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Ocean warming and acidification prevent compensatory response in a predator to reduced prey quality

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ABSTRACT: While there is increasing evidence for the impacts of climate change at the individual level, much less is known about how species' likely idiosyncratic responses may alter ecological interactions. Here, we demonstrate that ocean acidification and warming not only directly alter species' (individual) physiological performance, but also their predator–prey dynamics. Our results demonstrate that tissue production (used as a proxy for prey quality) in the barnacle *Semibalanus balanoides* was reduced under scenarios of future climate change, and hence their ability to support energy acquisition for dogwhelk *Nucella lapillus* through food provision was diminished. However, rather than increasing their feeding rates as a compensatory mechanism, consumption rates of *N. lapillus* were reduced to the point that they exhibited starvation (a loss of somatic tissue), despite prey resources remaining abundant. The resilience of any marine organism to stressors is fundamentally linked to their ability to obtain and assimilate energy. Therefore, our findings suggest that the cost of living under future climate change may surpass the energy intake from consumption rates, which is likely exacerbated through the bottom-up effects of reduced prey quality. If, as our results suggest, changes in trophic transfer of energy are more common in a warmer, high CO_2 world, such alterations to the predator–prey dynamic may have negative consequences for the acquisition of energy in the predator and result in energetic trade-offs. Given the importance of predator–prey interactions in structuring marine communities, future climate change is likely to have major consequences for community composition and the structure and function of ecosystems.

KEY WORDS: Predator–prey · Climate change · Ocean warming · Ocean acidification · Trophic interactions · Ecological interactions · Compensatory

INTRODUCTION

Ecosystems are structured by physical processes and interactions between co-existing species (McCann et al. 1998, Berlow et al. 2009). The strength and direction of these biotic interactions can determine the stability of populations and communities (de Ruiter et al. 1995, Rooney et al. 2006). Idiosyncratic responses to projected ocean acidification and warming (Harvey et al. 2013, Kroeker et al. 2013) due to differences in species' physiological tolerances and performance (Pörtner 2012) are likely to alter the outcomes of competitive (e.g. Diaz-Pulido et al. 2011, Connell et al. 2013) and trophic interactions (e.g. O'Connor 2009, Alsterberg et al. 2013). Hence, accurately predicting the consequences of climate change first requires an understanding of how local-scale changes to the environment can drive changes in

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community dynamics and the flow of energy in ecosystems.

Our understanding of the impacts of ocean acidification and warming on individual species is increasing rapidly (see Harvey et al. 2013, Brodie et al. 2014, Clements & Hunt 2015, Nagelkerken & Connell 2015 for reviews), and although empirical data on how these abiotic stressors affect species interactions is less common, the number of studies has increased substantially in the last few years (see Clements & Hunt 2015, Nagelkerken & Munday 2016 for reviews). The resilience of any heterotrophic marine organism to the combined effects of ocean acidification and warming is fundamentally linked to its ability to obtain and assimilate energy (Doney et al. 2012). Any changes in the consumption rates of a consumer due to abiotic stressors will not only directly alter the abundance of its prey (or resource), but it will also affect how much energy is transferred up the food chain. The effects of climate stressors on basal resources can therefore indirectly affect higher-order consumers through bottom-up effects (e.g. Beaugrand et al. 2003), or even allow organisms to maintain homeostatic physiological compensation if their food supply is sufficient (e.g. Melzner et al. 2011, Pan et al. 2015, Ramajo et al. 2016). Understanding the simultaneous responses of species at different trophic levels to environmental stressors will therefore better enhance our ability to predict patterns at more complex levels of organisation, such as entire communities and ecosystems (Harvey et al. 2014, Nagelkerken & Munday 2016).

Organisms are expected to incur increased energetic expenditures associated with climate change as a function of altered metabolic demands (Marshall et al. 2011), acid–base physiology (Miles et al. 2007) and calcification mechanisms (e.g. Ries et al. 2009). In order to balance energy intake and expenditure, consumption rates would be expected to increase (e.g. Sanford et al. 2014) at least until a threshold is exceeded and conditions begin to impact predator performance (Kroeker et al. 2014). The efficiency of energy transfer between trophic levels reflects the remaining energy following maintenance and growth (Jennings & Mackinson 2003) that can be passed along the food chain. The highest trophic level that can be supported in a system is one that can receive sufficient energy from lower trophic levels to support a minimum viable population (Kordas et al. 2011). For a given (fixed) resource base, any greater energetic demands due to climate change may result in constraints on the efficiency of trophic energy transfer (Dossena et al. 2012) and decrease food chain length (e.g. Petchey et al. 1999). Moreover, any direct disruptions to feeding rates (Siikavuopio et al. 2007, Miller et al. 2014) or changes in digestion efficiency (Stumpp et al. 2013) in response to climate change will likely cause complex changes in the energy allocation between individual-level processes (i.e. trade-offs) (e.g. Stumpp et al. 2012).

Here, we experimentally tested the effects of elevated pCO_2 and temperature on the energetic states of the rocky-shore intertidal predator, the dogwhelk *Nucella lapillus* (Linnaeus, 1758), and its principal prey, the acorn barnacle *Semibalanus balanoides* (Linnaeus, 1767), in order to provide information on the effects of predicted climate change on population dynamics and predator–prey interactions, and inform potential impacts for community structure.

MATERIALS AND METHODS

Experimental conditions and system design

An orthogonal experimental design was employed with 3 levels of CO_2 (400, 750 and 1000 ppm) and 2 levels of temperature (14 and 18°C). The experimental conditions of 400 ppm and 14°C represented the mean local ambient conditions for the duration of the study (September to November 2012). The 'warm' temperature (+4°C) and the levels of CO_2 were chosen based on the IPCC (2007) Special Report on Emissions Scenarios A2 and A1 for the year 2100.

