 348C) will cause some mortality in those populations but not in intermediate or lower latitude ones. Showing significant genetic adaptation across conspecific populations. 2.

Genetic adaptation between populations of the same species is often opposed by gene flow. In T. californicus, there is abundant evidence that gene flow is extremely restricted over the geographical range of the species [38–40]. 2.

While such fixation at early stages of population divergence is likely driven by neutral evolution, this process also affects genes underlying thermal tolerance, such as heat-shock proteins, which contain amino acid substitutions between the thermal-tolerant population of SD and the relatively thermal-sensitive population of SCN [34]. The populations studied here are distributed over a wider geographical and ecological range than previous studies and probably diverged in isolation over thousands or millions of years [42]. In this context, a combination of population demography, long divergence times and selection for alternative thermal regimes has apparently resulted in the accumulation of adaptive genetic differences among T. californicus populations and may explain the large difference in innate thermal tolerance observed here. 2.

Here, we showed that (i) performance curves of split-broods reared at different temperatures show significant differences of survivorship to acute heat-stress (figure 1) and (ii) reaction norms from all populations are positively sloped (figure 2), clearly supporting a significant beneficial contribution of phenotypic plasticity to thermal tolerance. Phenotypic plasticity in thermal tolerance is characterized by an increase both in thermal tolerance (LD50) and in thermal limit (LD10), generally leading to a shift of the whole performance curve to higher temperatures. 2.

These increases in thermal tolerance were not confounded by differential survivorship due to rearing condition (electronic supplementary material, figure S6), indicating that differences in phenotype are indeed caused by developmental phenotypic plasticity rather than selective mortality during development. Moreover, individuals reared at higher temperature show a significantly higher survivorship to acute heat-stress compared with individuals acclimated to the same temperature for 1 day (electronic supplementary material, figure S7), suggesting that developmental phenotypic plasticity can result in much larger effects than short-term plasticity. Yet, changes in thermal tolerance due to adaptive plasticity are only up to 1.348C, much smaller than the 3.838C inter-population difference due to gen- etic adaptation (electronic supplementary material, figure S2). Reviews on thermal adaptation to climate change suggest that plastic factors seem to be more to important than genetic factors [5]. 2.

Interestingly, our results show that the magnitude of phenotypic plasticity differs among populations, resulting in a significant interaction between genotype and environment and in crossed reaction norms (figure 2). This pattern is indicative of some genetic variation in plasticity [13,44], suggesting that populations of T. californicus differ genetically in the plastic response to heat-stress. Although the genetic basis of phenotypic plasticity remains largely unknown, genetic (heritable) variation is the minimal requirement for the maintenance of plasticity by natural selection [8,13,45]. 2.

When alterations in the environment are predictable, such as during global warming, the ability to flexibly and rapidly respond to a new environment will be associated with increased fitness, allowing plasticity to evolve via Darwinian evolution. Recent studies in cichlid fishes have shown that plasticity in feeding morphology is genetically determined and can evolve adaptively via genetic assimilation [16], leading to ecological diversification and eventually to species formation [22]. Our finding of genetic variance in plasticity for thermal tolerance, which has direct consequences to individual physiology and fitness, suggests that phenotypic plasticity may in fact evolve via natural selection and contribute to adaptation to heat-stress. 2.

Heritable clinal patterns for temperature stress resistance have been described in a number of terrestrial invertebrates. Such macro-ecological patterns are hypothesized to reflect both genetic adaptation to higher temperatures characteristic of lower latitude, and/or plastic adaptation to broader temperature ranges experienced at higher latitudes (termed the climatic variability hypothesis; [25]). 2.

In T. californicus, we find a strong and significant correlation of thermal tolerance, as reflected by LD50, both with mean air temperature (figure 3a) and with latitude (electronic supplementary material, figure S5a). These strong correlations between innate thermal tolerance and habitat measurements strongly suggest that mean temperatures experienced by local populations are a major driver of the large latitudinal gradients of thermal tolerance observed in this species. 2.

Studies in other species have shown similar correlation of innate, or environmentally independent, thermal tolerance with latitude (e.g. porcelain crabs [26], marine molluscs [46], amphibians [47] and fruit flies [48]), suggesting that genetic adaptation strongly contributes to large-scale latitudinal gradients observed across species. An emerging implication of latitudinal gradients of innate thermal tolerance across terrestrial insects [49], also supported by our results in this marine copepod, is that warm-adapted populations from lower latitudes are characterized by thermal limits that are frequently experienced in their local environments, suggesting that southernmost populations might be close to their innate adaptive capacity. 2.

The two critical assumptions of the climate variability hypothesis are that there is a gradient between latitude and thermal variability, and that there is a match between this cline and thermal physiological breadth of a taxon [25]. Although there is a clear correlation between latitude and temperature variability throughout the range of T. californicus (electronic supplementary material, figure S8), we do not find a correlation with performance breadth, as reflected by DLD50 (figure 3b), suggesting that phenotypic plasticity does not contribute to latitudinal gradients of thermal tolerance in this species. Our result contrasts with an earlier study using six populations from three similar environments [32], suggesting that broader sampling, a split-brood experimental design, parallel rearing conditions and the careful exclusion of maternal effects are required for appropriate tests of the contribution of phenotypic plasticity in adaptation to large-scale thermal gradients. 2.

The level of microclimate variability, such as the level of sun exposure of tide pools or pool size, varies strongly throughout the species range and can cause strong variation in temperature at finer spatial scales, which would not be recognized in the macro climatic variables used here. Other studies where genetic and plastic factors could be separated also did not show a correlation between latitude and thermal breadth (e.g. in amphibians [50] and in fruit flies [51]), suggesting that the climatic variability hypothesis might not explain the evolution of latitudinal gradients in thermal tolerance in all species and that its generalization to explain such a strong macro-ecological pattern is premature. 2.

Concerning current climate warming, species from lower latitudes are generally considered to be the biggest ‘losers’ of adaptive capacity [6]. Our results from T. californicus suggest that this generalization is only partially true. Although we confirmed that adaptive genetic capacity of southern populations might be limited because thermal limits lie near current thermal maxima, phenotypic plasticity is not more restricted, providing some, yet limited, capacity to accommodate increases in heat tolerance. 2.

1. **Life on the edge: Thermal optima for aerobic scope of sequatorial reef fishes are close to current day temperatures (Rummer *et al* 2014)**

Our results indicate that low-latitude reef fish populations are living close to their thermal optima and may be more sensitive to ocean warming than higher-latitude populations. Even relatively small temperature increases (2–3 °C) could result in population declines and potentially redistribution of equatorial species to higher latitudes if adaptation cannot keep pace. 3.

Species living at extreme latitudes (equator and poles) may be particularly sensitive to global warming because they evolved in a relatively stable thermal environment and are expected to exhibit narrow thermal tolerance ranges (Tewksbury et al., 2008). The thermal range for optimum aerobic performance (thermal optima; Topt) in such species may only span a few degrees, whereas temperate species need to perform over a much wider range of temperatures(Deutsch et al., 2008; Somero, 2010; Nguyen et al., 2011; Sunday et al., 2011). 3.

Furthermore, theory suggests that populations living at thermally stable latitudes (e.g., near the equator or poles) have less capacity for thermal acclimatization (i.e. physiological, anatomical, or biochemical modifications that occur within a lifetime to cope with natural changes in temperature) than populations living in more thermally variable, high-latitude locations (Portner, 2002; Stillman, 2003; Somero, 2010; Neuheimer et al., 2011; Nguyen et al., 2011). 3.

Moreover, there may be no selection pressure to tolerate temperatures outside of what the populations are regularly experiencing. Equatorial populations of marine species are predicted to be especially sensitive to rising temperature because they experience an even narrower temperature range than equatorial populations of terrestrial species (due to the large heat storage capacity of water). In addition, their geographical ranges more closely conform to organismal thermal tolerance limits than the geographical ranges of terrestrial species, especially near equatorial boundaries (Sunday et al., 2011, 2012). Consequently, the 2–3 °C warming of tropical oceans projected to occur by the end of this century due to cli- mate change (IPCC, 2007; Poloczanska et al., 2007; Ganachaud et al., 2011) could have serious impacts on equatorial populations of many marine organisms. 3.

For coral reef fishes, rising ocean temperatures may not be immediately lethal (Mora & Ospına, 2001), but could have significant impacts on individual performance that will ultimately affect population demography and biogeographic distributions (Munday et al., 2008b; Nilsson et al., 2009). For example, an increase in average temperature of 2–3 °C significantly com- promises growth and reproduction of some species (Munday et al., 2008a; Donelson et al., 2010; Pankhurst & Munday, 2011; Rushworth et al., 2011; Zarco- Perello et al., 2012). The mechanistic explanation for the effects on individual performance may be related to how temperature influences O2 uptake, transport, and delivery, also known as oxygen- and capacity- limited thermal tolerance (OCLTT) (Portner, 2001; Portner & Knust, 2007; Portner & Farrell, 2008; Elia- son et al., 2011). 3.

The physiological scope for aerobic performance (aerobic scope), calculated as the difference in O2 consumption between resting and maxi- mal performance (Fry & Hart, 1948; Priede, 1977), represents the oxygen available – in excess of that required for basic maintenance of the organism – for activities essential to support biological fitness (e.g., activity, feeding, and reproduction). In principle, a species may perform optimally at a particular temperature (Topt); above or below Topt, the aerobic scope narrows and therefore performance falls (P€ortner & Farrell, 2008). 3.

For example, aerobic scope may be reduced by as much as 65% in tropical reef fishes acclimated to temperatures only 2 °C above their Topt (Nilsson et al., 2009; Gardiner et al., 2010; Johansen & Jones, 2011). Temperature- induced reductions in aerobic scope have ecological consequences because less energy is available for vital life history processes that shape population dynamics and community structure (Portner & Peck, 2010). 3.

Many species also have large geographical ranges that span temperature ranges that are greater than the projected increase in ocean temperature due to global warming (Munday et al., 2008b). This suggests that populations are acclimatized or adapted to their local thermal environment along a latitudinal gradient. Adaptation to the very narrow equatorial temperature range may cause equatorial populations of reef fishes to be far more sensitive to global warming than populations of the same species from higher latitudes. 3.

Equatorial populations of four of the six species investigated in this study appear to be living at or above their optimal temperatures for aerobic performance. 3.

One species, A. polyacanthus, was unable to survive short-term exposure to 34 °C. This species is a direct developer, which is not the norm among reef fishes, and is known to exhibit strong genetic structure among populations (Bay et al., 2008). Consequently, A. polyacanthus populations may exhibit stronger local adaptation of their critical thermal limits than other species, leading to a very steep decline in performance at the higher temperatures. Aerobic scope has been classically referred to as a proxy for individual performance (Fry, 1971); although, potential limitations with this idea have been outlined in a recent review (Clark et al., 2013). Still, the significant tempera- ture-induced reductions in aerobic scope observed here in all species at 3 °C above current-day temperatures may be expected to have ecological consequences because less energy may be available for vital life history processes such as growth, reproduction, and predator-prey interactions (Portner & Peck, 2010). 3.

Our results suggest that equatorial populations may have optimized the rate functions that sustain metabolism to within or below the narrow temperature range they experience annually (27.9–31.3 °C). Within this range, resting O2 consumption rates (a proxy for basal metabolic needs) remain low, while maximum O2 consumption rates remain high. Beyond this temperature range, however, an increase in M˙ O2Rest, a decrease in M˙ O2Max, or both contribute to decreasing aerobic scope by 39–72% for four of the species we investigated. 3.

When M˙ O2Rest increases with temperature, the minimum energy required for basal maintenance of the organism is increased. In two of the damselfish species investigated here, the increase in M˙ O2Rest between 29 and 34 °C was dramatic (Q10 = 7.2, 4.8, Table 1).In other words, at 34 °C, over twice as much energy is required for these species to maintain routine metabolic processes than at 29 or 31 °C. Interestingly, this occurred in these two species with little change in M˙ O2Max. 3.

If tropical fishes are locally adapted to their thermal environment, do not regularly experience temperature fluctuations, and do not move far from these microhabitats, there would be no drive to possess such metabolic compensation. Therefore, the surprise might actually be the species exhibiting a Q10 of ca. 2. For example, D. melanurus held at 34 °C exhibited a moderate 45% increase in resting metabolic rates (Q10 = 2.1, Table 1); however, M˙ O2Max decreased such that no differences could be detected between M˙ O2Rest and M˙ O2Max and aerobic scope neared zero (Fig. 1b, 2b). Thus, in D. melanurus, the sharp decrease in M˙ O2Max contributed more to the diminished aerobic scope at 34 °C than the increase in M˙ O2Rest. 3.

As M˙ O2Max was largely temperature-dependent. The behavior and functional role of each species on the reef will dictate at which level saving energy will be most important. For example, the trade-off for some species may a loss of maximum aerobic performance to save energy at rest, whereas others may survive increased costs at rest as long as they can maintain maximum aerobic performance. It is therefore important to investigate both the trends in resting and maximum metabolic rates and each species’ behavior and functional role within its ecosystem when interpreting what is driving declines in their aerobic scope. 3.

It may be that A. polyacanthus, especially equatorial populations, will be especially vulnerable to ocean temperatures projected to occur by the end of this century. Our result show that the Topt for aerobic performance may closely resemble local temperature ranges for equatorial populations, but may also indicate that the area is not comprised strictly of equatorial specialists. 3.

First, all three populations seem to have approximately the same mean temperature range for optimal performance despite 21° of latitudinal separation (Fig. 3). Second, the optimal performance range only closely matched the range of summer temperatures experienced for the equatorial populations; whereas, the optimal performance range extended beyond local temperature maxima for higher latitude populations. At Heron Island, the site at the highest latitude, optimal performance ranges exceeded the maxi- mum summer temperature experienced in all but one species. Similar patterns have been described for terrestrial ectotherms, and suggest that, indeed, low latitude species are already living close to their thermal optima and will be most vulnerable to a changing climate (Deutsch et al., 2008; Tewksbury et al., 2008; Nguyen et al., 2011) if adaptation cannot keep pace with increasing temperatures. 3.

climate change increases in sea surface temperatures may even enhance fitness in high latitude populations. 3.

The similar optimal performance range among populations may suggest a lack of local adaptation in aerobic scope; however, our latitudinal comparisons did come with several assumptions, and there are alternative conclusions (Data S1). For example, because aerobic scope declined at temperatures lower than the highest experimental temperature used in the current study (34 °C), we assume we captured the upper limits to aerobic performance for the species we investigated. For some of the Lizard and Heron Island populations, however, the variation around the mean of the optimal performance range extended to the maximum experimental temperature (33 °C), suggesting that the upper thermal limit for aerobic performance could be even higher and therefore the optimal performance range broader in some of the high latitude populations. Furthermore, high latitude populations might be adapted to a greater range of seasonal temperatures that they would normally experience compared with low latitude populations, leading to improved capacity to perform at a range of temperatures, including higher temperatures outside the normal range experienced. This could produce an apparent mis- match between the average temperatures experienced in high latitude populations and the temperatures where aerobic scope is greatest. Consequently, our results could indicate that reef fish populations are more closely adapted to seasonal temperature variations than they are to the average temperatures they experience. 3.

Due to less thermal variability and thus, narrower thermal safety margins, the impact of global warming on coral reef fishes could be the greatest at low latitudes. If adaptation cannot keep pace with climate change, even relatively minor ocean warming (2–3 °C) could result in population declines and potentially the redistribution of equatorial populations to higher latitudes (Nilsson et al., 2009; Nguyen et al., 2011; Sunday et al., 2012). Thermal acclimation (plasticity) may assist some species and populations in coping with future temperature increases; however, thermal performance ranges of stenothermal (e.g., tropical, low latitude, polar) species are expected to be less plastic than eury- thermal (often temperate) species (Nguyen et al., 2011). Previous data exist to support minimal short-term capacity for acclimation in adults of two of the species we investigated, A. polyacanthus and P. moluccensis (Nilsson et al., 2010; Donelson et al., 2011). However, there could be an ontogenetic or trans-generational component, which may be more relevant to keeping pace with the rate of change occurring due to climate change. 3.

Exposure to elevated temperatures during the early stages of development may condition enzymatic processes to operate more efficiently later as adults (Nilsson et al., 2010), but there may be a cost at the level of diminished growth rates (Munday et al., 2008a; Donelson et al., 2011). 3.

If aerobic scope is closely linked to individual performance (Portner & Farrell, 2008; reviewed in Clark et al., 2013), then declines in this trait could have implications for long-term sustainability of equatorial fish populations and could drive a range shift of species away from their equatorial boundary (Munday et al., 2008b; Nguyen et al., 2011; Sunday et al., 2012). 3.

1. **Adaptive phenotypic plasticity and local adaptation for temperature tolerance in freshwater zooplankton (Yampolsky 2014)**

Among abiotic factors that affect living organisms, temperature plays a unique role because of its profound effect on the organisms’ biochemistry and physiology through fundamental physical and chemical constraints [1,2]. Most species experience daily or seasonal temperature changes and are generally assumed to have temperature ranges in which they perform best, whereas exposure to temperatures outside this range has costs [1,3,4]. Many poikilotherms experience enormous daily and seasonal variation in temperature, which will select for minimizing the fitness costs associated with the exposure to suboptimal temperatures. Selection for tolerance to suboptimal temperatures may take two forms of evolutionary responses: phenotypic plasticity or local adaptation. 4.

