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Effects of Habitat and Temperature on Reproductive Success of Fucus distichus in Central California

Acy E. Wood

EFFECTS OF HABITAT AND TEMPERATURE ON REPRODUCTIVE SUCCESS OF
***FUCUS DISTICHUS* IN CENTRAL CALIFORNIA**

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A Thesis

Presented to the

Faculty of

Moss Landing Marine Laboratories

California State University Monterey Bay

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In Partial Fulfillment

of the Requirements for the Degree

Master of Science

In

Marine Science

————————————

By

Acy E. Wood

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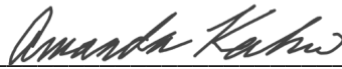The Undersigned Faculty Committee Approves the

Thesis of Acy E. Wood:

EFFECTS OF HABITAT AND TEMPERATURE ON REPRODUCTIVE SUCCESS OF
***FUCUS DISTICHUS* IN CENTRAL CALIFORNIA**

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DEDICATION

This thesis is dedicated to the network of people who stood by me throughout the tribulations of this project. The Moss and SERC communities helped remind me why we get up at 3AM to slog through mud and discover a finish line. My family and friends kept me alive and pulled me to my feet after stumbling over and over. I will be forever grateful to all of you. This work would not be completed without your insight and kindness.

Abstract

Effects of Habitat and Temperature on Reproductive Success of *Fucus distichus* in Central California
by
Acy E. Wood
Master of Science in Marine Science
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Rapid changes in environmental climate trends have influenced the temperature and salinity of marine ecosystems across the globe. This ongoing shift is predicted to have implications for the reproductive success of species that are integral to both the generation and identity of their ecosystem; namely, foundation species. Coastal marine foundation species, such as macroalgae, are expected to experience drastic environmental changes. Of particular interest to central Californian shores is the foundation species *Fucus distichus* (Family Fucaceae). This alga serves as a community builder residing in the upper intertidal throughout the Northern Hemisphere. While *F. distichus* residing within San Francisco Bay (SFB) have been determined to be genetically well-mixed, populations within the Bay are currently declining, so a better understanding of what affects their reproductive success is needed. This research explored how the reproductive success of *F. distichus* in SFB and along nearby open coast is influenced by habitat (i.e., sites that vary in their location and salinity), temperature, and the interaction between these factors to better understand how the reproductive success of coastal marine foundation species may respond to predicted future climate regimes.

Samples of *F. distichus* were collected from three habitat types (i.e., Outer Coast, Inner Coast Full-Salinity, and Inner Coast Low-Salinity) with three haphazardly-selected replicate fields per habitat over the course of 7 sampling cycles. Randomly-selected receptacles from the *F. distichus* samples were processed according to standardized protocols. They were then randomly sorted and incubated in two different temperature treatments that resemble current (12°C) and predicted (15°C) environmental conditions in SFB and nearby open coastline. For each cycle, the total number of eggs and embryos released by each receptacle (defined as reproductive output) along with the fertilization success of embryos was observed after 96 hours. The resulting data were analyzed using a series of three-way ANOVAs that investigated the effects of temperature, habitat type, and sampling cycle, and their multi-way interactions.

Both reproductive output and fertilization success were determined to have significant three-way interactions between the three factors analyzed. Reproductive output primarily was driven by a relationship between temperature and habitat, whereas fertilization success was primarily influenced by relationships involving sample cycle. In general, receptacles in the 15°C group experienced greater reproductive output and fertilization success than those in the 12°C group. Additionally, individuals from more saline habitat types experienced higher reproductive output and fertilization success than those from fresher conditions. These findings align with previous hypotheses that *F. distichus* may respond favorably to warmer future conditions. Future research should add more *F. distichus* populations or survey related genera to determine how predicted environmental conditions may influence reproductive success of coastal marine foundation species.

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Introduction

Rapid intensification of anthropogenic climate change is triggering substantial shifts in many of Earth's ecosystems (IPCC 2014). For the last century, the world has experienced climate-related increases in environmental temperature, intensification of storms, and proliferation of heatwaves (Harley et al., 2006; Lejeusne et al., 2010; Vergés et al., 2014; Hughes et al., 2017). Investigations into the effects of climate change have primarily focused on terrestrial ecosystems, while relatively few have detailed the impacts on marine ecosystems and their communities (Hoegh-Guldberg & Bruno, 2010; Thomson et al., 2015). These rapid changes have significantly altered oceanic conditions (Harley et al., 2006; Abraham et al., 2013; Stuart Chapin & Díaz, 2020). For example, the ocean has served as a heat reservoir, and increasing sea surface temperatures have resulted in increased ocean stratification (Abraham et al., 2013; Stuart Chapin & Díaz, 2020; IPCC 2014). Likewise, the ocean acts as a CO_2 store absorbing increased amounts of anthropogenically generated CO_2, resulting in progressively higher amounts of ocean acidification (Harley et al., 2006; Gaylord et al., 2011; Lopes et al., 2020; IPCC 2014). In addition to changes in sea water composition, marine ecosystems have also experienced an increased frequency of warming events with mounting evidence characterizing future warming events as more intense and longer lasting (Ready et al., 2010; Thomson et al., 2015; Smale et al., 2019; Jacox et al., 2022; Petsas et al., 2022). Accordingly, these shifting environmental conditions threaten to disrupt marine ecosystems globally (Harley et al., 2006; Lejeusne et al., 2010; Abraham et al., 2013; IPCC 2014; Stuart Chapin & Díaz, 2020; Braun de Torrez et al., 2021).

Shifting oceanic conditions are jeopardizing marine biodiversity and marine ecosystems all over the world (Harley et al., 2006; Tribbia & Moser, 2008; Stuart Chapin & Díaz, 2020). For

instance, the shrinking volume of the world's sea ice is resulting in heavy modification of ecosystems that have adapted to require the existence of sea ice (Perovich & Richter-Menge, 2015; Fernández-Méndez et al., 2018). Along with changing sea level, coastal communities are experiencing major shifts in species ranges as climate-related factors alter environmental conditions (Lonhart et al., 2019; Beas-Luna et al., 2020; Cimino et al., 2021; McPherson et al., 2021). Ecological communities commonly associated with southern California coasts are being observed progressively further north as species ranges shift poleward with ocean warming (Lonhart et al., 2019; Beas-Luna et al., 2020; Cimino et al., 2021). Coastal ecosystems such as kelp forests, both subtidal and intertidal, are particularly at risk as the life histories of critical community members are interrupted by shifting environments (Harley et al., 2006; Hughes et al., 2017; Stuart Chapin & Díaz, 2020).

Certain species that are common in their ecosystems are integral for both the generation and identity of an ecosystem (Ellison, 2019). These species, which account for the majority of the biomass in their communities and disproportionately affect the ecosystems they reside in, are referred to as foundation species (Dayton, 1972; Thomson et al., 2015; Ellison, 2019) since they constitute the foundation of the system upon which community interactions are formed (Stachowicz, 2001). Due to their central role in the provision habitat and energy to support the structure and function of ecosystems, if a foundation species experiences changes in physiology or the geographic extent of their species range, their dependent ecosystems often experience drastic shifts (Bulleri et al., 2016). The concept of foundation species was first identified in deep-water benthic environments (Dayton, 1972) and they are now recognized to occur in ecosystems worldwide (Bruno & Bertness, 2000; Bulleri et al., 2016; Thomsen et al., 2018). Foundation species are usually situated at low trophic levels (i.e., kelps, mangroves, seagrass, corals,

sponges, etc.) that operate in central roles to the maintenance of their communities (Ellison et al., 2005; Angelini et al., 2011; Ellison, 2019). Specifically, in addition to their contributions to food webs, their non-trophic interactions serve a multitude of roles such as stabilizing shorelines (Orth et al., 2006; Koch et al., 2009), filtering water (Altieri & Witman, 2006), providing nursery habitat (Boesch & Turner, 1984; Carr, 1989; Beck et al., 2001), and carbon sequestration (Ellison et al., 2005). Thus, foundation species characterize and modify their environment by creating physical structures and modulating ecosystem processes independent of trophic interactions (Baiser et al., 2013). For example, forests are defined by the dense presence of trees that provide shelter for community inhabitants, alter temperature and light levels beneath the canopy by casting shade, and modify the soil through nutrient uptake (Stachowicz, 2001). Through these non-trophic interactions, ecosystems can support extensive diversity that would collapse if the foundation species was suddenly removed (Ellison et al., 2005).

Previous research has defined a foundation species as "… a species (or group of functionally similar taxa) that dominates an assemblage numerically and in overall size (usually mass), determines the diversity of associated taxa through non-trophic interactions, and modulates fluxes of nutrients and energy at multiple control points in the ecosystem it defines" (Ellison, 2019). To qualify as a foundation species, a species must meet three criteria (Angelini et al., 2011; Ellison, 2019). First, the species must be common in the environment and dominate the biomass. Second, they must be at or near the base of the ecological web that characterizes the environment. Third, the majority of the interactions associated with the putative foundation species must be non-trophic, such as providing structural support to other species, altering the environment to facilitate other species, or mediating fluxes of energy or nutrients. In other words, the foundation species must be common and must interact with many members of the

community outside of trophic interactions (Ellison et al., 2005). Seaweeds also are common foundation species in intertidal and subtidal habitats (Scrosati, 2016; Weitzman et al., 2021). Like terrestrial plants, seaweeds commonly engineer their environments and can serve as the foundation for complex ecosystems (Daleo et al., 2006; Bellgrove et al., 2017; Pocklington et al., 2018; Shelamoff et al., 2019).

The factors that allow marine foundation species to serve their roles also makes them vulnerable to stressors affected by climate change (Miner et al., 2021). Global sea-level rise is predicted to cause entire coastal ecosystems, such as seagrass meadows and kelp forests, to shift as their foundation species redistribute to their optimal depths and conditions (Braun de Torrez et al., 2021). Intertidal ecosystems are predicted to undergo drastic shifts as sea level rise and temperature increases (Laughinghouse et al., 2015; Jueterbock et al., 2016). Changes in temperature, sea level, and salinity threaten to redefine coastlines and consequently, the organisms found there. The inhabitants of the intertidal are commonly existing at environmental tolerance limits, such as thermal or wave energy thresholds, and even a slight shift in an environmental condition can drive significant change in life history or range (Harley et al., 2012). For example, a warming planet is predicted to affect salinity throughout the oceans through changes to evaporation rates (IPCC 2014). Depending on the location, this can affect local conditions in different ways. If evaporation exceeds precipitation, then already saline conditions will become more saline through this process. The opposite is also a risk; if precipitation exceeds evaporation, then local conditions will get fresher (IPCC 2014). Phenomena like this are a threat to any organisms that rely on a certain local salinity to persist, such as stenohaline organisms that reside in environments that already experience dynamic salinity ranges (Cloern & Jassby, 2012; Harley et al., 2012; Whitney et al., 2016). In particular,

the impact of climate change on key intertidal organisms, such as foundation species found along coastlines, is of concern (Harley et al., 2012; Lonhart et al., 2019; Beas-Luna et al., 2020; Cimino et al., 2021).

The reproductive output of foundation species may vary as environmental conditions shift. Adults may need to reallocate energy that would typically go towards reproductive efforts (e.g., egg and sperm production, preparation of environment, or migration) to surviving their new environmental conditions (Johansson et al., 2014; Storch et al., 2014). Phenological shifts with climate change, such as the timing of the spring transition, have led to asynchronous mismatches in organisms that rely on cues such as daylength, light levels, and temperature to trigger reproduction. For instance, some photosynthesizers receive environmental cues triggering earlier reproduction with warming temperatures, leading to reduced reproductive performance as light and temperature requirements are different than what their offspring require (de Bettignies et al., 2018). Increased marine heatwaves may also coincide with reproductive windows for organisms that are sensitive to temperature extremes, due to a narrow thermal limit for their reproductive period (Nievola et al., 2017). As temperatures increase, such organisms are at higher risk for reproductive failure (Grazer & Martin, 2012; Nievola et al., 2017; Scrosati, 2017). Changes in reproductive output can shift population size over time (Sibly & Hone, 2002; Westerbom et al., 2021) as gradual changes in reproductive conditions can result in altered rates of recruitment within a population (Ibáñez et al., 2007; Matías & Jump, 2014).

The effects of climate change on recruitment are not universal, as a population in one area may respond to shifting conditions differently than one in a different area, if they are locally adapted to specific environmental conditions (Matías & Jump, 2014). A subpopulation's recruitment must match or exceed its death rate to prevent population loss or extinction (Harley

et al., 2012). This principle is of particular importance for foundation species (Ellison et al., 2005; Ellison, 2019), given their critical role within ecosystems. A decline in recruitment and resulting decrease in population size or density affects the whole community that is supported by the foundation species (Ellison et al., 2005). It is thus vital to investigate how reproductive output of foundation species will be affected by climate change to understand how whole ecosystems will transform in the coming decades (Ellison et al., 2005; Ibáñez et al., 2007; Ellison, 2019).

