Journal of Experimental Marine Biology and Ecology 449 (2013) 28–35

Contents lists available at ScienceDirect

Journal of Experimental Marine Biology and Ecology

journal homepage: www.elsevier.com/locate/jembe

Early benthic phase mortality of the barnacle *Balanus glandula* is influenced by *Fucus* spp. cover but not by weather-related abiotic conditions

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ARTICLE INFO

Article history:
Received 2 May 2013
Received in revised form 10 August 2013
Accepted 18 August 2013
Available online xxxx

Keywords:
Early postsettlement mortality
Mortality factors
Physiological stress
Population regulation
Recruitment
Weather

ABSTRACT

This study aimed to improve our understanding of the factors that influence mortality of the acorn barnacle, *Balanus glandula*, during the first days after the transition from pelagic to benthic environments. This was accomplished by examining the mortality of barnacle cyprids from settlement to metamorphosis, as well as mortality of early juveniles up to the age of 10 d after metamorphosis. A field survey of *B. glandula* recruitment was conducted from 1 to 23 June 2011 at Wizard Islet in Barkley Sound, British Columbia, Canada. We also documented the range of weather-related abiotic conditions that occurred in the intertidal zone during the recruitment survey. These weather-related abiotic conditions were highly variable during the survey, indicating that each daily cohort of barnacle settlers experienced conditions after settlement that differed from those experienced by the other daily cohorts. Cyprid cohort mortality was high, averaging 52.7 ± 22.7% (SD), and differed greatly among the daily cohorts. Contrary to expectations, cyprid mortality was not significantly influenced by weather-related abiotic conditions. This was likely due to the study being conducted during a La Niña cycle that may have had lower temperature and desiccation levels than are typical for Barkley Sound. Overall, an average of 70.6 ± 16.3% (SD) of all metamorphosed individuals were alive 10 d after metamorphosis. Although the direct cause of high mortality could not be determined, *Fucus* spp. cover negatively influenced the survival of both newly-settled cyprids and juveniles. A decline of fucoid algae populations due to changing climate may therefore result in an increase in barnacle survival through the early benthic phase and may subsequently affect annual variation in barnacle population abundance.

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1. Introduction

Many benthic marine invertebrates, including barnacles, have pelagic larvae that eventually settle into benthic habitats and undergo metamorphosis. The process of settlement to benthic habitats constitutes a dramatic ecological transition to a habitat with very different biotic and abiotic conditions. For those species settling in intertidal habitats, settlement involves the transition from a consistently aquatic habitat to one exposed to aerial conditions for several hours per day (Werner and Gilliam, 1984). During the first few hours and days after settlement, mortality can be severe with most cohorts typically experiencing 60–99% mortality (Gosselin and Qian, 1997; Pedersen et al., 2008), but mortality is also often highly variable among cohorts. For example, two separate studies reported that during the first day after settlement, mortality of the barnacle *Balanus glandula* varied by up to 40% among daily cohorts (Gosselin and Jones, 2010; Gosselin and Qian, 1996), and mortality during the second day varied by up to 20% among daily cohorts (Gosselin and Qian, 1996). Similarly, mortality of *Semibalanus balanoides* cyprids during the 2 d period from settlement to metamorphosis differed by up to 28% among 5 daily cohorts (Jarrett, 2000).

Several factors have been proposed as potential causes of the high levels of mortality during the first few hours and days after settlement. These include dislodgement (Dayton, 1971; Hawkins, 1983), predation (Gosselin and Qian, 1997; Hunt and Scheibling, 1997), poor physiological condition (Jarrett, 2000), and abiotic stress (Denley and Underwood, 1979; Gosselin and Jones, 2010; Gosselin and Qian, 1997; Hunt and Scheibling, 1997). In particular, newly-settled juveniles of some invertebrate species are known to be sensitive to abiotic factors such as heat (oysters, Roegner and Mann, 1995; barnacles, Chan and Williams, 2003), desiccation (whelks, Gosselin and Chia, 1995; barnacles, Shanks, 2009; mussels, Jenewein & Gosselin, 2013), reduced salinity (barnacles, Berger et al., 2006; Thiyagarajan et al., 2007), and both ultraviolet radiation and visible light (tunicates, Hurlbut, 1993; Bingham and Reitzel, 2000; barnacles, Gosselin and Jones, 2010). However, the role of most of these abiotic factors as causes of variation in early benthic phase mortality in the field is not known.

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http://dx.doi.org/10.1016/j.jembe.2013.08.012

Of all benthic invertebrate species, intertidal barnacles are perhaps the most directly exposed to abiotic stress during the early benthic phase; most barnacle species occupy exposed surfaces, and once the cyprid larva has attached itself it cannot move to a more suitable microhabitat if conditions become unfavorable. Several experiments have determined that newly-settled barnacles are unable to survive prolonged periods of high heat (Crisp and Ritz, 1967; Foster, 1969; Shanks, 2009) and desiccation (Foster, 1971). Other studies have reported a conflicting influence of weather conditions on barnacle survivorship, with some suggesting a negative influence of gales (Connell, 1961) and sun exposure (Denley and Underwood, 1979), while others suggest strong winds may in fact promote recruitment by driving cyprids onshore (Hawkins and Hartnoll, 1982). Given that weather conditions at any location can vary considerably from day to day, daily cohorts of settlers in the intertidal zone would differ substantially in the conditions they experience during the first hours and days after settlement. Weather conditions at a given site may therefore be responsible for high early benthic phase mortality in the intertidal zone, but also for the observed high levels of variation in early benthic phase mortality. Understanding the role of weather-related abiotic conditions in controlling post-settlement mortality will help clarify the mechanisms responsible for variation in early benthic phase mortality, and may also provide insight into the sensitivity of this phase of life to the effects of climate change.