The experimental system was in a constant temperature room with 300 W aquarium heaters (Eheim Jäger) used in the footer tank to maintain elevated temperature treatments. The pH of the mesocosms was set by continuous bubbling of a known air–CO_2 mix (following Findlay et al. 2008). In brief, the required atmospheric CO_2 was obtained by using a series of Erlenmeyer flasks to mix 100% CO_2 gas with CO_2-free air (CO_2 was removed by passing the air over soda lime), using a closed path infrared CO_2 gas analyser (LiCOR 820 IRGA; LiCOR Biosciences) to constantly monitor the level of atmospheric CO_2. By regulating the level of atmospheric CO_2 (ambient: 400 ppm, or elevated: 750 and 1000 ppm) being continuously bubbled into the mesocosms, it was possible to set the appropriate pH treatment of the seawater at equilibrium.

Measurements of pH_{NBS} (SevenGo Pro pH meter with Inlab 413SG probe; Mettler-Toledo), temperature and salinity (Cond 3210; WTW) were recorded daily, and total alkalinity (A_T, acid–base titration) was measured weekly. The pH potentiometric probe

was 3-point calibrated (pH_{NBS} 4.01, 7.00 and 9.21 buffer solution, carried out at 20°C) prior to every set of measurements. A_T was measured by manual titration with HCl (using 100 ml samples) and calculated from the Gran function between pH 4.2 and 3.0 (measured in triplicate, A_T precision: ±4.97 µmol kg^{-1}). The additional carbonate chemistry parameters were calculated using the software CO_2Calc (Robbins et al. 2010), with the measured pH_{NBS} and A_T as the input variables (Table 1). We used disassociation constants from Mehrbach et al. (1973), as adjusted by Dickson & Millero (1987), and KSO_4 using Dickson (1990) (Table 1). Light conditions were adjusted weekly to maintain seasonal natural light:dark cycles (decreasing from 12:12 to 8:16 h over the duration of the experiment), seawater was replenished weekly, and de-ionised water added every 2 to 3 d to account for any salinity increases due to evaporation.

Animal collection and experimental design

Nucella lapillus individuals and *Semibalanus balanoides* (on rock chippings) were collected from the low intertidal and sub-tidal fringe of the rocky shore at Borth, Wales, UK (52° 47.96′ N, 4° 5.52′ W) during September 2012, and held for 3 d in a flowing aquarium system. These species were chosen to represent model, ubiquitous, temperate rocky-shore intertidal species.

Two experiments were carried out. Expt 1 maintained *S. balanoides* and *N. lapillus* separately under experimental conditions for 80 d, using 5 replicate tanks per experimental treatment (for each species). For *S. balanoides*, each replicate tank (10 l: 36.5 × 26.5 × 14.5 cm) contained 2 rock chippings (approximately 500 individuals on each; length: 2.28 ± 0.46 mm), and for *N. lapillus*, each replicate tank (4.5 l: 26 × 17 × 18 cm) contained 12 individuals (shell length: 24.91 ± 0.48 mm). Throughout this experiment, both species were fed ad libitum, which for *S. balanoides* consisted of supplementing unfiltered seawater with a mix of microalgae and zooplankton (Gamma NutraPlus Complete Feed; TMC) every other day (0.5 ml added to each replicate tank, with additional 2 ml added to the header tank of each experimental system). *N. lapillus* individuals were fed *S. balanoides* that had been collected (also on rock chippings) at the same time as all of the experimental individuals. The rock chippings used for the 'food supply' were randomly allocated between experimental treatments, and held in holding tanks that were maintained at the same environmental conditions as the experimental replicate tanks (4 holding tanks per experimental treatment). Therefore, the *N. lapillus* individuals were always feeding upon individuals of *S. balanoides* under (and from) the same experimental conditions.

We confirmed that our feeding protocol did indeed result in ad libitum feeding for *N. lapillus* by monitoring the number of *S. balanoides* individuals (used for feeding) to ensure that an excess of food was available at all times, with rock chippings replaced with

Table 1. Seawater properties during Expt 1. pH_{NBS}, temperature, salinity and total alkalinity (A_T) are measured values. Seawater pCO_2, dissolved inorganic carbon (C_T), bicarbonate (HCO_3^-), carbonate (CO_3^{2-}), carbon dioxide (CO_2), saturation states for calcite ($\Omega_{calcite}$) and aragonite ($\Omega_{aragonite}$) are values calculated using the carbonate chemistry system analysis program CO_2Calc (Robbins et al. 2010). Numbers in parentheses represent SD