Intertidal seaweeds are excellent subjects to investigate potential effects of climate change on reproductive output of foundation species. Their distribution on shorelines makes them ideal for field work and laboratory experiments. Many seaweeds meet the criteria for foundation species and ameliorate the stressful conditions of the intertidal zone (Eckman et al., 1989; Dudgeon & Petraitis, 2005; Jueterbock et al., 2016; Scrosati, 2017). In particular, intertidal members of the Order Fucales make excellent candidates for study; there is a well-established library of work that has investigated numerous roles they serve within their ecosystems (Dudgeon & Petraitis, 2005; Coleman & Wernberg, 2017; Scrosati, 2017; Thomsen & South, 2019). The order Fucales (i.e., fucoids) contains eight families (Ascoseiraceae, Cystoseiraceae, Durvillaeaceae, Fucaceae, Hormosiraceae, Himanthaliaceae, Sargassaceae, and Seirococcaceae), making fucoids one of the largest and most diverse orders within the brown algal class, Phaeophyceae (Cho et al., 2006). For example, fucoids create three dimensional, heterogenous structures that diversify the environments they grow in (Edelstein & McLachlan, 1975; Ang, 1991; Coleman & Wernberg, 2017). Fucoids inhabiting the intertidal provide shade and shelter to organisms that would otherwise be exposed to desiccation and predators (Scrosati, 2017; Thomsen & South, 2019). This combination of the important role in engineering ecosystems,

extensive history of research into their life history, demography, and ecology, and ease of accessibility make them ideal candidates to explore the effects of climate change on coastal ecosystems.

Fucoid reproduction begins within structures called conceptacles, flask-like cavities that house the production of male antheridia and female oogonia (Edelstein & McLachlan, 1975; Feis, 2010; Baweja et al., 2016). Conceptacles can either be dioecious, with separate conceptacles developing either antheridia or oogonia, or monoecious, developing both within the same structure (Pearson & Brawley, 1996; Coleman & Brawley, 2005; Feis, 2010). Conceptacles are usually limited to the tips of branches or on inflated tip structures referred to as receptacles, although in some species conceptacles can be scattered throughout the thallus (Pearson & Brawley, 1996; Baweja et al., 2016). Mature antheridia and oogonia are shed as conceptacles swell with mucilage, such as when receptacles are exposed to low water energy environments during low tides or within pools of water (Edelstein & McLachlan, 1975; Pearson & Brawley, 1996; Baweja et al., 2016). Shedding during periods of minimal water movement reduces gamete dilution and increases fertilization success (Pearson & Brawley, 1996; Balina et al., 2018). Once shed, the antheridia and oogonia burst, releasing spermatozoids and eggs into the water (Feis, 2010). Eggs release a pheromone to attract spermatozoids, which then fuse with eggs to produce a zygote (Pollock, 1970; Lee, 2008). Once formed, zygotes settle onto nearby surfaces and develop into germlings (Ang, 1991; Edelstein & McLachlan, 1975; Pearson & Brawley, 1996). Typically, individuals will take 2-3 years to sexually mature. The strategy of synchronizing fertilization with events of low water movement allows established populations of fucoids to reliably recruit new generations to the local area over time (Ang, 1991; Feis, 2010). Shifting global conditions are predicted to allow select fucoid populations to expand their range as

environmental conditions create new potential habitat that fucoids are 'pre-adapted' to exploit (Weitzman et al., 2021). Intertidal fucoids, especially upper intertidal ones, are adept at managing heat related stress (Sideman & Mathieson, 1983; Baweja et al., 2016). They can withstand extended periods of heat exposure and desiccation during low tide, then return to normal functioning when resubmerged in seawater (Sideman & Mathieson, 1983; Baweja et al., 2016). As conditions warm, fucoids are predicted to experience a poleward expansion as new coastlines become suitable for their survival (Harley et al., 2012).

Numerous intertidal and subtidal fucoids have been studied for their roles as foundation species within their communities (Dudgeon & Petraitis, 2005; Coleman & Wernberg, 2017; Scrosati, 2017; Thomsen & South, 2019). They are known to vary across geospatial sites with the same species exhibiting local adaptations just meters apart from sibling populations (Wolcott, 2007; Whitaker et al., 2017). Previous studies have established that egg release of *Fucus distichus* occurs during daytime low tides throughout the year (Sideman & Mathieson, 1983; Pearson & Brawley, 1996; Coleman & Brawley, 2005). Optimal reproductive output occurs during late spring and early to mid-autumn, with early summer experiencing a drop in output followed by an increase in late summer (Sideman & Mathieson, 1983; Ang, 1991; Pearson & Brawley, 1996). Due to their role as foundation species for shorelines around the world, investigations into how fucoids may respond to predicted climate regimes are critical to predict climate change related impacts along coastlines (Harley et al., 2006; Tribbia & Moser, 2008). Prior investigations have examined how climate-related environmental changes will impact fucoidan life cycles and history. For example, shifting conditions are predicted to result in range expansions for multiple fucoid species (Laughinghouse et al., 2015; Jueterbock et al., 2016; Kashutin et al., 2019), as fucoids exhibit higher rates of reproductive output at higher

temperatures than those observed in the field, suggesting that fucoids are 'preadapted' to cope with increased temperatures (Smolina et al., 2016). This study aims to further understand and define the reproductive output and fertilization success of fucoid gametes and zygotes under estimated climate shifts by focusing on changes in temperature and salinity across different seasons, and geographic differences caused by the intensity of wave exposure.

San Francisco Bay (SFB) is home to a well-studied fucoid, *Fucus distichus* (Whitaker et al., 2017). Previous investigations have explored how the range of *F. distichus* may expand as global conditions shift, although it remains unclear if those same shifting conditions will affect reproductive output (Jueterbock et al., 2016). Changes in local salinity initiate gamete release for *F. distichus*, so these potential changes in local salinity raise important reproductive questions. Due to their foundational role, investigation of *F. distichus* reproductive output is needed to properly manage this critical community member of SFB shores (Visser, 2008; Coleman & Wernberg, 2017; Spinks et al., 2021). Populations of *F. distichus* within SFB are distinct from populations found throughout the North Pacific, exhibiting low genetic diversity within SFB compared to the non-SFB populations and occur in a variety of habitat types. The morphology of adult *F. distichus* can present as phenotypically plastic and differ in response to local environmental conditions. These factors make SFB an ideal system to study the effects and possible interactions of temperature and the salinity of rearing conditions on reproductive output of a foundation species (Giesel, 1976; Greene et al., 2013; Whitaker et al., 2017). Since the SFB populations are genetically similar, any observed differences between the two should be a phenotypically-plastic response to local environmental conditions. This study will use a series of field surveys and laboratory experiments to investigate how temperature and local environment affect reproductive success of *F. distichus* in SFB throughout one reproductive season, which

will improve our understanding of the effect of climate change on population dynamics of this foundation species in central California.

Objectives

The overarching goal of this project is to explore intra-seasonal patterns of reproductive output of *Fucus distichus* in San Francisco Bay and nearby open coastline. This work addresses three specific objectives:

1. To examine differences in reproductive output of *F. distichus* (a) *within* and (b) *between* three habitats found along the coast of central California, i.e. Outer Coast (OC), Inner Coast Full-Salinity (ICFS), Inner Coast Low-Salinity (ICLS).

2. To examine the influence of temperature on reproductive output of central California *F. distichus* by assessing fertilization rates and embryo survival in controlled rearing experiments

3. To explore the interaction between habitat and temperature on the reproductive output of central California *F. distichus* by assessing fertilization rates and embryo survival in controlled rearing experiments.

Due to their genetic and morphological similarities, it is hypothesized that ICFS and ICLS would display similar amounts of reproductive output. Alternatively, ICLS could display the lowest amount of reproductive output due to growing in less saline water. Since the populations found in the OC have distinct morphology presenting with wider, rounded receptacles at the end of thick, strap-like stipes and are likely less genetically similar, they will likely respond

differently. In contrast, it is hypothesized that the OC and the ICFS have similar levels of reproductive output due to being raised in similar saline conditions. In addition, it is hypothesized that sites within habitat type would display similar rates of reproductive output. The locations of the sites within habitat are not far from each other and experience similar environmental conditions, and for the ICFS and ICLS sites, are known to be genetically similar to each other. Therefore, similar amounts of reproductive output are likely to be observed.

Fucus distichus is already predicted to experience an expanded range as climate change warms the environment (Jueterbock et al., 2016). For this reason, individuals cultured at a projected higher temperature of 15°C should release higher number of embryos and eggs released than a cooler current environmental temperature of 12°C, regardless of habitat type. Less has been explored about the competency of embryos at higher temperatures, although it is predicted that they are tolerant of warming due to *F. distichus* being adapted to growing in the upper intertidal, where they can experience long periods of exposure to high temperatures. Therefore, it is predicted that the embryos cultured at 15°C would have similar fertilization success to those cultured at 12°C. Lastly, it is hypothesized that if there is an effect of temperature on reproductive output, it will become more apparent as culturing time passes. If there is a difference in the number of embryos released or percent fertile, then over time, the differences should be amplified as each treatment results in more embryo release or survival, resulting in progressively larger gaps between the two treatments.

Materials and Methods

Study Sites

Three different habitat types (Outer Coast [OC], Inner Coast Full-Salinity [ICFS], and Inner Coast Low-Salinity [ICLS]) were studied, with three (3) haphazardly selected replicate

field sites per habitat (9 field sites total; Figure 1). Field sites were selected from initial assessments identifying existing populations of *Fucus distichus* and from sites of relevant scientific and ecological history. All 9 sites were sampled within a single tidal cycle. Potential sites that required extended time to access were dismissed. The site sampling route began at Davenport, California and concluded at San Quentin, California (Figure 1). The OC sites (Davenport Crack, Whaler's Cove Beach, and Pigeon Point Bluff) all have established *F. distichus* populations located throughout the upper intertidal that are exposed to full marine conditions along the outer coast. The ICFS sites (Marina Green Degaussing Station, Pier 94 Wetlands, and Point San Bruno Park) all have bands of *F. distichus* in the upper intertidal, are exposed to salinity conditions the same or close to the OC sites, and are located within San Francisco Bay (Table 1). The ICLS sites (Coyote Point, San Quentin Beach, and John & Jean Starkweather Beach) have sparse populations of *F. distichus* throughout the upper intertidal and have been exposed to less saline conditions (3-6 psu lower on average) than either the OC sites or the ICFS sites, and are located within San Francisco Bay (Table 1). The OC sites face south to southwest while the ICFS and ICLS sites face north to northeast.

Sample Collection

Collections were conducted every 2 weeks, weather conditions permitting, from June 2021 to September 2021 for a total of 7 sampling cycles. All 9 sites were sampled in the following order: (1) Davenport Crack, (2) Whaler's Cove Beach, (3), Pigeon Point Bluff, (4) Coyote Point, (5) Point San Bruno Park, (6) Pier 94 Wetlands, (7) Marina Green Degaussing Station, (8) San Quentin Beach, (9) John & Jean Starkweather Beach. This order was chosen to allow a single vehicle to be able to depart MLML, sample all sites and return to MLML within a single tidal cycle.

Receptacles were collected from 10 *Fucus distichus* individuals per field site for a total of 90 individuals per cycle. A 10-m transect was run parallel to the shore through each population. PVC quadrats (0.5 m^2) were placed at 10 predetermined randomly-selected points along transects. An individual from each quadrat was randomly selected by counting the number of individuals within the quadrat that possess 4+ receptacles, assigning numbers to them, then randomly generating selection numbers. The selected individual's receptacles were collected and placed into a plastic bag for a total of 10 bags per site (McLachlan et al., 1971; Balina et al., 2018). All bags from a single site were wrapped in seawater-soaked hand towels, then stored within a container labeled with the site name. Site containers were placed in a cooler for transportation (Fulcher & McCully, 1969).

Sample Processing

After sample collection was concluded for all 9 sites, receptacles were prepared for culturing. All receptacles were separately washed by hand under cold running freshwater to remove invertebrates and other algae attached to the thalli (Jaffe & Neuscheler, 1969; Quatrano, 1980; Sideman & Mathieson, 1983; Steen & Rueness, 2004; Balina et al., 2018). Once washed, individuals were blotted dry with paper towels (Quatrano, 1980; Balina et al., 2018). Four (4) receptacles per individual were chosen at random to be excised and placed into a plastic petri dish (Kloareg & Quatrano, 1987; Tarakhovskaya et al., 2012; Balina et al., 2018). The remaining receptacles were discarded. This was repeated until 4 receptacles were prepared for each of the 90 *F. distichus* individuals, for a total of 360 receptacles within 90 petri dishes (i.e., 10 individuals per each of 9 replicate field sites). The 90 dishes were left to air dry further for 30 minutes (Balina et al., 2018). Twenty-five (25) mL of sterilized 20-μm sand-filtered seawater was added to each dish using a glass pipette, then covered with a petri dish cover. The

receptacles were partially submerged with one half under water and the other half left exposed to air for 2 hours (Jaffe & Neuscheler, 1969; Quatrano, 1980; Ang, 1991; Pearson & Brawley, 1996; Balina et al., 2018). Five of the ten individuals from each field site were randomly sorted into either a 12°C or a 15°C treatment, for a total of 45 individuals per temperature treatment (i.e., 5 individuals per each of 9 replicate field sites per each of 2 temperature treatments). 12°C was a reasonable approximation of local upper intertidal conditions throughout the range of sites, while 15°C was chosen as an elevated temperature based off predicted IPCC modeling of what SFB environmental conditions will be by the end of the century (Reay et al., 2007; Cloern & Jassby, 2012; Vaz et al., 2015). Cultures were grown in two Haier thermoelectric incubators (Model HVTECO6ABS/HVTECO8ABS), which have a programable temperature range from 10-19° C. Each incubator was equipped with LED lights (MingDak LED Aquarium Light, Model# B00X84LMHK) set to a 16-hour light/8-hour dark light cycle (McLachlan et al., 1971; Ang, 1991; Steen & Rueness, 2004). The 5 dishes from each site were randomly stacked and placed into an incubator set to their treatment temperature. Placement of the site-stacks was randomized each cycle.