In addition to weather effects on newly-settled invertebrates, algal cover may also influence early benthic phase mortality. Cyprid mortality has been attributed to "whiplash" during immersion, in which algal fronds dislodge and sweep cyprids off the rock surface (Grant, 1977; Hancock and Petraitis, 2001; Hawkins, 1983; Jenkins et al., 1999; Leonard, 1999), and Grant (1977) suggested that canopy cover might increase mortality by siltation on small barnacles. On the other hand, macroalgae might also have a positive effect on settler survival by moderating the microclimate and protecting barnacles from environmental stress (Dayton, 1971; Grant, 1977; Hawkins, 1983; Leonard, 1999). The role of algal cover as a mechanism causing variation in barnacle survivorship through the early benthic phase is therefore uncertain.

This study aims to improve our understanding of the factors responsible for variation in mortality during the first days after the transition from pelagic to benthic environments. It builds on the earlier work of Gosselin and Jones (2010), which specifically examined the influence of solar radiation on barnacle settlement and mortality; our study expands this work by determining the influence of multiple factors simultaneously. This was accomplished by studying the intertidal barnacle *B. glandula*, wherein we examined the mortality of cyprids from settlement to metamorphosis as well as the mortality of juveniles up to the age of 10 d after metamorphosis. The specific goals of the study were to: (1) determine the range of weather-related abiotic conditions occurring daily in the upper intertidal zone, a habitat heavily colonized by barnacles in the study area; (2) determine daily settlement and mortality rates of barnacle cyprids and juveniles in the upper intertidal zone; (3) characterize the role of temperature, relative humidity, wind speed, solar radiation, ultraviolet radiation, and rainfall at low tide in controlling variation in mortality of daily cohorts; and (4) determine the importance of cover by the macroalgae *Fucus* spp. in controlling variation in settlement and mortality of barnacle cyprids and juveniles.

2. Methods

2.1. Study site and organism

This field study was conducted from May to August 2011 in Barkley Sound along the west coast of Vancouver Island, British Columbia. Field work was carried out on Wizard Islet (N 48° 51′ 27″, W 125° 09′ 38″), a small islet with moderate exposure to waves (Gosselin and Rehak, 2007) and wind (authors' pers. obs.). The intertidal zone at the field site consists of a long, gently sloping bench that is not shaded by trees or rocky cliffs. The mid-intertidal zone is colonized by 2 species of fucoid algae (*Fucus gardneri* and *Fucus spiralis*), hereon referred to as *Fucus* spp., which can create an extensive canopy of branching fronds over the rock surface. This algal cover is typically greatest in the spring; it is often considerably reduced by the high heat of mid-summer, but may persist all season when summer temperatures are below average (Haring et al., 2002; L. Gosselin, pers. obs.). A dense canopy cover of *Fucus* spp. was present in the mid-intertidal zone in the spring of 2011 and persisted much longer than usual, up to late July. This allowed us to test for the effects of *Fucus* spp. cover on barnacle settlement and early benthic mortality (see Section 2.5 below).

The study organism, the acorn barnacle *B. glandula* Darwin 1854, is well suited to address the goals of this study because new settlers are exposed to abiotic stress daily and for extended periods. *B. glandula* densely colonizes the upper intertidal zone from approximately 2.4 m–3.0 m above mean lower low water (MLLW) (Gosselin and Jones, 2010; authors' pers. obs.). The barnacles are occasionally exposed to air for up to 13 h when the water level at the lower high tide of the day is below the vertical range of distribution of this animal, though typical emersion time is 8–9 h per low tide (Gosselin and Jones, 2010; authors' pers. obs.).

2.2. Weather-related abiotic conditions in the upper intertidal zone

To document the range of weather conditions occurring throughout the summer, a weather station (Davis Instruments Vantage Pro2 Plus Integrated Sensor Suite 6327) was mounted on Wizard Islet approximately 45 m inland from the field site. Wizard Islet was used as a common monitoring site for the present study and also for a separate study of mussel mortality (Jenewein and Gosselin, 2013). From 4 May to 20 August 2011, the weather station recorded the following weather parameters: air temperature, relative humidity (RH), wind speed, ultraviolet radiation, solar radiation, and rainfall. Temperature was also monitored on intertidal rock surfaces using 3 Thermochron® iButton (DS1921G) data loggers, and intertidal RH was monitored using 2 Lascar Electronics (EL-USB-2) data loggers. Weather stations and small button-type temperature data loggers have been used in many studies to monitor ambient weather conditions and intertidal temperatures (e.g., Denny et al., 2006; Jones et al., 2009; Wethey et al., 2011). The intertidal temperature and the RH loggers were placed at 2.75 m above MLLW, which is roughly the midpoint of the vertical distribution of *B. glandula*. The iButton data loggers were secured to the rock surface by placing them in tight-fitting gray mesh bags, which resembled the color of the rock surface, and bolting these to the rock surface. The mesh bags were stiff and kept the iButton loggers in good conductive contact with the rock surface during low tide. These loggers remained in the intertidal zone at all times during the same dates as the weather station. The RH data loggers, however, were only placed in the intertidal zone during daytime low tides on 6 consecutive days in June 2011 because they would be damaged if submerged in water. All devices were set to record data at 15 minute intervals, and data from the weather station and iButtons were downloaded every 2 weeks.

Data for temperature and RH at the intertidal rock surface were used in combination with weather station data to estimate the heat and desiccation conditions experienced by settlers at low tide on bare surfaces during the settlement season, from May to June 2011. Intertidal temperature and RH data were recorded at 15 min intervals over 6 low tides in June 2011. Multiple regression models were then developed using either intertidal temperature or intertidal RH as the response variable and the weather conditions recorded by the weather station as explanatory variables. The best-fit models obtained from multiple regression analysis were developed into predictive equations for intertidal temperature and intertidal RH (Jenewein and Gosselin, 2013).