Treatment (ppm CO_2, Temperature)	pH_{NBS}	Temp (°C)	Salinity (psu)	A_T (µmol kg^{-1})	pCO_2 (µatm)	C_T (µmol kg^{-1})	HCO_3^- (µmol kg^{-1})	CO_3^{2-} (µmol kg^{-1})	CO_2 (µmol kg^{-1})	$\Omega_{calcite}$	$\Omega_{aragonite}$
400 Ambient	8.111 (0.019)	14.19 (0.06)	34.93 (1.01)	2067.35 (61.46)	411.16 (14.07)	1894.84 (52.35)	1755.59 (45.48)	123.44 (7.97)	15.82 (0.54)	2.96 (0.19)	1.90 (0.12)
750 Ambient	7.881 (0.017)	14.21 (0.07)	34.04 (0.59)	2118.29 (53.78)	764.72 (27.62)	2027.71 (49.63)	1918.99 (46.12)	79.31 (4.35)	29.41 (1.07)	1.90 (0.10)	1.22 (0.07)
1000 Ambient	7.758 (0.014)	14.01 (0.15)	34.65 (0.68)	2112.56 (52.68)	1034.27 (25.99)	2060.77 (49.28)	1960.16 (46.46)	60.60 (3.12)	40.02 (0.99)	1.45 (0.07)	0.93 (0.05)
400 Warm	8.148 (0.017)	17.96 (0.07)	34.87 (0.44)	2210.77 (55.05)	409.05 (14.39)	1991.32 (46.25)	1819.44 (39.56)	157.81 (8.42)	14.07 (0.49)	3.79 (0.2)	2.45 (0.13)
750 Warm	7.938 (0.021)	17.90 (0.16)	34.47 (0.39)	2336.07 (67.52)	754.08 (27.64)	2202.05 (59.42)	2065.91 (53.37)	110.16 (7.27)	25.98 (0.94)	2.65 (0.17)	1.71 (0.11)
1000 Warm	7.812 (0.018)	18.12 (0.12)	34.44 (0.48)	2278.89 (71.11)	1012.35 (33.41)	2191.50 (65.5)	2073.41 (60.79)	83.42 (5.32)	34.66 (1.15)	2.01 (0.13)	1.30 (0.08)

those from the holding tanks (held at the same environmental treatment) when required. For *S. balanoides*, we provided approximately 30% of dry body mass in fresh food per experimental treatment to insure sufficient supply (with any excess food removed prior to the addition of new food).

Expt 2 was a feeding trial, using individuals of *S. balanoides* and *N. lapillus* taken from the first experiment (described fully in 'Predator feeding and ingestion efficiency' below). In brief, rock chips of *S. balanoides* (~300 individuals) were placed into tanks (2 l: 22.5 × 16.5 × 7.8 cm) for 28 d under (the same) experimental conditions. We used 10 replicate tanks per experimental treatment, and carried out our feeding trial using paired replicates (5 replicate tanks each) with *N. lapillus* either present (1 individual) or absent (control). The food supply for *S. balanoides* during the second experiment was maintained as above.

Prey growth, calcification and survival

Following the completion of Expt 1, *S. balanoides* growth rates and survival were ascertained by comparing the digital images taken with a PowerShot A2300 HD camera (Nikon) at the start and end of the first experiment (similar to Findlay et al. 2010), using ImageJ for the measurements (version 1.47; Abràmoff et al. 2004). Growth was measured by comparing the length (barnacle rostro-carinal diameter; RCD) of the same individuals in both the initial and final image (n = 200 ind. measured tank^{-1} treatment^{-1}). Length–weight relationships were established for *S. balanoides* to relate the RCD (mm) with both dry body tissue mass (mg) and shell mass (mg) (see Golléty et al. 2008). We found a significant relationship between the barnacle size (RCD length) and both their body mass (R^2 = 0.803, $p < 0.0001$), and shell mass (R^2 = 0.688, $p < 0.0001$). Therefore changes in RCD (final RCD – initial RCD) over the experiment were used to describe changes in tissue production and calcification (for model fit, regressions and pairwise test results see Tables S5-S9 in the Supplement at www.int-res.com/articles/suppl/m563p111_supp.pdf). Starting tissue and shell mass were initially established by length–weight relationship (dry body tissue mass [mg] = 0.1026 × RCD$^{3.0137}$ [mm], n = 100; shell mass [mg] = 1.3982 × RCD$^{2.7390}$ [mm], n = 100) using barnacles collected at the same time as the experimental organisms. Since we expected treatment-specific changes in the length–weight relationships, final measurements used treatment-specific length–weight relationships (see Figs. S2–S7 for tissue mass and Figs. S9–S14 for shell mass in the Supplement), which were established by sacrificing a sub-sample of barnacles (ash-free dry mass; 6 h, 500°C) that were collected across replicates from each treatment at the completion of the 2 experiments. We additionally used the tissue production of *S. balanoides* as a proxy to represent their prey quality. Survival was measured as the remaining percentage of barnacle individuals (compared to the starting abundance) after the first experiment. Following Findlay et al. (2010), prior to photography, the ability of barnacle individuals to close their operculum was tested, with any individual unable to close their operculum classed as dead.

Predator growth and calcification

Before the first experiment, each experimental *N. lapillus* was labelled with a numbered, coloured queen bee tag (EH Thorne; Rand) and measured for starting shell length (digital calliper, ±0.1 mm), and starting dry shell mass and wet body mass using the non-destructive methodology of Palmer (1982). Starting dry shell mass was calculated using linear regression with buoyant weight (previously calculated by destructively sampling individuals collected at the same time and place as the experimental individuals; dry shell mass = 1.6317 × buoyant weight – 0.0949 g, n = 50; R^2 = 0.9895, $p < 0.001$). Starting wet body mass was calculated by subtracting the estimated dry shell mass from the total mass of the individual in air. Starting wet body mass was then converted to dry body mass with linear regression (dry body mass = 0.2142 × wet body mass – 0.006 g, n = 50; R^2 = 0.9870, $p < 0.001$; this regression was established with the same individuals that were used for the dry shell mass to buoyant weight relationship). At the end of the experiment, all individuals were measured for final (individual) length, and then sacrificed for dry mass (48 h at 60°C) and ash-free dry body mass (6 h at 500°C). Therefore, (individual) shell length was measured as final length – initial length, while dry shell growth (i.e. net calcification) and wet body growth were calculated as final mass – initial mass.