Reproductive Output

Embryo and egg release can begin as early as 30 minutes after partial submergence and last for multiple days (McLachlan et al., 1971; Quatrano, 1980; Balina et al., 2018). Due to operational constraints imposed by the COVID-19 pandemic, the room containing the microscope and incubators was scheduled to be available for a maximum of 96 hours after culturing begins. Because of these restraints, observation of reproductive output took place every 24 hours for 96 hours.

Site-stacks were removed from the incubator in the same order they were placed in. Dish covers were removed, and receptacles were temporarily removed and placed onto their covers. Afterwards, the dishes were placed individually under a Leica DM IL inverted microscope at 400x for observation (Steen & Rueness, 2004; Tarakhovskaya et al., 2012; Balina et al., 2018). Individuals were monoecious and self-fertilizing as embryos were released. Reproductive output of each *Fucus distichus* individual was determined by counting: (1) the total number of fertilized embryos released into dish seawater, and (2) the total number of unfertilized eggs released into dish seawater (McLachlan et al., 1971; Pearson & Brawley, 1996).

Embryos detected in the visual field were then observed at 1000x to determine if they were fertilized (Quatrano, 1980; Tarakhovskaya et al., 2012) either through the presence of cell division or by polarization of the embryo, which only occurs after being released from an egg (Jaffe & Neuscheler, 1969; Kloareg & Quatrano, 1987; Tarakhovskaya et al., 2012). Any unfertilized eggs were also counted. Fertilization success for each *F. distichus* was then calculated using:

$$Fertilization\ Success = \frac{Fertilized\ Embryos}{Fertilized\ Embryos + Unfertilized\ Eggs}$$

Once observations concluded, the site-stacks were reassembled and placed back into their respective incubators. This process was repeated until all 90 dishes had been observed. After 96 hours, dishes were discarded.

Statistical Analyses

A series of three-way ANOVAs were used investigate the effects habitat type (fixed factor, 3 levels), temperature (fixed factor, 2 levels), and cycle (fixed factor, 7 levels) and their multi-way interactions on (1) reproductive output (total number of released embryos and eggs)

and (2) fertilization success. Data were averaged among all 5 replicate dishes per site on any

given habitat type, temperature, and cycle combination, since site (n=3) is the statistical

replicate. Data were graphed for each of the daily observational periods per cycle to study

embryo formation and gamete release. Graphs were compared to each other to determine if the

results of each daily period differed from each other or if gamete release had ceased. Since

significant gamete release continued to occur up to the final day of observation, the 96-hour (i.e.,

cumulative total of gamete release over the past 4 days) surveys were used for statistical

analyses. Separate three-way ANOVAs were conducted for total reproductive output and

fertilization success. In each ANOVA, data were tested to determine if they met assumptions of

normality and homoscedasticity. The data for reproductive output were log transformed to meet

normality assumptions. The data for fertilization success met normality assumptions. Post-hoc

multiple comparisons and magnitude of effects tests were used to determine which treatment

combinations were most important in driving *Fucus distichus* reproductive output, and residual

analyses were used to assess the assumptions of normality and equal variances.

Results

Reproductive Output

Reproductive output data (the total number of embryos and eggs released) were analyzed

with a three-way ANOVA with two levels of temperature (12ºC, 15ºC), three levels of habitat

types (OC, ICFS, ICLS), and seven levels of cycles (Cycle 1 through Cycle 7). A three-way

interaction between temperature, habitat type, and cycle was significant ($F_{12, 578}$=5.812; p<0.001,

Figure 2, Table 2). Another interaction between temperature and habitat type was significant, ($F_{2, 578}$=4.342; p=0.013, Table 2), indicating that the reproductive output of *F. distichus* in a habitat

type changes depending on the temperature. The OC and ICFS habitat types exhibited higher

reproductive output at 15º C than at 12º C, while the ICLS habitat type exhibited higher reproductive output at 15º C than at 12º C only for Cycles 1, 4, 5, and 7 (Figure 2). This temperature and habitat type interaction appeared to be the key driver behind the interaction found between all three variables. No significant relationship was found between the interactions of cycle and either temperature or habitat type, indicating that cycle served less of a role within the three-way interaction.

The main effect of temperature was significant ($F_{1,578}$=6.618; p=0.01, Table 2, Figure 3), suggesting that reproductive output at 15º C (Table 4) was greater than at 12º C (Table 4, p<0.001), in all cases except a few cycles at ICLS, where the pattern was reversed. The main effect of habitat type was also significant, ($F_{2,578}$=372.67; p<0.001, Table 2, Figure 3), suggesting that different habitats resulted in different rates of reproductive output, despite some complexity in the pattern during cycle 2. A post-hoc Tukey test revealed that the reproductive output of the OC habitat type (Table 4) differed from the ICFS habitat type (Table 4, p<0.001), and the ICLS habitat type (Table 4, p<0.001). The reproductive output of the ICFS habitat type also differed from the ICLS habitat type (p<0.001). Overall, ICFS had the highest total number of eggs and fertilized embryos, OC had the second highest, and ICLS had the lowest. The main effect of cycle (i.e., date) also was significant, ($F_{6,578}$= 41.364; p<.001, Table 2, Figure 3). A post-hoc Tukey test revealed that reproductive output in Cycle 2 (Table 4) was significantly lower than Cycle 1 (Table 4, p<0.001), Cycle 4 (Table 4, p=0.015), Cycle 5 (Table 4, p<0.001), and Cycle 7 (Table 4, p=0.015).

Fertilization Success

Fertilization success data were analyzed with a three-way ANOVA with two levels of temperature (12ºC, 15ºC), three levels of habitat types (OC, ICFS, ICLS), and seven levels of

cycles (Cycle 1 through Cycle 7). The three-way interaction between temperature, habitat type, and cycle was significant ($F_{12, 578}$=5.121; p<.001, Figure 4, Table 3). Most cycles were similar to each other except for Cycle 2, which suggests that the period in which Cycle 2 took place produced conditions that resulted in lower fertilization success (Figure 4, Figure 5, Table 5). An additional three-way ANOVA with the Cycle 2 data was performed to investigate if the differences observed within that time period was responsible for three-way interaction, however, the interaction persisted. The most probable explanation for this persistence is due to the fertilization success of ICLS habitat types being higher within the 12º C treatment during earlier cycles, then higher within the 15º C treatment during later cycles, while the fertilization success of the OC and ICFS habitat types were consistently higher within the 15º C treatment through all cycles.

Another interaction between temperature and cycle on fertilization success was significant ($F_{6,578}$=7.82; p<.001, Table 3), indicating that fertilization success at a given temperature differs from cycle to cycle. In earlier cycles, the 12º C treatment occasionally resulted in higher fertilization success than the 15º C treatment, however, from Cycle 3 through Cycle 7, the 15º C treatment had higher fertilization success than the 12º C treatment. Lastly, the interaction between habitat type and cycle was also significant, ($F_{12,578}$=5.6; p<.001, Table 3), indicating that fertilization success within a habitat type also differs from cycle to cycle. The OC and ICFS habitat types typically outperformed the ICLS habitat type within the 12º C treatment. The patterns within the 15º C treatment were more variable, although for most cycles, the OC and ICLS also outperformed the ICLS habitat type. Cycle 5 was a notable difference to this trend with the ICLS 15º C treatment outperforming the OC and ICFS habitat types. Unlike the results of reproductive output, temperature and habitat type did not have a significant interaction,

indicating that individuals from a given habitat type expressed similar fertilization success regardless of culturing temperature. Since cycle was determined to have significant interactions with the other two variables, it was determined to be the key driver behind the significant three-way interaction.

The main effect of temperature was significant ($F_{1,578}$=34.16; p<0.001, Table 3, Figure 5), suggesting that, as with reproductive output, fertilization success was higher at 15º C than at 12º C (Table 5, p<0.001). Specifically, this trend was for all cycles across the OC and ICFS habitat types except for Cycle 1 where the 12º C treatment yielded higher fertilization success. Cycles 1 through 3 for the ICLS habitat type also yielded higher fertilization success within the 12º C treatment than the 15º C treatment. Throughout Cycles 4 through 7, every habitat type yielded higher fertilization success within the 15º C treatment. The main effect of habitat type was also significant ($F_{2,578}$= 42.46; p<0.001, Table 3, Figure 5). A post-hoc Tukey test revealed that the fertilization success of the ICLS habitat type (Table 5) was significantly lower than both the OC habitat type (Table 5, p<0.001) and ICFS habitat type (Table 5, p<0.001). The main effect of cycle also was significant, ($F_{6,578}$= 88.57; p<0.001, Table 3, Figure 5). A post-hoc Tukey test revealed that Cycle 1 was significantly different than Cycle 2 (Table 5, p-adj.<0.001) and Cycle 3. Cycle 2 was also significantly different from Cycle 3, Cycle 4, Cycle 5, Cycle 6, and Cycle 7. Lastly, Cycle 3 was also found to be significantly different from Cycle 5, Cycle 6, and Cycle 7.

Discussion

This study aimed to elucidate how critical ecosystem builders may be affected by shifting environmental conditions by observing differences in reproductive output and fertilization

success of the foundation species *Fucus distichus* set in current and predicted future climate

conditions. A significant relationship between temperature and habitat type was determined to

play a role in the total number of eggs and embryos released by *F*. distichus receptacles. This

relationship was further strengthened when sampling cycle, a proxy for date, was introduced into

the statistical model. Contrary to this, no significant relationship between temperature and habitat

type existed for the fertilization success of released embryos. Interactions between these factors

were only found when sampling cycle was included in my statistical model. These results

suggest that *F. distichus* may spread to new shoreline areas that are warmer or more saline, but

that seasonal variation in reproduction may amplify variations in reproductive cycles across

seasons. Additional studies should be performed to better elucidate how the potential impact of

seasonality could affect the potential response of algae to shifting environmental conditions.

Furthermore, additional investigations could be conducted to determine if the results presented

here for *F. distichus* are applicable to other regions, to related fucoids, or are specific to these

local populations.

Reproductive Output

The interaction between temperature and habitat type significantly affected reproductive

output, and notably, a further significant interaction was found between cycle and the

temperature and habitat type interaction, meaning that the interaction between temperature and

habitat type on reproductive output varied depending on the cycle. In particular, the significant

three-way interaction between cycle, temperature, and habitat type occurred because Cycle 2

significantly differed from all other cycles (Table 2, Figure 2). Cycle 2 occurred in midsummer,

when gamete production typically drops relative to other times of the year, which conforms with

previous studies of the optimal timing of fucoid gametic production (Edelstein & McLachlan,

1975; Pearson & Brawley, 1996; Coleman & Brawley, 2005). Previous studies have suggested

that *F. distichus* dedicates energy towards growth during summer months instead of towards

reproduction, which could explain the smaller reproductive output during Cycle 2 (Edelstein &

McLachlan, 1975; Pearson & Brawley, 1996; Coleman & Brawley, 2005). No significant

interaction was found between cycle and either temperature or habitat type, meaning that cycle

only plays a role in determining reproductive output when interacting with the temperature and

habitat type. It is unclear if the effect of the timing of sampling (cycle) on the temperature and

habitat interaction is physiological or environmental. The middle of summer is the least optimal

time for reproductive release of fucoids, so it is possible the populations did not have mature

gametes ready for release (Edelstein & McLachlan, 1975; Feis, 2010; Baweja et al., 2016).