In local adaptation, on the other hand, populations show genetic differences for temperature tolerance corresponding to location-specific temperature variations, e.g. local mean or maximum temperature [7–11]. Local adaptation and phenotypic plasticity may evolve together [12–16] and it is often difficult to disentangle their relative contributions [13,17,18]. Furthermore, phenotypic plasticity may also adapt locally. It has been suggested that the interplay between plastic response and local adaptation with regard to temperature will be key in determining the fate of species and populations exposed to global temperature increase [9]. 4.

How a species copes with such strong environmental variation is a key question. If it copes only by phenotypic plasticity, then global temperature changes within the plastic tolerance range will not threaten the survival of local populations. However, if populations show a signature of adaptation to local temperatures, then global warming will put local populations under stress. It is therefore necessary to conduct studies that allow us to disentangle local adaptation and phenotypic plastic response to temperature. 4.

We also found a strong signature of local adaptation, with clones from warmer climatic backgrounds having higher tolerance. 4.

In selection experiments, different temperature regimes can quickly shape genotype composition, life-history traits and temperature tolerance in Daphnia [56–58]. 4.

We observed that a high tolerance to temperature correlates with the average high air temperature of the warmest month at the site of clone origin, suggesting that D. magna from warmer climates are able to tolerate a lethal temperature longer than those from colder climates, even though all animals were pre-acclimatized in the laboratory to the same temperatures. 4.

Furthermore, D. magna is known to exhibit extensive gene flow and very little geographical structure across Europe [59], making it unlikely that temperature tolerance reflects common ancestry. Thus, we strongly believe that the described pattern of high temperature tolerance is the result of local natural selection. 4.

However, we uncovered a further effect: the upregulation of haemoglobins during acclimatization to higher temperature revealed significant genotypic variation (table 4 and figure 3) in which some clones acclimatized to 288C did not respond by increasing haemoglobin, whereas others increased it three- to fourfold. The strength of this upregulation correlates positively with temperatures at the sites of origin (figure 3), suggesting that plasticity in upregulation of haemoglobin might be locally adapted. 4.

Daphnia magna from cold climates are able to acclimatize to high temperatures equally well as D. magna from warm climates, but without upregulation of haemoglobin. Thus, haemoglobin upregulation is not the only, or perhaps even not the most important, mechanism of heat acclimatization in this system, and there are apparently different mechanisms that Daphnia from different climatic regions use to differing degrees. 4.

An obvious speculation is that haemoglobin synthesis is costly. Selection, therefore, should favour plasticity in haemoglobin expression in habitats with variable temperatures (i.e. in seasonal environments), and constitutive expression in more constant habitats (less seasonal environments). This is opposite of what we found. Northern populations undergo extreme seasonal fluctuations but show the least plasticity in haemoglobin expression in our study. It has also been suggested that the higher visibility of haemoglobin-rich Daphnia is costly in the presence of visual fish predators so that haemoglobin production should be avoided as much as possible in habitats with such predators. Again, this is not in line with our findings. Our northern Daphnia populations all come from fishless ponds, whereas the more southern populations differed widely in this respect. The costs of over-expressing haemoglobins at low temperatures may also include other factors than the direct metabolic costs of haemoglobin synthesis. For example, overexpression of haemoglobin may cause an over- supply of oxygen to tissues in normoxic conditions. Indeed, heat-acclimatized Daphnia were found to perform worse than cold-acclimatized ones at lower temperatures [51], but it is not clear if the higher haemoglobin level in the heat-acclimatized animals caused this result. 4.

Thermal acclimatization and local adaptation are believed to determine the fate of species facing climatic change [9,73]. We demonstrated that high temperature tolerance in geographically diverse genotypes of D. magna shows evidence for local, climatically determined adaptation. Animals from warmer climates show tolerance, but also higher plasticity for haemoglobin upregulation. This raises questions about the mechanisms and costs of such adaptation and about the species’ ability to evolve to new conditions, which will be important for predicting the evolutionary response of plankton to rising temperatures. 4.

1. **Elevated temperature reduces the respiratory scope of coral reef fishes (Nilsson *et al* 2009)**

Populations of thermally tolerant species are likely to persist at higher temperatures, but populations of thermally sensitive species could decline on low-latitude reefs if individual performance falls below levels needed to sustain viable populations 5.

Tropical organisms are expected to be particularly sensitive to elevated temperatures because they inhabit a relatively thermostable environment (Huey & Hertz, 1984; Bush & Hooghiemstra, 2005; Hoegh-Guldberg et al., 2007; Tewksbury et al., 2008). 5.

Changes of a few degrees Celsius can influence the physiological condition, developmental rate, growth rate and reproductive performance of fishes (Wood & McDonald, 1997), all of which could affect the structure of adult populations. 5.

A decreased capacity to perform aerobically (reduced aerobic scope) is hypothesized to be the key physiological mechanism that will determine the response of marine fishes to increased ocean temperature (Portner, 2001; Portner & Knust, 2007). The limited capacity of the circulatory and ventilatory systems to keep pace with the increased oxygen demands of basal metabolism at higher temperatures causes a reduction in aerobic scope, allowing less energy to be devoted to, for example, feeding, growth and reproduction (Fry, 1971; Portner & Knust, 2007). 5.

reduced aerobic scope is the primary mechanism that controls the thermal niche for marine fishes and, thus, their potential geographical distributions. 5.

A general trend for all five species examined was that they were unable to increase their MO2Max when faced with a temperature-induced rise in MO2Rest, with the result that their scope for oxygen uptake became con- strained as ambient temperature increased. 5.

Thus, at least A. polyacanthus could become limited in its capacity for foraging, growth and reproduction at water temperatures that are likely to be regularly experienced on the northern GBR in the next 50–100 years. This is consistent with observations that growth and body condition of juvenile and adult A. polyacanthus are significantly reduced when exposed to temperatures just several degrees above the average summer temperature they usually experience (Munday et al., 2008b). 5.

some species, and perhaps some families of fishes, have greater thermal tolerance than others. 5.

Thus, fundamental shifts in community structure might occur on low-latitude reefs if, as our results suggest, some families of coral reef fishes are more sensitive to increased temperature than others. 5.

Two mechanisms could work against fundamental changes to fish populations and communities in response to rising sea temperature: (1) phenotypic temperature acclimation and (2) genotypic temperature adaptation through natural selection (Hawkins, 1996; Skelly et al., 2007; Visser, 2008). 5.

However, ectothermic vertebrates adapted to a life at relatively constant temperatures typically lack or have a very limited capacity for temperature acclimation (Johnston & Bennett, 1996; Tewksbury et al., 2008). 5.

stress response genes were up-regulated and did not indicate changes in gene expression that would function to reduce resting metabolic rate (i.e. temperature acclimation) (Kassahn et al., 2007). All this evidence suggests that populations of tropical marine fishes have limited capacity to acclimate their metabolic rates to future temperature increases. 5.

Genotypic adaptation through natural selection may secure the long-term prospects of species that show reduced respiratory scopes at elevated sea temperatures, provided there is appropriate genetic variation in respiratory capacity for selection to work on. A. polyacanthus appeared to be more sensitive to a temperature increase from 29 to 31 1C than the other two damselfish species examined, although it seemed to enable to maintain this reduced aerobic scope when exposed to 32 and 33 1C. A. polyacanthus exhibits significant local genetic structure on the GBR (Bay et al., 2006; Van Herwerden & Doherty, 2006), and a major reason for this is that A. polyacanthus, unlike most other damselfishes, does not have a dispersive larval phase. Therefore, populations of this species are more likely to be adapted to the local thermal environment than are populations of species with strong genetic connectivity across latitudinal and temperature gradients (Choat & Robertson, 2002; Planes, 2002; Rocha et al., 2007). 5.

Local adaptation probably increases the physiological performance at specific environmental conditions. However, it might also make populations more susceptible to rapid environmental change because gene variants that could prove useful under new conditions might have been selectively removed (Jump & Penuelas, 2005; Visser, 2008). Indeed, theory predicts that specialization to a narrow temperature environment leads to a reduced ability to acclimatize or adapt to temperature change (Huey & Hertz, 1984). In addition to greater sensitivity to increased water temperature by A. polyacanthus, reduced gene flow between populations compared with other coral reef fishes would reduce the potential for A. polyacanthus populations to receive favorable genotypes from other populations as local environmental conditions change. 5.

Consequently, a reduction in aerobic scope of the magnitude we observed (43%) between 29 and 31 1C might be sufficient to cause significant declines in A. polyacanthus populations at many locations on the GBR. This conclusion is supported by experimental evidence for significant reductions in the growth of juvenile and adult A. polyacanthus at water temperatures just 1.5 1C above the long-term summer average (Munday et al., 2008b).5.

Many coral reef fishes have latitudinal ranges that span a wide temperature gradient (Choat & Robertson, 2002; Munday et al., 2008a), and exhibit considerable genetic connectivity among populations (Planes, 2002). 5.

The combination of equatorial populations already living at water temperatures likely to become average conditions on high-latitude reefs over the next 100 years plus high levels of gene flow among populations provides hope that populations currently living at higher latitudes might adapt to increased water temperature through a combination of local adaptation and gene flow from low-latitude populations (Munday et al., 2008a). It seems unlikely, however, that adaptation in aerobic capacity will be able to keep pace with increasing temperatures in equatorial and low-latitude populations. Instead, we expect to see geographic range shifts in thermally sensitive species as a result of population decline at low latitudes and population expansion at higher latitudes. 5.

1. **A quantitative survey of local adaptation and fitness trade-offs (Hereford 2009)**

often show that genotypes are better adapted to their native environments than are genotypes from other populations (Linhart and Grant 1996; Van Zandt and Mopper 1998; Schluter 2000). 6.

Theory suggests that the magnitude of local adaptation will increase with greater genetic variation within populations and with greater environmental and phenotypic divergence between populations (Lande 1976; Endler 1977; Slatkin 1985; Garcia-Ramos and Kirkpatrick 1997). Low genetic variation due to genetic drift can limit adaptation. Small populations may not be well adapted to their native environment because drift can make it difficult for advantageous alleles to reach high frequency (Whitlock 2003) or because genetic load due to the chance fixation of deleterious alleles leads to low fitness or extinction (Lynch and Gabriel 1987; Lande 1994; Whitlock et al. 2000). Gene flow can also prevent local adaptation by homogenizing allele frequencies and limiting the response to selection within environments (e.g., Stanton and Galen 1997; Hen- dry and Taylor 2004). 6.

Divergent selection leads to local adaptation when environmental heterogeneity is coarse grained relative to gene flow (Bradshaw 1984; Endler 1986), and local adaptation should be more pronounced between populations from more strongly divergent environments (Becker et al. 2006; Hereford and Winn 2008). 6.

Local adaptation to one environment may cause lower relative fitness in alternative environments, resulting in a trade-off or cost of adaptation. These trade-offs are thought to maintain genetic variation among populations within species, leading to morphological or physiological specialization (Futuyma and Moreno 1988; Day 2000; Jas- min and Kassen 2007), and may promote ecological speciation (Rundle and Nosil 2005). 6.

First, how common and how strong is local adaptation? Second, does the magnitude of differences in the native environments of populations influence the degree of adaptation? Third, are populations that have undergone extensive phenotypic di- vergence more locally adapted than populations that have undergone less divergence? Finally, are there costs of local adaptation that could prevent a population from being well adapted to multiple environments? 6.

The frequency of fitness trade-offs can be measured by comparing the local adaptation of pairs of populations when raised in each other’s native environments. If both populations have greater relative fitness in their native environments, I conclude that adaptation to one environment results in a cost of adaptation to the other environment. This measure of trade-offs is specific to a pair of populations. Therefore, a trade-off may be apparent when comparing populations A and B but not when comparing A and C. 6.

The survey of the literature suggests that local adaptation is common and that, on average, a local population has 45% greater fitness than a foreign population. 6.

The magnitude of differences between the home environments of populations in reciprocal transplant studies had a small but significant positive effect on the magnitude of local adaptation, suggesting that greater local adaptation results from greater differences between environments. Phenotypic differences between populations were not associated with the magnitude of local adaptation. Finally, local adaptation often resulted in trade-offs, though the magnitude of the cost of local adaptation was small. 6.

Thus, if there is a random distribution of local adaptation in nature, the frequency and magnitude reported here are likely to be overestimates. Similarly, the strength of trade-offs or costs of adaptation estimated here are likely to be greater than in a random sample of populations. 6.

The average magnitude of local adaptation depended on the measure used to quantify fitness. Local adaptation measured with viability as fitness was smaller than with fecundity or composite fitness (fig. 2), suggesting that the overall magnitude of local adaptation would have been greater had more studies included fecundity or a composite measure of fitness. 6 .

Viability selection and local adaptation based on viability may be weaker because there is less variance in viability than in fecundity or other fitness measures. Because organisms have to survive to reproductive age in order to produce offspring, fecundity or population growth may capture more of the underlying variation in fitness, resulting in more accurate estimates of selection and local adaptation. Alternatively, past selection may have eliminated variation in traits that influence survival, resulting in little contemporary viability selection. Future studies should include the most comprehensive measure of fitness possible, given that the fitness metric influences the interpretation of experiments. 6.

However, the frequency of maladapted populations reported here suggests that foreign population advantage may not be rare. It appears that selection acts on most measurable phenotypic traits (Endler 1986; Hoekstra et al. 2001; Kingsolver et al. 2001) and can often be exceptionally strong (Hereford et al. 2004). 6.

The high frequency of local maladaptation suggests that stochastic processes such as genetic drift often limit local adaptation (e.g., Travisano et al. 1995). 6.

If alleles can spread readily throughout the species range (e.g., McDaniel and Shaw 2005), then gene flow can prevent populations within a species from evolving as independent units. 6.

The small amount of variation in local adaptation explained by environmental and phenotypic differences suggests that it may sometimes be difficult to identify the environmental gradients on which local adaptation occurs or that differences in the expression of phenotypic traits may not be associated with differences in relative fitness. I found that environmental and phenotypic divergence explained little variation in the magnitude of local adaptation (figs. 3, 4). Though environmental variation is not a direct measure of divergent selection, stronger environmental differences might be expected to result in more divergent selection (e.g., Schluter and Grant 1984), and divergence between populations in at least some phenotypic traits should be associated with local adaptation (de Jong 2005). Many of the phenotypic traits in the data were related to size, which is often positively correlated with fitness (Kingsolver et al. 2001; Hereford et al. 2004). 6.

The lack of a significant relationship between local adaptation and phenotypic divergence may not be due to a lack of selection on these traits. Instead, differences in the expression of these traits may not contribute to differences in relative fitness. Individuals may be able to grow to large sizes in novel environments but may not be able to get the same fitness benefit from large size in novel environments that they could gain in their native environment. 6.

Costs of adaptation or adaptive trade-offs do not appear to be strong enough to prevent simultaneous adaptation to multiple environments. The correlation between a population’s relative fitness in its native environment and its relative fitness in a foreign population’s environment was significant but weak. One of the underlying assumptions in the theory of the evolution of specialist phenotypes is that specialists suffer a cost, in that they cannot be well adapted to alternate environments or resources (Lynch and Gabriel 1987; Futuyma and Moreno 1988). Weak costs of adaptation may explain why the pre- dictions of theory relating evolution of specialization to costs of adaptation are frequently not met (Futuyma and Moreno 1988). 6.

Trade-offs associated with local adaptation were stronger when environmental differences between populations’ native sites were larger. 6.

Costs of adaptation will increase when a population adapts to environments that are drastically different from its ancestral environment. 6.

The presence of trade-offs is environment dependent. In their study, adaptation always led to trade- offs when bacteria adapted to the lowest pH, but trade- offs were present only one out of five times when adapting to a pH treatment that was more similar to the ancestral pH. 6.

Local adaptation is common but that many populations may be prevented from adapting to their local environment. This study also confirms theory that has shown that adaptive divergence not only depends on environmental differentiation and limited gene flow but also may be influenced by genetic drift. Studies that do not demonstrate local adaptation should not be looked on as failed experiments but as demonstrations that populations may be prevented from reaching adaptive optima. Future reciprocal transplant experiments should explicitly investigate the mechanisms that inhibit local adaptation. 6.

1. **Integrating patterns of thermal tolerance and phenotypic plasticity with population genetics to improve understanding of vulnerability to warming in a widespread copepod (Sasaki and Dam 2019)**

Characterizing patterns of thermal adaptation and determining their underlying causes are, therefore, directly related to our ability to predict vulnerability and responses of the biota to climate change (Moran, Hartig, & Bell, 2016; Sorte, Jones, & Miller, 2011) 7.

Macrophysiological studies, investigations of variation in physiological traits across space and time (Chown, Gaston, & Robinson, 2004), often yield evidence for adaptation across environmental gradients. Latitudinal thermal gradients, for example, are well‐known drivers of local thermal adaptation (Addo‐Bediako, Chown, & Gaston, 2000; Castañeda, Rezende, & Santos, 2015; Gaitán‐Espitia et al., 2017; Pereira, Sasaki, & Burton, 2017; Thomas, Kremer, Klausmeier, & Litchman, 2012; Thomas, Kremer, & Litchman, 2016; Yampolsky, Schaer, & Ebert, 2013). These pat‐ terns in adaptation across large spatial scales are often attributed to selection acting on a set of populations, as gene flow is assumed to be relatively low over large distances. 7.

