Intraspecific response of colonial ascidians to variable salinity stress in an era of global change

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ABSTRACT: Extreme or seasonal climatic events can lead to abrupt changes in environmental conditions. These events can produce a range of organismal responses that may help to protect local-scale populations against changes in climate. Empirical studies examining intraspecific variation in reproductive and physiological responses to varying durations of environmental stress are rare. We performed laboratory experiments under varying episodic and chronic salinities using the botryllid ascidians, *Botrylloides nigrum* and *Botryllus planus*. Our study illustrates intraspecific phenotypic variation to salinity stress. Respectively 40 and 20% of *B. nigrum* and *B. planus* colonies exhibited a distinct physical behavior when exposed to low salinity treatments. They distended their cloacal cavities, exposing their pharyngeal baskets and neural glands. Physiological signs of salinity stress included higher mortality, lower heart rates and limited asexual reproduction in both species. The physical and physiological differences among clones and colonies highlight phenotypic variation within and between genotypes to selective environmental pressures in real time. Our results underscore the need to examine physiological responses of species under varying durations of environmental stress. Plastic responses of species to fine-scale environmental change may aid their persistence in a future where extreme climatic events are likely to be more common and acute.

KEY WORDS: Intraspecific variation · Phenotypic plasticity · Local adaptation · Salinity · Climate extremes · Ascidians

INTRODUCTION

One of the pressing challenges in climate change research is to determine the effect of shifts in environmental parameters on maintaining species populations and local communities. Much effort has been made to empirically investigate the performance of species under a range of current and future climate conditions (after Graham et al. 2010, Sorte et al. 2010, Willis et al. 2010, Dijkstra et al. 2011, Pandolfi et al. 2011, Reyer et al. 2013). However, the degree to which species or individuals within species can acclimate in response to climate-related environmental factors is largely unknown (Visser 2008, Hofmann & Todgham 2010, Hoffmann & Sgro 2011, Vedder et al. 2013). While population-level responses of species to

changing climate conditions has received much attention in terrestrial systems (e.g. Etterson 2004, Bischoff et al. 2006, Charmantier et al. 2008), fewer studies have empirically investigated intraspecific physiological or phenotypic responses within marine species populations (but see Peck et al. 2015). Organisms respond to changes in abiotic conditions through a variety of mechanisms that include, but are not limited to, altered growth (e.g. Lord & Whitlatch 2015), physiology (Helmuth et al. 2005, Stenseng et al. 2005, Somero 2010, Tomanek 2010), reproduction and other related fitness traits (e.g. Westerman et al. 2009, Wrange et al. 2014). These adaptive shifts in behavior and life-history traits can lead to phenotypic plasticity and eventual genetic changes (Pigliucci 2001, Kelly et al. 2012). Recent findings indicate phe-

notypic differences exist between individuals within the same population (Bolnick et al. 2011, Richardson et al. 2014), suggesting a greater need for a better understanding of intraspecific trait variation within and among species.

Environmental factors affect biological processes more strongly in ectothermic species whose metabolism and reproduction are closely tied to ambient environmental conditions. In some ecosystems, extreme or seasonal climatic events such as flooding or heat waves can lead to episodic changes in abiotic factors such as temperature or salinity (Goodbody 1961, Garrabou et al. 2009). Such extreme climatic events may affect the physiological performance of the species or exceed its physiological threshold, resulting in contraction of the population (e.g. Smale & Wernberg 2013, Wernberg et al. 2013). The frequency and magnitude of these events is expected to increase, and in some areas these trends are already apparent (IPCC 2014). During a heavy rain event, abrupt salinity change can affect mortality rates, metabolic function, and may produce an adaptive or plastic response in the affected species (Livingstone et al. 1979, Boeuf & Payan 2001, Hassell et al. 2006, Dijkstra et al. 2008). Further, the duration of environmental stress may affect the potential for organisms to directly respond to abrupt shifts in environmental conditions.

Most studies that focus on the adaptive response of species to environmental variables have focused on temperature (e.g. Kelly et al. 2012); fewer have focused on salinity (but see Renborg et al. 2014). Extreme fluctuations in the duration and magnitude of precipitation events in near-shore tropical systems is expected to increase (IPCC 2014). In these systems, precipitation can fluctuate dramatically throughout the year (IPCC 2014), which can lead to depressed salinity during and after a heavy rainfall event (Goodbody 1961). Salinity affects the physiological function of many ecothermic species such as mussels, ascidians, and snails, often with species-specific responses (e.g. Braby & Somero 2006, Dijkstra et al. 2008, Groner et al. 2011). Laboratory studies relating salinity to growth and physiology indicate salinity may negatively affect physiological function and growth (Livingstone et al. 1979, Boeuf & Payan 2001, Hassell et al. 2006, Dijkstra et al. 2008). Colonial ascidians in the northeast Atlantic experienced species-specific differences in mortality when exposed to episodic stress events (10 ppt for 2 h every second day; Groner et al. 2011). These and other studies suggest that depressed salinity may negatively affect population growth in marine species. Given that the frequency of extreme precipitation events will likely

become more intense and more frequent (IPCC 2014), it is important to evaluate the resilience of individuals within a population to salinity stress.