Fucus distichus had greater reproductive output under warmer temperatures (Table 2), which

aligns with previous studies that have predicted that global warming conditions may be

beneficial to fucoids or that fucoids may be 'pre-adapted' to warmer climate regimes (Jueterbock

et al., 2016). Higher temperatures may facilitate gametic release mechanisms of fucoids. *Fucus*

distichus gametes are discharged as the conceptacles constrict, forcing gamete-laden mucilage

out of each conceptacle's pit-like structure (Pearson & Brawley, 1996; Baweja et al., 2016). The

warmer environment may increase the mucilage discharge rate, or the rate that gametes release

into the mucilage (Pearson & Brawley, 1996; Edelstein & McLachlan, 1975; Feis, 2010). These

findings are contradictory to the observed life history of *F. distichus*. Although higher

temperatures resulted in higher reproductive output, winter has been observed to be the optimal

time for reproduction of *F. distichus* while late spring to early summer is a period of low

reproduction (Pearson & Brawley, 1996; Steen, & Rueness, 2004; Feis, 2010). One possible

explanation is that colder temperatures prolong the period during which adhesion and zygote

attachment takes place (Pearson & Brawley, 1996). The tradeoff of diminished reproductive success to allow for more attachment appears to make winter the more favorable time to reproduce. Further studies investigating success beyond the embryonic stage may elucidate this seasonal paradox.

Reproductive output also changed depending on habitat type (Table 2), with *Fucus distichus* from more saline conditions outperforming the *F. distichus* originating from fresher conditions. Release of gametes is initiated by a change in salinity (Ang, 1991; Edelstein & McLachlan, 1975; Pearson & Brawley, 1996). A rapid shift in salinity when exposed to seawater causes the membranes containing developed gametes to burst, releasing embryos, sperm, and unfertilized ova into the environment (Pearson & Serrão, 2006; Feis, 2010). Usually, this is associated with a low tide event when fertile adults are exposed to the air, or when individuals are isolated in tidepools with a drop in local salinity, for example from deposition of freshwater from rain or nearby waterways, and consequently release of gametes (Pearson & Brawley, 1996; Balina et al., 2018). For this experiment, this process was simulated in the lab by washing fertile receptacles with fresh water, then letting them dry out to initiate gametic release, as is standard practice in fucoid studies (Jaffe & Neuscheler, 1969; Quatrano, 1980; Sideman & Mathieson, 1983; Steen & Rueness, 2004; Balina et al., 2018). Within this context, the lower reproductive output of individuals from low salinity sites was not surprising. It is possible that residing in a fresher environment results in less of a dramatic shift in salinity when exposed to freshwater compared to individuals that occur in full marine conditions.

The analysis also revealed that reproductive outputs were similar to each other across most cycles (Table 2). Individuals from all sampling cycles had a broad range of reproductive output as seen in their standard deviations (Table 2). The differences that were observed

between cycles illustrate how reproductive output can vary through time resulting in the quantity of gametes contained within receptacles to be unpredictable when gathering individuals from the field. Future studies could attempt to mitigate this large range of reproductive output within cycles by standardizing the amount of receptacle material placed into petri dishes. Although the same number of receptacles were gathered from each individual, the random determination of which receptacles would be used from each individual resulted in a variety of receptacle sizes being utilized for culturing. Any noise produced from using multiple receptacle sizes influencing the reproductive output signal could be reduced by ensuring that every dish received the same weight of reproductive material.

Fertilization Success

The results of the fertilization success three-way ANOVA also yielded significant interactions between temperature, habitat type, and cycle (Table 3, Figure 4). Taken along with the reproductive output interactions, this reinforces that midsummer is a period during which lower amounts of reproductive output occur with diminished fertilization success rate when compared to other times of the year. Cycle was determined to have a significant interaction with temperature on fertilization success along with another significant interaction with habitat type. Notably, the interaction between temperature and habitat type had no significant effect on fertilization success, meaning that any effect of temperature should be observable regardless of habitat type and vice versa.

Greater fertilization success could be attributed to many factors. For example, a positive relationship is known between fucoid zygote adhesion and temperature, which suggests cooler temperatures slow rates at which zygotes will settle (Pearson & Brawley, 1996; Coleman & Brawley, 2005; Pearson & Serrão, 2006). Typically, fertilization success in fucoids has been

measured by counting the number of fertilized embryos that have polarized or started dividing cells (Pearson & Brawley, 1996; Coleman & Brawley, 2005). If warmer temperatures encourage zygotes to settle faster, they could be exhibiting signs of fertilization more quickly than counterparts observed in cooler settings. Warmer conditions could also be a signal for receptacles to initiate gamete release mechanisms (Pearson & Brawley, 1996; Coleman & Brawley, 2005; Pearson & Serrão, 2006).

The topography of different habitat types may influence the rate at which adhesion or fertilization occurs (Pearson & Brawley, 1996; Coleman & Brawley, 2005; Pearson & Serrão, 2006). Typically fucoids release gametes in calm, low energy environments that facilitate encounters between gametes (Pollock, 1970; Edelstein & McLachlan, 1975; Sideman & Mathieson, 1983; Feis, 2010). The discrete tidepools that occur at low tide in rocky intertidal habitats are semi-protected, closed systems that experience relatively broad changes in temperature and salinity during a tidal cycle—optimal for gamete release. Environments with more gradual changes in water level or currents, such as estuaries, lead to weaker signaling which could result in less reproductive output or fertilization success (Marshall et al., 2004; Pearson & Serrão, 2006). Lower salinity environments may also promote polyspermy which could further reduce fertilization success (Brawley, 1987). A sodium-dependent fast block typically prevents multiple sperm from inseminating fucoid eggs, however low sodium environments can delay this mechanism resulting in incompetent embryos (Brawley, 1987, 1990).

This observed pattern of greater reproductive success under warmer temperatures supports previous studies investigating the impact of climate change on fucoid population size and range (Harley et al., 2012; Jueterbock et al., 2016; Lonhart et al., 2019). Previous studies

determined that predicted coastlines will be suitable for the expansion of *Fucus distichus* into rocky upper intertidal areas that have previously been uncolonized by this already wide-ranging fucoid and the outcomes of this investigation further confirm predictions that *F. distichus* will be a dominant player in intertidal ecosystems in the coming decades (Jueterbock et al., 2016). As temperatures continue to rise, the receptacles of *F. distichus* of SFB will experience an increase in reproductive output and fertilization success. Specifically, local conditions of SFB are predicted to increase in salinity as climate change continues to alter the environment (Cloern & Jassby, 2012; Vaz et al., 2015). Shifting precipitation regimes, lesser snowpack, and encroaching seawater are predicted to result in higher salinity in what have historically been estuarine environments throughout SFB (Knowles & Cayan, 2002, 2004; Cayan et al., 2007). Therefore, the combination of warming conditions and higher salinity should produce higher rates of reproductive success of SFB *F. distichus*.

Limitations and Future Directions

Due to financial and epidemiological constraints, the scope of this study was restricted to observing the reproductive output of *Fucus distichus* of SFB from late Spring to early Fall of 2021. This four-month window within a singular year lacks a robust, continuous dataset. The optimal season to observe maximum reproductive output of *F. distichus* is typically from Winter to late Spring, which was only partially captured during the period of this study. Due to this, a level of noise inevitably affects any results and conclusions reached. It is possible that some habitat types may have respond differently during different seasons, or that the 2021 output was an outlier in some fashion. Future repeated studies would need to be conducted over longer timespans and in additional seasons to adequately determine if the results of this study can be generalized.

The nature of specimen collection dictated that a pre-set route would need to be utilized to adequately visit each site within a tidal cycle. Because of this, the same sites were always sampled first at the beginning of the tidal cycle, and the same sites were always collected last at the end of the tidal cycle. Typically, this realistically meant the OC sites were gathered during daybreak or the early morning while the ICLS sites were collected by midday or in the afternoon. Partial submergence and air exposure are components of the instigation of gamete release and can occur daily (Edelstein & McLachlan, 1975; Pearson & Brawley, 1996; Baweja et al., 2016). It is possible that receptacles gathered at OC sites had not had an opportunity to shed gametes yet as they were collected first, while ICLS sites, which had lower reproductive success overall compared to the other two habitat types, had begun to release gametes before the sites were visited. Future studies could incorporate alternative collection routes or additional people collecting at different sites to help eliminate this collection bias and further confirm the findings of this investigation.

Similarly, the restricted route and timespan of this study resulted in sites only located in central California as suitable. While previous investigations into the *Fucus distichus* of San Francisco made studying the San Franciscan populations particularly interesting regarding environmental responses, it is outside the scope of this study to universally apply the effects and interactions observed to all *F. distichus* populations located throughout their entire range, which encompasses the Northern Hemisphere. Future studies throughout the rest of *F. distichus*' range, such as the Pacific Northwest, the East Coast, or throughout Europe, could replicate the methods presented here and determine if similar outcomes are observed.

Determining if warmer conditions are conductive to other *Fucus distichus* life stages also falls out of the scope of this project. Reproductive output may have increased in warmer

environments, however, this project terminated culturing subjects after 96 hours. Future studies may investigate how life stages past the embryonic stage fare when subjected to different temperature regimes or originate from different habitat types. While the species is expected to overall increase in range, populations within the southern part of the current range are predicted to experience northward shifts as conditions warm, especially in the presence of direct competitors (Coleman & Brawley, 2005; Jueterbock et al., 2016).

Additional work comparing how local environments are predicted to change and how local *Fucus distichus* respond should better elucidate how the species' range will shape. Investigations into other parts of *F. distichus* life history, such as growth rates of germlings or development of plastic morphology, in response to warming conditions would better elucidate the overall response of *F. distichus* to climate change. Surviving in warmer conditions may have a cost that was not detected in this study due to terminating subjects before they reached stages where such costs would become relevant. Determination of adult survival in response to warming conditions is particularly important. Throughout the course of this study, I observed deceased *F. distichus* at low tide at several sites within San Francisco Bay, in accordance with observers working on other concurrent within San Francisco Bay. Higher temperatures may increase reproductive output and early life stage success, but if warming conditions cause adults to perish, then populations and ranges may not expand in the future.

This study assessed the response of one life stage of the coastal foundation species, *Fucus distichus,* to climate change. Similar work investigating the life history and predicted range of other intertidal foundation species will be important to accurately predict how and where shoreline ecosystems will form as global conditions continue to shift. Understanding how foundation species will respond to future climate regimes will be critical in determining how

potential competitors will interact as new coastline becomes available or as *F. distichus* is introduced to areas with other, established ecosystem engineers.

Any shift in population dynamics of a foundation species will ripple throughout the resulting ecosystems they engineer (Ellison, 2019). The creation of new populations or increase in population size creates more suitable habitat for the ecosystem the foundation species builds (Stachowicz, 2001). The predicted increase in range and reproductive success should result in similar expansion opportunities for organisms that reside in *Fucus distichus* beds or lead to novel interactions as analogues of existing community members take residence in the habitat that is created. To generate accurate estimations of what future *F. distichus* beds may look like, the life histories of existing members should be investigated through a similar climate-driven lens determining if predicted shorelines are suitable or if physiological processes will continue to operate as they currently do. Depending on how existing community members respond to climate change, new *F. distichus* beds may have different community compositions and dynamics.

Conclusions

In this study I found that reproductive success of *Fucus distichus* within central California is affected by the environmental conditions of temperature, habitat type, date, and their interactions. All had significant influence on the reproductive output and fertilization success of *F. distichus*. Receptacles exposed to warmer temperatures had greater reproduction output and fertilization success. Receptacles from more saline habitat types outperformed receptacles gathered from estuarine habitats when reared under common garden conditions. The optimal conditions for both reproductive output and fertilization success were warmer temperatures in marine conditions during the late spring and early summer. The results of this

study indicate that *F. distichus* should flourish under predicted climate change regimes within its current range. *F. distichus* is poised to experience increased rates of reproductive success as the potential range of the species expands over time.