Adaptive genetic differentiation and phenotypic plasticity are two of the main mechanisms used by organisms to cope with variation in the thermal environment (Angilletta, 2009; Dam, 2013; Magozzi & Calosi, 2014; Somero, 2010; Sparks, Westley, Falke, & Quinn, 2017). Adaptive genetic differentiation is well known to produce significant variation in phenotypes (Hochachka & Somero, 2002). 7.

he climate variability hypothesis (CVH; Janzen, 1967; Stevens, 1989) posits that thermal tolerance, the ability of an organism to withstand exposure to high temperatures, should correspond to the mean temperature experienced by a population whereas phenotypic plasticity should evolve in response to variability in the thermal environment. This hypothesis has accumulated support over time, especially in terrestrial and freshwater systems (Deutsch et al., 2008; Sunday, Bates, & Dulvy, 2010), but still lacks robust experimental validation in the marine realm. 7.

Patterns in adaptation can, however, also be strongly influenced by gene flow (Lenormand, 2002). The “Gene Flow versus Selection” issue has been at the heart of evolutionary ecology for decades successful gene flow between populations can strongly impede local adaptation (Garant, Forde, & Hendry, 2007; Hendry & Taylor, 2004; Lenormand, 2002; Moore, Gow, Taylor, & Hendry, 2007; Nosil & Crespi, 2004). 7.

However, low levels of gene flow might also promote local adaptation by increasing the genetic diversity contained within a population (Garant et al., 2007; Tallmon, Luikart, & Waples, 2004). Taking both selection and gene flow into account may be needed to explain observed patterns of adaptation (Dionne, Caron, Dodson, & Bernatchez, 2008; Moore & Hendry, 2005). The potential for interaction between selection and gene flow makes integrated approaches to studying evolutionary physiology critical for robust characterization of spatial patterns in adaptation. 7.

Understanding which populations are more vulnerable, and why, is critical for effective management and conservation of diversity. 7.

Previous work has suggested that warm‐adapted, low‐latitude species or populations are more vulnerable to climate change as they already experience temperatures near their thermal maxima (Comte & Olden, 2017; Tewksbury, Huey, & Deutsch, 2008; Vinagre et al., 2016). However, this is not a universal observation, and populations from mid‐ to high latitudes have also been predicted to be more vulnerable (Bennett, Wernberg, Joy, Bettignies, & Campbell, 2015; Calosi, Bilton, & Spicer, 2007; Fusi et al., 2015). These predictions are often based on measurements of thermal tolerance alone. This is insufficient, however, as phenotypic plasticity may also play a large role in determining vulnerability to cli‐ mate change (Burggren, 2018; Chown et al., 2007; Magozzi & Calosi, 2014; Sparks et al., 2017). Examining spatial patterns in both thermal tolerance and the strength of phenotypic plasticity may provide more robust estimates of vulnerability. 7.

Key Largo, the southernmost population, had the highest thermal tolerance of the 10 populations examined, followed by 3 populations from the Gulf of Mexico. The northernmost population, SB, had the lowest thermal tolerance but the largest strength of phenotypic plasticity. 7.

The CVH (Janzen, 1967; Stevens, 1989) predicts higher thermal tolerance in warmer environments and increased phenotypic plasticity in more variable environments. The thermal tolerance results of our study are consistent with these predictions. 7.

The negative relationship between thermal tolerance and the strength of phenotypic plasticity might reflect a role of genetic accommodation or “plasticity first” evolutionary change (Kelly, 2019; Levis & Pfennig, 2016; Levis, Serrato‐Capuchina, & Pfennig, 2017; Pfennig et al., 2010; Pigliucci, Murren, & Schlichting, 2006; Price, Qvarnström, & Irwin, 2003; Scheiner, Barfield, & Holt, 2017; West‐Eberhard, 2005, 2003), wherein phenotypic modification by plasticity becomes canalized or fixed by genetic mechanisms, resulting in the loss of capacity for plastic change. 7.

Local adaptation within the range of dispersal, so‐called microgeographic adaptation (Richardson, Urban, Bolnick, & Skelly, 2014), has garnered increased attention. “Microgeographic” may be a misleading term in marine systems, though, as dispersal kernels can encompass hundreds of kilometers (Cowen & Sponaugle, 2009; Kinlan & Gaines, 2003; Kinlan, Gaines, & Lester, 2005). 7.

The wide distribution of genetic clades, several instances of shared haplotypes between distant populations, and the negative relationship between the estimated number of migrants and the pair‐ wise difference in LD50 suggests that gene flow can be strong enough to constrain the adaptive divergence of TPCs in this taxon. 7.

Reductions in gene flow may promote local adaptation, thus reducing vulnerability, while an increase in gene flow could strongly increase vulnerability to climate change if existing local adaptation is eroded by gene swamping (Lenormand, 2002). 7.

In general, local adaptation to increased temperature does not appear to increase vulnerability to warming, contrary to what has been previously suggested for warm‐adapted tropical species (Nguyen et al., 2011; Somero, 2010; Tewksbury et al., 2008). However, this is likely highly regionally specific; the second largest decrease in survivorship was predicted for one of the locally adapted populations, PR, from the Gulf of Mexico. 7.

determining vulnerability to climate change. Importantly, survivor‐ ship is only one component of fitness. Reproductive output also constitutes an important component, and changes in traits like egg production, hatching success, and offspring survival will also undoubtedly have strong effects on organismal responses to climate change. Trade‐offs between fitness metrics like survivorship at high temperature and egg production could offset any buffering capabilities of plasticity, and bias estimates of vulnerability. 7.

1. **Evolutionary responses to global change: lessons from invasive species (Moran and Alexander 2014)**

Even populations that are able to migrate to areas with climates similar to their current habitat will likely experience novel selection pressures due to altered biotic interactions (Parmesan 2006; Williams & Jackson 2007), as well as novel combinations of photoperiod cues and cli- mate, which means that plastic responses alone are unlikely to be sufficient in the long term (Visser 2008). 8.

There has recently been much interest in the role of genetic diversity and gene flow in determining species’ responses to climate change (Kremer et al. 2012). 8.

There is sometimes very low variation in particular ecologically important traits even if overall genetic diversity is high – for instance, tropical Drosophila often exhibits low genetic variation and thus low heritability in desiccation and heat tolerance (Merila 2012). Some authors have suggested that a lack of genetic diversity or a need to adapt to local conditions could be partly responsible for the long lags between establishment and spread in some invasive species (Ellstrand & Schierenbeck 2000), and while direct evidence for this is scarce, indirect evidence of the potential importance of genetic diversity and/or adaptation is mounting (Crooks 2005). 8.

Multiple selection pressures acting on a trait in different directions can prevent changes in the trait from occurring or lead to maladaptation with respect to a particular selection factor. 8.

Reduced gene flow makes the depletion of local genetic diversity by selection and drift more likely, and this could cause the rate of adaptation to increasingly lag behind the rate of environmental change, increasing the risk of extinction (Jump & Penuelas 2005). If the highly fragmented nature of many landscapes today selects against dispersal, this would tend to reduce the capacity for range shifts following climate change, weaken demographic rescue effects and increase genetic isolation. 8.

Correlations between traits such that the major axes of variation are not aligned with the selection gradients could impede evolutionary responses of native species to climate change. 8.

While local adaptation may be important for populations throughout a species’ range as climate warms (Jiguet et al. 2010), it is likely to be particularly important for populations at the trailing edge (e.g. at low latitude). Here, populations will be exposed to conditions that are not only locally novel, but that are more extreme than those experienced by populations anywhere else in the species’ range (Fig. 2). If the species’ distribution limit reflects limits to adaptation (Soberon 2010), such populations will need to evolve new species-level climatic niche limits in order to persist. Some have argued that this is unlikely, as evidenced by the apparent stability of species’ thermal limits in the fossil record (Parmesan 2006). Here again invasive species are instructive. 8.

Species that have undergone relatively recent range expansions often exhibit a gradient of progressively lower genetic diversity from the original core distribution towards the new range edge, resulting from sequential founder effects (Huchon et al. 1999; Hampe & Petit 2005). 8.

The factors affecting the likelihood and extent of an evolutionary response include a) the strength of selection, b) the amount local genetic variation and gene flow, c) demographic traits such as lifespan, generation time, and fecundity, and d) genetic correlations in the traits under selection. 8.

It may be possible to draw generalisations about what kinds of populations or species exhibit ecologically relevant evolutionary change under particular types of environmental change, what types of change are more likely and what constraints tend to limit evolutionary responses. 8.

The ability of populations to adapt to rapid environmental change will be limited by the availability of functional genetic variation on which selection can act. However, we still know very little about the amounts of additive genetic variation in ecologically important traits (Dlugosch & Parker 2008a), and how this variation is distributed across a species’ range in either native or invasive species. Comparisons of functional diversity in introduced populations (that do or do not evolve) to that of native populations could illuminate what levels of diversity are required and the effect of bottlenecks, admixture and gene flow on this diversity. 8.

1. **The effects of phenotypic plasticity and local adaptation on forecasts of species range shifts under climate change (Valladres *et al* 2014)**

However, species are usually treated as if individuals from all populations respond equally to environmental pressures (Kawecki 2008; Banta et al. 2012). There is ample evidence, though, that populations within a species experiencing different environmental conditions often differ in phenotypic characters and genetic structure (Linhart & Grant 1996). 9.

At species range edges, where the limits of the distribution are imposed by environmental constraints, individual fitness is generally lower than in the center of its distribution (Kawecki 2008). However, geographically peripheral populations do not always occur in unfavourable habitats (Jump & Woodward 2003; Granado-Yela et al. 2013). The fitness decline in populations at the environmental margin will depend on the extent of local adaptation of the populations, their phenotypic plasticity, the steepness of environmental gradients, and gene flow, amongst other factors (Kawecki 2008; Lenoir & Svenning 2013). 9.

Populations and genotypes that experience the greatest extent of variability in a given environmental condition are expected to be most plastic in traits adaptive in those conditions (Van Tienderen 1991; Sultan & Spencer 2002). In the face of change, plasticity may play a key role enabling persistence of remnant individuals or populations (Rubio de Casas et al. 2009; Chevin et al. 2010; Matesanz et al. 2010). Thus, patterns of plasticity of populations at the distribution margin will influence species responses to a changing climate, and will be important in determining species distributions under novel climates. 9.

Most models assume that species responses to climate changes are similar across distributional ranges. 9.

Atkins & Travis (2010) modelled the impact of local adaptation on climate change response in a theoretical species and found counter-intuitively that broadly distributed species can have greater range reductions because cooler adapted genotypes may block the potential for range shift by locally adapted genotypes. These studies demonstrate that the predictions of habitat suitability for a given species in future scenarios can be highly affected by intraspecific variation. 9.

Populations within a single species may differ in trait means across the species range. 9.

It has likewise been predicted that core and margin populations will differ significantly in life-history traits and plasticity pat- terns, as population genetic structure and selection pressures related to environmental heterogeneity are likely to vary along the distribution range of a species (Purves 2009). 9.

It is assumed that species abundance and genetic variation

decline towards low quality habitats at the range edge (Sagarin & Gaines 2002; Vucetich & Waite 2003). However, peripheral populations may experience favourable conditions, exhibiting higher levels of fitness and phenotypic plasticity. 9.

High quality habitats can thus exist in both peripheral and core locations, which is consistent with the observations that species often persist at the marginal rather than at the central parts of their range (Channel & Lomolino 2000). Populations at range limits are structured in metapopulations, constituting a shifting mosaic of source and sink populations held together by migration (Holt et al. 2005). 9.

However, at historical limits, where relict peripheral populations have been confined for long periods of time in habitat refugia, a combination of reproductive isolation, small population size, lower genetic variation, founder effects, and genetic drift often results in genetic divergence (Reisch et al. 2003). 9.

In summary, studies of fitness, local adaptation and phenotypic plasticity of populations across the entire range of a species are scant and while important phenotypic differences within species are evident, we lack a comprehensive picture of what the impact of those differences would be on forecasts of species distributions under climate change, and how intraspecific variation in phenotypic plasticity and thermal niche optima affects forecasts. 9.

When relating the current distributions to environ- mental variables, a model that does not consider intraspecific variation may smooth across fitness-environment curves of the individual sub taxa (populations), and, consequently, may not capture the intraspecific niche diversity very well. Atkins & Travis (2010) showed in a simulation model that when there is local adaptation (and restricted dispersal), a species may fail to survive a period of climate change, even when there is an overlap between its range prior to climate change and the area where climate is predicted to be suitable following climate change. This agrees well with our conceptual model. 9.

1. **Conserving biodiversity under climate change: the rear edge matters (Hampe 2005)**

There is now ample evidence that modern climate change is reshuffling the geographic distributions of plant and animal species world-wide (Parmesan & Yohe 2003). 10.

A major paradigm of this research is the centre- periphery hypothesis, which predicts that marginal populations are more prone to extinction and genetically less diverse than those from the centre, because they tend to occur in less favourable habitats and at lower and more variable densities (Lawton 1993; Vucetich & Waite 2003). 10.

In particular, phylogeographic surveys show that rangewide patterns of population genetic diversity are usually shaped by past climate-driven range dynamics (Hewitt 2000, 2004) rather than bydemogenetic stochasticity perse, as proposed in the centre-periphery model. As a consequence, marginal rather than central populations commonly harbour the bulk of species genetic diversity (e.g. Petit et al. 2003; Hewitt 2004). In summary, the utility of the deterministic centre-periphery- model is limited in the context of range modifications driven by climatic changes. 10.

The “leading edge” model of colonization, which states that range expansions involve mostly populations from the colonization front and are largely controlled by rare long-distance dispersal events followed by exponential population growth, has become a central paradigm in phylogeography, as it helps to explain the commonly observed poleward decrease of genetic diversity both within and among populations (Hewitt 1993, 2000). 10.

Rear edge populations are typically small and so isolated that regional population dynamics cannot easily compensate local extinction events. Their successful long-term persistence in spite of fairly small population sizes, at least during interglacial periods, indicates that extinction because of demographic stochasticity has played a relatively minor role (contradicting the centre- periphery-model). However, their small size and prolonged isolation have resulted in reduced within-population genetic diversity (see e.g. Castric & Bernatchez 2003; Petit et al. 2003; Chang et al. 2004). On the other hand, disproportionately high levels of genetic differentiation are observed among such populations, even between nearby ones, leading to exceptionally high levels of regional genetic diversity (Comps et al. 2001; Castric & Bernatchez 2003; Hampe et al. 2003; Petit et al. 2003; Martin & McKay 2004). 10.

Appropriate conservation strategies need to be designed that consider the peculiarities of rear edge populations. For instance, the particular genetic structure of rear edge populations requires conservation strategies directed towards the detection and maintenance of the greatest possible number of local populations, regardless of their size or performance, instead of focusing on the most viable core populations. 10.

1. **Conceptual issues in local adaptation (Kawecki and Ebert 2004)**

Local adaptation may be hindered by gene flow, confounded by genetic drift, opposed by natural selection due to temporal environmental variability, and constrained by lack of genetic variation or by the genetic architecture of underlying traits. 11.

Thus, although divergent natural selection is the driving force, these other forces, in particular gene flow, are integral aspects of the process of local adaptation. 11.

Because of those other forces, the pattern of local adaptation is not a necessary outcome of evolution under spatially divergent selection. 11.

Generally, an adaptation is a phenotypic feature which is functionally designed by past natural selection, and which improves Darwinian fitness relative to alternative features (Williams 1966). 11.

The study of local adaptation offers the more feasible alternative of comparison between local populations, which have evolved under different conditions. In the absence of divergent (i.e. spatially heterogeneous) natural selection, genetic differentiation in fitness-related traits is expected to be obliterated by gene flow. Therefore, local adaptation in a set of demes connected by gene flow must be due to ongoing (or very recent) natural selection related to differences in environmental conditions experienced by different demes. 11.

In contrast, traits that are unconditionally adaptive will tend to become fixed within the species. 11.

First, gene flow hinders local adaptation. Therefore, the existence of a pattern of local adaptation despite gene flow certifies to the strength of natural selection imposed by particular environmental factors. Second, it is sometimes possible to infer the age of a deme from geological or historical data; this allows one to estimate the rate of adaptive evolutionary change (e.g. Stearns 1983; Gomi & Takeda 1996). Third, local adaptation has been recognized as an important mechanism maintaining genetic variation (reviewed by Felsenstein 1976; Hedrick et al. 1976; Hedrick 1986). Finally, a number of scenarios for allopatric and sympatric speciation (reviewed by Schluter 2001; Turelli et al. 2001; Via 2001) assign local adaptation a crucial role in initiating the divergence of incipient species. 11.

Genotype · environment interaction for fitness is an obvious pre-requisite for local adaptation. 11.

Of several forms such an interaction can take, the most important for local adaptation is antagonistic pleiotropy, whereby the alleles have opposite effects on fitness in different habitats. Such antagonistic pleiotropy implies that no single genotype is superior in all habitats, leading to trade-offs in adaptation to different habitats. 11.

Have shown that spatial heterogeneity facilitates maintenance of polymorphism that shows such antagonistic pleiotropy, provided that density-dependence (population regulation) operates within demes (Christiansen 1975; Pimm 1979; Karlin & Campbell 1981). 11.

Thus, restricted gene flow is a pre-requisite for local adaptation. Restricted gene flow (due to low passive dispersal or active habitat choice) also makes the conditions for maintenance of polymorphism more favourable (e.g. Maynard Smith 1966). 11.