Here, we use an experimental laboratory study to investigate the intraspecific response of colonial invertebrates to abrupt chronic and episodic changes in salinity, using 2 ascidian species, *Botrylloides nigrum* and *Botryllus planus*, as models. Ascidians are ideal species to study physiological responses to climate-related factors, as they have accelerated substitution rates across genes (Tsagkogeorga et al. 2010, 2012). Further, they have relatively fast generation times (Dijkstra et al. 2011) and can quickly amass large local populations, as they have lecithotrophic larvae that spend less than 24 h in the water-column before settling on suitable substrate. They make up an important component of subtidal habitats and are frequently exposed to variable salinity. Though relatively little is known about the adaptive responses of marine species to changes in coastal waters, they are increasingly considered to be an important component to forecast the effects of climate change on population dynamics. Given the high mutation rates and local retention of larvae, we predict that ascidian species are capable of responding to fine-scale environmental pressures.

MATERIALS AND METHODS

Experiments were conducted at the Smithsonian Tropical Research Institute (STRI) in Bocas del Toro, Panama (9° 21′ 05″ N, 82° 15′ 24″ W) in October 2011. Two local botryllid ascidian species were used in experimental trials. *Botrylloides nigrum* is a tropical to sub-tropical cosmopolitan species with a wide global range (Carman et al. 2011), occurring in Florida, USA, the Caribbean Sea, both coasts of Panama, Brazil, the Mediterranean Sea, West Africa, South Africa, Madagascar, Australia and Polynesia (Fofonoff et al. 2003). Due to its widespread distribution, its native range is currently unknown. In contrast, *Botryllus planus*, also a tropical to sub-tropical species, exhibits a more restricted distribution, being native to warm western Atlantic waters from North Carolina, USA, to Brazil (Fofonoff et al. 2003), with one introduced population known from the Pacific side of the Panama Canal (Carman et al. 2011).

A total of 20 colonies each of *B. nigrum* and *B. planus* were collected along several pier pilings of the Bocas Marina (9° 20′ 07″ N, 82° 14′ 47″ W). Colonies were taken from the same location in order to reduce differences in the historical environmental con-

ditions experienced by each population. Genetic analysis has not been conducted on this population so the amount of genetic differentiation between colonies is unknown. Once collected, colonies were immediately brought to the lab, cut into 5 equal-sized subcolonies (clones) ~2 cm^2 in size and placed on microscope glass slides in a closed container to facilitate their attachment. Once the clones were reattached, slides were labeled for differentiation and placed in open microscope slide boxes hung from a floating dock (2–3 d) until the beginning of the experiments. Prior to the beginning of each experiment, the general condition of individuals was assessed, and only healthy and attached clones were chosen (see Brunetti et al. 1980). All excess colonies and their associated clones were bagged and put in the trash.

We tested 2 scenarios of low-salinity stress: (1) a chronic treatment whereby colonies of both species were exposed to different salinities over 9 d; and (2) an episodic treatment whereby colonies were exposed to 3 and 12 h durations of lower salinity. The durations of salinity stress, chronic and episodic, were chosen to mimic the natural durations of low salinity (Fig. 1). For both experimental studies (chronic and episodic), heart rates, indicators of overall colony health (see Brunetti et al. 1980, Dijkstra et al. 2008), were recorded under a dissecting microscope. Heart beats were measured from 3 haphazardly selected zooids lining the edge of each ascidian colony.
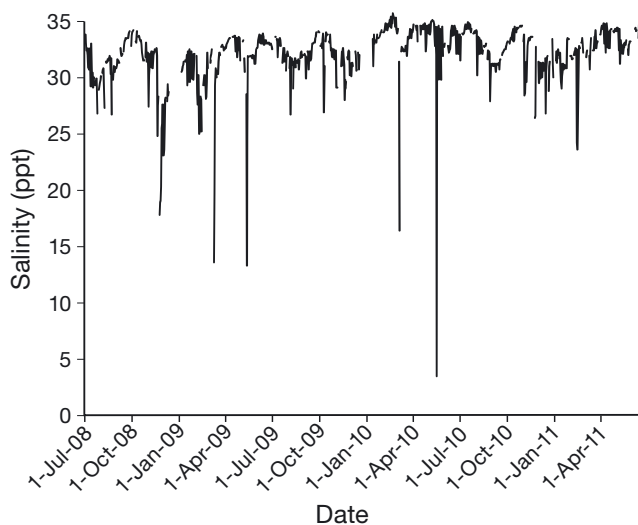

Fig. 1. Salinity range at Bocas del Toro, Panama, between 2008 and 2011. During heavy storm events salinity dropped below 25 ppt for several hours and in November 2008 for several days. Environmental data for this figure was obtained from the Smithsonian Tropical Research Institute physical monitoring website (http://biogeodb.stri.si.edu/physical_monitoring/research/bocas#parameters)

Counts from 3 zooids were averaged, and the average number of beats per colony was used for statistical analysis. Heart beats were recorded at 15 s intervals, and a single peristaltic wave (undulation) was considered 1 heartbeat. Ascidian hearts are tubular and have 2 pacemakers, one on each end of the tube, that prompt the heart to reverse direction. During the chronic experiment, rate of asexual reproductive development was recorded by identifying different stages of palleal budding (i.e. asexual phases; see Sabbadin 1955, Manni et al. 2007). Although both species differ in some morphological features (Van Name 1945), they exhibit the same bilateral budding to replace adult zooids during asexual reproduction (as in Brunetti et al. 1980).