References

Abraham, J. P., Baringer, M., Bindoff, N. L., Boyer, T., Cheng, L. J., Church, J. A., Conroy, J. L., Domingues, C. M., Fasullo, J. T., Gilson, J., Goni, G., Good, S. A., Gorman, J. M., Gouretski, V., Ishii, M., Johnson, G. C., Kizu, S., Lyman, J. M., Macdonald, A. M., … Willis, J. K. (2013). A review of global ocean temperature observations: Implications for ocean heat content estimates and climate change. *Reviews of Geophysics*, *51*(3), 450–483. https://doi.org/10.1002/rog.20022

Altieri, A. H., & Witman, J. D. (2006). Local extinction of a foundation species in a hypoxic estuary: Integrating individuals to ecosystem. *Ecology*, *87*(3), 717–730. https://doi.org/10.1890/05-0226

Ang, P. O. (1991). Natural dynamics of a Fucus distichus (Phaeophyceae, Fucales) population: reproduction and recruitment. *Marine Ecology Progress Series*, *78*(1), 71–85. https://doi.org/10.3354/meps078071

Angelini, C., Altieri, A. H., Silliman, B. R., & Bertness, M. D. (2011). Interactions among Foundation Species and Their Consequences for Community Organization, Biodiversity, and Conservation. *BioScience*, *61*(10), 782–789. https://doi.org/10.1525/bio.2011.61.10.8

Baiser, B., Whitaker, N., & Ellison, A. M. (2013). Modeling foundation species in food webs. *Ecosphere*, *4*(12), 1–14. https://doi.org/10.1890/ES13-00265.1

Balina, K., Boderskov, T., Bruhn, A., & Romagnoli, F. (2018). Increase of Fucus vesiculosus fertilization success: Testing of different receptacle drying methods to increase spore release. *Energy Procedia*, *147*, 282–287. https://doi.org/10.1016/j.egypro.2018.07.093

Baweja, P., Kumar, S., Sahoo, D., & Levine, I. (2016). Chapter 3 - Biology of Seaweeds. In J. Fleurence & I. B. T.-S. in H. and D. P. Levine (Eds.), *Seaweed in Health and Disease*

Prevention (pp. 41–106). Academic Press. https://doi.org/https://doi.org/10.1016/B978-0-12-802772-1.00003-8

Beas-Luna, R., Micheli, F., Woodson, C. B., Carr, M., Malone, D., Torre, J., Boch, C., Caselle, J. E., Edwards, M., Freiwald, J., Hamilton, S. L., Hernandez, A., Konar, B., Kroeker, K. J., Lorda, J., Montaño-Moctezuma, G., & Torres-Moye, G. (2020). Geographic variation in responses of kelp forest communities of the California Current to recent climatic changes. *Global Change Biology*, *26*(11), 6457–6473. https://doi.org/10.1111/gcb.15273

Beck, M. W., Heck, K. L., Able, K. W., Childers, D. L., Eggleston, D. B., Gillanders, B. M., Halpern, B., Hays, C. G., Hoshino, K., Minello, T. J., Orth, R. J., Sheridan, P. F., & Weinstein, M. P. (2001). The identification, conservation, and management of estuarine and marine nurseries for fish and invertebrates. *BioScience*, *51*(8), 633–641. https://doi.org/10.1641/0006-3568(2001)051[0633:TICAMO]2.0.CO;2

Bellgrove, A., McKenzie, P. F., Cameron, H., & Pocklington, J. B. (2017). Restoring rocky intertidal communities: Lessons from a benthic macroalgal ecosystem engineer. *Marine Pollution Bulletin*, *117*(1–2), 17–27. https://doi.org/10.1016/j.marpolbul.2017.02.012

Boesch, D. F., & Turner, R. E. (1984). Dependence of fishery species on salt marshes: The role of food and refuge. *Estuaries*, *7*(4), 460–468. https://doi.org/10.2307/1351627

Braun de Torrez, E. C., Frock, C. F., Boone, W. W., Sovie, A. R., & McCleery, R. A. (2021). Seasick: Why Value Ecosystems Severely Threatened by Sea-Level Rise? *Estuaries and Coasts*, *44*(4), 899–910. https://doi.org/10.1007/s12237-020-00850-w

Brawley, S. H. (1987). A sodium-dependent, fast block to polyspermy occurs in eggs of fucoid algae. *Developmental Biology*, *124*(2), 390–397. https://doi.org/10.1016/0012-1606(87)90491-X

Brawley, S. H. (1990). The polyspermy block in fucoid algae. In W. Wiessner, D. G. Robinson, & R. C. Starr (Eds.), *Cell Walls and Surfaces, Reproduction, Photosynthesis* (pp. 134–144). Springer Berlin Heidelberg. https://doi.org/10.1007/978-3-642-48652-4_10

Bruno, J. F., & Bertness, M. D. (2000). Habitat modification and facilitation in benthic marine communities. *Marine Community Ecology*, *January 2001*, 201–218.

Bulleri, F., Bruno, J. F., Silliman, B. R., & Stachowicz, J. J. (2016). Facilitation and the niche: Implications for coexistence, range shifts and ecosystem functioning. *Functional Ecology*, *30*(1), 70–78. https://doi.org/10.1111/1365-2435.12528

Carr, M. (1989). Effects of macroalgal assemblages on the recruitment of temperate zone reef fishes. *Journal of Experimental Marine Biology and Ecology*, *126*, 59–76. https://doi.org/10.1016/0022-0981(89)90124-X

Cayan, D. R., Maurer, E. P., Dettinger, M. D., Tyree, M., & Hayhoe, K. (2007). Climate change scenarios for the California region. *Climatic Change*, *87*(1 SUPPL). https://doi.org/10.1007/s10584-007-9377-6

Cho, G. Y., Rousseau, F., De Reviers, B., & Boo, S. M. (2006). Phylogenetic relationships within the Fucales (Phaeophyceae) assessed by the photosystem I coding psaA sequences. *Phycologia*, *45*(5), 512–519. https://doi.org/10.2216/05-48.1

Cimino, M. A., Jacox, M. G., Bograd, S. J., Brodie, S., Carroll, G., Hazen, E. L., Lavaniegos, B. E., Morales, M. M., Satterthwaite, E., & Rykaczewski, R. R. (2021). Anomalous poleward advection facilitates episodic range expansions of pelagic red crabs in the eastern North Pacific. *Limnology and Oceanography*, *66*(8), 3176–3189. https://doi.org/10.1002/lno.11870

Cloern, J. E., & Jassby, A. D. (2012). Drivers of change in estuarine-coastal ecosystems:

Discoveries from four decades of study in San Francisco Bay. *Reviews of Geophysics*, *50*(4), 1–33. https://doi.org/10.1029/2012RG000397

Coleman, M. A., & Brawley, S. H. (2005). Variability in temperature and historical patterns in reproduction in the Fucus distichus complex (Heterokontophyta; Phaeophyceae): Implications for speciation and the collection of herbarium specimens. *Journal of Phycology*, *41*(6), 1110–1119. https://doi.org/10.1111/j.1529-8817.2005.00147.x

Coleman, M. A., & Wernberg, T. (2017). Forgotten underwater forests: The key role of fucoids on Australian temperate reefs. *Ecology and Evolution*, *7*(20), 8406–8418. https://doi.org/10.1002/ece3.3279

Daleo, P., Escapa, M., Alberti, J., & Iribarne, O. (2006). Negative effects of an autogenic ecosystem engineer: Interactions between coralline turf and an ephemeral green alga. *Marine Ecology Progress Series*, *315*, 67–73. https://doi.org/10.3354/meps315067

Dayton, P. K. (1972). Toward An Understanding of Community Resilience and the Potential Effects of Enrichments tot he Benthos at McMurdo Sound, Antarctica. *Proceedings of the Colloquium on Conservation Problems in Antarctica*, 81–96.

de Bettignies, T., Wernberg, T., & Gurgel, C. F. D. (2018). Exploring the influence of temperature on aspects of the reproductive phenology of temperate seaweeds. *Frontiers in Marine Science*, *5*(JUN), 1–8. https://doi.org/10.3389/fmars.2018.00218

Dudgeon, S., & Petraitis, P. S. (2005). First year demography of the foundation species, Ascophyllum nodosum, and its community implications. *Oikos*, *109*(2), 405–415. https://doi.org/10.1111/j.0030-1299.2005.13782.x

Eckman, J. E., Duggins, D. O., & Sewell, A. T. (1989). Ecology of under story kelp environments. I. Effects of kelps on flow and particle transport near the bottom. *Journal of*

Experimental Marine Biology and Ecology, *129*(2), 173–187. https://doi.org/10.1016/0022-0981(89)90055-5

Edelstein, T., & McLachlan, J. (1975). Autecology of Fucus distichus ssp. distichus. *Marine Biology*, *30*(4), 305–324. https://doi.org/10.1007/BF00390636

Ellison, A. M. (2019). Foundation Species, Non-trophic Interactions, and the Value of Being Common. *IScience*, *13*, 254–268. https://doi.org/10.1016/j.isci.2019.02.020

Ellison, A. M., Bank, M. S., Clinton, B. D., Colburn, E. A., Elliott, K., Ford, C. R., Foster, D. R., Kloeppel, B. D., Knoepp, J. D., Lovett, G. M., Mohan, J., Orwig, D. A., Rodenhouse, N. L., Sobczak, W. V., Stinson, K. A., Stone, J. K., Swan, C. M., Thompson, J., Von Holle, B., & Webster, J. R. (2005). Loss of foundation species: Consequences for the structure and dynamics of forested ecosystems. *Frontiers in Ecology and the Environment*, *3*(9), 479–486. https://doi.org/10.1890/1540-9295(2005)003[0479:LOFSCF]2.0.CO;2

Feis, M. E. (2010). *Reproduction in the Genus Fucus* (Issue July). University of Groningen.

Fernández-Méndez, M., Olsen, L. M., Kauko, H. M., Meyer, A., Rösel, A., Merkouriadi, I., Mundy, C. J., Ehn, J. K., Johansson, A. M., Wagner, P. M., Ervik, Å., Sorrell, B. K., Duarte, P., Wold, A., Hop, H., & Assmy, P. (2018). Algal hot spots in a changing Arctic Ocean: Sea-ice ridges and the snow-ice interface. *Frontiers in Marine Science*, *5*(MAR). https://doi.org/10.3389/fmars.2018.00075

Fulcher, R. G., & McCully, M. E. (1969). Laboratory culture of the intertidal brown alga Fucus vesiculosus. *Canadian Journal of Botany*, *47*(1), 219–222. https://doi.org/10.1139/b69-028

Gaylord, B., Hill, T. M., Sanford, E., Lenz, E. A., Jacobs, L. A., Sato, K. N., Russell, A. D., & Hettinger, A. (2011). Functional impacts of ocean acidification in an ecologically critical foundation species. *Journal of Experimental Biology*, *214*(15), 2586–2594.

https://doi.org/10.1242/jeb.055939

Giesel, J. T. (1976). Reproductive Strategies as Adaptations to Life in Temporally

Heterogeneous Environments. *Annual Review of Ecology and Systematics*, *7*(1), 57–79.

https://doi.org/10.1146/annurev.es.07.110176.000421

Grazer, V. M., & Martin, O. Y. (2012). Investigating climate change and reproduction:

Experimental tools from evolutionary biology. *Biology*, *1*(2), 411–438.

https://doi.org/10.3390/biology1020411

Greene, H. G., Endris, C., Vallier, T., Goldern, N., Cross, J., Ryan, H., Dieter, B., & Niven, E.

(2013). Sub-tidal benthic habitats of central San Francisco Bay and offshore Golden Gate

area - A review. *Marine Geology*, *345*, 31–46. https://doi.org/10.1016/j.margeo.2013.05.001

Harley, C. D. G., Anderson, K. M., Demes, K. W., Jorve, J. P., Kordas, R. L., Coyle, T. A., &

Graham, M. H. (2012). Effects Of Climate Change On Global Seaweed Communities.

Journal of Phycology, *48*(5), 1064–1078. https://doi.org/10.1111/j.1529-8817.2012.01224.x

Harley, C. D. G., Hughes, A. R., Hultgren, K. M., Miner, B. G., Sorte, C. J. B., Thornber, C. S.,

Rodriguez, L. F., Tomanek, L., & Williams, S. L. (2006). The impacts of climate change in

coastal marine systems. *Ecology Letters*, *9*(2), 228–241. https://doi.org/10.1111/j.1461-

0248.2005.00871.x

Hoegh-Guldberg, O., & Bruno, J. F. (2010). The impact of climate change on the world's marine

ecosystems. *Science*, *328*(5985), 1523–1528. https://doi.org/10.1126/science.1189930

Hughes, T. P., Barnes, M. L., Bellwood, D. R., Cinner, J. E., Cumming, G. S., Jackson, J. B. C.,

Kleypas, J., Van De Leemput, I. A., Lough, J. M., Morrison, T. H., Palumbi, S. R., Van

Nes, E. H., & Scheffer, M. (2017). Coral reefs in the Anthropocene. *Nature*, *546*(7656), 82–

90. https://doi.org/10.1038/nature22901

Ibáñez, I., Clark, J. S., LaDeau, S., & Hille Ris Lambers, J. (2007). Exploiting temporal variability to understand tree recruitment response to climate change. *Ecological Monographs*, *77*(2), 163–177. https://doi.org/10.1890/06-1097

Jacox, M. G., Alexander, M. A., Amaya, D., Becker, E., Bograd, S. J., Brodie, S., Hazen, E. L., Pozo Buil, M., & Tommasi, D. (2022). Global seasonal forecasts of marine heatwaves. *Nature*, *604*(7906), 486–490. https://doi.org/10.1038/s41586-022-04573-9

Jaffe, L. F., & Neuscheler, W. (1969). On the mutual polarization of nearby pairs of fucaceous eggs. *Developmental Biology*, *19*(6), 549–565. https://doi.org/10.1016/0012-1606(69)90037-2

Johansson, J., Smith, H. G., & Jonzén, N. (2014). Adaptation of reproductive phenology to climate change with ecological feedback via dominance hierarchies. *Journal of Animal Ecology*, *83*(2), 440–449. https://doi.org/10.1111/1365-2656.12151

Jueterbock, A., Smolina, I., Coyer, J. A., & Hoarau, G. (2016). The fate of the Arctic seaweed Fucus distichus under climate change : an ecological niche modeling approach. *Ecology and Evolution*, *6*(6), 1712–1724. https://doi.org/10.1002/ece3.2001

Kashutin, A. N., Klimova, A. V, & Klochkova, N. G. (2019). The Seasonal Growth Dynamics of Fucus distichus subsp. evanescens (C. Agardh) H.T. Powell, 1957 (Phaeophyceae: Fucales) in the Avacha Bay (Southeastern Kamchatka). *Russian Journal of Marine Biology*, *45*(4), 275–282. https://doi.org/10.1134/S1063074019040096

Kloareg, B., & Quatrano, R. S. (1987). Enzymatic removal of the cell walls from zygotes of Fucus distichus (L.) Powell (Phaeophyta). *Hydrobiologia*, *151–152*(1), 123–129. https://doi.org/10.1007/BF00046117

Knowles, N., & Cayan, D. R. (2002). Potential effects of global warming on the Sacramento/San

Joaquin watershed and the San Francisco estuary. *Geophysical Research Letters*, *29*(18), 2–

5. https://doi.org/10.1029/2001GL014339

Knowles, N., & Cayan, D. R. (2004). Elevational dependence of projected hydrologic changes in

the San Francisco Estuary and watershed. *Climatic Change*, *62*(1–3), 319–336.

https://doi.org/10.1023/B:CLIM.0000013696.14308.b9

Koch, E. W., Barbier, E. B., Silliman, B. R., Reed, D. J., Perillo, G. M. E., Hacker, S. D.,

Granek, E. F., Primavera, J. H., Muthiga, N., Polasky, S., Halpern, B. S., Kennedy, C. J.,

Kappel, C. V., & Wolanski, E. (2009). Non-linearity in ecosystem services: Temporal and

spatial variability in coastal protection. *Frontiers in Ecology and the Environment*, *7*(1), 29–

37. https://doi.org/10.1890/080126

Laughinghouse, H. D., Müller, K. M., Adey, W. H., Lara, Y., Young, R., & Johnson, G. (2015).