Therefore, loci with large effects on fitness should disproportionally contribute to local adaptation (Macnair 1991). This is indeed the case in the classic examples of local adaptation of plants to sites contaminated with heavy metals (reviewed in Macnair 1987, 1991). 11.

Nonetheless, many fitness-related characters likely to play a role in local adaptation show polygenic variation. In contrast to single-locus models, the theory of polygenic traits under divergent selection remains relatively unexplored. 11.

Population differentiation corresponding to local adaptation is promoted by low dispersal and strong selection (Brown & Pavlovic 1992; Day 2000; Kisdi 2002; Spichtig & Kawecki 2004). However, if selection is very strong (i.e. fitness falls off very quickly as the phenotype deviates from the local optimum), intermediate genotypes have low fitness in all habitats. This makes it difficult for a population initially adapted to one habitat to invade other habitats and evolve into a set of locally adapted demes, promoting the stability of an asymmetric equilibrium with a single phenotype specialized on one habitat (Day 2000; Kawecki 2000, 2003; Ronce & Kirkpatrick 2001; Kisdi 2002). 11.

Therefore, the conditions for local adaptation mediated by polygenic traits are most favourable when selection in habitat 1 against genotypes well adapted to habitat 2 and vice versa is strong, but selection against intermediate (recombinant) genotypes is moderate. 11.

If selection against intermediate genotypes is weak, intermediate generalist phenotypes are likely to be favoured, leading to loss of genetic variance and little differentiation (Spichtig & Kawecki 2004). If it is too strong, the population is likely to be trapped in a source-sink situation with little differentiation among demes (in a single- locus model this case corresponds to loss of polymorphism because of excessive marginal underdominance for fitness averaged between habitats; Christiansen 1974). An asymmetric equilibrium is also promoted by differences in size and quality of habitats, so local adaptation is most likely when such differences are small (Kawecki 1995, 2000, 2003; Ronce & Kirkpatrick 2001; Kisdi 2002). 11.

In addition to gene flow, other forms of selection may act against local adaptation. In particular, temporal variation in natural selection favours generalist phenotypes (e.g. Kisdi 2002). Furthermore, temporal fluctuations in habitat quality favour increased dispersal (unless the fluctuations are strongly positively correlated across habitats; e.g. Levin et al. 1984), and thus act against local adaptation. In contrast, spatial environmental heterogeneity favours reduced dispersal and habitat fidelity (e.g. Hastings 1983), which make conditions for local adaptation more favourable. Such feedbacks lead to coadaptation between dispersal rates and traits involved in habitat adaptation (Kisdi 2002). 11.

Finally, it should be noted that environmental heterogeneity favours the evolution of adaptive phenotypic plasticity. In the absence of costs of and constraints on plasticity, a genotype that in each habitat produces the locally optimal phenotype would become fixed in all demes. 11.

To summarize, ecological factors predicted to promote local adaptation include: low gene flow (i.e. low dispersal or strong habitat fidelity), strong selection against genotypes optimally adapted to other habitats but moderate selection against intermediate genotypes (most likely under moderate differences between habitats with respect to traits under selection), little temporal variation in the forces of selection, small differences between habitats in size and quality (e.g. the amount of resources), and costs of or constraints on adaptive plasticity. We know much less about the effects of genetic architecture, as even the models with explicit genetics typically assume a simplistic genetic architecture (additivity and unlinked loci). One may expect that loci with large effects may be more important – polymorphism is more easily maintained and greater allele frequency differentiation is possible. Similarly, one could conjecture that linkage will be favourable for local adaptation as it reduces the power of recombination to break up locally adapted gene combinations (for a simple model see Dickinson & Antonovics 1973). Further theoretical work specifically addressing local adaptation mediated by polygenic traits with more complex genetic architecture is needed to substantiate these conjectures and generate new predictions. 11.

First, the key comparison from the viewpoint of local adaptation is between the relative fitness of local vs. immigrant genotypes within each test habitat, not between the performance of a given genotype at home and away. Second, the unit of biological eplication is a deme, and more than two demes need to be studied to distinguish the pattern of local adaptation from other forms of deme · test habitat interactions. 11.

In each habitat the local deme is expected to show higher fitness than demes from other habitats. In contrast, the home vs. away criterion emphasizes the comparison of a deme’s fitness across habitats: local adaptation would be said to occur if each deme had a higher fitness in its own habitat (at home) than in other habitats (away). 11.

In general statistical terms, local adaptation implies a specific form of deme · habitat interaction: mean deme fitness should be systematically higher for the sympatric deme · habitat combinations (i.e. a deme is tested in its habitat of origin) than in the remaining, allopatric cases. 11.

However, we do not agree with the proposition that they are equally relevant for testing the pattern of local adaptation. Rather, we believe that the local vs. foreign criterion should be regarded as diagnostic for the pattern of local adaptation. This criterion is directly relevant to the driving force of local adaptation – divergent natural selection – which acts on genetic differences in relative fitness within each habitat. The local vs. foreign criterion addresses the efficacy of divergent selection relative to other evolutionary processes. In contrast, the home vs. away criterion confounds the effects of divergent selection with intrinsic differences in habitat quality. Survival or fertility of a genotype optimally adapted to a poor-quality habitat may still increase following a transplant to a resource-rich habitat, although in the poor habitat this genotype is favoured (i.e. has higher relative fitness than other genotypes) while in the rich habitat it would be outcompeted by other genotypes. 11.

In contrast to genetically- based differences among demes in overall performance, which are a product of evolution, differences in intrinsic habitat quality are a property of the environment. 11.

Theory of local adaptation predicts evolutionary changes in the metapopulation, but not changes in the environment. We, therefore, propose that a pattern that satisfies the local vs. foreign but not home vs. away criterion (like that in Fig. 1b) offers as much support for local adaptation, as a pattern that satisfies both criteria (like that in Fig. 1a). 11.

In contrast, a pattern that satisfies the home vs. away but not the local vs. foreign criterion (Fig. 1c) implies that some demes consistently outperform others in all habitats, in contrast to what the theory predicts. 11.

Therefore, independent of the issues discussed in the preceding section, it is desirable to show that the

sympatric vs. allopatric difference is unlikely to be explained by deme · test habitat interaction unrelated to local selection. This requires replication at the level of the deme; if only two demes are studied, these two interaction terms are impossible to separate. The lack of replication prevents one from concluding that the differentiation is because of divergent selection, rather than chance events in the demes history. 11.

Nonetheless, replication at the level of the deme is needed to demonstrate local adaptation on the basis of the fitness pattern alone. 11

Because the focus in parallel local adaptation is on the specific ecological factors which define habitat types, the main effect of the habitat is treated from the statistical viewpoint as fixed (type I) factors (Sokal & Rohlf 1981, section 8.6). In contrast, the demes included in the study will usually be treated as a sample of all demes evolved in the focal habitat types; one would usually want to generalize the findings to other demes. This perspective implies that deme should be treated as random (type II) statistical factor (Sokal & Rohlf 1981, section 8.7). 11.

The geographic or spatial distance between the habitat of origin and the test habitat can be incorporated as an explanatory variable (for various designs and statistical approaches see e.g. Ebert 1994; Kaltz et al. 1999; Joshi et al. 2001; Thrall et al. 2002; Belotte et al. 2003). 11.

Finally, we would like to reiterate that local adaptation as defined above is not a property of individual populations, but of a set of demes (i.e. a metapopulation). Nonetheless, it may be of interest to identify subsets of demes that do show a pattern of local adaptation vs. those that do not, especially if these subsets can be characterized by specific properties such as history, spatial arrangement, habitat size, spatial isolation, or deme size or age (see below). 11.

Examples range from major fitness components like juvenile survival or fecundity (e.g. Mopper et al. 2000; Leiss & Muller-Scharer 2001), through life history traits such as age at first reproduction or, for a parasite, infectivity (e.g. Lively 1989; Mopper et al. 1995; Kaltz et al. 1999), to traits such as body size, root growth or number of leaves (e.g. Gomez- Mestre & Tejedo 2003; Berglund et al. 2004) or resistance to local parasites and herbivores (e.g. Roy 1998). A working assumption behind using such traits as measures of performance is that they are monotonically related to fitness, i.e. are under directional selection in all demes. However, fitness-related traits are often under stabilizing selection and/or are trade-off with other fitness components (reviewed in Roff 1992; Stearns 1992). In this case, different intermediate trait values may be optimal in different locations; treating these traits as measures of performance (e.g. the bigger the fitter) may be misleading. However, if the habitat-specific optima of a trait are known, the degree to which each deme matches the optimum for its habitat is highly informative about local adaptation (e.g. Dias & Blondel 1996). Some traits (e.g. juvenile survival or parasite infectivity) will in general be more often under directional selection than others (e.g. root size, phenological traits or parasite virulence). In any case careful consideration should be given to the relationship of a given performance trait to actual fitness. This relationship can often be verified through measurements of selection gradients (see below). 11.

Ideally, each sample would be acclimated under the conditions under which its fitness is to be measured. This is often possible if the fitness assays take place in the laboratory, but will usually be impractical if fitness is measured in the field (but see Karban 1989). 11.

Furthermore, a metapopulation may fail to show genetic differentiation for fitness traits because of lack of divergent selection, too much gene flow, or temporal variation in selection, which favours generalist genotypes. 11

More recently established demes may show poorer adaptation to their habitat than older ones. A beneficial mutation may be spreading in the metapopulation, being already fixed in some demes (which thus would show higher fitness) while absent in others. 11.

Finally, different demes may have reached alternative adaptive peaks of different height, i.e. if they have evolve alternative epistatic gene combinations that result in different fitness. Thus, the absence of the pattern does not necessarily mean that the, process of divergent natural selection is not operating. Studying the processes driving, hindering, and interacting with, local adaptation would help to understand why local adaptation is apparent in some metapopulations but not in others. This involves asking questions and testing hypotheses about ecological factors responsible for divergent natural selection, traits under selection and their genetic architecture, gene flow, and processes affecting immigrants (such as heterosis or outbreeding depression). 11.

Traits mediating local adaptation should show genetically based phenotypic differences between demes evolved in different habitats, the phenotype being understood broadly to include physiological and biochemical characteristics and patterns of gene expression. However, not all genetically based phenotypic differences between demes must be adaptive. Instead they may represent the costs of adaptive traits, mediated by pleiotropic effects of underlying genes. They may also be because of genetic hitchhiking of genes linked to those favoured by divergent selection. Finally, such differences may be produced by processes not related to local adaptation (such as drift or evolution of alternative coadapted gene combinations). 11.

In the context of local adaptation we are interested in differences in fitness gradients between habitats (e.g. Kalisz 1986; Petit & Thompson 1998; Caruso 2001). 11.

Finally, local adaptation requires that spatial variation in selection is substantially greater than temporal variation. Both theoretical arguments (Gillespie 1973) and experimental data (reviewed in Kassen 2002) show that temporal variation in selection favours generalist genotypes and thus hinders local adaptation. Thus irrespective of the approach used to study divergent selection, it is desirable to address the issue of its constancy through time. 11.

In particular, latitudinal clines and other forms of spatial variation correlated with environmental factors are often observed for allele frequencies at allozyme loci (reviewed in Eanes 1999). 11.

The role of candidate loci in local adaptation can be verified by demonstrating differential survival or reproduction of genotypes (e.g. Lenormand et al. 1998; Schmidt & Rand 2001). 11.

Even if the genes responsible for local adaptation remain unknown, useful information about the genetic aspects of traits mediating local adaptation can be learned with the methods of quantitative genetics. First, how much additive genetic variation for this trait exists and how is it distributed within vs. among demes? The former indicates the ability of the trait to respond to selection (for estimation see Falconer & Mackay 1996; Lynch & Walsh 1998, part III). The latter, which can be quantified as Qst (Merila & Crnokrak 2001; McKay & Latta 2002), measures the degree of genetic differentiation of quantitative traits between populations. Traits under strongest divergent selection are expected to have the highest Qst, which is another way of identifying traits mediating local adaptation. 11.

Second, what is the genetic architecture of diverged traits? Is it mostly because of few major loci or are many loci with small effects involved? What are the patterns of dominance and epistatic interaction between loci? Are the traits affected by genetically-based maternal effects? These questions can be addressed with the analysis of crosses between genotypes originating from different demes (for methods see Lynch & Walsh 1998, Chapter 9). 11.

Third, do these traits show phenotypic plasticity and is it adaptive? As discussed above, adaptive plasticity may be seen as an evolutionary alternative to local adaptation. 11.

Selection will counteract such maladaptive plasticity, so local adaptation will in this case be manifested as reduction of phenotypic differences between demes living in different habitats. Selection will thus be divergent at the genetic level, but not at the phenotypic level, and will thus not be detectable as a difference in fitness gradients. This type of local adaptation has been termed countergradient variation (Conover & Schultz 1995). 11.

Fourth, are the traits mediating local adaptation involved in genetically-based trade-offs with other traits relevant for fitness. 11.

Many fitness-related traits like the number and quality of offspring are positively correlated with fitness, but trade off with each other, so the effective selection on them is stabilizing. Also, many specific adaptations, like heavy metal tolerance or herbivore resistance, have physiological costs. In environments where these adaptations are not needed these costs translate into a fitness disadvantage (e.g. Strauss et al. 2002), and thus are the reason why such adaptations are local rather than global. 11.

Divergent selection is the driving force of local adaptation, but the outcome depends on the interaction between divergent selection and other forces of evolution, in particular gene flow. Therefore, quantitative estimates of gene flow provide important insights in the process of local adaptation. Gene flow is usually estimated indirectly based on differentiation at (presumably) neutral genetic marker loci. 11.

Genetic differentiation at marker loci is often inversely related to the geographic distance among populations, an observation termed isolation by distance. In the context of local adaptation gene flow may be, however, confounded by asymmetric dispersal among demes and by selective processes acting on the fate of immigrants. 11.

Another reason for deviations from a simple isolation by distance pattern is habitat choice. Genetic variation for habitat choice automatically becomes non-randomly distributed among habitats, and can cause gene flow to be greater between distant patches of similar habitats than between neighbouring patches of different habitats. 11.

Gene flow is, however, not only a function of dispersal, but also of the success of the migrants in their new habitat. A number of other evolutionary processes will affect the fate of migrants and their offspring, and thus influence the effective gene flow. 11.

Genes flow from one deme to another packaged in migrating individuals or propagules (seeds, spores, pollen, etc.), and all genes carried by a propagule initially share the same fate. Because local adaptation is characterized by the inferiority of immigrants relative to locals, effective gene flow is reduced by the presence of locally adapted residents. 11.

A different mechanism influencing gene flow is related to the fact that immigrants are usually rare, so their fitness may be biased by frequency-dependent selection. For example, if different demes have evolved different sexually selected ornament-preference systems, immigrant males will be discriminated against by local females; given that most females will be local, this will create sexual selection against immigrants. The converse is also possible, as females may show preference for males they perceive as unusual (e.g. Sinnock 1970; Ball et al. 2000). In general, frequency dependent selection will tend to obscure local adaptation (if it favours rare genotypes), or to create an appearance of one (if it discriminates against rare genotypes). This calls for studies designed to disentangle local adaptation from frequency dependent selection (e.g. Roy 1998). 11.

Furthermore, emigrants will often not be a representative sample of their deme. In species with contest competition poorer competitors will often be more likely to emigrate because they are unable to gain a territory or a breeding site in their native habitat (e.g. Serrano et al. 2003). 11.

Finally, the effective gene flow will not only depend on the dispersal rate and the performance of immigrants, but also on the fitness of their offspring and later descendants. 11.

There are three general reasons why fitness of such hybrid genotypes may deviate from a simple average of the two parental genotypes. First, the phenotype for the traits mediating local adaptation may deviate from the mid-parent value because of dominance and epistatic interactions (see above); even if it does not, the effects on habitat-specific fitness will not be additive if the relationship between the phenotype and fitness is not linear (e.g. Hartfield & Schluter 1999). Second, offspring of immigrants may enjoy hybrid vigour (heterosis). Hybrid vigour usually reflects complementation of recessive deleterious mutations whose frequency differentiated between demes due to drift. Hybrid vigour favours immigrant genes and thus magnifies the effective gene flow (e.g. Ebert et al. 2002). Third, hybrid genotypes, especially those of second and later generations, may suffer from outbreeding depression not related to traits under divergent selection. Outbreeding depression is expected if, due to their initial genetic makeup or historical contingencies, the parental demes have evolved alternative coadapted gene combinations (i.e. reached alternative ‘adaptive peaks’; Goodnight 2000). Breakdown of those beneficial epistatic interactions would reduce the fitness of recombinant genotypes, especially in the second and following generation of immigrant offspring backcrossed into the local gene pool. Outbreeding depression will thus cause selection against immigrant genes for reasons unrelated to local adaptation 11.

If many demes are studied, the degree to which individual demes show local adaptation can be correlated with their characteristics such as size, age, demography, isolation, and habitat quality. In the spirit of this approach Mopper et al. (2000) have demonstrated that older demes of a leaf mining lepidopteran (those on older trees) show more pronounced local adaptation to their individual host trees than young demes, despite being less differentiated from one another in neutral markers. 11.