Chronic treatments of low-salinity tress

We carried-out a 9 d chronic salinity stress experiment, exposing colonies of *B. nigrum* (n = 5) and *B. planus* (n = 5) to 5 different salinities (20, 24, 28, 32 and 35 ppt) under ambient temperatures (~28°C). Salinities were chosen to capture the range of salinities that occurred annually in Bocas del Toro. Only colonies with 5 healthy and attached clones were chosen for experiments. One clone from each of 5 individual colonies was placed in a separate aquarium at each salinity level—there were 5 replicate aquaria per salinity treatment. Heart rates, reproduction (asexual developmental phase) and mortality were recorded once a day for a period of 9 d. The water in each experimental aquarium was changed every other day using unfiltered marine water that contained natural levels of phytoplankton as a food source. To be certain colonies were not food limited, we added 2–3 drops of Invertebrate Smorgasborg (Coralife®) twice a day to each aquarium. Prior to water replacements, salinity was reduced to treatment levels using deionized (DI) water.

Episodic treatments of low-salinity stress

To investigate the ability of each species to recover from short-term salinity stress, such as that experienced during a strong rain event, healthy colonies of *B. nigrum* and *B. planus* were exposed to the lowest treatment salinities, 20 ppt (n = 6/species/time period) and 24 ppt (n = 6/species/time period), for 2 inundation times (3 and 12 h). Clones were not used during the episodic salinity experiment, and care was taken to ensure that replicates were unique individu-

als and not sub-colonies. These salinity levels were chosen because in our preliminary studies (earlier experiments conducted at Bocas del Toro in June 2011) both species experienced mortality and physiological challenges, such as higher rates of heart rate reversal and slower asexual reproduction, at these salinities. Furthermore, duration of exposure was chosen to mimic short (3 h) and longer (12 h) periods of rain events that are typical for tropical environments (Kauffman & Thompson 2005). After exposure, colonies were returned to ambient salinity. Mortality and heart rates were recorded prior to exposure to low salinity at the end of the exposure period (3 or 12 h) and then measured repeatedly every 2 h in ambient salinity for a period of ~8 h. Heart rate was chosen as an indicator of environmental stress, since it shows immediate response to changes (Dijkstra et al. 2008, J. A. Dijkstra unpubl. data). Asexual reproduction was not measured, as the recovery time was too short to observe change in asexual phases (Sabbadin 1955, J. A. Dijkstra & C. Simkanin pers. obs.).

Statistical analyses

Statistical analyses were generated using JMP software (JMP 11, SAS Institute, Cary, NC, USA). To detect differences in physiology (i.e. heart rates) among salinities, we used a 2-way repeated measures analysis of variance (ANOVA) with salinity and clones of individual colonies as the fixed factors and time as the repeat factor. Response variables were the average heart rate measured from 3 zooids lining the edge of each clone (n = 5 colonies per salinity treatment). Variances remained heterogeneous (Levene's test, $p < 0.05$) despite transformation, so untransformed heart rates were used for all univariate analyses. Though ANOVA is relatively robust to heterogeneous variances (Box 1953), results were evaluated at a conservative significance level of 0.01. The raw data for asexual phases met assumptions of equal variances (Levene's test, $p < 0.05$). A 1-way block ANOVA with individual colony number as block was used to assess the effect of chronic salinity level on total number of phases that occurred within a clone during the experiment. On finding a significant difference, post-hoc Tukey-Kramer tests, set to 0.01 significance, were used to assess pairwise differences between treatment means. To examine differences in initial and end heart rates of *B. nigrum* and *B. planus* during episodic exposure to low salinity, paired *t*-tests were run using square root-transformed heart rate data.

RESULTS

Chronic treatments of low-salinity stress

Physical responses

Mortality of *Botrylloides nigrum* colonies exposed to 20 ppt was 100% after 3 d of exposure, while colonies exposed to 24 ppt experienced 80% mortality by Day 9 (Fig. 2A). Colonies exposed to salinities between 28 and 35 ppt experienced 0% mortality. Mortality of *Botryllus planus* colonies exposed to 20 ppt was 20% after 3 d of exposure, increasing to 40% at Day 4 and remained at 40% for the remainder of the experiment. Colonies exposed to 24 ppt experienced 40% mortality by Day 4 (Fig. 2B). Mortality did not increase with longer exposure time. Colonies exposed to salinities between 28 and 35 ppt experienced 0% mortality. Intraspecific response to salinity stress was observed for one colony of *B. planus*. The clone of a
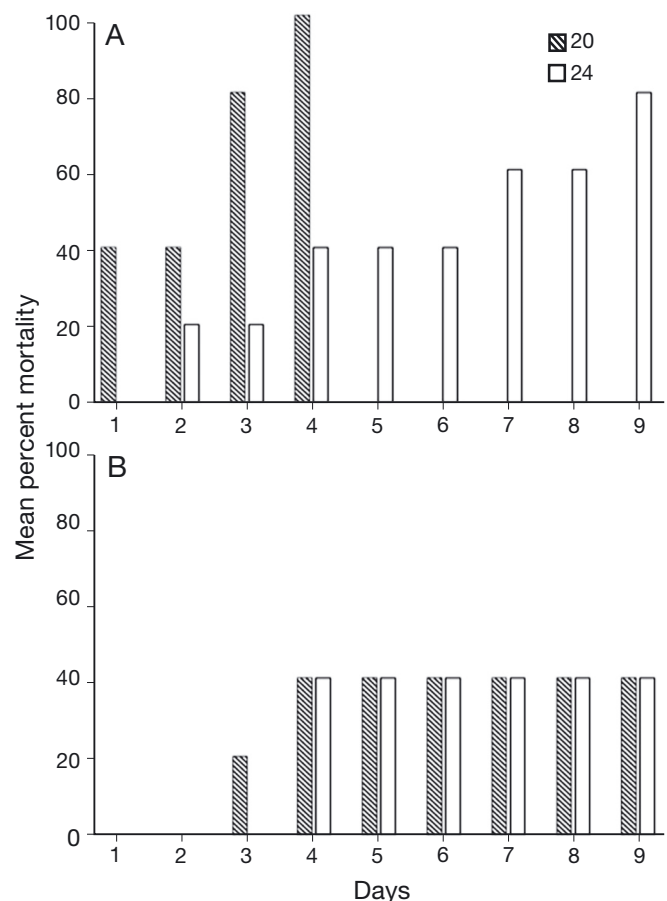

