Celestial mechanics affects emersion time and cover patterns of an ecosystem engineer, the intertidal kelp *Saccharina sessilis*

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ABSTRACT: Understanding the factors that control the performance and abundance of important community members such as ecosystem engineers is critical for understanding ecosystem dynamics in a changing climate. Oscillation of the moon's declination over 18.6 yr periods directly affects emersion time in intertidal systems. Here we document the direct influence of this predictable emersion time cycle on the cover of the dominant intertidal kelp and ecosystem engineer *Saccharina sessilis*. Field surveys over 14 yr showed large changes in the kelp canopy (between a maximum of 84 % and a minimum of 21 % cover) that were tightly linked to changes in annual emersion time. In laboratory experiments, we found evidence of a mechanistic link between emersion and *S. sessilis* canopy cover, as even short exposure to realistic low-tide conditions reduced physiological performance and caused substantial biomass loss. Our field data show a strong negative relationship between annual emersion time and kelp canopy cover. The emersion time cycle had cascading effects on the community, as shown by a strong positive correlation between kelp canopy cover and the abundance of the chiton *Katharina tunicata*, a major herbivore that depends on the canopy for shade. Recognizing the effects of natural, decadal-scale cycles on habitat-modifying species is an especially important step in achieving an understanding of the ecological consequences of climate change.

KEY WORDS: Celestial mechanics · Ecosystem engineer · Emersion time · Habitat modification · Kelp · Maximum quantum yield · Rocky intertidal zone · Sub-lethal stress

INTRODUCTION

Aquatic and terrestrial ecosystems are affected by many natural environmental oscillations which drive patterns of primary productivity and standing biomass of vegetation (Dayton et al. 1999, Paine & Trimble 2004, Edwards & Estes 2006, Woodward et al. 2008, de Jong et al. 2012) and consequently affect the performance of organisms in higher trophic levels (Holmgren et al. 2006, White 2008). The potential for abrupt regime shifts and the challenge of restoring ecosystem function in the face of hysteresis have been well documented for cycles ranging in scale from global (e.g. the El Niño/La Niña Southern Oscillation [ENSO] and Pacific Decadal Oscillation [PDO]) to regional (e.g. the North Atlantic Oscillation [NAO] and temporary climatic effects of volcanic eruptions) to local (e.g. periods of drought and recovery) (Woodward et al. 2008, de Jong et al. 2012). From a community perspective, whatever the spatial scale, cycles that affect key species (e.g. keystone species, ecosystem engineers, and foundation species; Elmqvist et al. 2003) are especially important, as these effects have repercussions for the entire community.

Unambiguously identifying the effects of environmental cycles on natural systems is critical to understanding ecosystem dynamics and developing informed strategies for management, especially in a changing climate (Folke et al. 2004). Differentiating between responses to environmental cycles and directional changes in climate parameters can be especially challenging when cycles overlap or cause incremental effects over long temporal scales. A natural environmental cycle on a decadal scale may temporarily counter (mask) or exacerbate the effects of shorter cycles (e.g. ENSO or PDO) or longer-term climatic change. Alternatively, a natural environmental cycle in an unchanging environment, undetected due to limited resolution or scope of data collection, could be misinterpreted as directional climate change (Denny & Paine 1998). Though clearly important, partitioning the effects of overlapping environmental cycles and long-term directional climate trends is only possible with an understanding of each cycle′s timing and intensity.

Emersion time is one of the primary structuring forces in intertidal ecosystems, which are subjected to well-understood and strong effects of daily and monthly tidal cycles (Stephenson & Stephenson 1972). On a longer time scale, oscillation of the moon′s declination over 18.6 yr periods directly affects emersion time (Denny & Paine 1998); surprisingly, the ecological effects of this cycle are poorly documented despite their potential to be pervasive. This celestial phenomenon can cause a doubling or more in the annual low-tide emersion time at a given location over the 9 yr encompassing the cycle extremes. Increased emersion time results in longer periods of exposure to terrestrial conditions (including high temperatures, solar radiation, and wind) for marine organisms. The effect of longer exposure time over the celestial cycle could easily be misinterpreted as a response to directional climate change (Denny & Paine 1998). In contrast, a thorough understanding of the decadal emersion time cycle and its ecological effects could give us a valuable preview of the ecosystem responses we can expect with a changing climate, as well as insights into the potential for mitigation and recovery of ecosystem function.

Here we document the first example of the influence of celestial mechanics on the abundance of a primary producer foundation species, the canopy-forming intertidal kelp *Saccharina sessilis* (formerly *Hedophyllum sessile*; hereafter *Saccharina*). Over a 14 yr *in situ* study we quantified changes in kelp canopy cover which we hypothesized were tightly linked with the lunar-influenced cycle of emersion time. We also used laboratory experiments to test the hypothesis that sub-lethal stress during low tide emersion reduced kelp physiological performance, providing a mechanistic link between emersion and canopy cover. As a canopy-former, *Saccharina* is both a foundation species (Dayton 1972) and a physical ecosystem engineer (Jones et al. 1994, 1997), and the provision of shade by the kelp controls the distribution of the major herbivore in this system, the chiton *Katharina tunicata* (Burnaford 2004). Therefore, we predicted that we would see an indirect influence of celestial mechanics on the system in inter-annual changes in the abundance of the chiton in conjunction with changes in canopy cover. Because the data that are needed to detect the influence of long time-scale cycles on ecological systems (and distinguish them from climate change) are rare, the influence of cycles such as this one may be under-appreciated.

