

1 **Commentary Functional ecology**

2 **'Winners' and 'losers' in the Anthropocene: understanding adaptation through**
3 **phenotypic plasticity**

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5 Being able to make accurate predictions about the success of a species in the face of climate
6 change and other stressors is a major focus of ecological research. Integral to the approach
7 is to identify the mechanisms by which organisms respond to change. To persist under new
8 conditions (for example, increased ocean temperatures) a species will either need to shift its
9 geographic distribution (Poloczanska et al., 2013), adapt through genetic evolution (Muñoz
10 et al., 2015), or exhibit adaptive phenotypic plasticity in response to the stressor (Palumbi et
11 al., 2014). Range shifts have been documented for a number of marine species (e.g.
12 Mieszkowska et al., 2013), however, for most the bulk of their geographical distribution will
13 remain unchanged (Munday et al., 2017). Genomic evolution may not be possible for
14 individuals 'trapped' in their current distribution, because of a mismatch between
15 generation time and the speed of changes. Studies which assess the genomic and epigenetic
16 mechanisms that underpin species' plasticity in response to rapidly changing environmental
17 conditions are, therefore, particularly relevant. Ultimately, the flexibility and strength of
18 these responses will be critical to becoming a 'winner' under unprecedented rates of
19 change.

20 In this issue of *Functional Ecology*, Clark et al (2018) report on a creative experiment that
21 takes significant steps towards understanding the molecular basis of phenotypic plasticity.
22 Polar habitats are at the forefront of anthropogenic-driven change, with the Antarctic
23 Peninsula having experienced some of the most rapid warming relative to baseline for any

24 region on Earth (Meredith and King, 2005). It is, therefore, no surprise that scientists have
25 focussed on the ability of polar species to acclimatize. Clark et al.'s selection of the
26 Antarctic limpet *Nacella concinna* to investigate the cellular and molecular mechanisms
27 underpinning plasticity is perfectly aligned to this aim. This species inhabits both inter-tidal
28 and sub-tidal zones, with two morphotypes that differ in a suite of physiological and
29 morphological characteristics that make them suited to the specific environment's
30 requirements. Phenotypic variation such as this is not unusual for marine species (e.g. De
31 Wolf et al., 1998), but critically, *N. concinna* is a broadcast spawner; producing a planktonic
32 larval stage that disperses over 1-2 months; thus contributing to its genetically
33 homogeneous background across the habitats (Hoffman et al. 2010).

34 Gene expression profiles following reciprocal transfer experiments between the two
35 habitats show the up-regulation of cellular stress response genes reflect individuals being
36 moved from the relatively benign sub-tidal to their new stressful inter-tidal home.
37 However, these changes also persisted in the inter-tidal animals transplanted to the sub-
38 tidal. Epigenetic differentiation (methylation patterns) also showed differences after
39 transplantation, thus indicating its role in an organism's ability to respond to new
40 environments and also in habitat-specific phenotype differentiation.

41 What this study has also done, which makes it stand out not only from other polar studies,
42 but for marine invertebrates generally, was to include a long term common garden
43 experiment. This has enabled the authors to investigate if the expression profiles had
44 become fixed. The nine months of being in aquarium conditions did not remove
45 transcriptomic differences between the sub-tidal and inter-tidal groups. The epigenetic
46 differences seen at the start of the transplant experiments did not persist, although the

47 authors do acknowledge that they may have missed some methylation as it can be extensive
48 across the genome (Huang et al., 2017).

49 Clark et al. (2018) have addressed fundamental issues of adaptation but, as is often the
50 case, the animals did not always stick to the plan. The fact that individuals of both
51 transplanted groups began to move back to their source habitats (travelling several metres)
52 highlights some interesting future research themes. For example: i) why would an organism
53 return to an environment that is demonstrably more stressful; and ii) how does an organism
54 initiate novel behavioural strategies (i.e., start homing) that contribute to phenotypic
55 plasticity?

56 Our world is changing rapidly not just in terms of average meteorological quantities, e.g.
57 temperature, precipitation etc., but also with variability of these quantities e.g., the
58 intensity and frequency of extreme climatic events (Jentsch et al., 2007; Thompson et al;
59 2013; Leung et al., 2017). Studies using transcriptomic and epigenetic methods that show
60 species *can* respond to change in relatively short time scales are currently in the minority,
61 but the results of Clark et al (2018) and others will have significance as they give hope that
62 many more species have the potential to be 'winners'. Indeed, rapid stress-induced
63 epigenetic changes are thought to contribute to the fast acclimatisation experienced during
64 biological invasions: an extreme form of winning (Huang et al 2017). However, what is
65 missing from being able to identify 'winners' at a broader scale is if the transcriptomic and
66 epigenetic resilience can be routinely passed to offspring. Some marine species have
67 capacity for trans-generational acclimation (Munday et al., 2013; Veilleux et al., 2015), but
68 multi-generational experiments are required for many more marine species in line with
69 mammalian studies (Metzger and Schulte, 2016).