Fig. 2. Mean percent mortality in colonies of (A) *Botrylloides nigrum* and (B) *Botryllus planus* exposed to 20 and 24 ppt. Colonies exposed to salinities above 24 ppt did not experience mortality

Fig. 3. Physical response of colonies exposed to similar salinities: (A) *Botrylloides nigrum* with distended cloacal cavities when exposed to 24 ppt; (B) an intact *B. nigrum* colony when exposed to 24 ppt; (C) *Botryllus planus* with distended cloacal cavities, showing their exposed pharyngeal baskets when exposed to 24 ppt; and (D) an intact *B. planus* colony when exposed to 24 ppt
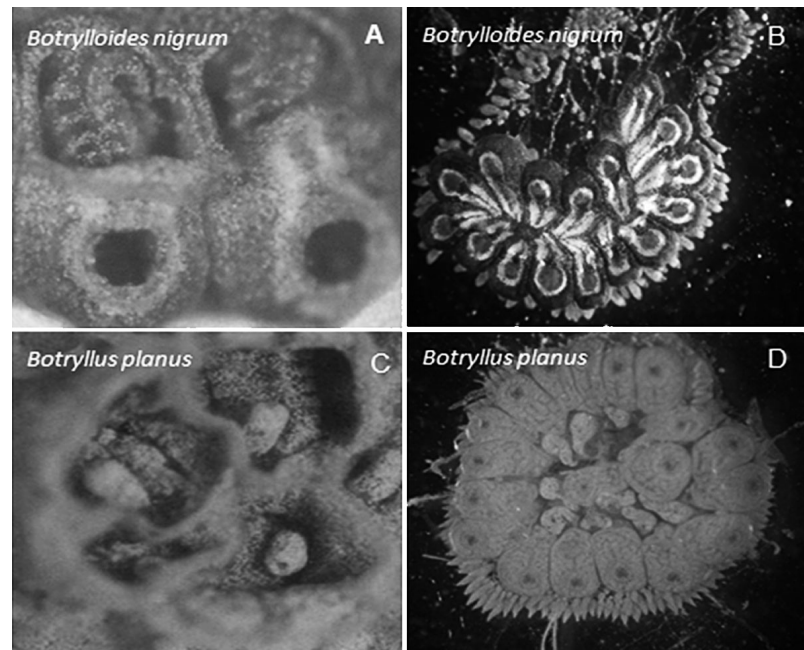
colony exposed to 20 ppt survived, while another clone of the same colony died when exposed to 24 ppt.

Within 48 h, *B. nigrum* and *B. planus* displayed physical responses to salinity stress. Forty percent of *B. nigrum* colonies exposed to 24 and 28 ppt exposed their pharyngeal baskets (Fig. 3A). The other 60% did not exhibit this behavior, and their appearance and heart rate was more similar to that of colonies exposed to 32 and 35 ppt (Fig. 3B). Similarly 20% of *B. planus* colonies exposed to 24 ppt opened their cloacal cavities, exposing their pharyngeal basket and neural glands (Fig. 3C), while 80% did not (Fig. 3D). Neural glands in *B. planus* appeared to be inflated.