Predator standard metabolic rates

Rates of oxygen uptake for *N. lapillus* were measured, as a proxy for resting metabolic rate, using closed bottle respirometers. Individuals were placed in 250 ml respirometers (n = 25, with 5 additional

blanks to control for microbial respiration per experimental treatment), located in a flowing water bath to maintain their respective temperature and pCO_2 treatments. Respirometers were covered, but left open for 1 h to remove any potential handling stress. Before the respirometers were sealed, starting O_2 levels were measured using a dissolved oxygen meter (Orion Star A223 DO with polarographic O_2 electrode; Thermo Scientific), with the electrode standardised using aerated seawater (100% saturation) and oxygen-free seawater using sodium sulphite (0% saturation). The respirometers were sealed for 2 h, with the experimental duration chosen in order to maintain O_2 saturation above 80% and avoid hypoxic conditions (Gnaiger et al. 1989). A second oxygen concentration was measured, and the rates of oxygen uptake were calculated as the difference between the starting and final oxygen concentrations (accounting for microbial respiration). Measurements were then multiplied by the solubility coefficient for oxygen (corrected for temperature and salinity; Harvey 1955) and the respirometer volume, for standard temperature and (dry) pressure (STPD). Ash-free dry body mass was measured by sacrificing all individuals measured for their metabolic rate (6 h at 500°C), and final oxygen uptake was expressed in terms of µmol O_2 g^{-1} AFDW h^{-1} STPD.

Predator feeding and ingestion efficiency

The amount of *S. balanoides* consumed by *N. lapillus* was quantified by estimating the mass of somatic tissue eaten during the second experiment. The number of *S. balanoides* consumed was measured by changes in the final abundance (with predator present) compared to the starting abundance (determined from a digital image; Nikon PowerShot A2300 HD), after subtracting any deceased barnacles in the paired predator-free treatments (i.e. accounting for natural mortality). The somatic tissue was then estimated using the regression between the barnacle RCD and somatic tissue previously established for barnacle tissue production (see Figs. S2–S7 in the Supplement). Feeding rates were then converted to energy consumption by converting the estimated somatic tissue of ingested *S. balanoides* to energy units using 23 J mg^{-1} (Wu & Levings 1978). The value used above for the energetic content of tissue was assumed to not vary among the different experimental treatments.

Ingestion efficiency, the ratio of ingestion to metabolism (Yodzis & Innes 1992, Vasseur & McCann 2005, Rall et al. 2010), was also calculated for all *N. lapillus* individuals used in the feeding trials using the methodology of Vasseur & McCann (2005). Ingestion efficiency represents the ingestion gain of a consumer relative to metabolic demands, whereby ingestion efficiencies of 1 indicate that ingestion balances metabolic costs, while ratios below 1 indicate the metabolic costs exceed ingestion. We calculated ingestion gain by taking the energy units ingested (23 J mg^{-1}; Wu & Levings 1978) and used a previously established absorption efficiency (energy assimilated / energy ingested) of 0.4 for *N. lapillus* (Stickle & Bayne 1987). Similar to the energetic content of tissue, the value used was assumed to not vary among the different experimental treatments. For the metabolic costs, oxygen uptake was converted into joules by multiplying it by an oxycalorific coefficient of 21.10 mJ l^{-1} O_2, representing an accepted value for catabolism of carbohydrate (Elliott & Davison 1975). This value was chosen because most gastropods rely on glycogen stores for energy during activity (Carefoot 1987).

Statistical analysis

A 2-way ANOVA with CO_2 (3 levels: 400, 750 and 1000 ppm) and temperature (2 levels: 14 and 18°C) as fixed factors was employed to test for possible differences among all measurements (prey growth, calcification and survival; predator growth, calcification, standard metabolic rate, feeding rate and ingestion efficiency), with Tukey's HSD post hoc tests used to test pair-wise differences ($\alpha = 0.05$). Since tissue production and shell mass were related to RCD (in *S. balanoides*), an ANCOVA was employed to test for differences between treatments in the response of final barnacle tissue and shell mass, using length (RCD) as a covariate, with both length and weight log-transformed. All data was normally distributed (Kolmogorov-Smirnov) as well as displaying homogeneity of variance (Levene) in all cases ($p > 0.05$). Statistical analyses were conducted using R (version 3.2.3; R Development Core Team 2012).

RESULTS

Prey growth, calcification and survival

Elevated pCO_2 significantly reduced RCD growth in *Semibalanus balanoides* ($F_{2,24} = 12.56$, $p < 0.001$; Fig. 1a, Table S1 in the Supplement); however, growth