**Metabolic trait diversity shapes marine biogeography** Deutsch 2020

“The energetic demands of ectothermic organisms increase with temperature and activity, and must be met by an adequate supply of oxygen (O2) and food” (Deutsch et al., 2020, p. 557)

“At a minimum, physiological survival requires that the supply of energy matches the maintenance costs of an organism in a resting state; these energy demands vary by body size, temperature and species6,” (Deutsch et al., 2020, p. 557)

“Additional energetic costs are incurred by the growth and activity required for ecological survival, which depend on lifestyle and ecological niche and typically increase energy expenditure several-fold above resting rates8,” (Deutsch et al., 2020, p. 557)

“Energy provision can be limited by O2 if its availability falls short of the metabolic demands of the organism” (Deutsch et al., 2020, p. 557)

“A third component of the energetic balance of an organism is the O2 needed to fuel growth and essential ecological activities” (Deutsch et al., 2020, p. 557)

“The boundaries of the geographical ranges of species are more strongly aligned with the Metabolic Index than with either temperature or pO2 alone” (Deutsch et al., 2020, p. 559)

“That the species habitat boundaries coincide with a lower Φ value suggests that an aerobic barrier limits the geographical ranges of marine animals” (Deutsch et al., 2020, p. 560)

“We find a strong correlation between biogeographically inferred Φcrit and laboratory measured MMR/RMR values” (Deutsch et al., 2020, p. 560)

**The role of mechanistic physiology in investigating impacts of global warming on fishes**

“Warming of aquatic environments as a result of climate change is already having measurable impacts on fishes, manifested as changes in phenology, range shifts and reductions in body size” (Lefevre et al., 2021, p. 1)

“Secondly, there are latitudinal shifts in species distributions, notably a poleward invasion by temperate and sub-tropical species” (Lefevre et al., 2021, p. 1)

“The third phenomenon is a reduction in average body size, due to a decline in final adult size and increases in the proportion of younger and smaller individuals (Daufresne et al., 2009; Gardner et al., 2011; Audzijonyte et al., 2020” (Lefevre et al., 2021, p. 1)

**Intraspecific variation in tolerance of warming in fishes**

Annotations  
(8/21/2023, 11:41:21 AM)

“Fishes may be especially vulnerable to global warming because, as ectotherms, their physiology is determined by thermodynamic effects of the surrounding water temperature, which sets their” (McKenzie et al., 2021, p. 1536)

“body temperature” (McKenzie et al., 2021, p. 1537)

“Intraspecific variation exists both within and among individuals and populations of a species (Bolnick et al., 2011; Killen et al., 2016a; Mimura et al., 2017; Spicer & Gaston, 2000” (McKenzie et al., 2021, p. 1537)

“A second element is phenotypic plasticity, the ability of a given genotype to produce different phenotypes in response to the environment within an individual's lifetime (Stearns, 1989), which can be a source of variation both within and among individuals. A capacity for plasticity in tolerance can buffer against the immediate impacts of thermal stress, thereby reducing population sensitivity” (McKenzie et al., 2021, p. 1537)

“Thirdly, there is genetically based heritable variation among individuals, either within or between populations.” (McKenzie et al., 2021, p. 1537)

“Possessing a broad range of heritable tolerance genotypes will influence population adaptability and the capacity to adjust to new conditions over generational time scales (Bennett et al., 2019; Moran et al., 2016; Pacifici et al., 2015)” (McKenzie et al., 2021, p. 1537)

“These collective effects of individual variation in thermal tolerance can, therefore, have important implications for vulnerability of populations and species to both short-term extreme heatwaves and long-term gradual warming (Bennett et al., 2019)” (McKenzie et al., 2021, p. 1537)

“This then has far-reaching consequences. If broad functional variation among individuals increases the stability and resilience of a species in the face of environmental stressors, such as warming, this can stabilize the species’ ecological functions and, in turn, stabilize overall community and ecosystem function (Bolnick et al., 2011; Mimura et al., 2017; Pacifici et al., 2015).” (McKenzie et al., 2021, p. 1537)

“The prevailing theories for what defines thermal tolerance in fishes, the Fry Paradigm (Fry, 1947, 1957, 1971) and the oxygen and capacity-limited thermal tolerance (OCLTT) hypothesis (Pörtner, 2010), both focus on fish cardiorespiratory physiology and the capacity to meet the oxygen requirements of aerobic metabolism when a fish is subjected to the thermodynamic effects of water temperature” (McKenzie et al., 2021, p. 1538)

“A TPC can then identify a thermal optimum, the thermal range over which performance is near to optimal (thermal breadth), and temperature thresholds for alterations in performance (Figure 1) (Currie & Schulte, 2014; Pörtner et al., 2010; Schulte et al., 2011; Wang & Overgaard, 2007).” (McKenzie et al., 2021, p. 1538)

“The AAS is proposed to be of ecological significance because it defines the upper limit for oxygen allocation by a fish to sustain aerobic activities such as foraging, digestion, tissue deposition, migration, reproduction (Claireaux & Lefrançois, 2007; Farrell, 2009; Fry, 1971; Pörtner, 2010; Schulte, 2015)” (McKenzie et al., 2021, p. 1538)

“In fact, many fish species do not exhibit a unimodal TPC for AAS with a clear Topt (Lefevre, 2016) and, most notably, many show no decline in AAS as they are warmed towards their upper thermal tolerance limit (Gräns et al., 2014; Lefevre, 2016; Norin et al., 2014; Poletto et al., 2017; Verhille et al., 2016). That is, based on the available evidence, the Fry paradigm and OCLTT cannot be assumed to be universal principles and are currently a topic of debate in the literature (Clark et al., 2013; Farrell, 2016; Jutfelt et al., 2018; Pörtner et al., 2017)” (McKenzie et al., 2021, p. 1538)

“The fish heart assures oxygen delivery to all tissues in response to their demands, so cardiac performance is considered a central” (McKenzie et al., 2021, p. 1538)

“mechanism determining upper thermal tolerance in fishes (Eliason & Anttila, 2017; Farrell, 2009)” (McKenzie et al., 2021, p. 1539)

“Nonetheless, CT maximum (CTmax) and minimum (CTmin) have been used to interpret global warming impacts on fishes, such as range shifts (Sunday et al., 2011) or vulnerability to extreme warming events (Pinsky et al., 2019)” (McKenzie et al., 2021, p. 1539)

“Performance curves based on AAS have been used to interpret declines in species population abundance (Pörtner & Knust, 2007), failures of reproductive migrations (Eliason et al., 2011), how optimal habitats change with warming (Deutsch et al., 2015), and why particular species may be invading new areas (Marras et al., 2015” (McKenzie et al., 2021, p. 1539)

“A meta-analysis of thermal tolerance thresholds for 694 species (Dahlke et al., 2020) concluded that embryos and spawning adults have lower CTmax and a narrower thermal range (the difference in C between CTmin and CTmax) than larvae or adults (these latter defined as all animals post-metamorphosis, so from juveniles to mature adults that are not spawning).” (McKenzie et al., 2021, p. 1539)

“various studies have measured CTmax in larvae, few have considered how tolerance is affected by larval development (Moyano et al., 2017; Illing et al., 2020” (McKenzie et al., 2021, p. 1539)

“spiny chromis damsel Acanthochromis polyacanthus Bleeker 1855 (tropical) show no change in CTmax as they age (Moyano et al., 2017; Illing et al., 2020)” (McKenzie et al., 2021, p. 1539)

“olerance increases as development proceeds towards metamorphosis” (McKenzie et al., 2021, p. 1539)

“When comparing across fish species, CTmax can decline with body and consequent cell size (Leiva et al., 2019). There is also evidence that, within some species, CTmax declines with fish size or mass (Table 1).” (McKenzie et al., 2021, p. 1541)

“In marine tropical damselfishes, CTmax declined with size in spiny chromis Acanthochromis polyacanthus Bleeker 1855 and white damsel Dischistodus perspicillatus Cuvier 1830, but not in humbug Dascyllus aruanus L. 1758 (Clark et al., 2017)” (McKenzie et al., 2021, p. 1541)

“Thus, tolerance of warming declines with mass in many fish species, but more research is required to establish whether this is because of a reduced capacity of larger fishes to meet the oxygen demands of metabolism when water temperature rises” (McKenzie et al., 2021, p. 1541)

“Taken together, these data point to body size as another important factor that can lead to intraspecific variation in tolerance of warming in fishes” (McKenzie et al., 2021, p. 1541)

“Developmental plasticity occurs when conditions during early development cause the expression of a phenotype that is then fixed for the remainder of the animal's lifetime” (McKenzie et al., 2021, p. 1541)

“Transgenerational plasticity occurs when the environment experienced by the parent affects the phenotype of the offspring and can be mediated by epigenetic responses that affect gene expression and therefore the phenotype, but not the underlying genetic code (Donelson et al., 2018; Mimura et al., 2017; Moran et al., 2016)” (McKenzie et al., 2021, p. 1541)

“Epigenetic responses can contribute to immediate plastic responses but may also be heritable over a few generations (Donelson et al., 2018; Mimura et al., 2017; Moran et al., 2016)” (McKenzie et al., 2021, p. 1541)

“Nonetheless, one common pattern is that a given increase in acclimation temperature is not linked to an equivalent increase in CTmax, such that the thermal safety margin, the difference between acclimation temperature and CTmax, narrows as a fish is acclimated to progressively warmer temperatures across its thermal range (e.g., Habary et al., 2017; McArley et al., 2017; McDonnell et al., 2019; Spinks et al., 2019).” (McKenzie et al., 2021, p. 1541)

“Long-term acclimation to the temperatures is expected to provide adequate time for active plastic compensation of metabolic traits, presumably towards optimizing performance at the new temperature (Claireaux et al., 2006; Ferreira et al., 2014; Healy & Schulte, 2012; Norin et al., 2014; Sandblom et al., 2014, 2016; Slesinger et al., 2019)” (McKenzie et al., 2021, p. 1543)

“Studies have investigated how a TPC for AAS, measured over a range of acute temperature exposures, varies with thermal acclimation (Ferreira et al., 2014; Healy & Schulte, 2012; Poletto et al., 2017).” (McKenzie et al., 2021, p. 1543)

“Nonetheless, one response that appears to be observed in multiple species is that when acclimated chronically, the capacity to raise MMR appears to be finite so that plastic adjustments to maintain AAS are often linked to a capacity offset Q10 effects on SMR (Ferreira et al., 2014; Healy & Schulte, 2012; McArley et al., 2017; Norin et al., 2014; Sandblom et al., 2014, 2016; Slesinger et al., 2019)” (McKenzie et al., 2021, p. 1544)

“That is, the fishes recruit mechanisms to compensate for the thermodynamic effects of increased temperature on basal metabolic processes and their associated oxygen demand” (McKenzie et al., 2021, p. 1544)

“Reversible, developmental and transgenerational plasticity all contributes to intraspecific variation in tolerance of warming in fishes and has the potential to buffer species against the negative effects of climate warming” (McKenzie et al., 2021, p. 1544)

“In essence, “buying time” by allowing a species to persist as the environment changes. This may enable long-term evolutionary responses by populations, if it protects population size and underlying genetic diversity in the face of initial warming (Crispo, 2008).” (McKenzie et al., 2021, p. 1544)

“Thus, the question of whether intraspecific variation generated by plasticity will help or hinder long-term persistence of a species in the face of climate change remains far from settled (Fox et al., 2019” (McKenzie et al., 2021, p. 1544)

“At a geographic scale, variation in thermal tolerance is expected to be structured by large-scale environmental gradients and may reflect both plastic responses and underlying genetic diversity (Bennett et al., 2019).” (McKenzie et al., 2021, p. 1548)

“Tropical species also live closer to their upper thermal limits (Comte & Olden, 2017), such that there would be less thermal margin for standing variation in tolerance to persist in tropical latitudes.” (McKenzie et al., 2021, p. 1548)

“Greater variation within and among populations can buffer negative effects of climactic stressors and reduce the overall risk of negative effects on stability of the species.” (McKenzie et al., 2021, p. 1549)

“This effect does not require that variation is heritable, just that structured variation exists (Bolnick et al., 2011; Moran et al., 2016).” (McKenzie et al., 2021, p. 1549)

“For tolerance of warming, one example where a portfolio effect might contribute to differences in vulnerability is latitudinal structuring, with the greater variation in CTmax in temperate species compared to tropical species (Nati et al., 2020).” (McKenzie et al., 2021, p. 1549)

“The other major concept that defines vulnerability of a species to global warming is its adaptability or evolvability, which obviously focuses on heritable genetic variation (Bolnick et al., 2011; Mimura et al., 2017; Pacifici et al., 2015).” (McKenzie et al., 2021, p. 1549)

“The concept is simple; having a large degree of heritable variation can provide genotypes for new selections in a changing environment and contribute to populations fitting into the new environment (Bolnick et al., 2011; Mimura et al., 2017; Pacifici et al., 2015).” (McKenzie et al., 2021, p. 1549)

“Ongoing innovations in molecular biology may allow the direct investigation of functional genetic variants responsible for adaptation (Mimura et al., 2017; Razgour et al., 2019)” (McKenzie et al., 2021, p. 1549)

“For example, genomic studies of local adaptations can reveal the extent of molecular genetic diversity and how it relates to tolerance phenotypes and to prevailing environmental conditions at sites across a species’ range (Razgour et al., 2019).” (McKenzie et al., 2021, p. 1549)

“Phenotypic plasticity can reduce sensitivity to thermal stress, but there is an evidence that upper thermal tolerance has a “ceiling” in fishes, both in terms of CTmax and capacity to raise MMR when warmed.” (McKenzie et al., 2021, p. 1549)

“Effective plasticity in aerobic performance may involve maintaining broad thermal breadth in the short term and thermal compensation of basal metabolism by acclimation over th” (McKenzie et al., 2021, p. 1549)

“Having extensive heritable genetic variation is expected to improve the potential for adaptability; nonetheless, this remains to be demonstrated” (McKenzie et al., 2021, p. 1550)

“Advances in sequencing are opening up means to infer a role for physiological adaptation to the environment by linking genome-wide scans to prevailing environmental conditions (Mimura et al., 2017; Razgour et al., 2019” (McKenzie et al., 2021, p. 1550)

**Smaller adult fish size in warmer water is not explained by elevated metabolism**

# Annotations (8/31/2023, 3:54:55 PM)

“Fish and other ectotherms living in warmer waters often grow faster as juveniles, mature earlier, but become smaller adult” (Wootton et al., 2022, p. 1177)

“whether TSR-type body size changes (larger juveniles, smaller adults) are driven by some form of temperature-imposed limitation that has an overall negative impact on individuals, or whether it represents a potentially adaptive life-history optimisation or trade-off in warmer conditions (Audzijonyte et al., 2019; Verberk et al., 2020).” (Wootton et al., 2022, p. 1178)

“Known as the temperature-size rule (TSR), this pattern is commonly attributed to higher metabolism in warmer waters, leaving fewer resources for growth.” (Wootton et al., 2022, p. 1177)

“females at 30°C allocated more to reproduction, especially when maturing at the smallest sizes.” (Wootton et al., 2022, p. 1177)

“We show that elevated temperatures do not necessarily increase baseline metabolism if sufficient acclimation is allowed and call for an urgent revision of modelling assumptions used to predict population and ecosystem responses to warming.” (Wootton et al., 2022, p. 1177)

“The temperature-size rule (TSR) postulates that ectotherms living in warmer conditions grow faster as juveniles but attain smaller adult body sizes (Atkinson, 1994). This phenomenon has been observed in organisms ranging from bacteria to vertebrates (Atkinson, 1994) and is particularly pronounced in aquatic environments (Horne et al., 2015, 2017 ; Rollinson & Rowe, 2018)” (Wootton et al., 2022, p. 1177)

“The assumption that higher temperatures lead to higher metabolic rates is a central tenet of metaboli” (Wootton et al., 2022, p. 1178)

“theory of ecology (Brown et al., 2004). This assumption is so widely accepted that it is used in most models aiming to predict species and ecosystem responses to warming (DeLong et al., 2017; Sentis et al., 2021; WoodworthJefcoats et al., 2019; Zhang et al., 2017), including those that suggest >20% declines in body weight across hundreds of marine fish species (Cheung et al., 2013).” (Wootton et al., 2022, p. 1178)

“Yet, studies of hundreds of species show that metabolic rates can acclimate to temperature changes (Donelson et al., 2012; Scott & Johnston, 2012; Seebacher et al., 2015).” (Wootton et al., 2022, p. 1178)

“commonly observed higher metabolic rates in warm temperatures reflect an adaptive temperature-dependent selection for a faster pace of life rather than a physiological inevitability (Clarke & Fraser, 2004; Kingsolver & Huey, 2008; Schulte et al., 2011). Elevated metabolism at warmer temperatures then becomes an advantageous response that enables, for example, faster food intake rates (Denderen et al., 2020).” (Wootton et al., 2022, p. 1178)

“The alternative, life-history based, explanation for TSR emphasises how the trade-off in resource allocation to growth and reproduction is shaped to maximise individual fitnes” (Wootton et al., 2022, p. 1178)

“If higher temperatures enable” (Wootton et al., 2022, p. 1178)

“faster developmental rates (Kingsolver & Huey, 2008), this would allow earlier maturation and energy investment in reproduction at younger ages (Forster & Hirst, 2012). The resulting smaller adult body sizes would then not be driven by temperature-induced metabolic limitations, but rather adaptive energy allocation (Kingsolver & Huey, 2008; Kozlowski, 1992). Such shifts to earlier and potentially higher investment in reproduction can have important implications for population growth rates in warming environments (Engen & Saether, 2016; Oli et al., 2002).” (Wootton et al., 2022, p. 1179)

“Maximum metabolic rate always remained higher at warmer temperatures” (Wootton et al., 2022, p. 1183)