Metabolic response

In both *B. nigrum* and *B. planus* the severity of the physiological response to treatment salinity was inversely related to salinity (i.e. lower salinity results in reduced heart rates; Fig. 4). The pattern of slow heart beats in clones exposed to low salinity was similar across species and across time. A 2-way repeated measures ANOVA revealed a significant negative effect of low salinity on heart rates for *B. nigrum* and *B. planus* ($F_{3,141}$ = 46.9,
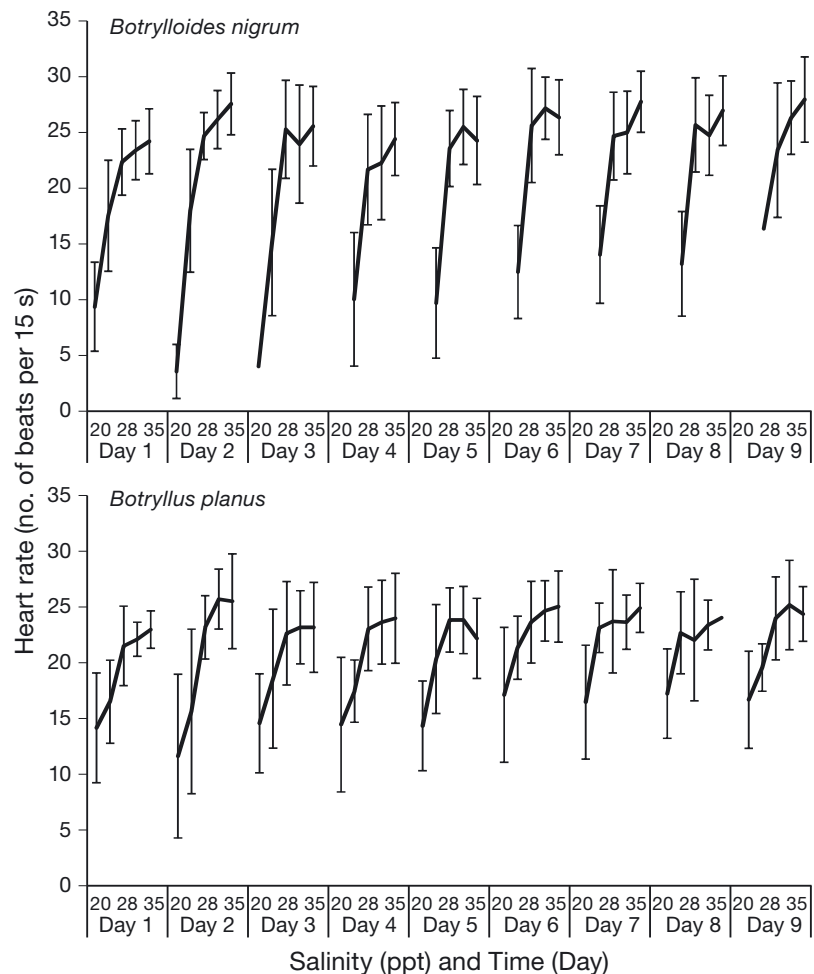

Fig. 4. Mean heart rate ± SD for *Botrylloides nigrum* and *Botryllus planus* for each day from all salinity treatments. Values without SD represent heart rates measured from a single treatment colony
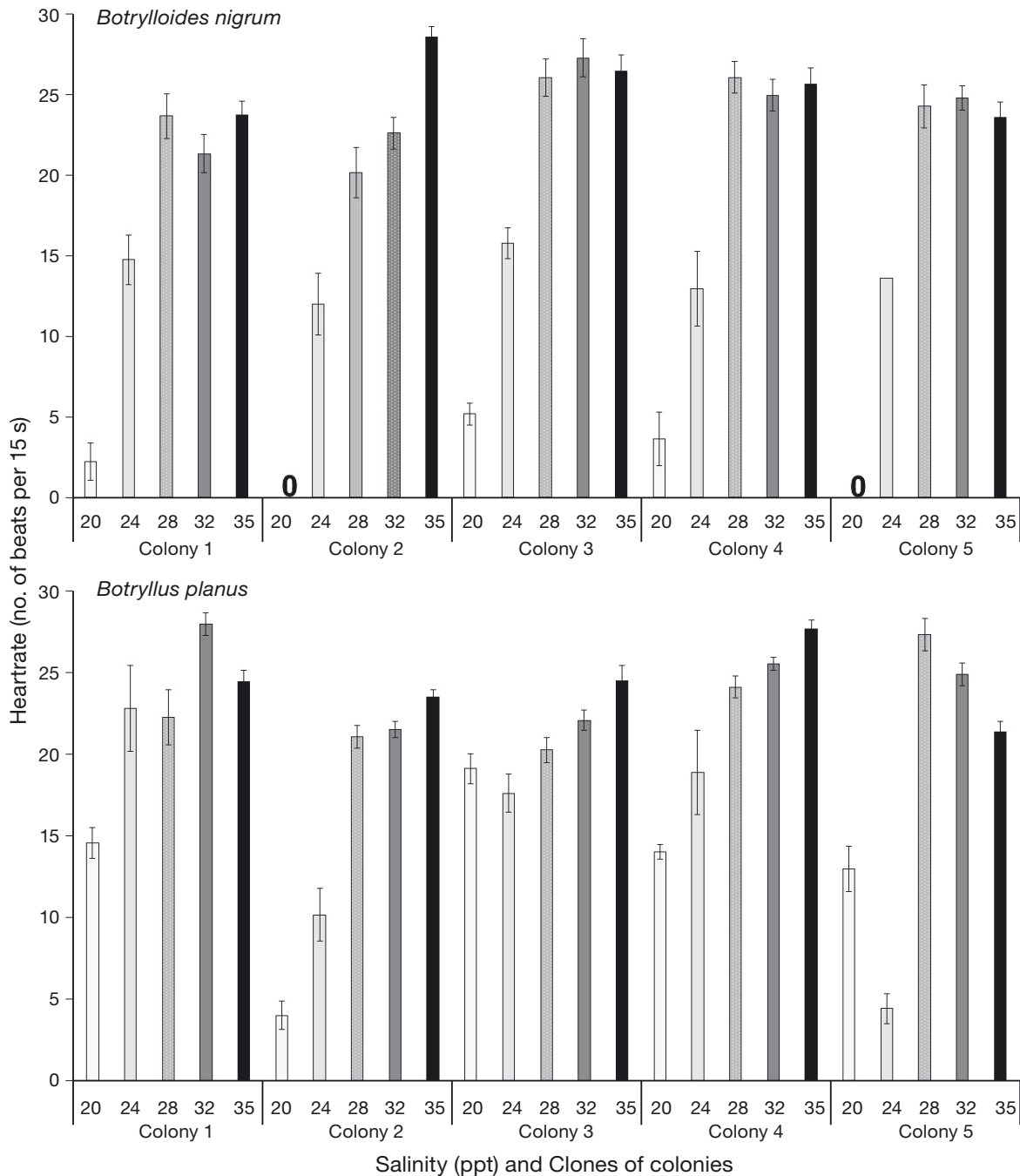
Fig. 5. Mean (±SE) heart rates of individual clones of 5 *Botrylloides nigrum* and 5 *Botryllus planus* colonies exposed to salinities between 20 and 35 ppt for 9 d. 0: all clones died