Evolution of the northern rockweed, fucus distichus, in a regime of glacial cycling:

Implications for benthic algal phylogenetics. *PLoS ONE*, *10*(12), 1–17.

https://doi.org/10.1371/journal.pone.0143795

Lee, R. E. (2008). *Phycology* (Fourth). Cambridge University Press.

Lejeusne, C., Chevaldonné, P., Pergent-Martini, C., Boudouresque, C. F., & Pérez, T. (2010).

Climate change effects on a miniature ocean: the highly diverse, highly impacted

Mediterranean Sea. *Trends in Ecology and Evolution*, *25*(4), 250–260.

https://doi.org/10.1016/j.tree.2009.10.009

Lonhart, S. I., Jeppesen, R., Beas-Luna, R., Crooks, J. A., & Lorda, J. (2019). Shifts in the

distribution and abundance of coastal marine species along the eastern Pacific Ocean during

marine heatwaves from 2013 to 2018. *Marine Biodiversity Records*, *12*(1), 1–15.

https://doi.org/10.1186/s41200-019-0171-8

Lopes, A. F., Faria, A. M., & Dupont, S. (2020). Elevated temperature, but not decreased pH, impairs reproduction in a temperate fish. *Scientific Reports*, *10*(1), 1–8. https://doi.org/10.1038/s41598-020-77906-1

Marshall, D. J., Semmens, D., & Cook, C. (2004). Consequences of spawning at low tide: Limited gamete dispersal for a rockpool anemone. *Marine Ecology Progress Series*, *266*(January 2004), 135–142. https://doi.org/10.3354/meps266135

Matías, L., & Jump, A. S. (2014). Impacts of predicted climate change on recruitment at the geographical limits of Scots pine. *Journal of Experimental Botany*, *65*(1), 299–310. https://doi.org/10.1093/jxb/ert376

McLachlan, J., Chen, L. C.-M., & Edelstein, T. (1971). The culture of four species of Fucus under laboratory conditions. *Canadian Journal of Botany*, *49*(8), 1463–1469. https://doi.org/10.1139/b71-206

McPherson, M. L., Finger, D. J. I., Houskeeper, H. F., Bell, T. W., Carr, M. H., Rogers-Bennett, L., & Kudela, R. M. (2021). Large-scale shift in the structure of a kelp forest ecosystem co-occurs with an epizootic and marine heatwave. *Communications Biology*, *4*(1), 1–9. https://doi.org/10.1038/s42003-021-01827-6

Miner, C. M., Burnaford, J. L., Ammann, K., Becker, B. H., Fradkin, S. C., Ostermann-Kelm, S., Smith, J. R., Whitaker, S. G., & Raimondi, P. T. (2021). Latitudinal variation in long-term stability of North American rocky intertidal communities. *Journal of Animal Ecology*, *90*(9), 2077–2093. https://doi.org/10.1111/1365-2656.13504

Nievola, C. C., Carvalho, C. P., Carvalho, V., & Rodrigues, E. (2017). Rapid responses of plants to temperature changes. *Temperature*, *4*(4), 371–405. https://doi.org/10.1080/23328940.2017.1377812

Orth, R. J., Carruthers, T. J. B., Dennison, W. C., Duarte, C. M., Fourqurean, J. W., Heck, K. L., Hughes, A. R., Kendrick, G. A., Kenworthy, W. J., Olyarnik, S., Short, F. T., Waycott, M., & Williams, S. L. (2006). A global crisis for seagrass ecosystems. *BioScience*, *56*(12), 987–996. https://doi.org/10.1641/0006-3568(2006)56[987:AGCFSE]2.0.CO;2

Pearson, G. A., & Brawley, S. H. (1996). Reproductive ecology of Fucus distichus (Phaeophyceae): An intertidal alga with successful external fertilization. *Marine Ecology Progress Series*, *143*(1–3), 211–223. https://doi.org/10.3354/meps143211

Pearson, G. A., & Serrão, E. A. (2006). Revisiting synchronous gamete release by fucoid algae in the intertidal zone: Fertilization success and beyond? *Integrative and Comparative Biology*, *46*(5), 587–597. https://doi.org/10.1093/icb/icl030

Perovich, D. K., & Richter-Menge, J. A. (2015). Regional variability in sea ice melt in a changing Arctic. *Philosophical Transactions of the Royal Society A: Mathematical, Physical and Engineering Sciences*, *373*(2045). https://doi.org/10.1098/rsta.2014.0165

Petsas, P., Doxa, A., Almpanidou, V., & Mazaris, A. D. (2022). Global patterns of sea surface climate connectivity for marine species. *Communications Earth and Environment*, *3*(1). https://doi.org/10.1038/s43247-022-00569-5

Pocklington, J. B., Jenkins, S. R., Bellgrove, A., Keough, M. J., O'Hara, T. D., Masterson-Algar, P. E., & Hawkins, S. J. (2018). Disturbance alters ecosystem engineering by a canopy-forming alga. *Journal of the Marine Biological Association of the United Kingdom*, *98*(4), 687–698. https://doi.org/10.1017/S0025315416002009

Pollock, E. G. (1970). Fertilization in Fucus. *Planta*, *92*(1), 85–99. https://doi.org/10.1007/BF00385566

Quatrano, R. S. (1980). Gamete release, fertilization, and embryogenesis in the Fucales. In

Handbook of Phycological Methods. Developmental and Cytological Methods (pp. 59–68). Cambridge University Press.

Ready, J., Kaschner, K., South, A. B., Eastwood, P. D., Rees, T., Rius, J., Agbayani, E., Kullander, S., & Froese, R. (2010). Predicting the distributions of marine organisms at the global scale. *Ecological Modelling*, *221*(3), 467–478. https://doi.org/10.1016/j.ecolmodel.2009.10.025

Reay, D., Sabine, C., Smith, P., & Hymus, G. (2007). Climate change 2007: Spring-time for sinks. In T. Z. and J. C. M. Edenhofer, O., R. Pichs-Madruga, Y. Sokona, E. Farahani, S. Kadner, K. Seyboth, A. Adler, I. Baum, S. Brunner, P. Eickemeier, B. Kriemann, J. Savolainen, S. Schlömer, C. von Stechow (Ed.), *Nature* (Vol. 446, Issue 7137, pp. 727–728). Cambridge University Press. https://doi.org/10.1038/446727a

Scrosati, R. A. (2016). The clonal seaweed Chondrus crispus as a foundation species. *Algae*, *31*(1), 41–48. https://doi.org/10.4490/algae.2016.31.2.10

Scrosati, R. A. (2017). Community-level facilitation by macroalgal foundation species peaks at an intermediate level of environmental stress. *Algae*, *32*(1), 41–46. https://doi.org/10.4490/algae.2017.32.2.20

Shelamoff, V., Layton, C., Tatsumi, M., Cameron, M. J., Wright, J. T., & Johnson, C. R. (2019). Patch size and density of canopy-forming kelp modify influences of ecosystem engineering on understorey algal and sessile invertebrate assemblages. *Marine Ecology Progress Series*, *632*(January), 59–79. https://doi.org/10.3354/meps13155

Sibly, R. M., & Hone, J. (2002). Population growth rate and its determinants: An overview. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *357*(1425), 1153–1170. https://doi.org/10.1098/rstb.2002.1117

Sideman, E. J., & Mathieson, A. C. (1983). The growth, reproductive phenology, and longevity of non-tide-pool Fucus distichus (L.) powell in New England. *Journal of Experimental Marine Biology and Ecology*, *68*(2), 111–127. https://doi.org/10.1016/0022-0981(83)90154-5

Smale, D. A., Wernberg, T., Oliver, E. C. J., Thomsen, M., Harvey, B. P., Straub, S. C., Burrows, M. T., Alexander, L. V., Benthuysen, J. A., Donat, M. G., Feng, M., Hobday, A. J., Holbrook, N. J., Perkins-Kirkpatrick, S. E., Scannell, H. A., Sen Gupta, A., Payne, B. L., & Moore, P. J. (2019). Marine heatwaves threaten global biodiversity and the provision of ecosystem services. *Nature Climate Change*, *9*(4), 306–312. https://doi.org/10.1038/s41558-019-0412-1

Smolina, I., Kollias, S., Jueterbock, A., Coyer, J. A., & Hoarau, G. (2016). Variation in thermal stress response in two populations of the brown seaweed, Fucus distichus, from the Arctic and subarctic intertidal. *Royal Society Open Science*, *3*(1), 10. https://doi.org/10.1098/rsos.150429

Spinks, R. K., Bonzi, L. C., Ravasi, T., Munday, P. L., & Donelson, J. M. (2021). Sex- and time-specific parental effects of warming on reproduction and offspring quality in a coral reef fish. *Evolutionary Applications*, *14*(4), 1145–1158. https://doi.org/10.1111/eva.13187

Stachowicz, J. J. (2001). Mutualism, Facilitation, and the Structure of Ecological Communities. *BioScience*, *51*(3), 235–246.

Steen, H., & Rueness, J. (2004). Comparison of survival and growth in germlings of six fucoid species (Fucales, Phaeophyceae) at two different temperature and nutrient levels. *Sarsia*, *89*(3), 175–183. https://doi.org/10.1080/00364820410005818

Storch, D., Menzel, L., Frickenhaus, S., & Pörtner, H. O. (2014). Climate sensitivity across

marine domains of life: Limits to evolutionary adaptation shape species interactions. *Global Change Biology*, *20*(10), 3059–3067. https://doi.org/10.1111/gcb.12645

Stuart Chapin, F., & Díaz, S. (2020). Interactions between changing climate and biodiversity: Shaping humanity's future. *Proceedings of the National Academy of Sciences of the United States of America*, *117*(12), 6295–6296. https://doi.org/10.1073/pnas.2001686117

Tarakhovskaya, E. R., Kang, E.-J., Kim, K.-Y., & Garbary, D. J. (2012). Effect of GeO 2 on embryo development and photosynthesis in Fucus vesiculosus (Phaeophyceae). *Algae*, *27*(2), 125–134. https://doi.org/10.4490/algae.2012.27.2.125

Thomsen, M. S., Altieri, A. H., Angelini, C., Bishop, M. J., Gribben, P. E., Lear, G., He, Q., Schiel, D. R., Silliman, B. R., South, P. M., Watson, D. M., Wernberg, T., & Zotz, G. (2018). Secondary foundation species enhance biodiversity. *Nature Ecology and Evolution*, *2*(4), 634–639. https://doi.org/10.1038/s41559-018-0487-5

Thomsen, M. S., & South, P. M. (2019). Communities and attachment networks associated with primary, secondary and alternative foundation species; A case study of stressed and disturbed stands of southern bull kelp. *Diversity*, *11*(4), 1–20. https://doi.org/10.3390/d11040056

Thomson, J. A., Burkholder, D. A., Heithaus, M. R., Fourqurean, J. W., Fraser, M. W., Statton, J., & Kendrick, G. A. (2015). Extreme temperatures, foundation species, and abrupt ecosystem change: an example from an iconic seagrass ecosystem. *Global Change Biology*, *21*(4), 1463–1474. https://doi.org/10.1111/gcb.12694

Tribbia, J., & Moser, S. C. (2008). More than information: what coastal managers need to plan for climate change. *Environmental Science and Policy*, *11*(4), 315–328. https://doi.org/10.1016/j.envsci.2008.01.003