“MMR showed a different temperature sensitivity compared to SMR across generations. Maximum rates of oxygen consumption did not differ across body size and generation at the two temperatures (test 5 in Table 1), nor was there an interaction of temperature and body size alone (test 6 in Table 1). MMR was always higher in fish from warmed populations, with this difference in adults appearing to increase as generations progressed, although the trend was not significant” (Wootton et al., 2022, p. 1183)

“Our multi-generational experimental results are therefore incompatible with the ‘limitation’ hypothesis or the narrow application of metabolic theory of ecology, where metabolic rates are seen as an inevitable consequence of environmental temperature, and smaller adult body sizes are a negative consequence of insufficient energy or oxygen available for growth.” (Wootton et al., 2022, p. 1184)

“In this study we confirmed, through a multi-generational experiment, that fish mature at smaller sizes and become smaller adults when exposed to elevated temperatures.” (Wootton et al., 2022, p. 1183)

“Our findings, therefore, better align with the argument that” (Wootton et al., 2022, p. 1184)

“an individual's baseline metabolism, and by extension its oxygen use, is determined by its needs (Bigman et al., 2021; Kingsolver & Huey, 2008) and not an inescapable effect of temperature. Still, the elevated SMR observed over the first few generations of our experiment suggest that acclimation to a 4°C higher temperature required time, even in a eurythermal species like zebrafish.” (Wootton et al., 2022, p. 1184)

“warminginduced increases in metabolism (baseline, or through digestion related energetic costs (Jutfelt et al., 2021)), and hence some form of ‘limitation’ are still considered the main explanation of TSR-type body size responses.” (Wootton et al., 2022, p. 1184)

“Limitation mechanisms are explained either directly (Pauly, 1981, 2021 ; Portner et al., 2004) or indirectly through ‘ghosts of evolutionary past’, where organisms grow to smaller sizes in response to historic selection (e.g. via past oxygen limitation (Verberk et al., 2020)).” (Wootton et al., 2022, p. 1184)

“Even inter-generational studies often only consider two or three generations, ye” (Wootton et al., 2022, p. 1184)

“the full range of responses in our study was observed only after three generations” (Wootton et al., 2022, p. 1185)

“If our experiment stopped sooner, it would be logical to conclude that smaller adult body sizes were driven by higher baseline adult metabolic rates. Yet, after six generations our results suggest the opposite – higher temperatures, if anything, actually increased size-specific aerobic scope and thus likely increased metabolic performance in zebrafish. In all, our study supports the view that the generally higher metabolic rates of organisms living in warmer conditions (Brown et al., 2004) are not directly caused by high temperatures. Rather, they more likely reflect an adaptive metabolic response to temperature-induced changes in community structure due to shifting predation rates or faster developmental rates (Clarke & Fraser, 2004).” (Wootton et al., 2022, p. 1185)

“It could be argued that even if the total SMR at higher temperatures remains the same, the proportion of oxygen used for repair increases, leaving less oxygen for growth. Teasing apart the relative demand of cellular repair and growth would require measurements of the proportion of SMR spent by separate physiological processes.” (Wootton et al., 2022, p. 1185)

“Adult fish had higher SMR sensitivity to temperature in the first generations, whereas for juveniles, elevated temperatures had virtually no effect on SMR. Our findings strongly support the body size dependency of metabolic rates, at least on acute, short time scales” (Wootton et al., 2022, p. 1185)

“These observations appear to support the life-history-based ‘optimisation’ explanation for TSR with a reproduction-growth trade-off at its core” (Wootton et al., 2022, p. 1185)

“Higher temperatures lead to faster developmental rates and earlier maturation in many ectotherms (Berrigan & Charnov, 1994; Forster & Hirst, 2012). Naturally, an earlier onset of reproductive allocation is expected to divert energy away from growth” (Wootton et al., 2022, p. 1185)

“although see Pauly (2021) for a list of arguments of why allocation to reproduction cannot explain TSR type growth trajectories in fish.” (Wootton et al., 2022, p. 1185)

“We note that this reproductive allocation is not only a direct expenditure on gonads but also includes other indirect costs of reproduction such as migration, reproductive behaviours and competition (Watson et al., 1998).” (Wootton et al., 2022, p. 1185)

“Zebrafish living at the warmer temperature always matured earlier, despite any ambiguity in observations of gonad weights across temperatures and adult sizes” (Wootton et al., 2022, p. 1185)

“All else being equal, an earlier onset of reproduction is advantageous because it increases an individual's chance to reproduce (Cole, 1954). However, earlier reproduction and a resultant smaller adult body size typically means lower fecundity later in life. One explanation for TSR-type growth could be that size-specific fecundity increases later in life at colder temperatures and hence the risks of delayed maturation are compensated for by higher overall reproductive output in these conditions (Arendt, 2011).” (Wootton et al., 2022, p. 1185)

“Although we did not test for such an increase in size-specific fecundity, females living at the control temperature grew to larger sizes and, therefore, had larger overall gonads which would suggest greater absolute reproductive potential.” (Wootton et al., 2022, p. 1185)

“Another adaptive pathway could lie in evolved responses to shorter lifespans in warmer waters. Reductions to longevity at higher temperature can occur through direct (e.g. oxidative stress: Monaghan et al., 2009) and indirect (e.g. increased predation: Walker et al., 2020) processes, and involve the expression of early maturation or increased reproductive allocation in response to reduced lifetime reproductive opportunity (Kozlowski, 1992” (Wootton et al., 2022, p. 1185)

“Despite earlier reproduction, warmed populations did not necessarily have higher reproductive output” (Wootton et al., 2022, p. 1186)

“In fact, after four generations of heating we observed a rapid decline in the recruitment (number of fish that reached 6 weeks of age) of our warmed experimental populations (see: Wootton et al., 2021). It is important to note that the observed decrease in recruitment was relative to the control populations and does not necessarily suggest that earlier maturation itself was disadvantageous” (Wootton et al., 2022, p. 1186)

“our findings challenge the prevailing view that smaller body sizes at warmer temperatures are driven by physiological limitations and are necessarily maladaptive. Instead, they highlight that the adaptive significance of a body size response to warming is complex. Our findings also strongly suggest that the TSR puzzle will remain unresolved if we keep attempting to explain the complexity of growth simply as a difference between anabolism and catabolism. Time is ripe for better growth models, which at least specifically include reproductive allocation and its costs (Audzijonyte & Richards, 2018; Marshall & White, 2019)” (Wootton et al., 2022, p. 1186)

**Physiology can predict animal activity, exploration, and dispersal**

# Annotations (8/22/2023, 3:53:06 PM)

“Physiology can underlie movement, including short-term activity, exploration of unfamiliar environments, and larger scale dispersal, and thereby influence species distributions in an environmentally sensitive manner.” (Wu and Seebacher, 2022, p. 1)

“Range edges differed from cores in traits that may be associated with dispersal success, including metabolism, locomotor performance, corticosterone levels, and immunity, and differences increased with increasing time since separation.” (Wu and Seebacher, 2022, p. 1)

“At a larger spatial scale, dispersal drives colonisation of novel habitats and impacts biogeography2. Dispersal within meta-populations determines rates of gene flow between individual populations and influences genetic variation and adaptation to different environments3” (Wu and Seebacher, 2022, p. 2)

“For example, low rates of gene flow may decrease genetic diversity within single populations and limit the potential for selection. Increased dispersal could “rescue” isolated populations by increasing genetic diversity4.” (Wu and Seebacher, 2022, p. 2)

“On the other hand, genetic variation between populations within a greater meta-population can increase resilience to environmental change of the metapopulation as a whole via the portfolio effect5.” (Wu and Seebacher, 2022, p. 2)

“Additionally, changing environmental conditions, such as changes in temperature, may cause unfavourable conditions in the original habitat and stimulate individuals to search for more favourable conditions” (Wu and Seebacher, 2022, p. 2)

“For example, mismatches between the parental environment and the actual environmental conditions experienced had negative influences on physiological performance and stimulated dispersal in guppies (Poecilia reticulata)12.” (Wu and Seebacher, 2022, p. 2)

“Energetics and aerobic energy (ATP) production are the most frequently recognised physiological constraints of movement1” (Wu and Seebacher, 2022, p. 2)

“muscle-powered locomotion, and muscles require ATP for contraction and relaxation so that energetics could pose a strong constraint24.” (Wu and Seebacher, 2022, p. 2)

“Other physiological constraints include cardiovascular function. The capacity of the heart to pump sufficient blood to sustain exercise (cardiac scope) may be constrained by environmental conditions and thereby limit” (Wu and Seebacher, 2022, p. 2)

“movement particularly under challenging conditions such as against high water flow29.” (Wu and Seebacher, 2022, p. 2)

“Physiological characteristics typically vary between individuals within populations, and these differences may impact the tendency and extent of movement. For example, there was a threefold difference in the metabolic cost of transport (i.e., the energy used to move a given mass for a given distance) among individual zebrafish, which influenced the distance individuals moved in an artificial stream30. Similarly, metabolic rates and locomotor performance can vary widely among individuals within species31–33” (Wu and Seebacher, 2022, p. 2)

“On the other hand, the movement itself may cause physiological differentiation within populations if it led to the separation between the expanding movement edge and the core of the distribution.” (Wu and Seebacher, 2022, p. 2)

“As briefly discussed above, individuals with a greater tendency to move may have particular physiological characteristics, leading to core-edge differences.” (Wu and Seebacher, 2022, p. 2)

“Ina species expanding into novel environments, conditions at the dispersal front may differ substantially from those of the core distribution. As a consequence, the phenotypes that are successful in environments at the range edges may be different to the most successful phenotype at the core of the distributions; these differences may arise because individuals with particular genetic make-ups or greater capacity for plasticity have greater fitness at the range edge36,37.” (Wu and Seebacher, 2022, p. 2)

“Potential differentiation in physiological phenotypes between the core and edges may influence animal ecology through a variety of underlying traits, from disease resistance to social behaviour38,39” (Wu and Seebacher, 2022, p. 2)

**Selection Experiments in the Sea: What Can Experimental Evolution Tell Us About How Marine Life Will Respond to Climate Change?**

“However, many marine organisms, including many that are long lived, have large effective population sizes and are able to produce tremendous numbers of larvae at one time. For example, the red sea urchin (Mesocentrotus franciscanus)can live for more than a century, but a single female can produce 2 106 eggs in a single spawning event (Ebert and Southon, 2003).” (Kelly and Griffiths, 2021, p. 33)

“For example, geographic range size is often assumed to be inversely correlated with extinction risk from climate change, because large geographic ranges are assumed to stem from a broad environmental tolerance at the species level. But in some species, genetic subdivision may produce a collection of locally adapted populations whose environmental niches are narrower than the species as a whole” (Kelly and Griffiths, 2021, p. 33)

“A 10-generation selection experiment revealed that heattolerant phenotypes observed in low-latitude populations could not be achieved in high-latitude populations, through either acclimation or selection; and many populations plateaued in their responses to selection, suggesting that standing variation had already been depleted. These experiments demonstrated that broad geographic ranges do not necessarily imply low extinction risk in every population of a widely distributed species.” (Kelly and Griffiths, 2021, p. 33)

“(Kelly et al., 2012).” (Kelly and Griffiths, 2021, p. 33)

“By measuring costs of adaptation, experimental evolution can help to improve predictions about climate change effects: even in the cases where populations are able to evolve greater stress tolerance, it may come at a cost of decreased growth rates” (Kelly and Griffiths, 2021, p. 34)

**Counter-Gradient Variation in Respiratory Performance of Coral Reef Fishes at Elevated Temperatures**

“The response of species to global warming depends on how different populations are affected by increasing temperature throughout the species’ geographic range.” (Gardiner et al., 2010, p. 1)

“Local adaptation to thermal gradients could cause populations in different parts of the range to respond differently” (Gardiner et al., 2010, p. 1)

“Therefore, respiratory performance is expected to vary between populations at different latitudes because they experience different thermal environments.” (Gardiner et al., 2010, p. 1)

“The effect of higher temperatures on species’ distribution and abundance includes range shifts, population collapses, local extinctions, and phase shifts [5–11” (Gardiner et al., 2010, p. 1)

“These patterns emerge from the combined responses of populations to increasing temperature throughout the species’ geographic range” (Gardiner et al., 2010, p. 1)

“Local adaptation to thermal gradients can cause populations in different parts of the geographic range to exhibit different responses to temperature variation [12–18].” (Gardiner et al., 2010, p. 1)

“Consequently, comparing the effects of temperature increases in different populations is essential for generating robust predictions about the impact of global warming on animal communities at large spatial scales” (Gardiner et al., 2010, p. 1)

“Thermal optima could be locally adapted to match the thermal environment, such that populations from warmer locations outperform populations from cooler locations at higher” (Gardiner et al., 2010, p. 1)

“temperatures, but populations from cooler locations outperform populations from warmer locations at cooler temperatures (F” (Gardiner et al., 2010, p. 1)

“Thermal performance curves could exhibit co-gradient variation, whereby populations from warmer locations tend to outperform populations from cooler locations at all temperatures (Fig. 1b).” (Gardiner et al., 2010, p. 1)

“This pattern of thermal performance is predicted when genetic and environmental influences on performance are positively associated across the thermal gradient [21]. (3) Thermal performance curves could exhibit counter-gradient variation, whereby populations from cooler locations outperform populations from warmer locations at all temperatures (Fig. 1c). This pattern of thermal performance is predicted when genetic and environmental influences on performance are negatively associated across the thermal gradient [20]. (4) Finally, there might be no difference in thermal performance curves between populations (Fig. 1d). This pattern would be predicted if populations do not acclimate to the local thermal environment and high gene flow between populations restricts local adaptation to a thermal gradient. Each of these alternatives has different implications for how species would respond to increasing average temperature across their geographic range.” (Gardiner et al., 2010, p. 1)

“n aquatic systems, comparisons of geographic variation amongst conspecific populations has predominantly focused on polar and temperate climates, and counter-gradient patterns have often been detected [22,23]. Counter-gradient variation can arise when there is a trade-off between traits or processes in order to compensate for detrimental effects of the environmental gradient on performance, such as that induced by temperatures above a population’s thermal optima [21,22]. For example, physiological processes may be locally adapted to maintain growth and developmental rates against a thermal gradient that has a negative effect on these traits [20,21]. Whether similar compensatory mechanisms occur in tropical marine species is largely unknown.” (Gardiner et al., 2010, p. 2)

“While some tropical species appear to live close to their upper thermal limits [23,24], the capacity to acclimate may increase species flexibility to succeed in warmer temperatures [20]. With tropical ocean temperatures predicted to increase up to 3uC over the next 100 years [3,4], investigating the response of tropical marine taxa to higher temperatures has become increasingly important” (Gardiner et al., 2010, p. 2)

“In water breathing animals, such as fish, a key mechanism affecting performance with increasing temperatures is aerobic capacity.” (Gardiner et al., 2010, p. 2)

“Their results predict rising sea temperatures will alter reef fish community structure by causing more substantial declines in cardinalfish populations than in the damselfish populations. Deleterious effects of rising temperature on aerobic performance has already led to population collapses and ecosystem shifts in polar and temperate regions [9], and similar effects might be expected to occur in tropical marine systems” (Gardiner et al., 2010, p. 2)

“We detected significant differences in respiratory performance of reef fish populations at two widely separated locations on the Great Barrier Reef, but generally not as predicted by optimality models of thermal adaptation.” (Gardiner et al., 2010, p. 9)

“Reef fish in the warmer, northern Great Barrier Reef location did not cope better with higher temperatures than their conspecifics in the cooler, southern region” (Gardiner et al., 2010, p. 9)

“the southern populations had either greater or equivalent aerobic scope than the northern populations when tested at common temperatures. This counter-gradient variation in absolute aerobic capacity was mostly driven by southern populations exhibiting up to 80% higher MO2Max compared with the northern populations. Southern populations generally also had higher levels of MO2Rest than northern populations when tested at common temperatures.” (Gardiner et al., 2010, p. 9)

“n contrast to the differences in aerobic scope seen in some Heron Island fish compared with Lizard Island fish, there was no clear evidence for differences in the thermal optima between fish from the two sites” (Gardiner et al., 2010, p. 11)

“Thermal optima of some ectotherms are finetuned to their local thermal environment” (Gardiner et al., 2010, p. 11)

“For example, the optimal thermal temperature of Pacific salmon populations varies in direct relationship with their historically experienced river temperatures [15]. If Heron Island fish populations were adapted to the average summer temperatures experienced at that location, MO2Max and aerobic scope should have been highest at 27uC.” (Gardiner et al., 2010, p. 11)

“Instead, aerobic scope for all six species at Heron Island was highest between 29–31uC, well above the average summer temperatures experienced at this latitude. Due to north - south dispersal gradients on the Great Barrier Reef (GBR) [27], Heron Island populations may receive considerable gene flow from northern populations causing their apparent thermal optimum to be more suited to the summer reef temperatures of lower latitude reefs (e.g. 29–31uC)” (Gardiner et al., 2010, p. 11)

“Overall, our results suggest that Heron Island fish may perform better under warmer water conditions likely to occur in the future” (Gardiner et al., 2010, p. 11)

“. local adaptation, developmental plasticity, or a combination of the two) remains to be determined. Testing between these alternative will require sophisticated breeding experiments where offspring from the two populations are reared throughout their entire life-span at a range of different temperatures” (Gardiner et al., 2010, p. 11)