Although RH values were measured and predicted, vapor pressure deficit (VPD) was used as the final estimate of desiccation because it is considered a better estimate of evaporation potential than RH. RH

values were therefore converted to VPD values using the method outlined by Jenewein and Gosselin (2013).

2.3. Daily settlement, cyprid mortality, and juvenile mortality

To determine patterns of mortality through the early benthic phase, a field survey of *B. glandula* recruitment was conducted in June 2011 at Wizard Islet using the transparency mapping technique (Gosselin and Qian, 1996). This consisted of using a 20× magnifying lens to identify settlers within a quadrat and then marking their position on clear transparency sheets. Within a long horizontal bench of the intertidal zone, 30 sites were selected between 2.5 m and 2.75 m above MLLW. These were selected so that each site was a flat, nearly horizontal surface colonized by *B. glandula*, based on the criteria outlined by Gosselin and Jones (2010). Of the 30 sites, 20 were then randomly chosen for this study using a random number generator. At each site, one 5 cm diameter circular quadrat was established, marked by a screw fastened into a hole drilled in the center of the quadrat. All barnacle cyprids and small (<3 mm diameter) juveniles were then removed from each quadrat using a needle probe; all larger juveniles and adults were left intact. Finally, to determine if cover by the macroalgae *Fucus* spp. affects cyprid settlement and mortality during the early benthic phase, all *Fucus* spp. were removed from within a 12 cm radius of half (10) of the quadrats. From 1 to 23 June 2011, new settlers and their subsequent fate were surveyed daily in each quadrat. A cohort of settlers was considered as all new barnacles (all quadrats pooled together) that had settled since the previous daily survey; thus, the fate of each daily cohort of settlers was monitored separately. New settlers were recorded up to June 13, after which only the fate of existing cohorts was monitored; we therefore monitored a total of 13 daily cohorts during the survey. The fate of individuals was categorized as (a) attached cyprid, (b) dead cyprid, (c) metamorphosed live early juvenile, or (d) metamorphosed dead early juvenile. A cyprid was considered dead if the carapace was shriveled, had been dislodged, or had not completed metamorphosis by the third day after settlement (Gosselin and Jones, 2010). Dead cyprids and early juveniles were then carefully removed using a needle probe.

2.4. Effect of weather-related abiotic conditions on cyprid mortality

To determine if variation in cyprid cohort mortality might be a consequence of variation in weather-related abiotic conditions, the conditions experienced by each cohort were estimated as the sum or average of measurements for each weather variable during low tide periods from 6 am to 8 pm (i.e., during daytime) over 2 consecutive days, starting on the day the cyprid cohort settled. The only exception to this was the calculation of wave height (m), which was based entirely on observations made during high tide (i.e., greater than 2.5 m above MLLW). The 2 d period took into consideration that the majority of cyprids able to complete metamorphosis would have done so within this time (Gosselin and Jones, 2010). Our initial analyses using extreme daily values for each variable did not reveal any significant trends and the models fit poorly (data not shown), therefore we opted to investigate the effect of cumulative exposure to each variable, similar to the study by Gosselin and Jones (2010). Several of the weather variables were highly correlated, which violates most parametric linear model assumptions. To analyze the effect of weather-related abiotic conditions on cyprid cohort mortality, we therefore began by employing principal component analysis (PCA) to eliminate multicollinearity among weather variables. A multiple linear regression was then performed using the uncorrelated PCA factors as explanatory variables and cyprid cohort mortality as the response variable. Prior to all statistical analyses, a modified Freeman and Tukey (1950) arcsine transformation was applied to cohort mortality data to meet the assumptions of normality and homogeneity of variance. Cyprids that settled in bare surface quadrats were analyzed separately from cyprids that settled in the *Fucus* spp. covered quadrats (see below).

2.5. Effect of Fucus cover on settlement and mortality of cyprids and juveniles

Cohort mortality data in quadrats of the same surface type (bare or *Fucus*-covered) were pooled together prior to analyses due to low settlement in some of the quadrats. Randomized complete block analysis of variance (ANOVA) was used to compare mortality between bare surfaces and *Fucus*-covered surfaces using the date of settlement as the blocking factor (n = 13). ANOVA and linear regression models were used to analyze potential causes of variation in mortality between surfaces.

3. Results

3.1. Weather-related abiotic conditions in the upper intertidal zone

Four of the 8 weather parameters recorded by the weather station were significantly related to intertidal temperature: air temperature, RH of air, wind speed, and solar radiation ($F_{4,132} = 356.4$, $R^2 = 0.913$, $n = 137$, $p < 0.001$). Three of these parameters were also significantly related to intertidal RH: air temperature, wind speed, and solar radiation ($F_{3,133} = 393.6$, $R^2 = 0.897$, $n = 137$, $p < 0.001$). The equations developed from these models predicted intertidal values very close to actual measured values, although they slightly underestimated temperatures above 27 °C and RH values below 48%. The predictive equation for temperature described above was used to estimate intertidal rock surface temperature from 9 to 21 June 2011 when iButton loggers failed. After calculation, the predicted values for intertidal RH were converted to VPD.