MATERIALS AND METHODS

Lunar declination, emersion time, kelp canopy cover, and herbivore abundance

We investigated the relationship between annual changes in emersion time and the canopy cover of the intertidal foundation species *Saccharina sessilis* as well as abundance patterns of its major herbivore, the chiton *Katharina tunicata*, at Pile Point, on the west side of San Juan Island, Washington, USA (48.481767° N, 123.093653° W). Over 18.6 yr, the angle of lunar declination cycles from a maximum of ~29° to a minimum of ~18° (see Fig. 1A in Denny & Paine 1998). Our study spanned almost the entire range of lunar declination (http://ssd.jpl.nasa.gov/horizons.cgi#top; see Fig. S1 in the Supplement at www.int-res.com/articles/suppl/m509p127_supp.pdf). Percent canopy cover of *Saccharina* and the abundance of *K. tunicata* were quantified every summer from 1998 to 2000 and again from 2007 to 2012 in 25 permanent plots of 1 m² which spanned the vertical range of *Saccharina* at our study site (approx. mean lower low water ±0.5 m). When the plots were established (in 1998), each was located at least 0.7 m inward from the edge of the *Saccharina* bed and 1.5 m from other plots. Throughout the study, a single investigator (J.L.B.) measured percent canopy cover of all kelps in each plot using the visual scanning method (Dethier et al. 1993) with a 1 m² quadrat divided into 100 squares. The number of plots included in our analysis varied from all 25 in 1998 and 2007−2012 to 5 (spanning the tidal range of *Saccha-*

rina) in 1999 and 2000. We excluded the remaining 20 plots in 1999 and 2000 because they were part of a manipulative experiment (the 5 plots used in this analysis were the unmanipulated controls; see Burnaford 2004 for details). No manipulations or collections occurred in any plots between 2000 and 2007, and in 2007 there was no difference in *Saccharina* cover between the formerly manipulated plots and the former controls (*t*-test, ln-transformed data, df = 23, $t = -0.83$, p = 0.42). For more detailed analysis we also identified the 5 study plots with the longest emersion times (those consistently emersed first and submerged last during low tide) and the 5 with the shortest emersion times (those consistently emersed last and submerged first during low tide) through direct observations of all 25 study plots (which spanned a large area of the intertidal zone) over 20 low tides.

To assess the relationship between abiotic conditions and our biological response variables, we calculated standardized metrics for July 1 (of year $x - 1$) through June 30 (of year x) for each 'year x' summer survey. Emersion times were calculated for +0.03 m tidal height (approximately the midpoint of the tidal distribution of our plots) using verified tidal height data recorded at 6 min intervals at a location 10 km from our study site (NOAA NOS station 9449880 in Friday Harbor, Washington; www.tidesandcurrents. noaa.gov). We calculated mean daily maximum air temperatures for each year using data from Anacortes, Washington (48.5119° N, 122.6136° W; www. ncdc.noaa.gov/cdo-web/datasets/GHCND/stations/ GHCND:USC00450176/detail; see details in the Supplement).

Sub-lethal stress effects on photosynthesis: laboratory experiments

To assess the impacts of emersion on *Saccharina* physiology, we conducted an experiment at the Bodega Marine Laboratory (University of California, Davis) simulating realistic stressful and benign conditions over a 2 d mock tidal series. We monitored net photosynthetic rate (NPR), recovery of maximum quantum yield (MQY), and changes in biomass over time as measures of sub-lethal stress.

Prior to the experiment, thalli from Kibesillah Hill, California (39.599881° N, 123.788875° W) were submerged in an outdoor flow-through seawater tank and acclimated to common conditions (daytime photosynthetically active radiation [PAR], mean ± SD: 1064.1 ± 677.6 µmol photons m^{-2} s^{-1}, water temperature: 9.9 ± 0.9°C; www.bml.ucdavis.edu/boon/index.

html) for 5 to 8 d. Blade dimensions (including rugosity) of these experimental thalli were well within the range for thalli at Pile Point (J. Stokes, K.J. Nielsen, J.L. Burnaford unpubl. data). To control for individual (genotypic) variation, thalli were divided into 3 sections (blades) after the holdfast was excised. Each blade was assigned at random to a treatment and given 24 h to heal before the experiment commenced. Blades remained in the outdoor tank during the day except during physiological measurements and (if relevant) periods of simulated low tide (see below). Starting at dusk, blades were maintained in complete darkness for 12 h in an indoor flow-through seawater tank covered with opaque black plastic to create a controlled dark recovery period.