“There is some evidence that the differences in respiratory performance could have a least some genetic basis. Three of the damselfishes species tested here (A. polyacanthus, C. atripectoralis, P. moluccensis) exhibit genetic structure between the northern and southern GBR [27,28]” (Gardiner et al., 2010, p. 11)

“Geographic range differences among the study species may also contribute to differences in thermal tolerance” (Gardiner et al., 2010, p. 11)

“Whether warming oceans will shift the distributions of tropical marine species polewards depends strongly on the metabolic capacity of populations to keep pace with increased oxygen demand” (Gardiner et al., 2010, p. 12)

“If the strong counter-gradient patterns seen here are prevalent among reef fish, and other tropical marine ectotherms, then lower latitude populations inhabiting warmer waters will be more sensitive to global warming than populations of the same species at higher latitudes. Where dispersal mechanisms permit we might expect species with distributions currently centered in low latitudes to expand their distribution polewards. The long term viability of populations at low latitudes will depend on their ability to acclimate or adapt to warmer seas. Given the lack of evidence we detected for fine-tuning of thermal optima to match average or maximum summer temperatures” (Gardiner et al., 2010, p. 12)

“prospects for rapid adaptation to warming ocean temperatures by low-latitude populations may be limited” (Gardiner et al., 2010, p. 12)

**The ecological importance of intraspecific variation**

“More recently, research has broadened the characterization of diversity to incorporate the considerable phenotypic and genotypic variation within and among populations of single species4, including those undergoing contemporary (rapid) evolution5–” (Des Roches et al., 2018, p. 57)

“Understanding the ecological effects of intraspecific variation is important for models predicting the consequences of biodiversity loss and rapid trait change19,2” (Des Roches et al., 2018, p. 57)

“For example,  recent studies have reported massive current and projected declines in population genetic diversity24. Thus, a thorough understanding of the ecological effects of intraspecific variation will be critical for predicting how rapid, widespread changes in biodiversity within species will impact communities and ecosystems25” (Des Roches et al., 2018, p. 57)

“nature, the generation of intraspecific variation can occur through a variety of mechanisms, including, local adaptation, artificial selection, parental conditions and phenotypic plasticity4” (Des Roches et al., 2018, p. 57)

“When generated by evolutionary mechanisms, intraspecific trait variation can reflect microgeographic adaptation, divergent selection and even incipient speciation26.” (Des Roches et al., 2018, p. 57)

“When generated by plasticity, traits can change rapidly within generations and differ drastically across populations in dissimilar habitats27.” (Des Roches et al., 2018, p. 57)

“ss of the mechanistic underpinnings, it is the phenotypic manifestation of this variation that generates ecological impacts28.” (Des Roches et al., 2018, p. 58)

**Local adaptation reduces the metabolic cost of environmental warming**

“Metabolism shapes the ecosystem role of organisms by dictating their energy demand and nutrient recycling potential.” (Moffett et al., 2018, pp. -)

“Metabolic theory (MTE) predicts consumer metabolic and recycling rates will rise with warming, especially if body size declines, but it ignores potential for adaptation” (Moffett et al., 2018, p. 2318)

“Concern over climate change has spurred interest in predicting how changing thermal regimes will influence ecological systems (Bellard et al. 2012).” (Moffett et al., 2018, p. 2318)

“Much of our current approach to making these predictions is based on studies that take subsets of communities from a single ecosystem, expose them to elevated temperature over relatively short periods of time (i.e., within the lifespan of some constituent organisms), and gauge ecological responses (Shurin et al. 2012, Yvon-Durocher et al. 2012)” (Moffett et al., 2018, p. 2318)

“In essence, this approach forces today’s organisms into the context of tomorrow’s climate. This may be a major shortcoming because it fails to account for potential adaptation” (Moffett et al., 2018, p. 2318)

“Here, we consider adaptation as trait change through either developmental plasticity or evolution of genetically fixed traits to a range of drivers (Palkovacs et al. 2012), including changing climate (Bradshaw and Holzapfel 2006).” (Moffett et al., 2018, p. 2318)

“Such contemporary adaptation can substantially alter ecological outcomes derived from expectations of fixed phenotypes (Woodward et al. 2005, Fryxell and Palkovacs 2017)” (Moffett et al., 2018, p. 2318)

“Anticipating future climate change outcomes may thus depend on our ability to develop a general mechanistic understanding of how contemporary thermal adaptation alters fundamental physiological and ecological functions of populations” (Moffett et al., 2018, p. 2318)

“MTE predicts that warming alone should drive up population-level metabolic rates due to the temperature dependence of metabolism (Fig. 1). If” (Moffett et al., 2018, p. 2318)

“Regardless of the mechanisms underlying the trait change, the ecological outcome suggests that ignoring predictable variation in metabolic scaling traits can vastly overestimate consumer population energy demand and nutrient cycling and may ultimately underestimate the scope for persistence under future warming” (Moffett et al., 2018, p. 2323)

**Local Adaptation in Marine Invertebrates**

Local adaptation is the fine-tuning ofpopulations to their local environment via natural selection. Natural environments are often heterogeneous, characterized by strong spatial variation in both abiotic and biotic factors. Persistent environmental gradients may impose divergent selection, such that populations evolve differences in morphology, physiology, behavior, or life history that provide a fitness advantage under those local conditions. Local adaptation thus results in resident genotypes that have a higher fitness in their native habitat than do foreign genotypes from more distant populations (Kawecki & Ebert 2004). Importantly, the diversifying effects of selection are opposed by the homogenizing effects of gene flow.

In contrast, until recently, local adaptation has received comparatively little attention in marinesystems (reviewed by Conover 1998, Sotka 2005, Conover et al. 2006). Most marine species have traditionally been viewed as a collection of demographically open populations that are interconnected by high gene flow. This expectation followed from the apparent lack of dispersal barriers in marine systems and the fact that most marine invertebrates and fishes have planktonic larvae that spend days to months in the water column (Grosberg & Cunningham 2001). However, this paradigm of well-mixed marine populations has changed considerably in recent decades as mul- tiple lines of evidence now suggest that many marine populations are less connected than once thought (reviewed by Palumbi 2004, Levin 2006).

Restricted connectivity among marine populations may arise from life history, larval behavior, and/or oceanographic features that lead to the retention of offspring near their natal habitats (Dawson 2001, Sherman et al. 2008, Morgan et al. 2009).

The idea that a few successful migrants per generation may be sufficient to maintain genetic homogeneity between two populations is a useful guideline that has been repeated frequently in the literature (e.g., D´ıaz-Viloria et al. 2009, Goldstien et al. 2009, Hellberg 2009). Although this is likely true for neutral molecular markers (the focus of most population genetic studies), it is unlikely to be true for loci under selection (Hedgecock 1986, Slatkin 1987).

This may contribute to the misconception that a few larvae traveling between sites during each generation may be sufficient to maintain homogeneity across the entire genome, thus precluding adaptive divergence.

It is critical to realize that differentiation in loci under selection can occur in the face of considerable gene flow, so that populations that appear homogenous for neutral loci may still exhibit local adaptation (Conover et al. 2006)

A growing awareness of restricted connectivity among marine populations has been accompa-nied by a parallel realization that environmental gradients in the sea may be more fine-grained than has been traditionally appreciated

An additional limitation of the common garden approach is that this design explicitly tests

the role of a focal selective factor(s), and thus may neglect the response to other key factors present in nature but not manipulated in laboratory treatments. Reciprocal transplant experi- ments circumvent this limitation by transferring individuals between source habitats in the field and subsequently quantifying their fitness at each location.

For species with broad geographic ranges, adaptive differentiation among populations can generate a variety ofspatial patterns, ranging from countergradient variation across a latitudinal gradient (Conover et al. 2006, 2009) to more complex geographic mosaics ofadaptation (Thompson 1999). Countergradient variation occurs when genetic influences on a trait oppose environmental influ- ences, such that phenotypic differences across the gradient are minimized. For example, it has long been recognized that geographically separated populations of animals can exhibit similar rates of respiration or growth in their native environments, despite experiencing vastly different temperatures (Bullock 1955). However, when animals from distant portions ofa geographic range are acclimated at a common temperature in the laboratory, populations from cooler environments often exhibit higher rates of respiration. Although such metabolic compensation may often reflect physiological acclimatization (i.e., phenotypic plasticity), in other cases, fixed genetic differences among populations appear to make a major contribution to this countergradient pattern (Somero 2005, 2010).

local adaptation lies on a continuum with balanced polymorphism (Figure 3). Location along this continuum depends on the scale over which gene flow occurs and the scale over which the selective regime varies. When gene flow is restricted to a scale that is less than the scale over which a strong selective force varies, then the potential for local adaptation is increased. In contrast, when gene flow occurs over a spatial scale that is larger than the scale of the selective gradient, local adaptation is impeded and differentiation (if it occurs) must be main- tained by purifying selection.

In addition to the homogenizing effects ofgene flow, other factors may constrain local adaptation, most notably temporal variation and phenotypic plasticity (Figure 4). In species with high levels of gene flow, phenotypic plasticity will be favored over local adaptation, as long as there are no great costs to plasticity (Warner 1997, Kawecki & Ebert 2004).

Plasticity should constrain the evolution of local adaptation because it represents an alternate mechanism for achieving adaptive phenotypes in heterogeneous environments.

Local adaptation will also be opposed by metapopulation dynamics because population extinction and recolonization will erase any adaptation that has occurred over the life span of the population (Sultan & Spencer 2002).

Finally, local adaptation may be constrained by temporal variation in environmental gradients (Kawecki & Ebert 2004).

A better understanding of local adaptation will also improve the accuracy of predictions about the impacts of climate change. Climate

Predictions ofrange shifts are based increasinglyon climate envelope models,which use a species’ current distribution to describe its environmental niche and then map that niche on to space under future environmental conditions (Pearson&Dawson 2003).These models assume that every population ofa species has the same environmental niche and may underestimate extinction risk in species with strong local adaptation, where individual populations have a narrower range of tolerances than the species as a whole (Figure 5). This problem may be especially important for corals and intertidal invertebrates, some ofwhich appear to be living close to the edge of their upper thermal limits (Hughes et al. 2003; Somero 2005, 2010). Recent

If differences among populations are due to phenotypic plasticity, each population has the potential to achieve the full range of tolerances found in the species as a whole. If differ- ences are due to local adaptation, poleward populations may be unable to achieve higher thermal tolerance without gene flow frommore tolerant populations.

Earlier in this review, we drew a distinction between true local adaptation and balanced poly- morphism, where maladapted genotypes arrive in a population every generation and are removed by selection. This distinction is also important to making accurate predictions about the effects of climate change. If interpopulation differences in environmental tolerance are due to balanced polymorphism, then the full range of phenotypes found in the species are available to each popu- lation every generation, and so the narrower tolerances of individual populations should not lead to a greater extinction risk

Improved knowledge of local adaptation will also likely inform the conservation and spatial management of natural populations. Efforts to design effective networks of marine protected areas have emphasized the importance ofdemographic connectivity (reviewed by Palumbi 2004). How- ever, there is growing interest in ensuring that reserve networks also protect genetic diversity to promote resilience to environmental change (Bell & Okamura 2005, Baums 2008, Miller & Ayre 2008). Although genetic diversity is generally assessed using neutral molecular markers, there is often a poor correlation between neutral genetic variation and quantitative genetic variation in functionally important traits (Hedgecock 1986, Conover et al. 2006). Thus, there is a need for management planning that addresses spatial patterns of local adaptation. In particular, locally adapted populations might be a conservation priority if they act as sources of genotypes that re- plenish areas following disturbance.

populations that are truly locally adapted might indeed hold novel stress-resistant genotypes, and such populations might merit special consideration for conservation.

There has also been considerable interest in the implications of local adaptation for both

fisheries management and restoration efforts.

**Local adaptation is the fine-tuning of populations to their local environment via natural selection and results in resident genotypes that have a higher fitness in their native habi- tat than genotypes from more distant populations. Experimental approaches (including common garden designs and reciprocal transplants) are effective tools for identifying local adaptation.**

**Although understudied, local adaptation has been documented in numerous marine in- vertebrates in response to selection imposed by strong gradients (and more complex mosaics) of abiotic and biotic conditions**

**Local adaptation is promoted when the spatial scale of gene flow is small relative to the scale over which a strong selective gradient varies. Local adaptation is impeded when the scale of gene flow is much greater than that of the selective gradient. However, genetic differentiation can still occur in the face of high gene flow when selection is strong; in this case, divergence is maintained by selection acting on early life stages during each generation, and the system is characterized as a balanced polymorphism. As a result of these combined processes, differentiation among populations is expected to occur across a broad range of spatial scales and life histories in marine organisms.**

**Addressing spatial patterns of local adaptation in the sea is central to advancing our un- derstanding ofcommunity ecology, climate change impacts, and the spatial management of marine populations.**

**Most marine species occur over broad geographic ranges and exhibit considerable spa- tial variation in key traits. In most cases, little is known about relative contributions of phenotypic plasticity versus fixed genetic variation to these differences. Although the importance of this question has been recognized for decades (Bullock 1955, Segal 1961), progress has been limited**

**Agrowing bodyofpopulation genetic studies demonstrates genetic differentiation among marine populations in neutral molecularmarkers. These studies provide important infor- mation regarding scales ofgene flow, yet information is needed regarding corresponding differentiation in functionally important traits related to life history, physiology, and ecology.**

**A small, but expanding, body of work uses whole-genome scans to identify candidate loci involved in local adaptation. This approach promises to connect disparate scales of ecology and evolution, linking divergent selection among populations to the functional basis of adaptation at the level of individual genes.**

**Finally, there is a critical need for studies that rigorously quantify the spatial scale over which adaptive differentiation occurs in marine systems. Prior studies of local adapta- tion have frequently used two or three populations, which provides little information to address this question. Resolving the spatial scale over which local adaptation occurs in marine species has broad implications ranging from improved prediction ofthe biological impacts of climate change to effective management planning.**

**Intraspecific variation in tolerance of warming in fishes**

Intraspecific variation in key traits such as tolerance of warming can have profound effects on ecological and evolutionary processes, notably responses to climate change.

There is also strong evi- dence of structured variation in tolerance of warming within species, which may have ecological and evolutionary significance irrespective of whether it reflects plasticity or adaptation

Fishes may be especially vulnerable to global warming because, as ectotherms, their physiology is determined by thermody- namic effects of the surrounding water temperature, which sets their body temperature

A capacity for plasticity in toler- ance can buffer against the immediate impacts of thermal stress, thereby reducing population sensitivity. A second ele- ment is phenotypic plasticity, the ability of a given genotype to pro- duce different phenotypes in response to the environment within an individual's lifetime (Stearns, 1989).

Thirdly, there is genetically based heritable variation among individuals, either within or between populations. Possessing a broad range of heritable tolerance geno- types will influence population adaptability and the capacity to adjust to new conditions over generational time scales (Bennett et al., 2019; Moran et al., 2016; Pacifici et al., 2015). These collective effects of individual variation in thermal tolerance can, therefore, have impor- tant implications for vulnerability of populations and species to both short-term extreme heatwaves and long-term gradual warming (Bennett et al., 2019)

If broad functional variation among individuals increases the stability and resilience of a species in the face of environmental stressors, such as warming, this can stabilize the species’ ecological functions and, in turn, stabilize overall community and ecosystem function (Bolnick et al., 2011; Mimura et al., 2017; Pacifici et al., 2015)

**A practical guide to measuring local adaptation (Blanquart 2013)**

Adaptation to local environmental conditions plays a fundamental role in the generation and maintenance of biodiversity (Levene 1953; Gavrilets 2003), the contraction and expansion of species geo- graphical ranges (Kirkpatrick & Barton 1997) and the ecological and evolutionary dynamics of species interactions (Kaltz & Shykoff 1998). In addition, because local adaptation measures the match between adaptive genetic variation and environmental variation, its magnitude depends on the interaction among evolutionary forces such as selection and gene flow (Kawecki & Ebert 2004) such that quantifying levels of local adaptation may provide important insight into the relative strengths of these evolutionary forces

For instance, adapta- tion to local environmental conditions can be inferred if greater divergence is observed for a candidate trait than can be explained by drift alone (Hendry et al. 2001; McKay & Latta 2002). Alterna- tively, support for local adaptation could be provided by evidence of strong correlations between a candidate trait and functionally rel- evant environmental variables (Fumagalli et al. 2011; Hancock et al. 2011).

Thus, local adaptation is not a property of a sin- gle population, but rather of a metapopulation where multiple envi- ronments and populations are sampled.

First, local adaptation is sensitive to the balance between gene flow and local selection

When gene flow is limited, specialised genotypes can be maintained in isolated populations and this favours local adaptation. When gene flow is very large, however, the genotype that is, on average, the best, invades the population and local adaptation van- ishes (‘gene swamping’, Lenormand 2002). Second, the amount of genetic drift may also act on local adaptation. Genetic drift is expected to reduce local adaptation by reducing additive genetic var- iance, and by causing the random fixation of a reduced number of genotypes (Yeaman & Otto 2011; Blanquart et al. 2012

If selection pressures change, gene flow can facilitate adaptation by augmenting local genetic variation. Rap- idly changing selective pressures are often found in the context of antagonistic interactions, where coevolution results in ‘arms race’ dynamics with constantly escalating traits in both partners, or ‘Red Queen’ dynamics with periodical fluctuations in allele frequencies

**Geographic variation in temperature tolerance as an indicator of potential population responses to climate change (sorte 2011)**

The temperature tolerances of individuals in geographically separated populations of a single species can be used as indicators of each population's potential to persist or become extinct in response to climate change.