$p < 0.001$; $F_{4,175} = 23.6$, $p < 0.001$, respectively; Fig. 4). There were significant differences in individual responses to salinity across colonies (and clones) for both species ($F_{2,141} = 46.9$, $p < 0.006$, $F_{4,175} = 3.8$, $p < 0.005$, respectively; Fig. 5). There was no significant interaction between salinity and individual colony on heart rates for *B. nigrum* ($F_{14,141} = 1.6$, $p = 0.07$), but there was a significant interaction of individual

colony and salinity on heart rates for *B. planus* ($F_{16,175} = 2.4$, $p < 0.003$), suggesting the response of clones within a colony is not consistent when exposed to varying salinity. Prior to 100% mortality at Day 4, heart rates of individual *B. nigrum* exposed to 20 ppt had the least number of heart beats (Tukey-Kramer test set to 0.01 significance), followed by heart rates in *B. nigrum* colonies exposed to 24 ppt and *B. planus*

colonies exposed to 20 ppt (Fig. 4). Overall, heart rates in 2 of the 5 replicate individual colonies were significantly lower than heart rates in the other 3 individual colonies across salinities (Tukey-Kramer test set to 0.01 significance).

Asexual reproduction

Clones of individual colonies of *B. nigrum* and *B. planus* exposed to low salinity had fewer asexual reproductive phases than clones of colonies exposed to greater salinities (Fig. 6). A 1-way block ANOVA revealed a significant negative effect of salinity on reproduction in *B. nigrum* (sum of squares [SS] = 44.24, $F_{4,24}$ = 24.04, p < 0.01) and *B. planus* (SS = 16.96, $F_{4,24}$ = 4.28, p < 0.01). Colonies of *B. nigrum* exposed to 20 and 24 ppt and *B. planus* colonies exposed to 20 ppt had significantly fewer asexual reproductive phases than colonies exposed to higher salinities (Tukey-Kramer set to 0.01 significance). Reproductive response of individual colonies was similar across salinities for *B. nigrum* (SS = 1.84, $F_{4,24}$ = 1.00, p = 0.44). In contrast, reproduction in 2 of the 5 *B. planus* replicate individual colonies were significantly lower than reproduction in the other 3 individual colonies across salinities (Tukey-Kramer test set to 0.01 significance).

Episodic treatments of low-salinity stress

During the experimental period, 0% mortality was observed for colonies exposed to 3 and 12 h. of low salinity. For both species, the severity of the physiological response (i.e. heart rate) to episodic low salinity depended on salinity treatment and duration of exposure (Fig. 7). Heart rates of *B. nigrum* exposed to 20 ppt for 3 and 12 h did not recover after 8 h to their pre-exposure values, t = −3.85, p < 0.01 (3 h); t = −10.09, p < 0.001 (12 h) (Fig. 7A,B). In contrast, colonies exposed to 24 ppt for 3 and 12 h did recover to their pre-exposure values after 8 h in seawater of 32 ppt, t = −0.20, p = 0.07 (3 h), t = −0.38, p = 0.72 (12 h) (Fig. 7A,B), although recovery after 3 h exposure is only slightly significant. Heart rates of *B. planus* colonies exposed to 20 and 24 ppt for 3 h did recover to their pre-exposure values, t = 0.374, p = 0.72, t = 1.72, p = 0.15, respectively (Fig. 7C,D). In contrast, heart rates in *B. planus* colonies exposed for 12 h to 20 ppt and 24 ppt did not recover to their pre-exposure values after 8 h, t = −6.79, p < 0.001, t = −4.85, p < 0.01, respectively (Fig. 7D).

DISCUSSION

In an era of global change, where storm events are expected to become more frequent and severe (IPCC 2014), our study highlights the need for experiments examining organism response to both chronic and episodic stress. By manipulating the duration of salinity stress, we have shown an adaptive plastic response within *Botrylloides nigrum* and *Botryllus planus* to variation in salinity. Ascidians are good candidates for a plastic response, as they have traits such as accelerated substitution rates across genes (Tsagkogeorga et al. 2010, 2012) and fast generation times (Sabbadin 1955, Dijkstra et al. 2011). Our study indicates intraspecific variation in the physical and physiological responses within species exposed to identical salinities. Some individuals exhibited a dramatic morphological response to low salinity, while other colonies did not. Responses included distension of ascidian cloacal cavities and exposition of their pharyngeal baskets and neural glands surrounding their zooids. An immediate response, such as observed swelling of the neural gland in *B. planus*, may aid in osmotic regulation. While ascidians lack excretory organs such as kidneys or nephridia for osmoregulation (exception is the renal sac in molgulids), their neural glands may act as an osmoregulatory organ (Ruppert 1990, Deyts et al. 2006). Variation among colonies that coexist on a local scale, especially the responses from the proportion of the population that demonstrated resilience to extreme salinity events, may promote persistence under stressful flood conditions. These traits, therefore, may help to buffer populations against the immediate impacts of a changing climate, particularly in shallow water ecosystems that are especially vulnerable to storm events.