was not significantly reduced by elevated temperature ($F_{1,24}$ = 2.17, p = 0.15; Fig. 1b, Table S1). No significant interaction was observed ($F_{2,24}$ = 1.29, p = 0.29; Table S1). After controlling for barnacle length, we observed a significant (negative) independent effect of both elevated pCO_2 (ANCOVA, $F_{2,574}$ = 10.46, p < 0.01) and warming (ANCOVA, $F_{1,574}$ = 43.46, p < 0.001) on barnacle tissue production (i.e. length–weight relationship; see Fig. S1 in the Supplement for regressions), such that *S. balanoides* individuals of the same length had significantly smaller body tissue mass with increasing pCO_2 levels and warming. Hence, independently elevated pCO_2 ($F_{2,24}$ = 10.01, p < 0.001; Fig. 1c, Table S2) and warming ($F_{1,24}$ = 13.83, p < 0.01; Fig. 1d, Table S2) significantly reduced barnacle tissue production (and by proxy, prey quality) compared to control conditions (non-significant interaction between elevated pCO_2 and warming; $F_{2,24}$ = 2.36, p = 0.12; Table S2). Even after standardising by length, barnacle shell mass was not significantly affected by warming ($F_{1,24}$ = 0.015, p = 0.90; Table S3), or elevated pCO_2 ($F_{2,24}$ = 3.36, p = 0.052; Table S3) with no significant interaction ($F_{2,24}$ = 0.49, p = 0.62; Table S3, see Fig. S8 in the Supplement for regressions). The marginal non-significance of elevated pCO_2 was likely due to the decreased (RCD) growth rates exhibited under elevated pCO_2, rather than an actual reduction in calcification rates per se. Survival rates of *S. balanoides* were significantly lower compared to control conditions when exposed to elevated CO_2 ($F_{2,24}$ = 9.88, p < 0.001; Fig. 1e, Table S4) and warming ($F_{1,24}$ = 53.28, p < 0.001; Fig. 1f, Table S4) independently of each other. There was no significant interaction between elevated CO_2 and warming ($F_{2,24}$ = 1.38, p = 0.27; Table S4).

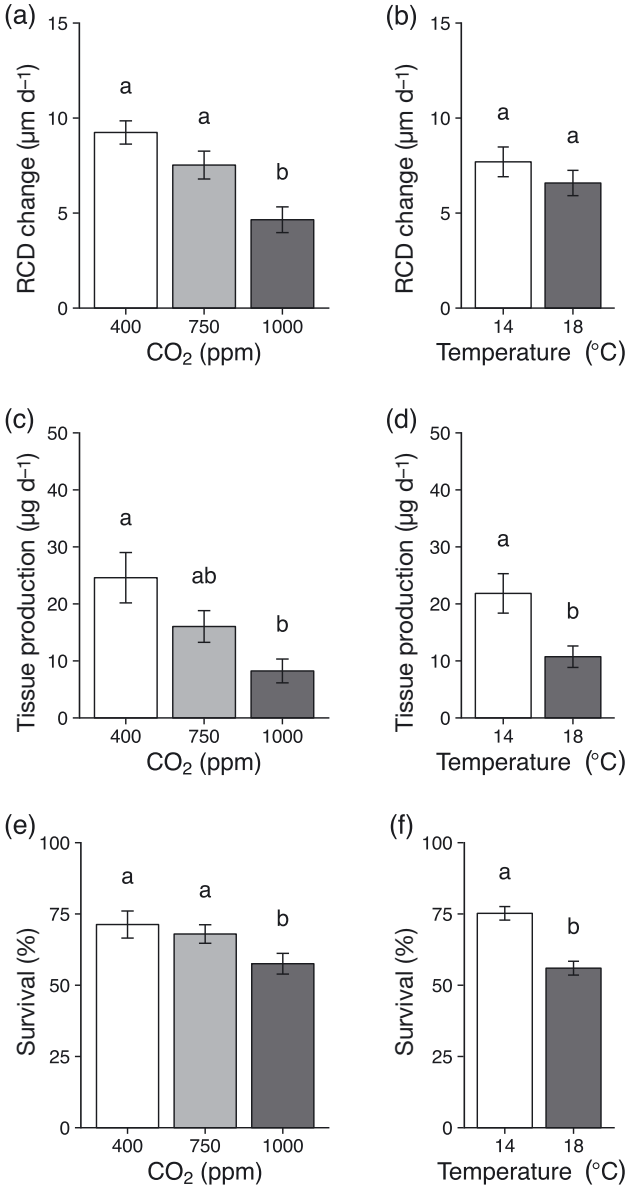

Fig. 1. Mean (±SE) (a,b) rostro-carinal diameter (RCD) change (µm d^{-1}), (c,d) tissue production (µg d^{-1}), and (e,f) survival rate (%) of *Semibalanus balanoides* in response to (a,c,e) different CO_2 concentrations (400, 750 and 1000 ppm) averaged across levels of temperature, or (b,d,f) different temperature treatments (14 and 18°C) averaged across levels of CO_2 concentration (n = 5 treatment^{-1}). A significant difference between treatments is indicated with a different letter (Tukey's HSD, p < 0.05)

Predator growth, calcification and standard metabolic rates

We observed a fairly complex response for tissue production in *Nucella lapillus*. Overall, there was a significant interaction between ocean warming and acidification ($F_{2,24}$ = 7.47, p < 0.001; Fig. 2, Table S10). When the elevated temperature and mid pCO_2 level (750 ppm) were combined, tissue production did not significantly differ from control conditions; however, when the elevated temperature and high pCO_2 level were combined, *N. lapillus* experienced negative growth, i.e. a loss of somatic tissue (Fig. 2, Table S10). While mortality was not a specific response variable in this experiment there was higher mortality in these treatments, with 6 *N. lapillus* dying in the high pCO_2 and warmer treatment, and only 1 individual dying in each of the other 5 treatments.