To examine the effects of single and repeated low-tide exposures, we compared the performance of fully hydrated (control) blades, which were maintained in flowing seawater, to blades exposed to simulated low tide treatments that mimicked realistic atmospheric field conditions over a 2 d tidal cycle. Low tide conditions simulated sunny, windy days (high-stress low tide treatment) or cloudy, calm days (low-stress low tide treatment). We recorded experimental conditions during low tide simulations using an LI-190 Quantum Sensor (LI-COR) to measure PAR and a Kestrel 4500 pocket weather tracker (Nielsen-Kellerman) to measure wind speed, relative humidity, and air temperature. During simulated low tides, blades in the low-stress low tide treatment were placed on an indoor laboratory bench with low light (mean ± SD: 11.5 ± 1.35 µmol photons m^{-2} s^{-1}), no wind (0 ± 0.0 m s^{-1}), and moderate relative humidity (RH, 48 ± 0.74 %) and temperature 22.14 ± 0.29°C). Blades in the high-stress low tide treatment were held in the laboratory suspended from monofilament flanked by lights (54 Watt T5 HO equipped with 4 SlimPaq 10 000 K daylight and four 460 nm actinic fluorescent bulbs [Model 1123: Current]) in front of a fan. This protocol created low tide conditions with high light (1036 ± 121.8 µmol photons m^{-2} s^{-1} on each side) and moderate wind (1.97 ± 0.3 m s^{-1}), relative humidity (45 ± 0.53%), and temperature (22.72 ± 0.3°C). Blades in the high-stress low tide treatment were maintained under experimental low tide conditions until they had lost ~50% of their wet mass (determined by periodic weight measurements), which typically took 30 to 50 min. Low tide exposure for the corresponding low-stress low tide blade was terminated at the same time as exposure for the high-stress low tide blade, such that the duration of low tide did not differ between treatments for blades from the same thallus.

Environmental conditions during our experimental low tides were within the range of values experienced by *Saccharina* in the field. Over 22 low tides during the summer of 2012 at Pile Point, Washington, relative humidity ranged from 46 to 100%, air temperature ranged from 10 to 28.7°C, wind speed ranged from 0 to 9.7 m s^{-1}, and irradiance (PAR) ranged from 0 to 1969 µmol photons m^{-2} s^{-1}. At Kibesillah Hill, California, over 6 summer low tides during 2011 and 2012, relative humidity ranged from 59 to 100%, air temperature ranged from 8 to 21°C, wind speed ranged from 0 to 2.7 m s^{-1}, and irradiance (PAR) ranged from 0 to 1400 µmol photons m^{-2} s^{-1}. A single *Saccharina* blade blocks transmission of >97% of ambient PAR (Burnaford & Vasquez 2008). The low-stress low tide laboratory treatment roughly mimicked conditions for top (canopy) blades during a moderate morning low tide or understory blades during a sunny afternoon low tide, while the high-stress low tide treatment corresponded to conditions for canopy blades during a sunny afternoon low tide.

To assess the physiological effect of stressful low tide conditions, we compared aerial (emersed) measurements of NPR of blades from the high-stress low tide treatment (desiccated to ~50% wet mass over a single low tide as described above) with aerial measurements of fully hydrated (control) blades which were removed from flowing seawater tanks immediately before measurement. NPR was measured following Williams & Dethier (2005) as CO_2 uptake (normalized to dry biomass) using an infrared gas analyzer (IRGA: Model LI-6400, LI-COR). During NPR measurement, blades were fully spread out on monofilament line in UV-transparent airtight Plexiglas chambers (30.5 × 30.5 × 4 cm) with air circulation provided by two 12-volt DC fans. Temperature varied slightly among trials with a mean (±SD) of 18.4 ± 1.4°C. There was no relationship between difference in temperature between blade pairs (from a single thallus) and the difference in their NPR measurements (correlation analysis, r = −0.06, p = 0.93). Relative humidity, which was affected by blade hydration state, varied among trials with a mean (±SD) of 41.44 ± 10.1%. There was no relationship between difference in RH between blade pairs (from a single thallus) and the difference in their NPR measurements (correlation analysis, r = 0.08, p = 0.86). Irradiance was provided by full-spectrum fluorescent lamps (mean ± SD: 330 ± 26 µmol photons m^{-2} s^{-1}).

We also assessed MQY (=F_v/F_m in Cosgrove & Borowitzka 2010) each morning immediately before exposing the blades to first light after the dark recovery period (Table S1). Inability to recover MQY by first light would indicate that energetic costs of metabolic repair (of damaged photosynthetic enzymes) were not balanced by daily energy or nutrient budgets. In a dimly lit room, under the opaque black plastic covering the flow-through tank, we placed 3 dark-adaptation clips on haphazardly chosen locations on each blade. To ensure full dark-adaptation, measurements were made at least 15 min after clipping. MQY was measured in air using a pulse-amplitude modulated (PAM) fluorometer (Diving-PAM Fluorometer, Heinz Walz GmbH). The 3 readings per blade were averaged prior to analysis. Immediately after MQY measurements, we measured biomass as wet weight of damp blades from which surface water had been removed.