The physical and physiological differences among clones and colonies highlight phenotypic variation within and between genotypes to selective environmental pressures in real time (Whitman & Agrawal 2009). This occurs in areas where the environment fluctuates over time scales shorter than an organism's lifetime (Meyers & Bull 2002, Piersma & van Gils 2011). Colonies of both species exhibited differential mortality at low salinity. One colony of *B. nigrum* exposed to 24 ppt and 3 colonies of *B. planus* exposed to 20 and 24 ppt persisted throughout the entire experimental period while the other colonies perished. This indicates colonies exposed to low salinity conditions experienced a wider range of physiological responses, which is observed in the variability of reproductive and heart rate responses among salinity
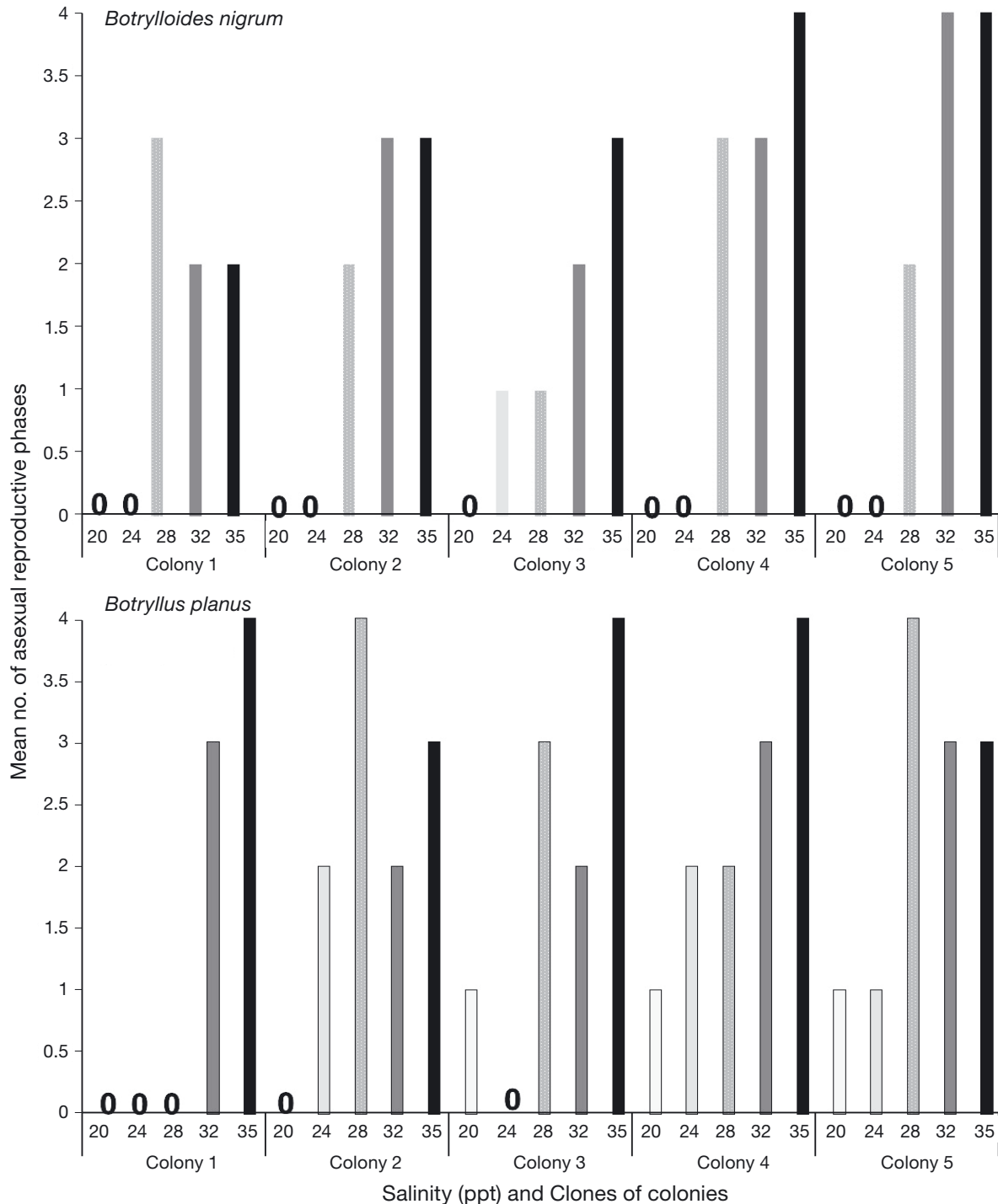
Fig. 6. Mean number of asexual reproductive phases in clones of 5 *Botrylloides nigrum* and 5 *Botryllus planus* colonies exposed to salinities between 20 and 35 ppt for 9 d. A positive gradient in asexual reproduction with salinity was observed with species-specific differences in reproduction at low salinity. Intraspecific differences in reproduction were observed for *B. planus*. 0: no reproductive phases

treatments. Colonies exposed to low salinity experienced greater variation in number of heart beats per 15 s than colonies exposed to high salinity. Colonial botryllid ascidians have short life-history stages and

