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Physiology of juvenile hydroids - High food availability mitigates stress responses of *Hydractinia echinata* to increasing seawater temperatures

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ABSTRACT

Ocean warming due to climate change is predicted to profoundly affect marine ecosystems. These effects are expected to be intensified for shelf seas like the North Sea, where sea surface temperatures are predicted to increase 3 °C by 2100. Increasing seawater temperature is suggested to alter physiological performance of benthic marine invertebrates, while predicted changes in ocean dynamics and primary production might limit nutrient availability. At present, the combined effect of temperature and nutrition stress on marine biota is largely understudied. We investigated physiological responses in highly polymorphic hydroids *Hydractinia echinata* from two locations in the North Sea in response to two temperatures (18 °C = ambient, 21 °C = increased) cross factored with two food regimes (high, low). After 50 days of experimental exposure, morphological (biomass), physiological (standard metabolic rate) and biochemical performance (contents of protein and protein carbonyl) was determined in juvenile hydroids. Reduced growth and low total protein contents combined with high standard metabolic rates and high protein carbonyl contents in *H. echinata* exposed to 21 °C/low food compared to 18 °C/high food point towards an energy deficiency in the former animals. Meanwhile, high food availability seems to mitigate negative effects of elevated temperature, as energy budgets were sufficient to maintain growth and to keep oxidative damage accumulation low at 21 °C/high food. Our results suggest that high nutrition will increase resilience in juvenile hydroids to seawater temperatures predicted for 2100 in the North Sea. This study illustrates that habitat energy availability is a major driver of species distribution ranges and should be considered in when predicting responses of marine invertebrates to future environmental stressors.

1. Introduction

Global climate change due to rising anthropogenic greenhouse gas emissions such as carbon dioxide (CO_2) is a major threat for marine ecosystems (IPCC, 2014). Since 1750, CO_2 concentrations increased by 40%, leading to atmospheric and ocean warming (0.11 °C per decade between 1970 and 2010; IPCC, 2014). By 2100, atmospheric CO_2 concentrations and ocean temperatures are predicted to rise higher than ever recorded. Globally, sea surface temperatures (SST) are predicted to increase by 1.5–2 °C (IPCC, 2014), and in the North Sea by 3 °C (Schrum et al., 2016) due to topographic conditions of shelf sea areas (e.g., shallow depths, high tidal ranges, large scale intertidal zones).

Further, future climate change scenarios predict a decrease in marine primary ($> 6\%$ since the early 1980) and secondary production in the northern Atlantic Ocean (Gregg et al., 2003), due to the influence of the North Atlantic Oscillation (Fromentin and Planque, 1996), as well as changes in ocean dynamics (e.g., wave action, storm events; Grabemann and Weisse, 2008; Woth et al., 2005). For example, the mean wave height of continuous waves in the North Sea is predicted to increase by up to + 18% by 2100 (Grabemann and Weisse, 2008) due to projected wind changes. Prey-capture success of sessile filter feeders is suggested to be highly affected by wave action (Sebens, 2002). As a result, higher waves in addition to a reduced food availability might limit feeding time and prey-capture success in benthic suspension feeders in the future.

It is strongly debated whether the potential for acclimation or adaption in marine organisms will cope with the rate of ecosystem changes (reviewed in Hoffmann and Sgro, 2011), which might be highly species specific. Evidence accumulates that ocean warming can drive species turnover (Hillebrand et al., 2010) influencing species

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specific changes in phenology and trophic mismatches (Edwards and Richardson, 2004). This might lead to shifts in ecological communities and ecosystems in the future. Marine organisms living in intertidal habitats tend to have wider tolerances and higher potentials for phenotypic plasticity due to larger (daily and seasonal) fluctuations in temperature, salinity and oxygen availability compared to those living in the subtidal. However, due to recent changes in environmental conditions (e.g., rising summer SST, lower nutrition; Puce et al., 2009) in intertidal zones, several studies have shown a decrease in ecosystem biodiversity but an increase of sessile organisms, leading to higher competition (Hawkins et al., 2009).

Numerous impacts of rising SST on marine biota are reported in the literature ranging from restricted physiological performance to reduced reproduction, growth and even survival (e.g., Chomsky et al., 2004b; Hofmann and Todgham, 2010). Higher seawater temperatures can alter the kinetics of biochemical processes and disrupt enzyme functions and cofactor binding in poikilothermic organisms, leading to increasing metabolic fluxes, and higher standard metabolic rates and increasing cell damage (Hofmann and Todgham, 2010). This in turn can induce higher production rates of harmful reactive oxygen species (ROS). In aerobic animal cells, ROS are mainly formed in the mitochondrial electron transport chain during the course of oxidative phosphorylation (Harman, 1956, 1972). Oxidative stress occurs in case of rising ROS production rates and/or an imbalance in the pro-oxidant/antioxidant ratio, which turn favours pro-oxidants and results in oxidative damage accumulation (e.g., protein carbonyls, Halliwell and Gutteridge, 1999).

In marine invertebrates, phenotypic plasticity – in other words, phenotypic changes of morphological, physiological, life history or behavioural traits based on the experienced environmental conditions and at a given genotype (Garland and Kelly, 2006; Pigliucci, 2005; Scheiner, 1993; West-Eberhard, 2003) - is an important strategy to withstand rapid environmental changes. For example, high morphological plasticity is an effective mechanism in scleractinian corals to cope with the heterogenic nature of the reef environment or with external environmental forces (e.g., differences in light, sedimentation, gravity, water flow, competition, Flot et al., 2011; Shaish et al., 2007; Todd, 2008). Another well-known example for acclimation by a high level of phenotypic plasticity is shown in plants, which can achieve optimal reproduction and growth according to different environmental conditions through structural and physiological modifications (Todd, 2008; Weaver and Kramer, 1932).