Statistical analysis

Data analysis was conducted using JMP v. 10.02 or SAS v. 9.2 (SAS Institute). We inspected residual plots to assess normality and equality of variances after fitting the data to statistical models. Standard data transformations and alternate statistical models (including different covariance structures, when appropriate) were used to meet model assumptions (Zuur et al. 2009). For linear mixed model analyses, we used Akaike's Information Criterion (corrected for small sample sizes; AIC_c) to select the most appropriate covariance structure for models that included random terms or repeated measures (Littell et al. 2002).

We used quadratic regression to model the relationship between exposure time and the percent cover of *Saccharina* at Pile Point, Washington. Total exposure time over the 12 mo preceding the summer cover surveys was regressed against mean percent cover of *Saccharina* in the 1 m^2 plots (N = 25 plots for all years except 1999 and 2000 when N = 5 plots). We used simple and multiple linear regressions to model the relationship between *K. tunicata* abundance and the percent cover of *Saccharina*. Mean number of *K. tunicata* ind. per plot was regressed against mean percent cover of *Saccharina* in the 1 m^2 plots. We then examined the influence of temperature on the relationship between *Saccharina* and *K. tunicata* using multiple regression analysis with mean cover of *Saccharina* and mean daily maximum air temperature as predictor variables and mean number of *K. tunicata* per plot as the response variable. We used correlation analysis to ensure that our predictor variables did not co-vary (r = −0.06, p = 0.86).

NPR (as μmol CO_2 g dry mass^{-1} h^{-1}, ln-transformed) were compared between hydrated (control) and high-stress low tide blades using a paired t-test (N = 8 blades per treatment). To determine if MQY recovery declined over time, we fit a linear mixed model with individual as a random factor (N = 8 blades per treatment for Day 1 and Day 2, 6 blades per treatment for Day 3) using maximum likelihood estimation and AIC_c to select the covariance structure that best matched the structure of the random and repeated factors in our data. We then fit a fully saturated linear mixed model (with treatment, time and time × treatment effects), with the selected covariance structure to model the random effect(s), using restricted maximum likelihood. We used contrasts of *a priori* hypotheses, least square means (and confidence intervals), and parameter estimates as appropriate to address questions of interest. We used the same approach to analyze changes in blade wet mass, which was expressed as the proportion of initial mass (on Day 1) on Days 2 and 3 of the experiment (N = 6 for Day 2, N = 4 for Day 3).

RESULTS

Emersion time, kelp canopy cover, and herbivore abundance

Kelp cover in the 1 m^2 plots changed greatly in concert with the change in emersion time over the study period, dropping from >70% mean cover down to a low of 21.5% mean cover before climbing upward again (Fig. 1A). Emersion time at the tidal height midpoint of the plots more than doubled over the course of the study, rising from 344 h of low tide exposure over 12 mo in 1998 to 818 h of low tide exposure over 12 mo in 2007 before declining again (Fig. 1A). Differences in annual emersion time between cycle low and high points (1998 vs. 2007) were due both to changes in the frequency of exposure to air (129 d with aerial exposure in 1998 vs. 241 d in 2007) and the duration of exposure during each low tide (mean emersion time of 2.67 h per low tide in 1998 vs. 3.39 h per low tide in 2007). Among our 25 study plots, those with the shortest emersion times during low tide retained higher kelp cover than plots with the longest emersion times for a large portion of the emersion time cycle (Fig. 1B).

There was a strong relationship between mean kelp cover and emersion time in the 12 mo preceding kelp surveys (Fig. 1C). There was no evidence that the inter-annual pattern of changes in kelp cover was
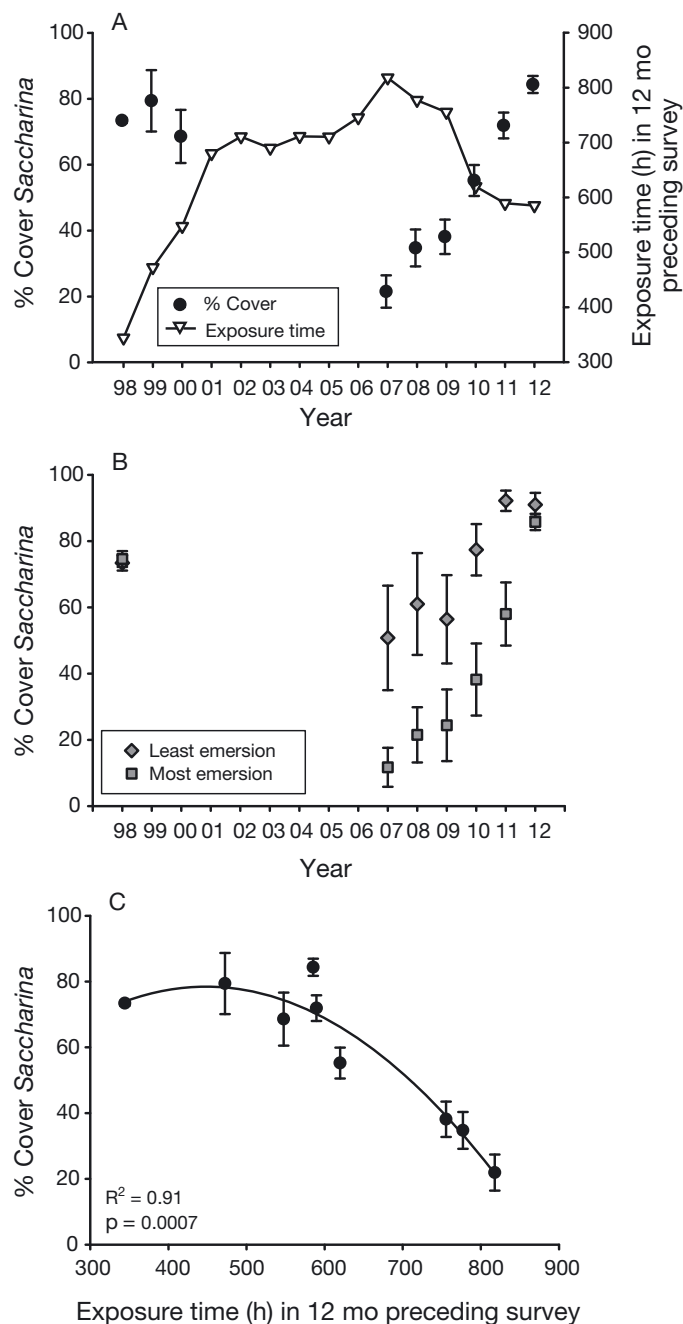