exhibit an immediate physiological response to environmental conditions (Grosberg 1988, Dijkstra et al. 2008), characteristics that may facilitate a rapid response to selective climate pressures. Clearly, the
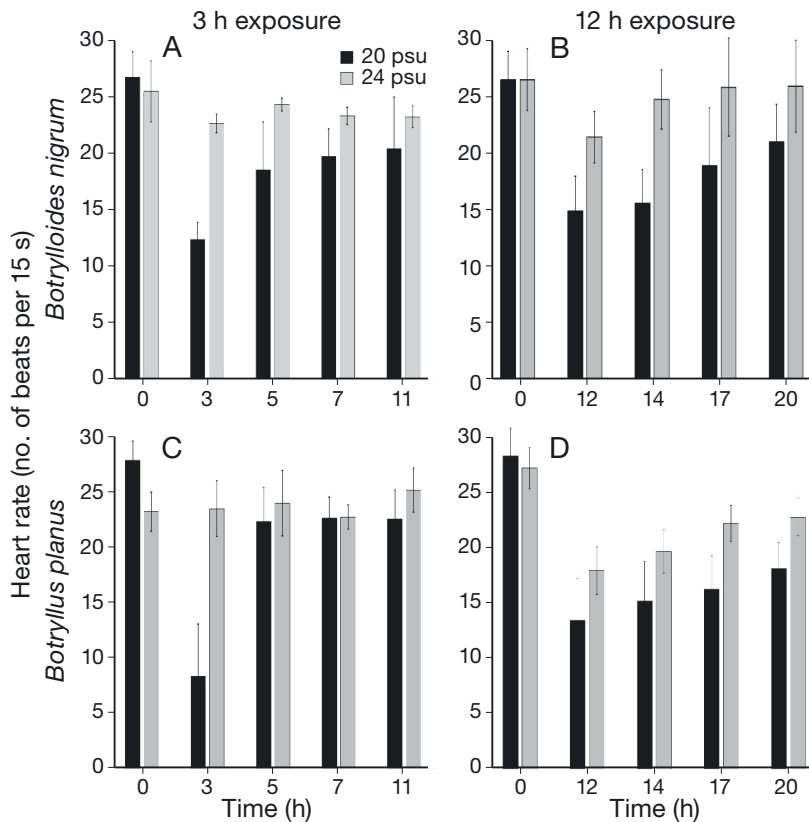
Fig. 7. Mean heart rates of (A,B) *Botrylloides nigrum* and (C,D) *Botryllus planus* colonies exposed to 20 and 24 ppt for (A,C) 3 and (B,D) 12 h

vorable conditions; however, despite this, many ascidians are widespread global invaders (Shenkar & Swalla 2011). The physical and physiological differences observed in our experiments may provide some insight into the ability of these species to expand their distributions. Variation in heart rates and asexual reproduction (*B. planus*) between individuals when exposed to varying salinity may increase the likelihood of survival during the transport and introduction stages of an invasion (sensu Blackburn et al. 2011). Recent meta-analyses of introduced plants, also sessile species, albeit in a very different system, show that increased plasticity and physiological performance have a positive influence on invasion success (Richards et al. 2006, van Kleunen et al. 2010). Intraspecific variation in survival and growth leads to a higher likelihood that one or more individuals will survive to reproduce during an environmentally stressful event, thus ensuring species survival. Variation in asexual reproduction in *B. planus* in response to varying salin-

species we evaluated are susceptible to mortality when salinity is reduced, but the persistence of these species in Bocas (which experiences periodic flooding) is aided by resilience demonstrated by a subset of colonies.

Our study, along with other empirical studies (Dijkstra et al. 2008, Groner et al. 2011), reveal that colonial ascidians can survive and reproduce at much lower salinities than previously recorded. This has important implications for projections of population growth in estuarine ecosystems. Most introductions occur in ports and estuaries, areas with widely varying environmental fluctuations such as salinity (Preisler et al. 2009). Our study suggests that models that predict species response to environmental change such as salinity are likely to underestimate the effect of changing environmental conditions on abundance due to the difficulties of incorporating trait variation responses. Modelling without taking adaptive processes into account may significantly reduce our predictive power, as they play key roles in modifying the impacts of climate change on species success (Hoffmann & Sgro 2011, Pandolfi et al. 2011).

As sessile species, ascidians cannot escape unfa-

ity is important to consider for viability and growth in response to environmental extremes. Some colonies of *B. planus* had twice the number of asexual phases at similar salinities than others. As many botryllids must undergo a number of asexual reproductive cycles prior to sexual reproduction (Saito et al. 1981, Yund et al. 1997, Westerman et al. 2009), greater rates of asexual reproduction in some individuals will lead to a dampening oscillation within the population, as at any one time, an individual will be reproducing.

Climate change will alter precipitation amounts and the frequency of extreme weather events (IPCC 2014). This may be particularly important for tropical ecosystems, as precipitation is expected to increase in frequency and intensity (IPCC 2014). Bocas del Toro is located on Isla Colon, an archipelago of 6 islands that separate the Lagune of Chiriqui and the Bay of Almirante, and much of the region of the Archipelago is shallow (Collin 2005). Large and more frequent storms, as predicted for the region (IPCC 2014), will depress salinity and may alter water pathways in watersheds to enhance flooding and threaten the survival and distribution of many nearshore-

dwelling species. Our study demonstrates intraspecific variation in physiology and asexual reproduction (*B. planus*) to salinity. Individual variation in asexual reproduction to environmental stress will help to stabilize populations due to their stochastic response to low salinity. Species with traits which elicit an adaptive plastic response to environmental pressures may help to buffer populations against the immediate impacts of a changing climate, particularly in shallow water ecosystems that are especially vulnerable to storm events.

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