Maximum mid-intertidal temperature and VPD on bare surfaces varied greatly during the settlement season. Both intertidal temperature and VPD generally increased from May to June, with peak values occurring in early June. The maximum rock surface temperature that occurred during May and June was 28.8 °C and 36.8 °C, respectively (Fig. 1A). VPD levels at the rock surface were also highest on the days

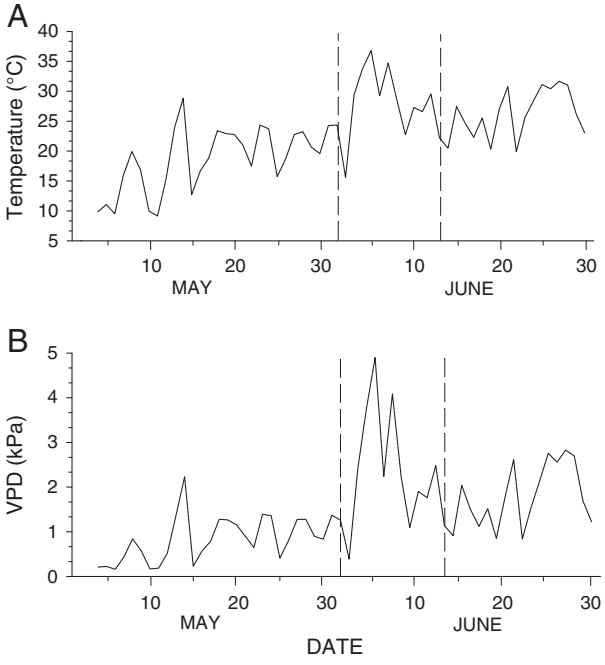

Fig. 1. (A) Predicted maximum daily mid-intertidal temperatures (°C) and (B) predicted maximum daily mid-intertidal VPD at the rock surface for May and June 2011. Vertical dashed lines indicate the start and end of the settlement period monitored during the recruitment survey.

when these maximum temperatures were observed; the maximum VPD level for May was 2.2 kPa and the maximum VPD level for June was 4.9 kPa (Fig. 1B). These peak temperature and VPD levels occurred on clear, sunny days during mid-day low tides.

During the field study of barnacle settlement and mortality, abiotic conditions in the intertidal zone were highly variable from day to day. June 2 and 9 were overcast days with some rainfall (<3 mm). June 3–5 were mainly sunny, whereas the remaining days were generally characterized by overcast mornings becoming sunny by 2 pm. The highest temperatures, VPD levels, solar radiation levels, and UV radiation levels occurred over June 4 and 5 (Fig. 2, cohort 4). Average wind speed generally increased throughout the survey, ranging from 9.1 to 16.7 km/h. Settlers were exposed to aerial conditions for at least 17.5 h over 48 h, up to a maximum total of 24 h in a 48 h period. The maximum duration of a single emersion event during daylight was 13 h. Given the high daily variability of abiotic conditions observed, each cohort of barnacle settlers experienced conditions after settlement that differed from those experienced by other cohorts.

3.2. Daily settlement, cyprid mortality, and juvenile mortality

Cyprid settlement and mortality varied greatly among daily cohorts. Daily monitoring for settlers before and after the survey period suggest the full settlement season for *B. glandula* in 2011 occurred over a period of ~5 weeks, from 23 May to 26 June. The 13 daily cohorts monitored during the settlement survey therefore represented ~43% of the total number of daily cohorts during the 2011 settlement season. A total of 2066 cyprids settled in our 20 quadrats during the survey. Two high-settlement events occurred on June 3 and 10 (Fig. 3A, cohorts 3 and 10), on the days immediately following the only high tide rainfall events in the study period. There was an average of 101.2 ± 83.6 (SD) cyprid settlers per daily cohort (in total within all 20 quadrats), with daily settlement slightly increasing during the latter half of the survey. Cyprid mortality was high, averaging 52.7 ± 22.7% (SD), and differed greatly among the daily cohorts (Fig. 3B). For those cyprids that did complete metamorphosis, an average of 70.6 ± 16.3% (SD) were still alive 10 d after metamorphosis.