Fig. 1. *Saccharina sessilis* cover and emersion time at Pile Point, Washington, USA. (A) Total number of hours of low tide exposure at 0.03 m tidal height over the 12 mo preceding each survey (1 July of year *x*–1 through 30 June of year *x*) calculated from verified tidal height data, and mean (±SE) *Saccharina sessilis* cover in 1 m^2 plots. N = 5 plots in 1999 and 2000, 25 plots in all other years except 2001 to 2006 (no data), see 'Materials and methods' for details. (B) Cover (mean ± SE) in the 5 plots regularly exposed first and submerged last during low tide ('most emersion') versus the 5 plots regularly exposed last and submerged first during low tide ('least emersion'). (C) Relationship between mean *Saccharina* cover and total emersion time in the preceding 12 mo (quadratic regression). Sample size as in (A)

related to wave action, air temperature, or water temperature (see the Supplement, Table S2, Figs. S2 & S3 at www.int-res.com/articles/suppl/m509p127_ supp.pdf). As percent cover of non-*Saccharina* kelps did not exceed 1% in any plot before 2008, there is no evidence that changes in *Saccharina* cover were related to competition from other canopy-forming species. Because the abundance of the major herbivore in this system, *Katharina tunicata*, was strongly and positively related to *Saccharina* canopy cover (Fig. 2A); there is no evidence that changes in kelp cover were caused by herbivory.
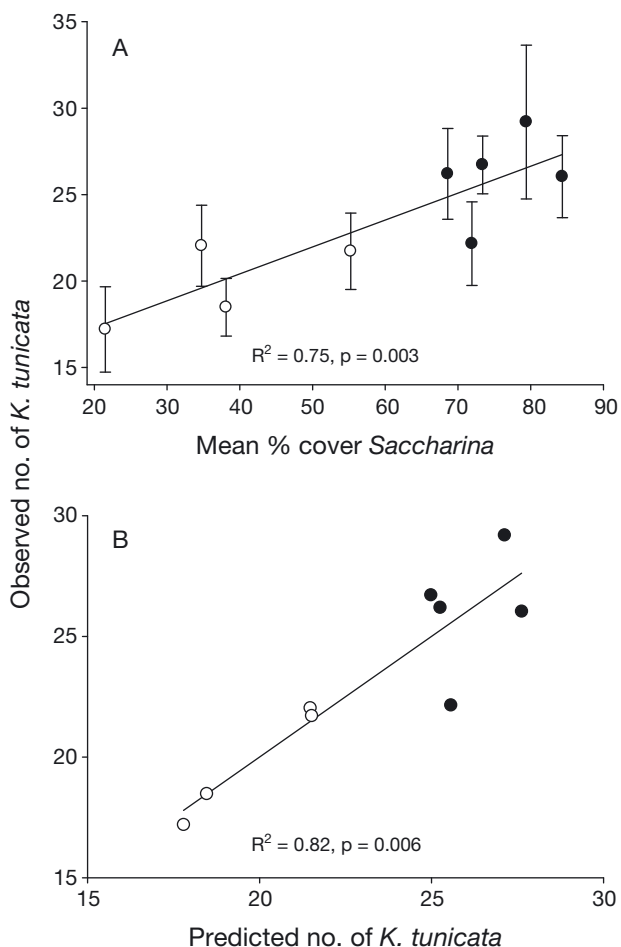
Multiple regression analysis with percent cover of *Saccharina* and mean daily maximum air temperature (in the 12 mo preceding the surveys) as predictor variables generated predicted mean *K. tunicata* abundances in our 1 m^2 study plots that were a good match to observed mean abundances (Fig. 2B). In years with low *Saccharina* cover (mean cover <56%), model fit was extremely tight (variance of residuals = 0.24), whereas in years with high *Saccharina* cover (mean cover >68%) model fit was not strong (variance of residuals = 5.58).