As mean and extreme temperatures increase in marine systems, the likelihood that a given population persists is partly related to the physiological capacity of organisms to tolerate elevated temperatures (Hutchins, 1947; Newell, 1969, 1979). Temperature clearly affects species' distribution patterns: a strong relationship between upper temperature tolerance and maximum habitat temperature has been demonstrated for many species

Shifts in species' ranges have been linked to rising mean temperatures (Southward et al., 1995; Herbert et al., 2003; Mieszkowska et al., 2005; Helmuth et al., 2006; Wethey and Woodin, 2008; Sorte et al., 2010a; Poloczanska et al., 2011-this issue).

It has been suggested that species with higher temperature tolerances will be better able to cope with global warming (Calosi et al., 2008) or, conversely, that more warm-adapted species will be at a disadvantage because they tend to live closer to their absolute tolerance limits (Stillman and Somero, 2000; Somero, 2005, 2010; Compton et al., 2007; Bonebrake and Mastrandrea, 2010) and have lower acclimation potentials (Stillman, 2003; Somero, 2005; Stenseng et al., 2005; Ghalambor et al., 2006).

Geographic variation in temperature tolerance, or differences in the average individual tolerances between geographically distinct populations, arises due to individual variation. This variation in temperature tolerance of an organism represents both adaptation (a distinct genotype) and phenotypic plasticity, or the range of phenotypes possible for a single genotype, which can be either fixed or variable over an individual's lifespan

At the species level, latitudinal distribution is often positively related to thermal tolerance range, although the implications for responses to climate change are equivocal given that this pattern is often driven by greater variation in lower, rather than upper, tolerance limits (Goto and Kimura, 1998; Gaston and Chown, 1999; Addo-Bediako et al., 2000; Kimura, 2004)

Thus, populations that are more prone to local extinction will be those in which individuals have low temperature tolerance, low acclimatization capacity, and/or low dispersal ability (Deutsch et al., 2008). We present three case studies in which we combine physiological thermotolerance data with current temperature data and climate change predictions.

Because geographic variation in temperature tolerance within a

species could be due to acclimation and/or adaptation (Kuo and Sanford, 2009), differences in life-history strategies will likely play an important role in the response of populations to increasing tempera- tures (Somero, 2010).

Organisms with reduced dispersal distances, limited acclimatization ability, and low thermal tolerances are considered to be at the greatest risk under a regime of climate warming (Harley et al., 2006; Deutsch et al., 2008; Somero, 2010). Conversely, organisms with pelagic larval dispersal, and therefore extensive gene flow and little genetic differentiation (Addison et al., 2008), are expected to have limited potential for local adaptation (Conover et al., 2006), and pelagic dispersal is only an advantage if gene flow is from more tolerant populations and towards less tolerant populations.

Sensitivity to climate change is determined by intrinsic factors

such as physiological limits, ecological traits, and genetic diversity (Williams et al., 2008)

**Can we predict ectotherm responses to climate change using thermal performance curves and body temperatures? (Sinclair2016)**

In studies with ecological applications, TPCs typically quantify whole-organism perfor- mance (e.g. speed, stamina, feeding rate, or growth) or some- times fitness proxies (e.g. reproductive output) because such integrative, higher level, traits are more directly related to eco- logical performance than are lower level ones such as enzyme activity.

DO TPCS REALLY ESTIMATE FITNESS?

Finally, some temperature-dependent traits may be poor proxies for fitness. For example, although resting or standard metabolic rates increase with temperature, higher rates indi- cate higher energetic expenditures as well as higher activity, and may not therefore translate to higher fitness, particularly during non-feeding life stages (Clarke 1991). Thus, identifying the most relevant fitness proxies is necessary when parsing contrasting – or even contradictory – signals from different traits (e.g. Fig. 3).

In fact, the ther- mal sensitivity of ectotherms sometimes varies markedly across their range, often in concert with local conditions. This variation can alter predictions of population dynamics at range edges under climate change (Pearson et al. 2009).

For example, thermal tolerance of barnacles is higher in subpopu- lations that experience more extreme temperatures (Schmidt et al. 2000), and thermal tolerances can vary widely among insect populations (reviewed by Sinclair et al. 2012). This local adaptation illustrates the evolutionary potential of thermal biology to shift over relatively short time scales – less than a century in the case of the cabbage white butterfly, Pieris rapae, in North America (Kingsolver et al. 2007). Thus, natu- ral selection might conceivably alter w(Tb) for species with short life cycles by the 2050 and 2100 dates used for most climate change projections.

The capacity for w(Tb) to evolve in this timeframe will vary

among taxa, habitats and traits (Hoffmann & Sgr?o 2011), and will also depend on the extent to which climate change affects p(Tb) – see below

Such duration effects imply that TPCs are tempo- rally dynamic, but this has been generally ignored in models

Although the broad physio- logical and biochemical mechanisms underlying these changes are reasonably well-understood, predicting how TPCs will shift is challenging, even in broad geographic comparisons (Somero 2010).

The capac- ity for plastic responses to changing temperatures can also depend on the rate of temperature change: emerald ash borer prepupae have relatively high heat tolerance when shifted slowly to a high temperature because slow warming allows them to mount a heat shock response (Sobek et al. 2011).

Both the order of thermal exposure and the rate of temperature change can affect w(Tb), but neither is usually accounted for in models (Assumptions 6 and 8 in Table 1), even though both vary in nature. Plastic responses to temperature fluctua- tions will likely bear costs and elicit trade-offs, not just as simple shifts in the instantaneous value of w(Tb), but in terms of long-lasting accumulation of fitness

Overall, a predictive understanding of how thermal fluctuations affect ectotherm fitness is still elusive (Kingsolver et al. 2013; Vasseur et al. 2014; Colinet et al. 2015), and empirical responses might well prove idiosyncratic.

Environmental physiology of ectotherms often focuses on temperature as a ‘master variable’ that dominates the performance, survival and fitness of organisms (Assumption 11, Table 1). Nevertheless, interactions involving numerous other environ- mental and biological factors can alter the shape of an organ- ism’s TPC and thus how an organism relates to its thermal environment (e.g. Fig. 4; Denny et al. 2009; Todgham & Still- man 2013; Gunderson et al. 2016).

When such interactions occur, the combined effect of two variables usually cannot be pre- dicted merely by summing the individual effects from single parameter experiments. Non-additive (synergistic) or even antagonistic outcomes in multiple stressor scenarios appear to be the norm, and varying a larger number of environmental parameters yields more substantial effects

Because of high interspecific variability in thermal perfor- mance, climate change is expected to result in ‘winners’ and ‘losers’ (Somero 2010). When performance differs among eco- logically important species such as structuring species, ecosys- tem engineers and keystone predators, differential vulnerability among interacting species can translate into dif- ferential vulnerability of entire assemblages (Monaco & Hel- muth 2011; Dell et al. 2014). Similarly, TPCs can be modified by interactions among species: shifts in food abundance (e.g. via predator–prey interactions, or competition) can modify the TPC (Fig. 6); non-consumptive effects (‘fear of being eaten’) can reduce foraging success and efficiency, or elicit other physiological costs (Rovero et al. 1999; Nelson et al. 2004); and parasites and pathogens can induce direct physio- logical costs (Vernberg & Vernberg 1963) that might modify the TPC.

**Intraspecific trait variation across scales: Implications for understanding global change responses (Moran 2016)**

some models are beginning to account for the fact that species’ traits are neither sta- tic nor homogenous in space or time (Bolnick et al., 2011; Violle et al., 2014).

Understanding and incorporating variation in traits is therefore important for basic science, for making predictions about global change impacts, and for managing species affected by global change

Intraspecific trait variation may be due to heritable differences between individuals, or it may be due to phenotypic plasticity in trait values across varying environmental conditions.

Understanding which of these sources is responsible for trait variability is crucial for predicting global change responses.

If differences in trait values within a population are due to genetic dif- ferences, they will be heritable, and therefore, popula- tion-level means will be subject to change through natural selection over generational timescales.

Plastic- ity, on the other hand, enables immediate adjustment of phenotypic traits, which can buffer a population against rapid environmental change. Plasticity tends to slow adaptive evolution in the short term by weakening selective pressures, but by preserving population size and genetic diversity may enable evolutionary responses in the long run (Crispo, 2008)

Epigenetic differences, which affect gene expression but not the underlying genetic code, can contribute to both categories of variation. They contribute to plastic responses, but some can also be heritable over inter- mediate time spans (~1–5 generations).

Within a population or geographic area, trait variation can be structured (varying in a consistent or predictable way) or unstructured (random) with respect to space, time, or kinship.

Structured variation in traits across populations or large geographic areas can often be related to environ- mental gradients (Fig. 1) or to geographic structure. If the variation is heritable and dispersal is very low, lack of genetic variation may inhibit adaptation to changing conditions; if dispersal is extremely high, the move- ment of alleles between heterogeneous environments may counteract local selective pressures (Aitken & Whitlock, 2013)

In many global change applications, the focus is not so much on describing the change in local populations, but rather on capturing spatial structure and large-scale dynamics.

**Causes and consequences of thermal tolerance limits in rocky intertidal porcelain crabs, genus Petrolisthes (Stillman 2002**)

Incorporation of the evolutionary history into any analysis follows from the ‘‘unarguable premise that species are not independent biological units that are devoid of history and genealogical affinities’

The evolutionary consequences of upper thermal tolerance limits and plasticity of thermal limits are large because only a single exposure to a temperature above the upper themal tolerance limit before repro- duction is required to lower fitness to zero. Thus, there is a great selective advantage for those individuals in a population that have thermal tolerance limits above the maximal habitat temperatures.

Organisms live within ecological communities and the strength of interaction among groups of organisms can be great. Small increases in temperature that occur well below the lethal limits and that affect the performance of a predator can have large changes in community dynam- ics (e.g., Sanford, 1999).

**Temperature dependence of fish performance in the wild: Links with species biogeography and physiological thermal tolerance (Payne 2016)**

for ectotherms, environmental temperature has a profound influence on physiology and fitness. The thermal sensitivity of ectotherm performance is often described by a thermal performance curve, which increases with temperature to a maximum (the temperature at maximum performance is defined as the optimum temperature, Topt), and declines at higher temperatures.

Because ectotherms can acclimate (phe- notypically) and adapt (genetically) to different tempera- tures (Angilletta 2009), there is a general expectation that optimal and critical temperatures will reflect, to some extent, the environmental temperatures an ectotherm expe- riences throughout its geographical range

Comparative and experimental studies support this expectation, with Topt shown to correlate positively with mean environmen- tal temperatures (Frazier, Huey & Berrigan 2006; Deutsch et al. 2008; Huey et al. 2012), and critical temperatures to correlate with latitude (Addo-Bediako, Chown & Gaston 2000; Sunday, Bates & Dulvy 2011).

Recent studies suggest tropical species may be more vulnerable to climate warming because average or maximum temperatures in their natural habitat are already closer to those that maximize physiological performance in the lab- oratory than are those of species from higher latitudes (Deutsch et al. 2008; Huey et al. 2009; Rummer et al. 2014).

Tempera- tures that maximize performance in the wild (i.e. ecologi- cally optimal temperatures, which we call ‘ToptE’) may largely depend on those that maximize a particular physio- logical performance measure in the laboratory (such as the optimum temperature for aerobic scope, ‘ToptAS’), but will also depend on food and habitat availability, community structure and various other ecological factors. An inability to move, grow or reproduce will ultimately define species range boundaries whether failure of performance is proxi- mally caused by a loss of intrinsic physiological capacity (e.g. biochemical reaction rates or scope for metabolism) or other ecological factors (e.g. a lack of food).

Thus, examining relationships between temperature and perfor- mance in wild, unrestrained animals could be informative or understanding how temperature regulates species distri- butions.

**Life on the edge: Thermal optima for aerobic scope of equatorial reef fishes are close to current day temperatures (Rummer 2014)**

Species living at extreme latitudes (equator and poles) may be particularly sensitive to global warming because they evolved in a relatively stable thermal environment and are expected to exhibit narrow ther- mal tolerance ranges (Tewksbury et al., 2008). The ther- mal range for optimum aerobic performance (thermal optima; Topt) in such species may only span a few degrees, whereas temperate species need to perform over a much wider range of temperatures(Deutsch et al., 2008; Somero, 2010; Nguyen et al., 2011; Sunday et al., 2011).

Furthermore, theory suggests that popula- tions living at thermally stable latitudes (e.g., near the equator or poles) have less capacity for thermal accli- matization (i.e. physiological, anatomical, or biochemi- cal modifications that occur within a lifetime to cope with natural changes in temperature) than populations living in more thermally variable, high-latitude loca- tions (P€ortner, 2002; Stillman, 2003; Somero, 2010; Neu- heimer et al., 2011; Nguyen et al., 2011)

Moreover, there may be no selection pressure to tolerate temperatures outside of what the populations are regularly experiencing. Equatorial populations of marine species are predicted to be especially sensitive to rising temperature because they experience an even narrower temperature range than equatorial populations of terrestrial species (due to the large heat storage capacity of water). In addition, their geographical ranges more closely conform to organismal thermal tolerance limits than the geographical ranges of terrestrial species, especially near equatorial boundaries (Sunday et al., 2011, 2012)

For coral reef fishes, rising ocean temperatures may not be immediately lethal (Mora & Osp?ına, 2001), but could have significant impacts on individual perfor- mance that will ultimately affect population demogra- phy and biogeographic distributions (Munday et al., 2008b; Nilsson et al., 2009). For example, an increase in average temperature of 2–3 °C significantly com- promises growth and reproduction of some species (Munday et al., 2008a; Donelson et al., 2010; Pank- hurst & Munday, 2011; Rushworth et al., 2011; Zarco- Perell?o et al., 2012). The

The mechanistic explanation for the effects on individual performance may be related to how temperature influences O2 uptake, transport, and delivery, also known as oxygen- and capacity- limited thermal tolerance (OCLTT) (P€ortner, 2001; P€ortner & Knust, 2007; P€ortner & Farrell, 2008; Elia- son et al., 2011).

The physiological scope for aerobic performance (aerobic scope), calculated as the differ- ence in O2 consumption between resting and maxi- mal performance (Fry & Hart, 1948; Priede, 1977), represents the oxygen available – in excess of that required for basic maintenance of the organism – for activities essential to support biological fitness (e.g., activity, feeding, and reproduction).

Temperature- induced reductions in aerobic scope have ecological consequences because less energy is available for vital life history processes that shape population dynamics and community structure (P€ortner & Peck, 2010).

many species also have large geographi- cal ranges that span temperature ranges that are greater than the projected increase in ocean tempera- ture due to global warming (Munday et al., 2008b). This suggests that populations are acclimatized or adapted to their local thermal environment along a latitudinal gradient. Adaptation to the very narrow equatorial temperature range may cause equatorial populations of reef fishes to be far more sensitive to global warming than populations of the same species from higher latitudes

Equatorial populations of four of the six species investi- gated in this study appear to be living at or above their optimal temperatures for aerobic performance.

Aerobic scope has been classically referred to as a proxy for individual performance (Fry, 1971); although, potential limitations with this idea have been outlined in a recent review (Clark et al., 2013).

Still, the significant tempera- ture-induced reductions in aerobic scope observed here in all species at 3 °C above current-day temperatures may be expected to have ecological consequences because less energy may be available for vital life history processes such as growth, reproduction, and predator-prey interactions (P€ortner & Peck, 2010).

When M˙ O2Rest increases with tempera- ture, the minimum energy required for basal mainte- nance of the organism is increased. In

If tropical fishes are locally adapted to their thermal envi- ronment, do not regularly experience temperature fluc- tuations, and do not move far from these microhabitats, there would be no drive to possess such metabolic com- pensation.

If aerobic scope is closely linked to individual performance (P€ortner & Farrell, 2008; reviewed in Clark et al., 2013), then declines in this trait could have implica- tions for long-term sustainability of equatorial fish populations and could drive a range shift of species away from their equatorial boundary (Munday et al., 2008b; Nguyen et al., 2011; Sunday et al., 2012).

**Testing for local adaptation and evolutionary potential along altitudinal gradients in rainforest Drosophila: beyond laboratory estimates (O’Brien 2017)**

Such models typically assume that the association between the environment and a species’ abundance (i.e. its niche) does not vary across the species’ geographical range and will remain stable in the future (but see Kear- ney et al., 2009). However, spatial variation in environ- mental tolerances is observed across many species’ ranges, demonstrating local niche differentiation (Banta et al., 2012; Kelly et al., 2012)

Ignoring variation in a species’ ecological niche within populations, or between populations across its geographical range, will have two contrasting conse- quences: (i) we may overestimate the geographical dis- tribution of a species if tolerances are assumed to be constant throughout the species’ range (i.e. that all pop- ulations can tolerate all currently occupied conditions: Hampe, 2004; Kelly et al., 2012); and (ii) we may under- estimate the potential for species to persist through evolutionary change, where extinction would be pre- dicted based on current distributions (Davis et al., 2005; Kearney et al., 2009; Hoffmann & Sgr?o, 2011).

In addition, laboratory assays have revealed lower levels of genetic variation in eco- logically important traits associated with tolerance of climatic stresses within populations close to the species’ range margin, which may constrain adaptation (e.g. Hoffmann et al., 2003; Kellermann et al., 2006).