70 Keystone species from other habitats also need to be investigated. Like Clark et al. (2018),
71 many marine studies have focussed on inter-tidal rocky shore species for their tractability
72 and obvious exposure to extreme conditions (Mieszkiowska et al, 2013), but other benthic
73 habitats are also at risk. Inter-tidal mudflats are traditionally thought to be buffered to
74 extreme climatic effects, but our own data show that temperatures within the top 5 cm of
75 the sediment (where many of the infaunal species live) are still susceptible to heat waves if
76 emersion corresponds with high solar radiation levels (White, 2018). As sediment is a sink
77 for many pollutants, these habitats have also suffered disproportionately from other
78 toxicological stressors (e.g. Vandegehuchte and Janssen, 2014). Cumulative effects of
79 multiple stressors should, therefore, be a priority for future epigenetic and transcriptomic
80 studies.

81 Although we are beginning to understand the role of variability (inter-individual, inter-
82 population and inter-species) that discriminates a 'winner' from a 'loser', it is clear that the
83 Anthropocene is taking us (science, species and communities) into uncharted waters. As
84 Clark et al. (2018) have accomplished for their polar limpet, it is imperative for ecologists to
85 understand if, and how, species can respond to an uncertain future. We can only hope that
86 many species do have the capacity to be future 'winners'.

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88 De Wolf, H., Backeljau, T. and Verhagen, R., 1998. Spatio-temporal genetic structure and
89 gene flow between two distinct shell morphs of the planktonic developing periwinkle
90 *Littorina striata* (Mollusca: Prosobranchia). *Marine Ecology Progress Series*, 163, 155-163.

91 Hoffman, J.I., Peck, L.S., Hillyard, G., Zieritz, A. and Clark, M.S., 2010. No evidence for genetic
92 differentiation between Antarctic limpet *Nacella concinna* morphotypes. *Marine Biology*,
93 157, pp.765-778.

94 Huang, X., Li, S., Ni, P., Gao, Y., Jiang, B., Zhou, Z. and Zhan, A., 2017. Rapid response to
95 changing environments during biological invasions: DNA methylation perspectives.
96 *Molecular Ecology*, 26, 6621-6633.

97 Jentsch, A., Kreyling, J. and Beierkuhnlein, C., 2007. A new generation of climate-change
98 experiments: events, not trends. *Frontiers in Ecology and the Environment*, 5, 365-374.

99 Leung, J.Y., Connell, S.D. and Russell, B.D., 2017. Heatwaves diminish the survival of a
100 subtidal gastropod through reduction in energy budget and depletion of energy reserves.
101 *Scientific reports*, 7, 17688.

102 Meredith, M.P. and King J.C., 2005, Rapid climate change in the ocean west of the Antarctic
103 Peninsula during the second half of the 20th century. *Geophysical Research Letters*, 32,
104 L19604.

105 Metzger, D.C. and Schulte, P.M., 2016. Epigenomics in marine fishes. *Marine Genomics*, 30,
106 43-54.

107 Mieszkowska, N., Firth, L. and Bentley, M., 2013. Impacts of climate change on intertidal
108 habitats. *MCCIP Science Review*, 2013, 180-192.

109 Munday, P.L., Donelson, J.M. and Domingos, J.A., 2017. Potential for adaptation to climate
110 change in a coral reef fish. *Global Change Biology*, 23, 307-317.

111 Muñoz, N.J., Farrell, A.P., Heath, J.W. and Neff, B.D., 2015. Adaptive potential of a Pacific
112 salmon challenged by climate change. *Nature Climate Change*, 5, 163.

113 Palumbi, S.R., Barshis, D.J., Traylor-Knowles, N. and Bay, R.A., 2014. Mechanisms of reef
114 coral resistance to future climate change. *Science*, 344, 895-898.

115 Poloczanska, E.S., Brown, C.J., Sydeman, W.J., Kiessling, W., Schoeman, D.S., Moore, P.J.,
116 Brander, K., Bruno, J.F., Buckley, L.B., Burrows, M.T. and Duarte, C.M., 2013. Global imprint
117 of climate change on marine life. *Nature Climate Change*, 3, 919.

118 Thompson, R.M., Beardall, J., Beringer, J., Grace, M. and Sardina, P., 2013. Means and
119 extremes: building variability into community-level climate change experiments. *Ecology*
120 *Letters*, 16, 799-806.

121 Vandegehuchte, M.B. and Janssen, C.R., 2014. Epigenetics in an ecotoxicological context.
122 *Mutation Research/Genetic Toxicology and Environmental Mutagenesis*, 764, 36-45.

123 Veilleux, H.D., Ryu, T., Donelson, J.M., Van Herwerden, L., Seridi, L., Ghosheh, Y., Berumen,
124 M.L., Leggat, W., Ravasi, T. and Munday, P.L., 2015. Molecular processes of
125 transgenerational acclimation to a warming ocean. *Nature Climate Change*, 5, 1074.

126 White, S.M. (2018). Drivers of past, present and future change in mudflat
127 macroinvertebrate diversity. PhD, University of Portsmouth, pp. 324.

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