Photosynthetic physiology of emersion stress

NPR of emersed, fully hydrated *Saccharina* blades were nearly 4 times higher than NPR of emersed blades that had been exposed to a single low tide under conditions that mimicked a sunny summer day: hydrated (control) treatment mean (±SE) = 48.06 ± 9.79 µmol CO_2 g dry mass^{-1} h^{-1}; high-stress low tide treatment = 12.18 ± 1.82 µmol CO_2 g dry mass^{-1} h^{-1}; paired t-test on ln-transformed data, df = 7, t = −5.57, p = 0.0008).

Low tide conditions had strong effects on MQY over the course of our simulated tide series (Table 1, MQY Treatment × Day effect). Before the start of the experiment, MQY values in all treatments were similarly high (Fig. 3A; least square mean [LSM] and 95% CI of hydrated blades = 0.62 [0.58–0.67], low-stress low tide blades = 0.66 [0.62–0.71] and high-stress low tide blades = 0.64 [0.60–0.68]). After exposure to only 1 low tide, MQY before first light for blades in the high-stress low tide treatment dropped

Fig. 2. Factors associated with abundance of the chiton *Katharina tunicata*. (A) Relationship between the number of *K. tunicata* (mean ± SE) and mean *Saccharina sessilis* cover in annual surveys of 1 m^2 plots (linear regression). (B) Relationship between observed mean *K. tunicata* abundance and predicted mean *K. tunicata* abundance based on multiple regression analysis with mean *Saccharina* cover and mean daily maximum air temperature as predictor variables. N = 5 plots in 1999 and 2000, 25 plots in all other years except 2001 to 2006 (no data), see 'Materials and methods' for details. (○) years with low *Saccharina* cover (mean <56%); (●) years with high *Saccharina* cover (mean >68%)

Table 1. Fixed effects from linear mixed model analysis of maximum quantum yield (MQY) and change in wet mass over 3 d of experimental treatments for the kelp *Saccharina sessilis*. Covariance of repeated measures was modeled as unstructured for MQY, and as auto-regressive (lag = 1) for wet mass. Individual was a blocked random factor in both analyses

Fixed Effects	df	F	p-value
MQY			
Treatment	2, 15.7	8.33	0.0034
Day	2, 16.1	12.18	0.0006
Treatment × Day	4, 17.8	5.15	0.0061
Wet mass			
Treatment	2, 8.94	62.79	<0.0001
Day	1, 8.31	5.63	0.0440
Treatment × Day	2, 9.28	5.44	0.0273

by 30% (Fig. 3A, difference in LSMs Day 1 vs. Day 2, df = 21.2, $t = 5.39$, p < 0.0001), while MQY of blades in the hydrated (control) and low-stress low tide treatments showed little change (difference in LSMs Day 1 vs. Day 2, hydrated: df = 21.1, $t = 0.93$, p = 0.36; low-stress low tide: df = 21.1, $t = 1.24$, p = 0.23). Even on the third day of the experiment, MQY of hydrated and low-stress low tide blades remained high (Fig. 3A, LSM [95% CI], hydrated = 0.60 [0.52–0.68], low-stress low tide = 0.61 [0.53–0.69]) and similar to each other (difference in LSMs, Day 3, hydrated vs. low-stress low tide: df = 15.7, $t = -0.20$, p = 0.85).

However, the cumulative effect of high-stress low tides over 2 successive days strongly reduced *Saccharina*'s capacity to recover MQY, which dropped to a mean of 60% of pre-experimental values even after 12 h in complete darkness each night (difference in LSMs Day 1 vs. Day 3, df = 17.2, $t = 6.72$, p < 0.0001).

Low-tide conditions also had strong effects on blade wet mass over the course of our simulated tide series (Table 1, wet mass Treatment × Day effect). Blade wet mass did not differ among treatments at the start of the experiment (ANOVA, df = 2,15, $F = 0.06$, p = 0.94). In high-stress low tide blades, loss of function as indicated by the decline in MQY at first light was paralleled by biomass loss (Fig. 3A,B), as damaged tissue, visible as discolored spots at the end of each low tide, sloughed off during simulated high tides. After only 1 d of exposure to experimental conditions, blades in the high-stress low tide treatment had lost, on average, 9% of their original biomass (Fig. 3B, retained biomass LSM [95% CI] = 91% [88–94] of Day 1 values). In contrast, there was no loss of biomass in the hydrated (control) or low-stress low tide treatments (LSM [95% CI] = 101% [97–104] and 100% [96–103] of Day 1 biomass, respectively; Fig. 3B). After a second day of exposure to experimental conditions, blades in the high-stress treatment lost on average another 4% of their original biomass (Tukey-adjusted comparison; p = 0.025, LSM [95% CI] = 4.0% [0.5–7.4]), exacerbating the differences among treatments (Fig. 3B).