Vaz, P. G., Kebreab, E., Hung, S. S. O., Fadel, J. G., Lee, S., & Fangue, N. A. (2015). Impact of nutrition and salinity changes on biological performances of green and white sturgeon. *PLoS ONE*, *10*(4), 1–17. https://doi.org/10.1371/journal.pone.0122029

Vergés, A., Steinberg, P. D., Hay, M. E., Poore, A. G. B., Campbell, A. H., Ballesteros, E., Heck, K. L., Booth, D. J., Coleman, M. A., Feary, D. A., Figueira, W., Langlois, T., Marzinelli, E. M., Mizerek, T., Mumby, P. J., Nakamura, Y., Roughan, M., van Sebille, E., Gupta, A. Sen, … Wilson, S. K. (2014). The tropicalization of temperate marine ecosystems: Climate-mediated changes in herbivory and community phase shifts. *Proceedings of the Royal Society B: Biological Sciences*, *281*(1789). https://doi.org/10.1098/rspb.2014.0846

Visser, M. E. (2008). Keeping up with a warming world; assessing the rate of adaptation to climate change. *Proceedings of the Royal Society B: Biological Sciences*, *275*(1635), 649–659. https://doi.org/10.1098/rspb.2007.0997

Weitzman, B., Konar, B., Iken, K., Coletti, H., Monson, D., Suryan, R., Dean, T., Hondolero, D., & Lindeberg, M. (2021). Changes in Rocky Intertidal Community Structure During a Marine Heatwave in the Northern Gulf of Alaska. *Frontiers in Marine Science*, *8*(February). https://doi.org/10.3389/fmars.2021.556820

Westerbom, M., Kraufvelin, P., Mustonen, O., & Díaz, E. (2021). Explaining Recruitment Stochasticity at a Species' Range Margin. *Frontiers in Marine Science*, *8*. https://doi.org/10.3389/fmars.2021.659556

Whitaker, S. G., Fong, D. R., Neiva, J., Serrão, E. A., Anderson, L. M., & Raimondi, P. T. (2017). Distribution and genetic structure of Fucus distichus Linnaeus 1953 (formerly F. gardneri) within Central San Francisco Bay. *San Francisco Estuary and Watershed Science*,

15(3). https://doi.org/10.15447/sfews.2017v15iss3art4

Whitney, J. E., Al-Chokhachy, R., Bunnell, D. B., Caldwell, C. A., Cooke, S. J., Eliason, E. J., Rogers, M., Lynch, A. J., & Paukert, C. P. (2016). Physiological Basis of Climate Change Impacts on North American Inland Fishes. *Fisheries*, *41*(7), 332–345. https://doi.org/10.1080/03632415.2016.1186656

Wolcott, B. D. (2007). Mechanical size limitation and life-history strategy of an intertidal seaweed. *Marine Ecology Progress Series*, *338*, 1–10. https://doi.org/10.3354/meps338001

Tables

Table 1: Salinity and Temperature of Sites. Mean and Standard Deviation of Daily Salinity (PSU) of San Rafael, Pier 17, and Alcatraz Island for each collection cycle. USGS Buoys 374938122251801 SAN FRANCISCO BAY A NE SHORE ALCATRAZ ISLAND CA and 374811122235001 SAN FRANCISCO BAY A PIER 17 A SAN FRANCISCO CA were used to determine ICFS salinity (PSU) and USGS buoy 375607122264701 SAN FRANCISCO BAY A RICHMOND-SAN RAFAEL BRIDGE CA was used to determine ICLS salinity. No USGS buoys were available to be used as an analogue for local OC salinity.

Cycle	Date	Salinity (PSU)			Temperature (°C)		
		San Rafael	Pier 17	Alcatraz Island	San Rafael	Pier 17	Alcatraz Island
1	June 12, 2021	29.6 ± 1.2	32.4 ± 0.5	32.4 ± 0.5	16 ± 0.8	15 ± 0.6	14.9 ± 0.7
2	July 3, 2021	28.3 ± 0.6	32.5 ± 0.5	32.5 ± 0.5	17.9 ± 0.5	16.8 ± 0.3	16.7 ± 0.4
3	July 17, 2021	27.5 ± 0.6	32.9 ± 0.3	32.7 ± 0.5	17.3 ± 0.7	16.3 ± 0.5	16.3 ± 0.7
4	July 30, 2021	N/A	33.0 ± 0.2	32.6 ± 0.5	17.4 ± 0.7	16.5 ± 0.5	16.4 ± 0.6
5	August 13, 2021	25.7 ± 0.8	33.0 ± 0.0	32.7 ± 0.5	18.5 ± 0.6	17.7 ± 0.5	17.6 ± 0.5
6	August 21, 2021	N/A	33.0 ± 0.0	32.6 ± 0.5	18.4 ± 0.4	17.8 ± 0.2	17.7 ± 0.3
7	September 5, 2021	27.9 ± 1.1	33.0 ± 0.0	32.7 ± 0.5	18.7 ± 0.4	18 ± 0.4	17.9 ± 0.4

Table 2: Reproductive Output ANOVA Results. Full factorial three-way ANOVA testing the effects of temperature, habitat type, time period (i.e., cycle) and their interactions on reproductive output of *Fucus distichus*. Significant p-values are in bold text.

OVA	DF	Sum of Squares	Mean Square	F Value	Prob > F
Temperature	1	1.248	1.248	6.618	**0.01**
Habitat type	2	140.589	70.295	372.674	**<0.001**
Cycle	6	46.813	7.802	41.364	**<0.001**
Temperature*Habitat type	2	1.638	0.819	4.342	**0.013**
Temperature*Cycle	6	1.388	0.231	1.227	0.291
Habitat type*Cycle	12	3.745	0.312	1.654	0.073
Temperature*Habitat type*Cycle	12	13.155	1.096	5.812	**<0.001**
Residuals	578	109.024	0.189		

Table 3: Fertilization Success ANOVA Results. Full factorial three-way ANOVA testing the effects of temperature, habitat type, time period (i.e., cycle) and their interactions on fertilization success of *Fucus distichus*. Significant p-values are in bold text.

| Source	DF	Sum of Squares	Mean Square	F Value	Prob > F
Temperature	1	0.2086	0.20863	34.169	**<0.001**
Habitat type	2	0.5185	0.25927	42.461	**<0.001**
Cycle	6	3.2449	0.54082	88.571	**<0.001**
Temperature*Habitat type	2	0.0043	0.00214	0.35	0.705
Temperature*Cycle	6	0.2865	0.04775	7.821	**<0.001**
Habitat type*Cycle	12	0.4103	0.03419	5.6	**<0.001**
Temperature*Habitat type*Cycle	12	0.3752	0.03127	5.121	**<0.001**
Residuals	578	3.5293	0.00611		

Table 4: Reproductive Output Means Within Variables. Mean and standard deviation of total number of eggs and fertilized embryos of each level of temperature, habitat type, and time period (i.e., cycle) of *Fucus distichus*.

Variable Type	Level	Mean Total Number of Eggs & Fertilized Embryos	Standard Deviation
Temperature	12º C	363.8	229.0
Temperature	15º C	461.0	395.2
Habitat Type	OC	460.3	269.3
Habitat Type	ICFS	590.6	384.9
Habitat Type	ICLS	176.6	79.9
Cycle	1	520.3	338.1
Cycle	2	261.3	362.4
Cycle	3	391.0	257.7
Cycle	4	421.6	309.4
Cycle	5	491.7	316.5
Cycle	6	393.4	326.7
Cycle	7	419.8	301.4

Table 5: Fertilization Success Means Within Variables. Mean and standard deviation of fertilization success of each level of temperature, habitat type, and time period (i.e., cycle) of *Fucus distichus*.

| Variable Type	Level	Mean Fertilization Success	Standard Deviation
Temperature	12° C	0.837	0.115
Temperature	15° C	0.873	0.118
Habitat Type	OC	0.875	0.093
Habitat Type	ICFS	0.876	0.099
Habitat Type	ICLS	0.813	0.144
Cycle	1	0.905	0.070
Cycle	2	0.687	0.168
Cycle	3	0.842	0.092
Cycle	4	0.876	0.094
Cycle	5	0.908	0.059
Cycle	6	0.886	0.051
Cycle	7	0.887	0.066