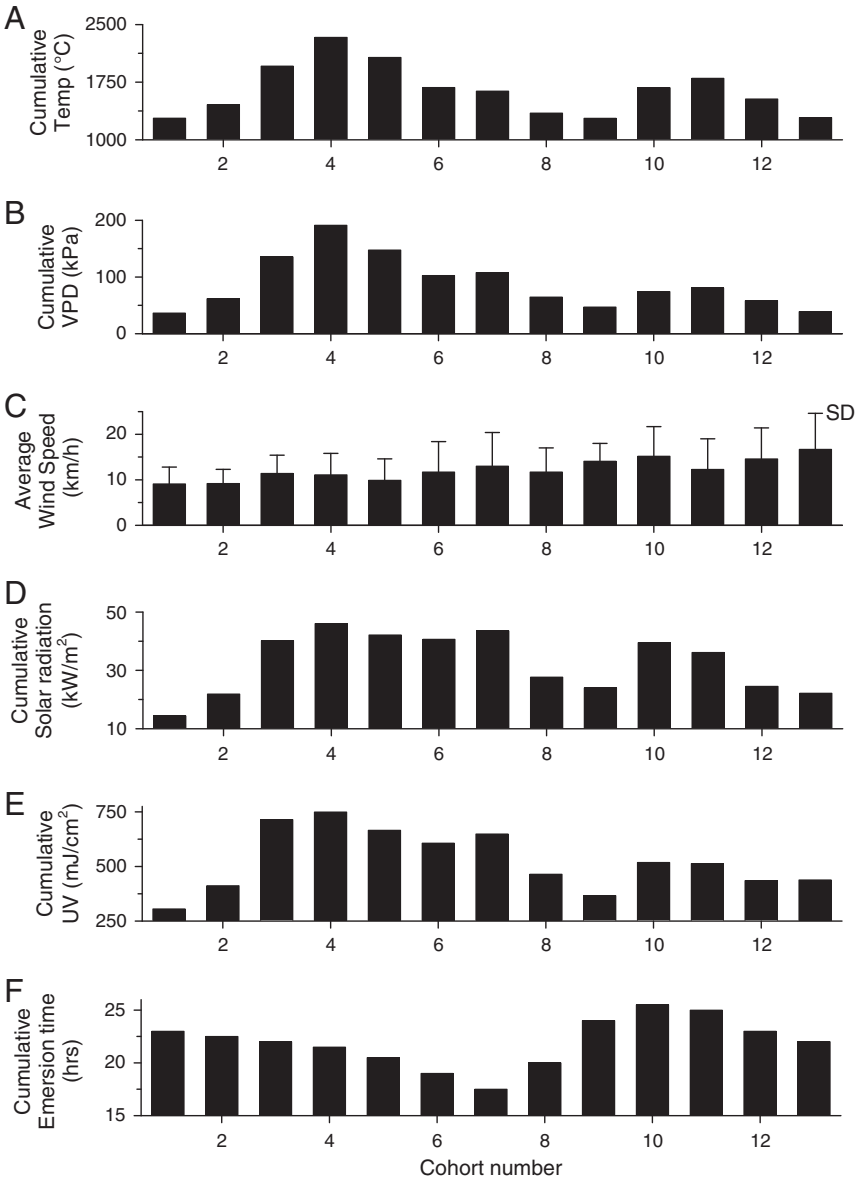

Fig. 2. Weather conditions experienced by each cohort of *Balanus glandula* on bare surfaces during the first 2 d after settlement. (A) Cumulative predicted intertidal temperature (°C). (B) Cumulative predicted intertidal VPD (kPa). (C) Average wind speed (km/h) ± SD. (D) Cumulative solar radiation (kW/m^2). (E) Cumulative UV dose (mJ/cm^2). (F) Total emersion time (h). Cumulative emersion time was determined from tide tables retrieved from the Canadian Hydrographic Service (2011).

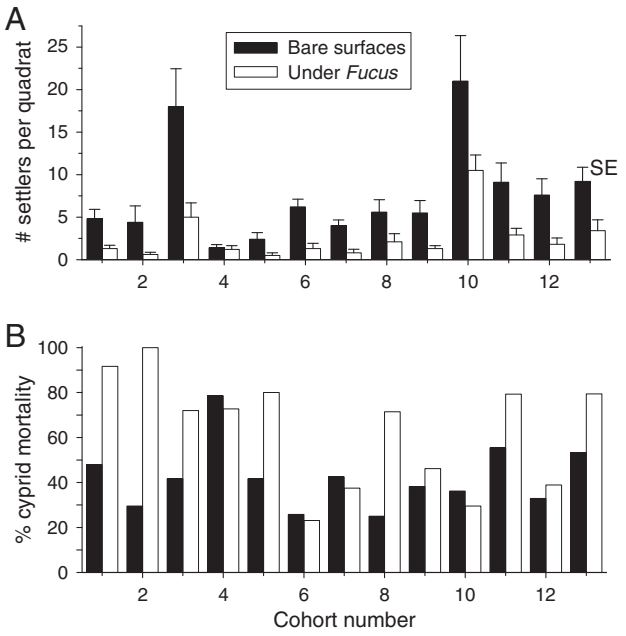

Fig. 3. Comparison of surfaces with and without the cover of *Fucus* spp. A) Number of *Balanus glandula* cyprid settlers in each daily cohort (average ± SE). B) Total mortality of *B. glandula* cyprids in each daily cohort.

3.3. Effect of weather-related abiotic conditions on cyprid mortality

Weather-related abiotic conditions did not significantly influence cyprid mortality on bare surfaces. Principal component analysis (PCA) revealed 3 factors that explained 91.4% of the variance in the weather-related abiotic conditions on bare surfaces (Table 1). Multiple regression then revealed that these 3 factors did not explain a significant proportion of the variation in cyprid mortality on bare surfaces (Table 2). The cyprid cohort that experienced the highest mortality (70.4%), however, also experienced the most stressful weather-related conditions during aerial exposure; in the first 2 d after settlement, these cyprids were exposed to the highest temperature, VPD, solar radiation, and ultraviolet radiation levels observed during the recruitment survey.

Weather-related abiotic conditions may have significantly influenced cyprid mortality under *Fucus* spp. cover. PCA revealed 3 factors that explained 90.3% of the variance in the weather-related abiotic conditions on *Fucus*-covered surfaces (Table 1). Multiple regression revealed that mortality under *Fucus* was significantly influenced by factor 3 ($F_{1,11} = 7.69$, $R^2 = 0.411$, $p = 0.018$), which had a strong negative association with average wind speed (km/h) and average wave height (m) (Table 1). Linear regression further resolved the role of these 2 parameters by revealing that average cyprid mortality was not related to wave height ($F_{1,11} = 1.73$, $R^2 = 0.06$, $p = 0.215$), but was related to average wind speed ($F_{1,11} = 4.65$, $R^2 = 0.23$, $p = 0.054$). High cyprid mortality under *Fucus* was therefore associated with low values of average wind speed.

Table 1
Results of PCA of weather parameters on bare surfaces and under *Fucus* at Wizard Islet. Only factors that explained >10% of the variance and components with loadings >0.2 or <−0.2 are shown, and components are listed in order of descending loadings. Weather parameters: AT = cumulative air temperature (°C); AV = cumulative air VPD (kPa); IT = cumulative intertidal temperature (°C); IV = cumulative intertidal VPD (kPa); W = average wind speed (km/h); SR = cumulative solar radiation (kW/m^2); UV = cumulative UV radiation dose (mJ/cm^2); ET = cumulative emersion time (h); WH = average wave height (m).