Linear shell extension of *N. lapillus* was not significantly affected by elevated pCO_2, temperature or their interaction (all p > 0.05; Table S11). Net calcification of *N. lapillus* was significantly reduced by the

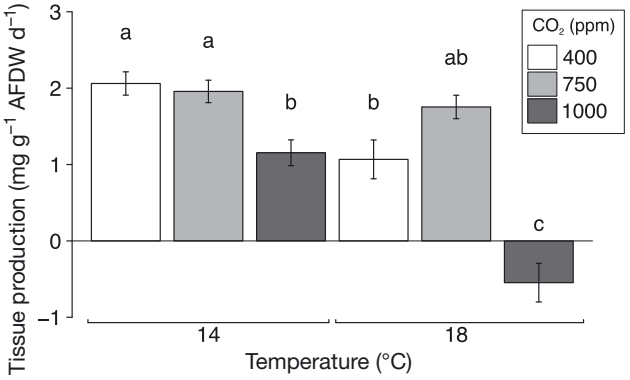

Fig. 2. Mean (±SE) change in tissue production (mg g^{-1} ash-free dry weight [AFDW] d^{-1}) of *Nucella lapillus* (n = 5). A significant difference between the treatments is indicated with a different letter (Tukey's HSD, p < 0.05)

highest pCO_2 levels ($F_{2,24}$ = 18.58, p < 0.001; Fig. 3a, Table S12), but was not significantly affected by elevated temperature ($F_{1,24}$ = 0.381, p = 0.54; Fig. 3b, Table S12), with no significant interaction ($F_{2,24}$ = 0.263, p = 0.77; Table S12). Rates of oxygen uptake in *N. lapillus* were elevated significantly when exposed independently to increased pCO_2 ($F_{2,24}$ = 8.44, p < 0.01; Fig. 3c, Table S13), and temperature ($F_{1,24}$ = 124.03, p < 0.001; Fig. 3d, Table S13) and there was no significant interaction ($F_{2,24}$ = 0.72, p = 0.50; Table S13).

Predator feeding and ingestion efficiency

The number of barnacles consumed was significantly reduced by elevated pCO_2 ($F_{2,24}$ = 3.56, p < 0.05; Fig. 4a, Table S14), but was not significantly affected by warming ($F_{1,24}$ = 2.41, p = 0.13; Fig. 4b, Table S14) or their interaction ($F_{2,24}$ = 2.66, p = 0.09; Table S14). Elevated pCO_2 ($F_{2,24}$ = 3.75, p < 0.05; Fig. 4c, Table S15) and increased temperature ($F_{1,24}$ = 8.89, p < 0.01; Fig. 4d, Table S15) independently reduced the feeding rates of *N. lapillus* in terms of estimated energy uptake, with the combination of elevated temperature and the high pCO_2 level causing a significant reduction in consumption rates compared to the control treatment (Tukey's HSD, p < 0.05; Table S15). Ingestion efficiency was diminished both by elevated pCO_2 ($F_{2,24}$ = 6.30, p < 0.01; Fig. 4e, Table S16) and ocean warming ($F_{2,24}$ = 39.01, p < 0.001; Fig. 4f, Table S16) independently of each other. There was no significant interaction between elevated pCO_2 and warming for ingestion efficiency ($F_{2,24}$ = 0.38, p = 0.69; Table S16).

DISCUSSION

Our findings suggest important changes in the energetic allocation of an intertidal predator and prey when exposed to elevated pCO_2 and warming. This was demonstrated through a reduction in the growth of somatic tissue for *Semibalanus balanoides*, reducing its quality as a food source. Simultaneously, the predator *Nucella lapillus* experienced increased energy expenditure due to higher maintenance costs, but appeared unable to initiate any compensatory mechanisms that would allow energy intake to match expenditure, and instead demonstrated reduced feeding rates and a subsequent loss of somatic tissue. Thus, in our study it was found that future climate change may indirectly cause (and exacerbate) negative influences on the fitness of the higher-order consumer through bottom-up effects on the basal resource.

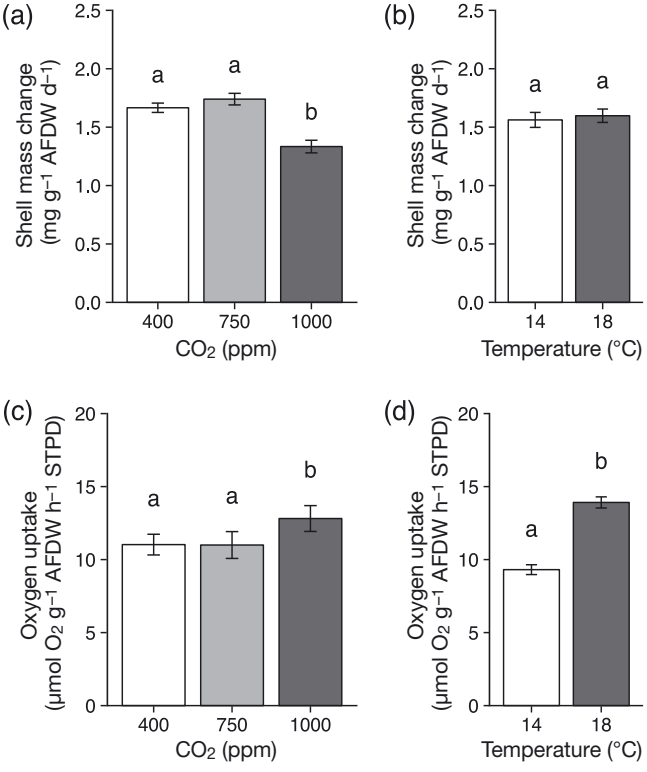

Fig. 3. Mean (±SE) (a,b) shell mass change (mg g^{-1} ash-free dry weight [AFDW] d^{-1}) and (c,d) metabolic rate (oxygen uptake, µmol O_2 g^{-1} AFDW h^{-1} at standard temperature and pressure [STPD]) of *Nucella lapillus* in response to (a,c) different CO_2 concentrations (400, 750 and 1000 ppm) averaged across levels of temperature, or (b,d) different temperature treatments (14 and 18°C) averaged across levels of CO_2 concentration (n = 5 treatment^{-1}). A significant difference between treatments is indicated with a different letter (Tukey's HSD, p < 0.05)