DISCUSSION

Large fluctuations in *Saccharina* canopy cover between 1998 and 2012 were tightly linked to the celestially driven 18.6 yr cycle of emersion time. Our decadal-scale data collection provided a perspective that could not have been gained from short-term (1 to 3 yr) studies, especially at the cycle extremes (around 1998 and 2007), when cover changed little between years. Furthermore, repeated observations led to the identification of the specific pattern of change in *Saccharina* cover, a critical step in identifying the cyclical driver. The dramatic change in cover between 1998 (mean = 73.4% cover) and 2007 (mean = 21.5% cover) could easily have been misinterpreted as a stable community regime shift in the direction that would be expected if the system was responding to global climate change. We repeat the call made by Denny & Paine (1998) for caution in the interpretation of data from studies in intertidal systems that compare communities at a single location at 2 time
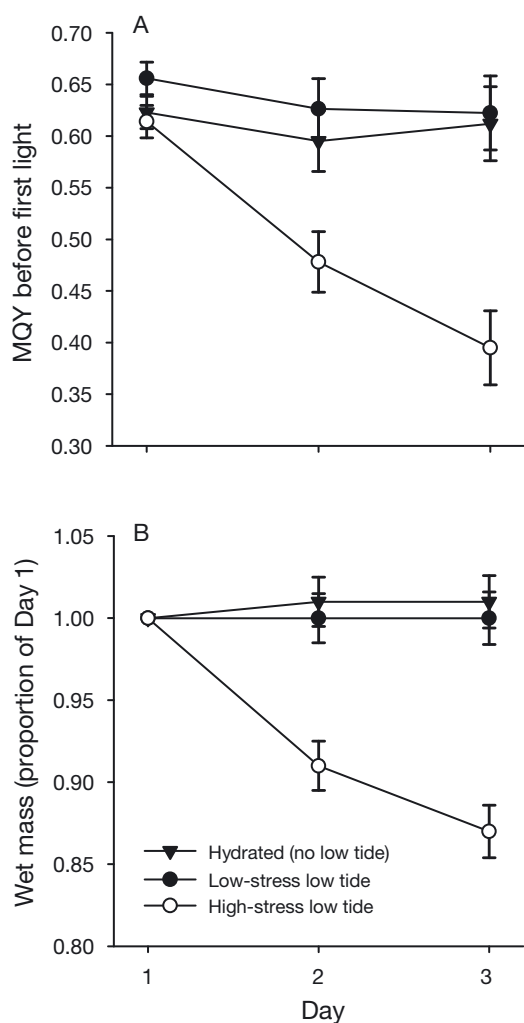

Fig. 3. *Saccharina sessilis* performance (least square means ± SE) over a simulated 2 d low tide series. Blades assigned to low tide treatments experienced simulated low tides after measurements on Day 1 and Day 2. (A) Maximum quantum yield (MQY) before first light. N = 8 thalli on Day 1 and 2, 6 thalli on Day 3. (B) Morning (= pre-low tide) wet mass of fully hydrated thalli expressed as a proportion of pre-experimental values. N = 6 thalli on Day 1 and 2, 4 thalli on Day 3

points to assess the impacts of climate change (e.g. Barry et al. 1995). In this system, an understanding of the emersion time cycle gives us the power to explain and predict temporal patterns of abundance of this ecosystem engineer.

In years with <590 h of emersion time, mean *Saccharina* cover exceeded 68%. The tight fit between our cover data and a curved (rather than a linear) model may indicate that there is an emersion time 'threshold' below which cover remains generally high. Additional insight into the effect of emersion time is provided by examining patterns among our study plots. Because the plots were spread across a large area of rocky shoreline, they naturally varied in the exact timing of emersion and submergence during each low tide, and one would predict that cover would differ slightly between plots which were consistently emersed first and submerged last during low tide (those with the most emersion) and those that were emersed last and submerged first (those with the least emersion). Our data show this predicted pattern.

In contrast, we found no evidence that any other environmental or biological factor was related to inter-annual changes in kelp cover. Wave forces recorded at our field site over the sample period were too low to dislodge a mature *Saccharina* sporophyte from the substratum (Burnaford 2001; see also the Supplement). Although *Saccharina* populations in other areas were reduced following the 1997/1998 El Niño (e.g. Paine & Trimble 2004), water temperatures in all years at our site remained well within the limits of sporophyte survival (−1.5 to 15°C, Lüning & Freshwater 1988) and gametophyte maximum fertility (7 to 12°C, Lüning & Neushul 1978). Although we do not have nutrient measurements at this field site, this region generally has high nutrient levels (Khangaonkar et al. 2012). Furthermore, nitrate concentrations are related to water temperature (Dayton et al. 1999)—which was not related to patterns of kelp cover (Supplement, Fig. S2). Thus, there is no indication that changes in nutrient availability are driving the pattern in kelp cover. Our data strongly indicate that emersion time, driven by celestial mechanics, affects the abundance of this kelp across years in a highly predictable fashion.