A well-studied model organism with a high polymorphic potential (e.g., morphological plasticity; Blackstone, 1998; Frank et al., 2001) is the hydroid *Hydractinia echinata* (Fleming, 1828). This colony forming species mostly encrusts gastropod shells inhabited by the hermit crab *Pagurus bernhardus* (Linnaeus, 1758). They occur in the intertidal (< 1 m depth) as well as in the subtidal (> 50 m depth) of the North Atlantic Ocean, including the North Sea. The colonies consist of different types of polyps with distinct functions – gastrozooids (feeding), gonozooids (sexual reproduction), dactylozooids and tentaculozooids (interaction / protection / capture of prey) – which are connected through a gastrovascular system (Frank et al., 2001). Before the age of 3 months, the colony consists of gastrozooids exclusively, while the other polyp types can be found, when they become sexual mature (Frank et al., 2001). Due to the high polymorphic potential, the different polyp types possess limited availability to convert into each other (Müller, 1961) and the shape of the colonies is highly variable (runner like vs. sheet like, Blackstone, 1998), partly dependent on the external environmental conditions.

In a controlled aquarium experiment, we investigated both morphological and physiological plasticity of juvenile *H. echinata* colonies in response to different temperature and food regimes. The parental colonies of these juveniles originated either from the subtidal around Helgoland or the intertidal around Sylt in the German Bight. Juveniles from Helgoland and Sylt were exposed to ambient (18 °C) and high (21 °C) temperatures, the latter according to predicted summer SST by 2100 in the German Bight, cross-factored with two food regimes (high and low). In order to assess potentials for acclimation to future environmental conditions and to estimate energetic costs of phenotypic plasticity, we determined morphological (growth), biochemical (contents of proteins and protein carbonyls) and physiological (standard metabolic rates) traits in juvenile *H. echinata* after 50 days of experimental exposure. In this study, we investigated how nutrition can alter physiological performance to cope with thermal stress.

2. Material & methods

2.1. Collection of parental colonies

As *H. echinata* are distributed in different habitats in the North Sea (intertidal and subtidal), 8–10 wildtype colonies of the hydroid growing on gastropod shells were sampled in April 2016 at two different locations within the German Bight. Staff of the Alfred Wegener Institute collected animals i. at a depth of around 50 m (subtidal) at Helgoland (54°07′–54°15′ N; 07°48′–07°57′ E) using the research vessel Uthörn and ii. at a depth of 1–3.5 m (intertidal) at Sylt (55°02′ N; 08°28′ E) using the research vessel MYA II. Gastropod shells colonized by living *H. echinata* colonies from Helgoland and Sylt were shipped to the University of Oldenburg; hermit crabs (*Pagurus bernhardus*) inhabiting the shells had been removed. At Helgoland, the annual sea surface temperature (SST) ranges from −1 °C to 19 °C and the salinity ranges from 30.8–33.5 (Becker et al., 1997). Around Sylt, the mean annual SST is +1 °C higher compared to Helgoland and ranges from 1 °C to 20 °C (Musat et al., 2006), while salinity ranges from 25 to 33 (Hickel, 1980). In contrast to Helgoland with solid, rocky seabed, the seabed of Sylt is dominated by sand flats. The hydroids were transported to the University of Oldenburg, and cultured in artificial seawater (Aqua Medic, Germany) at 12 °C and a salinity of 34. The colonies were fed daily with two-day old living *Artemia salina* nauplii.

2.2. Reproduction & larval settlement

Following the *Helgoland manual of animal development* (Plickert, 2013), spawning in *H. echinata* colonies was induced by an artificial light source (12/12 h light/dark cycle, 10.8 ± 3.5 μmol photons $m^{-2} s^{-1}$, T5 Razor, Giesemann, Germany). Wildtype colonies started to release eggs and sperm daily approximately one h after the onset of light. Four h after spawning, fertilized eggs were collected and washed in a 70 μm pore filter (Cell Strainers, Falcon™, Thermo Fisher Scientific, USA) and transferred into 100 ml of autoclaved artificial seawater at 18 °C and a salinity of 34. After two days, fertilized eggs had transformed into planula larvae and were collected and rinsed in a 200 μm pore filter (Luer, Süd-Laborbedarf GmbH, Germany).

The transformation of the planula larvae was induced by incubating them for 3 h in 116 mM caesium chloride at 18 °C following the protocol of Seipp et al. (2007). Larvae were then rinsed and transferred into a glass bowl containing artificial seawater and black glass tiles (dimensions 10 mm × 10 mm × 2 mm, Mosaikstein GmbH, Germany) for settlement. Prior to the experiment, consecutive numbers were engraved at the bottom side of the glass tiles for identification (population and individual) of juvenile colonies during the experiment. Rates of survival of the juvenile colonies is low within the first two weeks (pers. comm. Daniel Tschink). Therefore, approximately 5 planula larvae were settled onto each plate to ensure the settlement of at least 2–3 larvae on each tile.

2.3. Experimental setup

Overall 300 glass tiles colonized by juvenile *H. echinata* were distributed randomly into 24 holding tanks (100 ml, 5–7 glass tiles per tank and source population, Fig. 1). To be able to balance for tank specific effects, six replicate tanks were exposed to one of the four

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