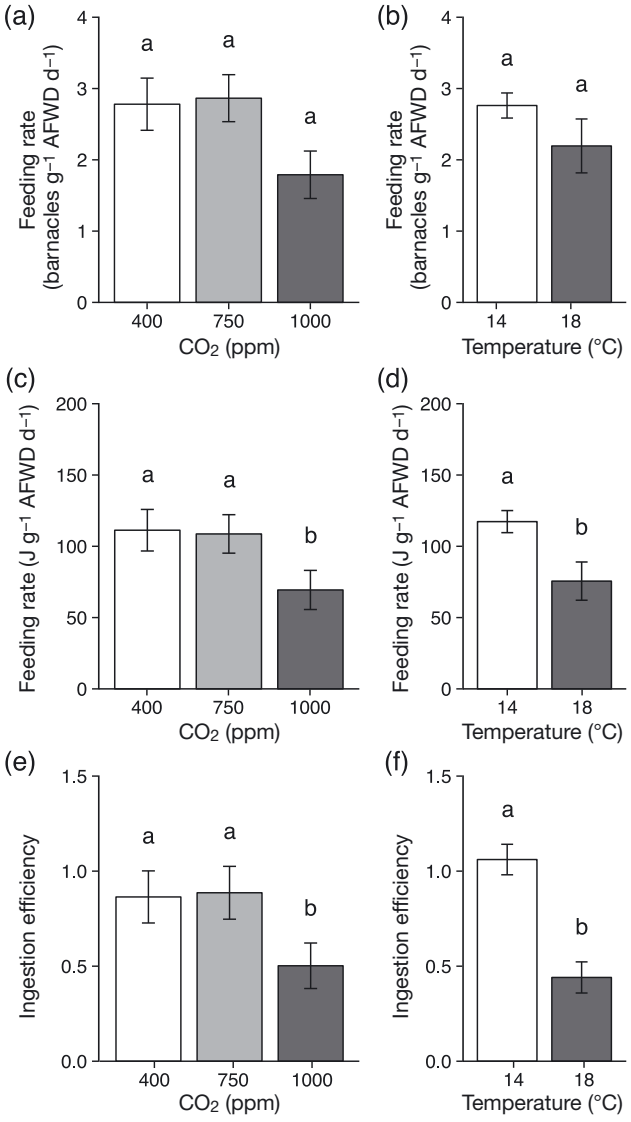

Fig. 4. Mean (±SE) (a,b) consumption rates (no. barnacles g^{-1} ash-free dry weight [AFDW] d^{-1}), (c,d) consumption rates (J g^{-1} AFDW d^{-1}) and (e,f) ingestion efficiency (ratio of ingestion to metabolism) of *Nucella lapillus* upon *Semibalanus balanoides* in response to (a,c,e) different CO_2 concentrations (400, 750 and 1000 ppm) averaged across levels of temperature, or (b,d,f) different temperature treatments (14 and 18°C) averaged across levels of CO_2 concentration (n = 5 $treatment^{-1}$). A significant difference between treatments is indicated with a different letter (Tukey's HSD, $p < 0.05$)

Prey responses

Although *S. balanoides* are capable of maintaining their calcification in response to ocean acidification (Findlay et al. 2009, present study), shell maintenance is still an energetically costly process (Palmer 1992). We found that tissue production in *S. balanoides* was significantly reduced by both elevated pCO_2 and warming, which suggests a reallocation of resources (e.g. use of lipid stores for energetic maintenance; Barnes et al. 1963) away from somatic growth, leading to a smaller (less energetically profitable) body size in future oceans (see also Daufresne et al. 2009). The warming treatment (in particular) had a prominent negative effect on somatic growth and survival of *S. balanoides.* This is possibly due to the fact that the high-temperature treatments used in this experiment exceed the temperatures presently experienced at their (current) southern range edge in the UK (Wethey & Woodin 2008). This is likely to reduce the abundance of *S. balanoides* and have important implications for their distribution, as well as for predators that utilise them as a prey resource.

Predator responses

The metabolic rates of *N. lapillus* were significantly stimulated by increased temperature and to a lesser extent elevated pCO_2, indicating an increased cost to sustain basic cellular functions (Hulbert & Else 2000). In order to balance this increase in energy expenditure, consumption rates might be expected to increase (e.g. Sanford et al. 2014); yet instead, a mismatch between consumption and metabolism was observed resulting in reduced ingestion efficiency. The implications of such a reduced ingestion efficiency are decreased individual fitness (Lemoine & Burkepile 2012), with energy needing to be reallocated towards the maintenance of acid–base and metabolic disturbances and away from vital biological processes such as protein synthesis, growth (somatic and shell) and reproduction (e.g. Stumpp et al. 2012, Calosi et al. 2013). A constant absorption efficiency of food was assumed across the different treatment groups in this study; however, it is possible that ocean acidification could either increase (e.g. Fernández-Reiriz et al. 2012) or decrease (e.g. Stumpp et al. 2013) absorption efficiency, resulting in changes to ingestion efficiency.

As energy is required to maintain physiological homeostasis in response to environmental change, the availability of food (along with food quality) will play a critical role in conferring calcifiers' resistance to elevated pCO_2 (Thomsen et al. 2013, Pan et al. 2015, Ramajo et al. 2016). Here, we showed that the net calcification rate of *N. lapillus* was significantly reduced under elevated CO_2, suggesting that the reduced energetic intake of *N. lapillus* could have been insufficient to maintain calcification. Due to the limited number of experiments that have considered

the role of food supply (see Ramajo et al. 2016 for a review), calcification in a warmer, more acidic ocean may be reduced even more than previously thought.