Our results align with the prediction made by Denny & Paine (1998) that changes in emersion time will affect the extent to which the physiological tolerance of intertidal organisms is stressed by the environment. In our laboratory study, only 2 short exposures to stressful conditions caused substantially reduced physiological performance and biomass

loss, indicating that *Saccharina* has limited resistance and resilience to low tide stress. We have observed similar patterns of biomass loss and MQY reduction in thalli in the Pile Point, Washington field population, with canopy blades losing more than 8% of their length per day during a low tide series and >50% reduction in MQY values in the 24 h following exposure to stressful low tide conditions (J. L. Burnaford unpubl. data). We suggest that emersion time is such a strong driver of cover for the Washington kelp population in this study because changes in annual emersion time in this region directly translate into changes in the duration of exposure to stressful conditions. In the San Juan Islands, with a mixed semidiurnal tidal cycle, the *Saccharina* zone is emersed once per day. From March to September, emersion occurs around midday, when air temperatures are up to 26°C higher than water temperatures (Burnaford 2004). Calm seas and mid-day low tides result in high body temperatures for ectothermic invertebrates (Helmuth & Hofmann 2001, Helmuth et al. 2002, Burnaford 2004) and a high likelihood of desiccation for macroalgae (Williams & Dethier 2005), resulting in high 'risk' of organismal stress (Mislan et al. 2009). Low-tide exposure from September to March occurs at night, when air temperatures are often lower than water temperatures, and though temperature differentials are smaller (around 13°C; Burnaford 2004), desiccation stresses are still high (Elsberry 2013) due to high winds. For example, winter 2011 monthly average wind speed ranged from 1.9 to 3 m s^{-1} with maxima between 9.94 and 15 m s^{-1} (www.depts. washington.edu/fhl/wx.html). Desiccation alone has been found to impose significant physiological stress on intertidal algae (e.g. Martone et al. 2010), and kelps (Order Laminariales) generally have low tolerance to desiccation (e.g. Dring & Brown 1982). Thus, throughout the year, during low tide, *Saccharina* thalli are likely to experience disruptive stress whereby abiotic conditions that exceed tolerance limits result in damage (Davison & Pearson 1996). Disruptive stress can also affect the performance of an alga after low tide if it is not resilient (Dring & Brown 1982, Bell 1993, Schagerl & Möstl 2011), and these 'hangover' effects can last for up to 10 h after the tide comes in (Dring & Brown 1982, Bell 1993, Peña et al. 1999). Additionally, for some intertidal seaweeds, photosynthetic rates in air are substantially lower than in water (Peña et al. 1999, Williams & Dethier 2005). If this pattern holds for *Saccharina*, longer emersion would result in reduced daily carbon acquisition even for thalli that experience low-stress low tides.

Low tide environmental factors that negatively impact individual performance clearly have consequences for population vital rates, even in the absence of mortality. The large increase in annual emersion time between 1998 and 2007 could have substantially affected *Saccharina* energy acquisition and rates of tissue production, which would affect canopy cover. Disruptive stress and low photosynthetic rates can result in populations of intertidal kelp with small blades and slow growth (Nielsen et al. 2006). *Saccharina* reproductive output is strongly correlated with blade area (Milligan 1998), and loss of biomass and reproductive potential is known to affect population sizes in some intertidal kelps (Thompson et al. 2010). *Saccharina* appears to have limited dispersal (Fox & Swanson 2007), and it is likely that year-to-year variation in abundance is controlled by site-specific factors. Thus limited physiological resistance and resilience of individuals to long emersion times could translate into large effects at the population level.

Our data also show that the fluctuation of shade availability as a result of this cyclical environmental phenomenon has real and predictable consequences in this community. There is a cascading effect of celestial mechanics on the ectotherm *Katharina tunicata*, an important herbivore in this system (Dethier & Duggins 1984, Paine 1984, 2002), which is known to be strongly and positively affected by the availability of shade, especially in warm years (Burnaford 2004). In years with low kelp canopy cover, mean chiton abundance in our study plots could be accurately predicted with knowledge of only 2 factors: mean canopy cover and mean daily maximum air temperature (Fig. 2B). In years with high canopy cover, chitons were less constrained by the availability of shade, and predicting *K. tunicata* abundance was more complicated. As the climate warms, ectothermic organisms are expected to rely more heavily on the use of shaded microhabitats as a means of avoiding stressful thermal conditions (Kearney et al. 2009, Sinervo et al. 2010, Sunday et al. 2011). Our data suggest that there is another aspect to the relationship between ectotherms and shade: not only is the importance of shade likely to increase with increasing temperature, but the effect (or importance) of temperature may in fact be determined by the availability of shade.

Detecting and predicting the response of intertidal systems to climate change depends on our ability to distinguish a response to non-climatic factors from a response to other changing conditions (Wernberg et al. 2012). For individuals living close to their physiological limits, even small changes in the duration of stress can have especially big consequences for individuals and populations. As global temperatures rise, pushing other intertidal species to their physiological limits, we predict that this emersion time cycle will increase in importance globally, affecting other species, populations, and communities. In addition, we suggest that greater consideration of the effects of long time-scale cycles on habitat-modifying species is a critical step in advancing our understanding of all ecological systems.

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