Surface		Eigenvalue	% variance explained	Components
Bare surfaces				
Factor	1	3.508	58.5	IV, IT, SR, UV, -ET
	2	1.057	17.6	W, ET, SR, IT
	3	0.915	15.3	ET, -W, -UV, IT
Under *Fucus*				
Factor	1	3.077	44.0	ET, -WT, -UV, -SR, -AV, AT
	2	2.257	32.3	-AT, -AV, -SR, WH, -ET, -UV
	3	0.984	14.1	-W, -WH

Table 2
Multiple regression best-fit model analyzing the influence of PCA factors on cyprid cohort mortality on bare surfaces. β = partial regression coefficient.

Coefficient	β	Estimate	Std. Error	t	p
Intercept	0.986	0.706	0.039	17.992	<0.001
Factor 1	0.392	0.028	0.022	1.278	0.233
Factor 2	0.340	0.043	0.040	1.084	0.307
Factor 3	0.299	0.040	0.043	0.939	0.372

$F_{3,9} = 1.231$, $n = 13$, $R^2 = 0.054$, $p = 0.354$.

3.4. Effect of Fucus cover on settlement and mortality of cyprids and juveniles

Data loggers placed in the intertidal zone during low tide revealed that both temperature and VPD levels were significantly higher on bare surfaces than under *Fucus* spp. cover (ANOVA: temperature: $F_{1,5} = 23.5$, $n = 12$, $p = 0.005$; VPD: $F_{1,5} = 64.1$, $n = 12$, $p < 0.001$). Under *Fucus* spp. cover, average temperature was up to 7.3 °C cooler and average VPD was up to 1.8 kPa lower than on nearby bare surfaces (Fig. 4). Differences between bare and *Fucus*-covered surfaces were greatest on afternoon low tides under clear, sunny weather (6–8 June 2013).

The presence of *Fucus* spp. cover also had a strong effect on cyprid settlement and mortality. Settlement in daily cohorts was significantly higher on bare surfaces than under *Fucus* spp. cover (Random complete block ANOVA: $F_{1,12} = 29.95$, $n = 26$, $p < 0.001$), with settlement being an average of 108.6 ± 34.5% (SD) higher on bare surfaces than under *Fucus* spp. cover (Fig. 3A). In addition, cyprid mortality was significantly higher under *Fucus* spp. cover than on bare surfaces (Random complete blocked ANOVA: $F_{1,12} = 9.34$, $n = 26$, $p = 0.01$), with mortality being an average of 21.0 ± 24.4% (SD) higher under *Fucus* spp. cover than on bare surfaces (Fig. 3B). Analysis of covariance using a model with common slopes and different intercepts revealed that differences in cyprid

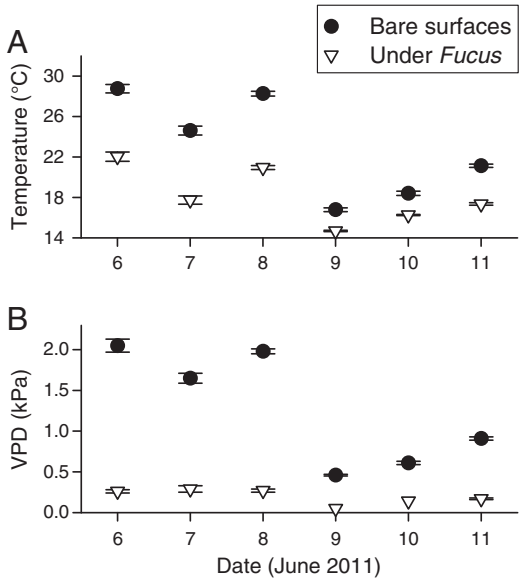

Fig. 4. Comparison of (A) average temperature (°C) ± SE and (B) average VPD (kPa) ± SE between rock surfaces with and without the presence of *Fucus* spp. from 11:30 am–12:30 pm during low tide on 6 of the settlement days in 2011. Weather on June 6–8 was clear and sunny, but was mainly overcast on June 9–11.

mortality between bare and *Fucus*-covered surfaces were not significantly related to temperature ($F_{1,9} = 0.54$, n = 12, p = 0.48) or VPD ($F_{1,9} = 0.29$, n = 12, p = 0.61). Of all the cyprids that died during the recruitment survey, 78.1% of cyprids disappeared from the substrate by day 2 after settlement; the other 21.9% of settlers that died as cyprids remained attached to the substrate up to day 3 after settlement. The number of cyprids that remained attached to the substrate up to day 3 after settlement differed between bare surfaces and *Fucus*-covered surfaces ($\chi^2 = 28.4$, df = 1, n = 580, $p < 0.001$), with 20.2% more cyprids remaining attached up to day 3 after settlement on bare surfaces than on *Fucus*-covered surfaces. Lastly, *Fucus* spp. cover also significantly influenced juvenile survivorship up to 10 d post-metamorphosis (ANOVA: $F_{1,10} = 79.1$, n = 22, $p < 0.001$); survivorship to day 10 (Fig. 5) was 27.6% greater on bare surfaces than under *Fucus* spp. cover.

4. Discussion

4.1. Weather-related abiotic conditions in the upper intertidal zone

Weather-related abiotic conditions varied considerably from day to day during the settlement and early growth period, indicating that each daily cohort experienced distinct levels of stress. A wide range of conditions were experienced by the daily cohorts during the survey; the weather parameters that varied the most during the survey were intertidal temperature, intertidal VPD, solar radiation, and ultraviolet radiation. Predicted intertidal temperature conditions during the settlement and early growth season were mostly within the known tolerance limit of newly-settled barnacles. Temperatures above 33 °C have been demonstrated to cause high mortality of *B. glandula* cyprids in the laboratory (Shanks, 2009); however, maximum surface temperatures above 33 °C occurred during only 3 out of 58 days (0.05%) of the settlement and early growth season at our field site. Heat is therefore unlikely to directly cause cyprid mortality at the study site. Desiccation conditions, however, occasionally exceeded levels expected to cause high cyprid mortality. Foster (1971) experimentally determined that VPD levels above 1.58 kPa (calculated from temperature and RH values provided by the author) can cause 50% mortality of cyprids of another mid-intertidal barnacle, *S. balanoides*, after an average of 6.6 h exposure; daily maximum surface VPD levels exceeding this threshold occurred during 18 out of 58 days (31%) of the settlement season. If *B. glandula* and *S. balanoides* have similar desiccation tolerance thresholds, the desiccation conditions at the study site would be stressful enough to cause frequent cyprid mortality in *B. glandula*. Our results on cyprid mortality (below), however, suggest this is not the case and *B. glandula* may therefore have a desiccation tolerance >1.58 kPa.