Mismatches between metabolism and consumption are being commonly observed at warmer temperatures (above summer ambient) for a range of marine ectotherms (see Lemoine & Burkepile 2012 for a review, but also see Iles 2014, Mertens et al. 2015) due to metabolism often scaling at a faster rate with temperature compared to consumption (Rall et al. 2010). As well as feeding being reduced at warmer temperatures, we also observed a large reduction in feeding rates of *N. lapillus* when exposed to the combination of high pCO_2 and warming, which may suggest that the combination of these stressors leads to limitations to consumption associated with either prey handling time, or the searching time required to find it (MacArthur & Pianka 1966). In this study, the calcification rates of *S. balanoides* were not significantly affected, which would suggest that handling times would not be expected to change (although other behavioural modifications may occur; see Kroeker et al. 2014, Clements & Hunt 2015). The decreased foraging rate exhibited is therefore more likely associated with some direct effects on the predator itself. Ocean acidification has been shown to induce complex changes in behaviour and chemoreception (e.g. Manríquez et al. 2014, Watson et al. 2014, and see Clements & Hunt 2015 for a review), including a lowered ability to locate food in *N. lapillus* (Queirós et al. 2015), and it is likely that similar processes may be operating here.

Likely as a consequence of the mismatch between basal metabolic demands and food consumption, we found that tissue production in *N. lapillus* was reduced in response to elevated pCO_2 and increased temperature, due to an altered energy reallocation (Yamane & Gilman 2009, Stumpp et al. 2012). When elevated pCO_2 was combined with increased temperature, *N. lapillus* individuals actually exhibited somatic tissue loss akin to starvation (e.g. Fussmann et al. 2014). Tissue loss is commonly observed in *N. lapillus* during the non-feeding overwintering period (Feare 1971), where body reserves are utilised as an energy source. With the majority of feeding (and growth) carried out during the summer months (Burrows & Hughes 1990, 1991), reduced foraging success during these times may not only reduce the capacity for storing energy for later use (such as for overwintering torpor, or reproduction), but may require foraging to be maintained for extended periods of the year (assuming water temperature is above the minimum temperature for feeding, thought to be ~3°C; Largen 1967), increasing the risk of predation and dislodgement during storm events.

It must be noted that the pCO_2-induced increase in metabolic rate is in contrast to the recent findings of Queirós et al. (2015), who found that *N. lapillus* exhibited metabolic depression following 14 mo exposure to elevated pCO_2 levels. Although the difference could possibly be linked to differences in the acclimation period (e.g. Dupont et al. 2013), we suggest it is more likely to be linked to differences in tidal regime, and represents a comparison in responses between subtidal (this study) and intertidal conditions (Queirós et al. 2015). As aerial conditions are considered more energetically costly for *Nucella* sp. (e.g. Yamane & Gilman 2009), it may become more important to conserve energy by resting rather than maximising energy gain during activity (Marshall & McQuaid 2011, Marshall et al. 2011), meaning that metabolic depression represents an energy conservation strategy more applicable for emersion periods. Our finding also concurs with a recent study which found increased metabolic rate for a subtidal gastropod species acclimatised to ocean acidification over multiple generations (Harvey et al. 2016).

Predator–prey interactions

The core assumption of predator–prey dynamics is that consumers will attempt to maximise their energy intake in comparison to their energy expenditure (Gaylord et al. 2015), i.e. optimal foraging theory (MacArthur & Pianka 1966). Here, prey quality (measured as changes in tissue production) was reduced due to elevated pCO_2 and temperature; however, rather than compensating for the reduced prey quality by increasing their feeding rate (e.g. Cruz-Rivera & Hay 2000), a reduced feeding rate was observed. Future climate change may therefore represent an important shift that is capable of not only influencing the energetic demands of all trophic levels, but also simultaneously affecting the ability of higher trophic levels to respond to changes in both resource availability and quality.

Energy gain may be constrained by food availability, digestive efficiency and digestive rate (Calow 1975). Our observations of reduced predator foraging rates resulting in somatic tissue loss, suggesting the possibility of consumer starvation (e.g. Fussmann et al. 2014), was reflected in diminished ingestion efficiency. This meant that as metabolic costs increased, and feeding rates concurrently decreased, the en-

ergy available for performance-related activities (e.g. growth) declined. Any attenuations in the energy moving up a food chain (due to reduced feeding or prey quality) would likely result in an increased mortality rate due to starvation and a diminished investment into reproduction; the combination of these population-level consequences could then cause a positive feedback loop that would result in the rapid non-linear decline of this species, and could have fundamental consequences for community dynamics.

In conclusion, experimental manipulation of temperature and pCO_2 to represent realistic scenarios of future climate change resulted in a reduction in the survival and somatic growth, and likely quality, of the prey barnacle *S. balanoides*. At the same time, the metabolic rate of the predatory gastropod *N. lapillus* increased, and despite prey resources remaining abundant, consumption rates of *N. lapillus* were reduced to the point that they exhibited starvation (a loss of somatic tissue). Our findings suggest that the cost of living under future climate change may surpass the energy intake from consumption rates (resulting in a mismatch), and that it is likely facilitated through bottom-up effects by having a reduced quality of basal resources. If responses such as those observed here are more common in a warmer, high CO_2 world, and given the importance of predator–prey interactions in structuring marine communities, future climate change will have major consequences for community composition and the structure and function of marine ecosystems.

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