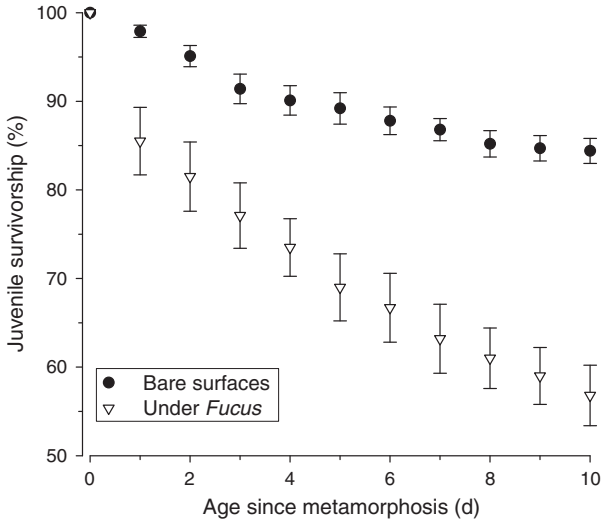

Fig. 5. Survivorship of juvenile *Balanus glandula* up to 10 d post-metamorphosis on bare surfaces and under *Fucus* spp. cover. Data points represent the average proportion alive ±SE.

4.2. Daily settlement, cyprid mortality, and juvenile mortality

The number of cyprids that settled during the survey varied greatly from day to day. Settlement slightly increased during the latter half of the survey, with an average of 101 settlers per daily cohort on bare and *Fucus*-covered quadrats combined. The 2 d of peak settlement occurred on the days immediately following high tide rainfall events, suggesting a possible effect of rainfall on settlement intensity. Reductions in sea surface salinity to values as low as 15 and extending 2 m below the surface following summer storm events have been observed in Barkley Sound (Garza and Robles, 2010), and Thiyagarajan et al. (2007) discovered that temporary exposure to similarly low salinity of 10 caused *Balanus amphitrite* cyprids to metamorphose upon transfer back to full strength seawater at a salinity of 34. The rainfall events in the present study, however, did not result in a large quantity of rain and only lasted up to 4 h; it is not known if the amount of rainfall that occurred in this study could have induced settlement by causing a rapid drop and recovery of salinity near the sea surface during high tide. Onshore winds can also influence settlement by pushing cyprids onshore (Hawkins and Hartnoll, 1982); during these rainfall events the wind direction was primarily onshore (from SW, data not shown), but this did not differ much from the other days of the study. Therefore, it seems unlikely that wind direction influenced the high settlement rates observed on these days.

A substantial proportion of cyprid settlers were unable to survive the transition from pelagic to intertidal habitat. Settled cyprid mortality was high, with an average of 53% mortality per daily cohort. This is consistent with the high cyprid mortality rates obtained in previous recruitment studies (Gosselin and Jones, 2010; Gosselin and Qian, 1996; Jarrett, 2000; Minchinton and Scheibling, 1993; Young, 1991). In addition, daily mortality after metamorphosis was much lower than cyprid mortality, with an average of 71% of all metamorphosed individuals still alive 10 d after metamorphosis. These findings therefore suggest that the transition from pelagic to intertidal habitat is a critical period for survival in barnacles, and may constitute a bottleneck period for recruitment (Gosselin and Qian, 1997).

Finally, we also noted (Jenewein, 2013) that overall survivorship at 10 d post-metamorphosis did not differ significantly between cyprids that completed metamorphosis within 24 h of settlement and those that spent 24–48 h in the intertidal zone before completing metamorphosis. This contrasts with the findings of a number of earlier studies that suggested cyprids delaying metamorphosis have lower post-metamorphic survival due to limited energy reserves (Jarrett and Pechenik, 1997; Pechenik, 2006; Pechenik et al., 1993, 1998; Qiu et al., 1997; Thiyagarajan et al., 2003, 2007).

4.3. Effect of weather-related abiotic conditions on cyprid mortality

Cyprid mortality on bare surfaces was not significantly influenced by the weather-related abiotic conditions experienced during the transition from pelagic to intertidal habitat. The 2 factors hypothesized to cause cyprid mortality, heat and desiccation, did not explain the observed variation in mortality among daily cyprid cohorts. This was surprising given that cyprids on bare surfaces were directly exposed to these factors, which are generally considered major stresses and causes of early benthic phase mortality (Denley and Underwood, 1979; Gosselin and Chia, 1995; Gosselin and Jones, 2010; Somero, 2002). This may have occurred because cyprids preferentially settle in small crevices and depressions (Raimondi, 1988; Savoya and Schwindt, 2010; Wethey, 1986), which can be more shaded and retain moisture longer than raised areas and smooth surfaces (Foster, 1971). In addition, the same high ultraviolet radiation (UVR) levels that influenced cyprid mortality in the study by Gosselin and Jones (2010), >650 mJ/cm^2, did

not correlate with high levels of cyprid mortality in the present study, supporting their conclusion that UVR is not an important factor affecting variation among daily cohorts in cyprid mortality. The cyprid cohort that experienced the highest mortality (70%, cohort 4), however, also experienced higher intertidal temperature, VPD, solar radiation, and UVR within the first 2 d after settlement than the 12 other cyprid cohorts. This suggests that cyprids are tolerant to most of the range of weather-related abiotic conditions experienced in the mid-intertidal zone, but that conditions may occasionally exceed cyprid tolerance limits and cause high mortality. Further, the conditions prevailing at low tide during most of the present study may not have exceeded tolerance limits to cause mortality, but might do so more often in other years if the conditions are more stressful (e.g., in El Niño years).

4.4. Effect of Fucus cover on settlement and mortality of cyprids and juveniles

Fucus spp. cover had a negative impact on cyprid mortality. We had expected that fucoid algae cover would reduce environmental stress and thus might decrease early benthic phase mortality. Our study confirmed that heat and desiccation were much lower under *Fucus* spp. cover. However, mortality under *Fucus* spp. cover was higher, not lower, than on bare surfaces. We also found the proportion of settled cyprids that remained attached to the substrate up to day 3 after settlement without completing metamorphosis to be significantly lower under *Fucus* cover than on bare surfaces, suggesting that more of the cyprids under the macroalgae canopy were being dislodged than on bare surfaces. Our initial hypothesis was that this could occur if wave action caused the algal fronds to beat against the rock surface, thus dislodging cyprids (i.e., algal whiplash) during high tide (Grant, 1977; Hancock and Petraitis, 2001; Hawkins, 1983; Jenkins et al., 1999; Leonard, 1999). However, cyprid mortality was not related to wave action, and thus it is unlikely that increased algal whiplash caused by increased wave action led to increased cyprid mortality. Other factors related to *Fucus* spp. cover were likely responsible for the elevated cyprid mortality in this treatment. For example, intertidal organisms such as limpets and snails that prey upon cyprids or dislodge cyprids from the rock surface while grazing ("bulldozing", Hawkins, 1983) are more active under fucoid algae canopy than on open surfaces (Jernakoff, 1985; Leonard, 1999; Menge, 1978; Miller and Carefoot, 1989) and may have caused greater cyprid mortality under *Fucus* spp. cover than on exposed surfaces. Alternatively, barnacle settlement cues such as the biofilm layer (Crisp, 1974; Thompson et al., 1998) and the presence of conspecifics (Raimondi, 1988; Thompson et al., 2005) on rock surfaces covered by *Fucus* spp. can be weaker than the settlement cues on bare surfaces (Thompson et al., 2005). This may have prevented the cyprids from achieving firm adhesion to the rock surface, increasing the likelihood of cyprids being swept away during the next high tide.

4.5. Interspecific comparison of responses to abiotic stress

Compared to newly-settled mussels examined in a parallel study in Barkley Sound (Jenewein & Gosselin, 2013), newly-settled barnacles in the present study appear to respond similarly to heat but differently to desiccation. The desiccation threshold for newly-settled mussels was frequently exceeded during the recruitment season, suggesting that desiccation on bare surfaces would be lethal to early benthic phase mussels. Barnacle cyprid mortality on bare surfaces, however, was not significantly influenced by desiccation.

The differing response of these 2 co-occurring species to desiccation, with threshold tolerance levels of *B. glandula* estimated at >1.58 kPa (Foster, 1971) and *Mytilus trossulus* at 1.01 kPa (Jenewein & Gosselin, 2013), is likely due to differences in coping mechanisms. Mussels settle within filamentous algae that retain moisture during low tide, which reduces exposure to potentially lethal levels of desiccation (Jenewein & Gosselin, 2013). Barnacle cyprids, on the other hand, experience reduced early survival in structurally complex habitats (i.e., under *Fucus* spp. cover). Rather, cyprids rely on physiological mechanisms (Foster, 1971) and an exoskeleton that are probably more effective at minimizing evaporative water loss than in newly-settled mussels.

Finally, future changes to weather-related abiotic conditions caused by climate shifts (Rodenhuis et al., 2007) could increase the levels of heat and desiccation in the intertidal zone during low tide aerial exposure on the west coast of North America. Although modest increases in heat and desiccation might not directly influence early benthic phase mortality in barnacles, these changes could have indirect effects. Specifically, additional stress may lead to a decrease in the population of fucoid algae. Several studies suggest that the growth and survival of juvenile intertidal seaweeds are related to heat and desiccation stress experienced during emersion (Brawley and Johnson, 1991; Lamote et al., 2007, 2012), and that abundance of fucoid algae is sensitive to changes in temperature regime, timing of tides, and wave action (Hawkins et al., 2008, 2009; Helmuth et al., 2006). A recent study reported some dominant populations of intertidal algae on the California coast, including those in the genus *Fucus*, have declined by over 50% in the 10 y following ocean warming (Schiel et al., 2004); this suggests that future increases in heat and desiccation may reduce the abundance and limit the distribution of fucoid algae populations on the west coast of North America (Haring et al., 2002; Martinez et al., 2012). The negative influence of *Fucus* spp. cover on the survival of cyprid and early juvenile barnacles revealed in the present study suggests that future declines in fucoid and other algal populations may result in an increase in barnacle survival through the early benthic phase and could potentially increase barnacle population abundance or reduce annual variation in population abundance.

Acknowledgments

We would like to thank the director and staff of the Bamfield Marine Sciences Centre for providing facilities, equipment and support during this study. The present study was conducted in compliance with the research ethics requirements of the Animal Care Committee of Thompson Rivers University. This work was supported by a NSERC Strategic Project grant to LAG, a Robert Frazier Memorial Fellowship from Thompson Rivers University to BTJ, and a John Boom Memorial Scholarship from the Bamfield Marine Sciences Centre to BTJ. **[ST]**

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