Figures
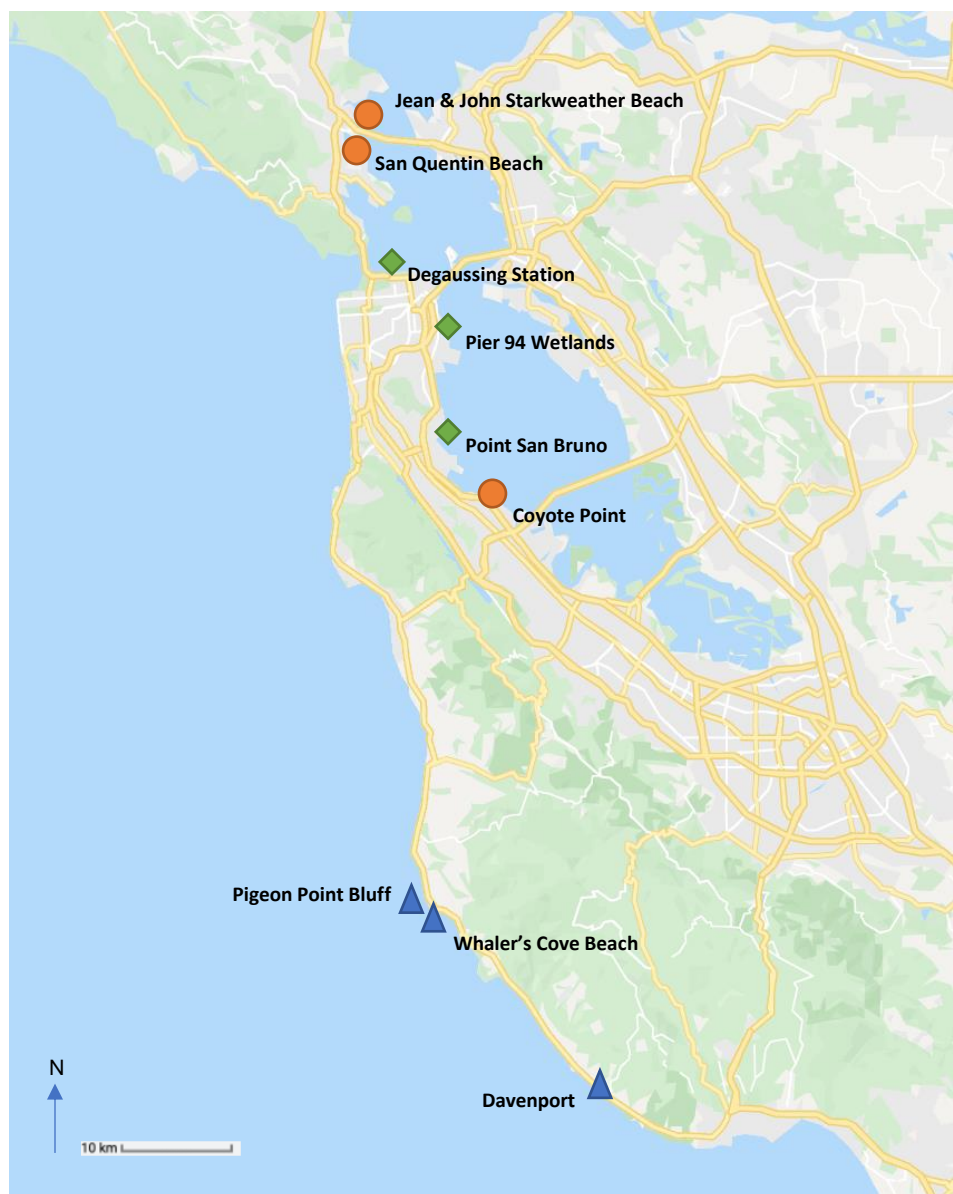
Figure 1: Map of Field Sites

Outer Coast field sites are marked with a blue triangle. Inner Coast Full-Salinity field sites are marked with a green diamond. Inner Coast Low-Salinity field sites are marked with an orange circle.
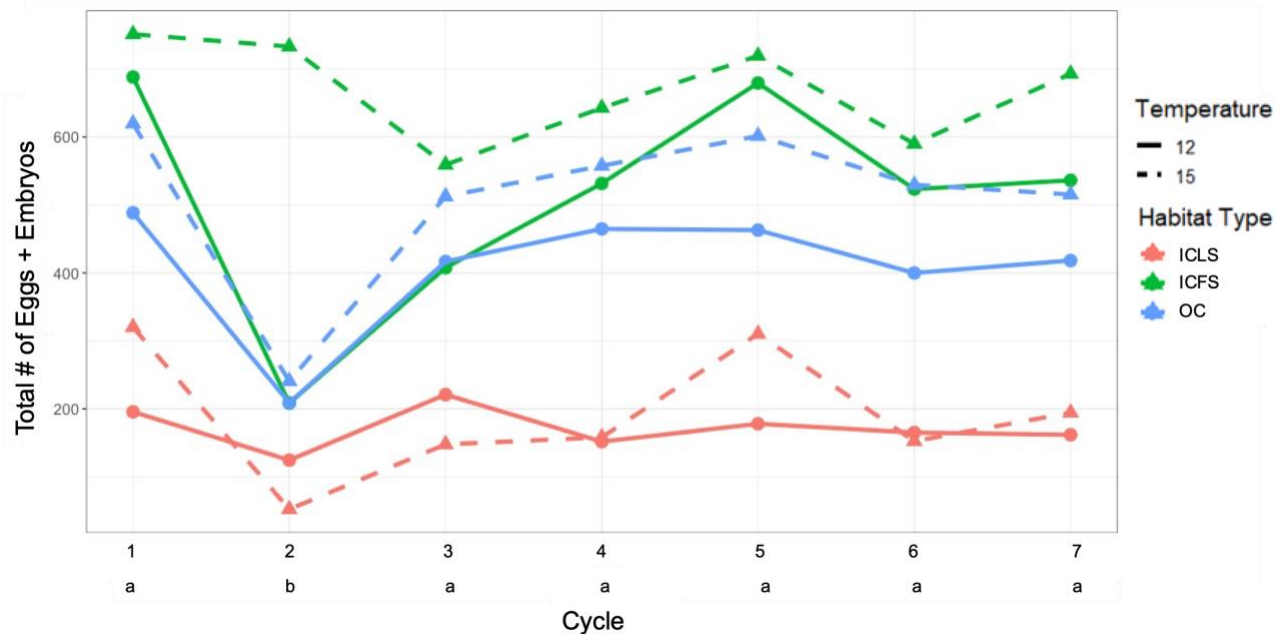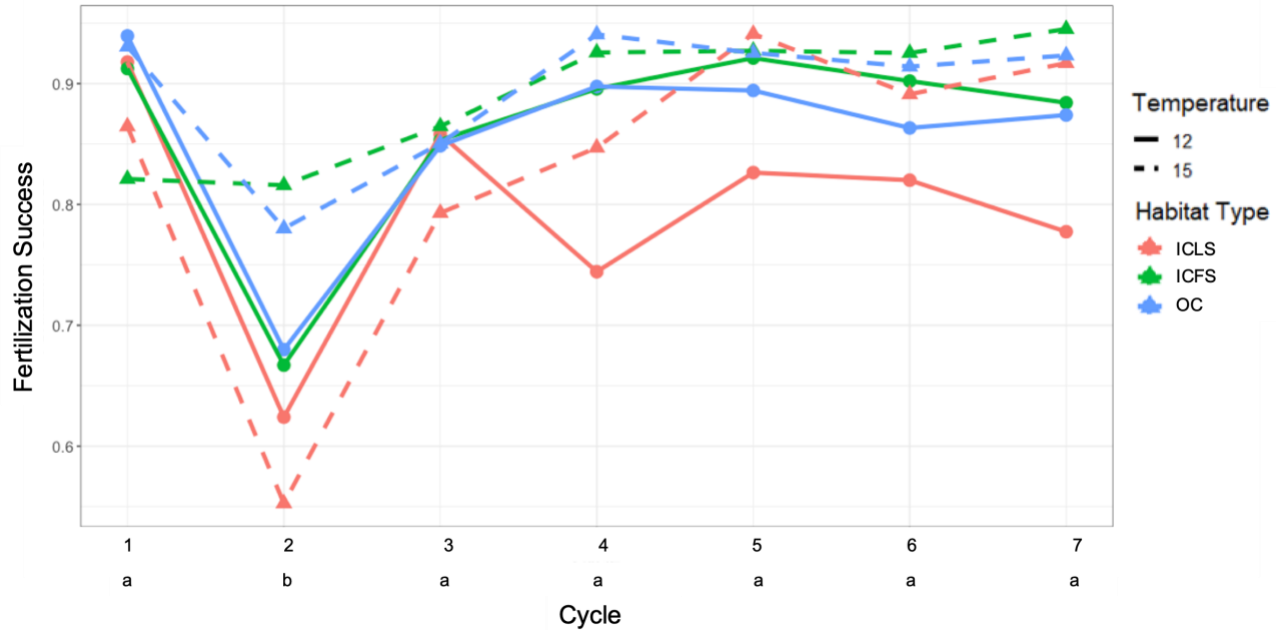
Figure 2: Three-Way Interaction of Temperature, Habitat and Date on Reproductive Output of *Fucus distichus*

Visualization of the three-way interaction of temperature, habitat, and cycle on the reproductive output of *Fucus distichus*. Solid colored lines represent the average reproductive output of the 12ºC treatments and dashed colored lines represent the average reproductive output of the 15ºC treatments. Red lines represent the average reproductive output of the Inner Coast Low-Salinity (ICLS) sites (n = 3), green lines represent the average reproductive output of the Inner Coast Full-Salinity (ICFS) site (n = 3), and blue lines represent the average reproductive output of the Outer Coast (OC) sites (n = 3). The relationship between Habitat and Temperature was affected by the Cycle, with the Habitat-Temperature interaction differing during Cycle 2 from all other cycles (Cycle 1: $p<0.001$, Cycle 3: $p<0.05$, Cycle 4: $p<0.01$, Cycle 5: $p<0.001$, Cycle 6: $p<0.05$, Cycle 7: $p<0.01$). Comparisons between cycles marked with the same letter (i.e., a or b) are not significantly different from each other.
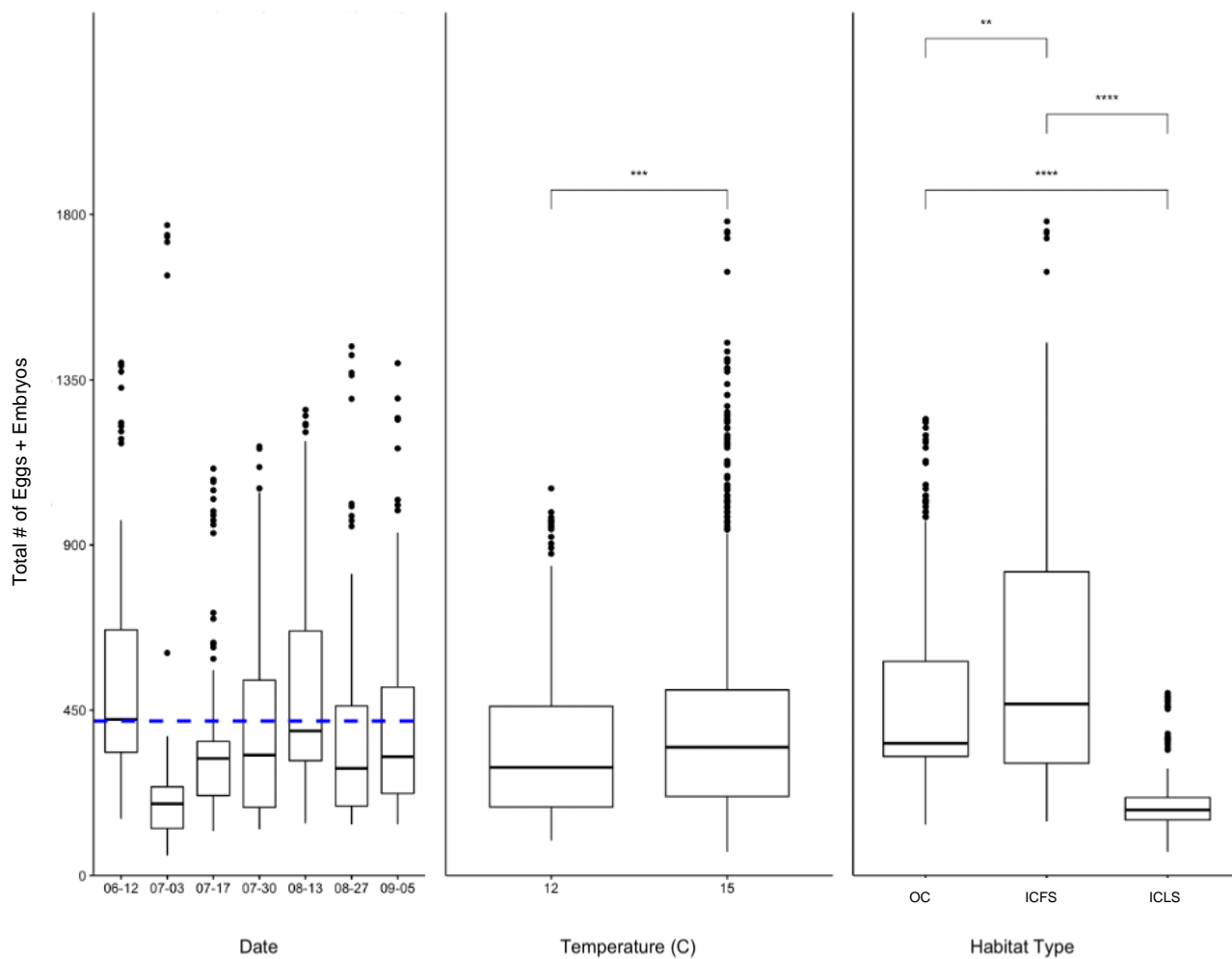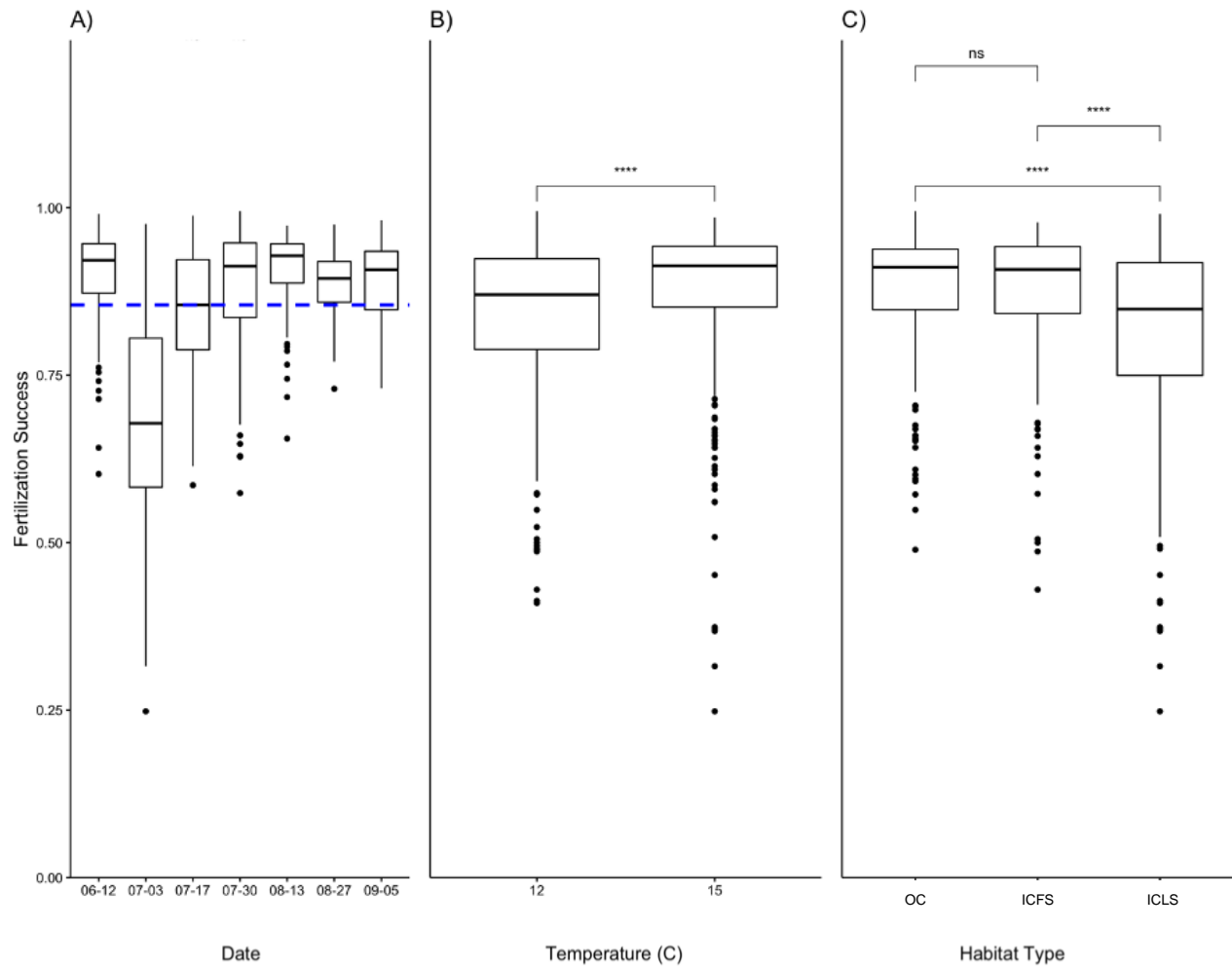
Figure 3: Reproductive Output Treatment Comparisons

Mean *Fucus distichus* reproductive output (total number of eggs and embryos of 4 receptacles from a single individual) of each A) Cycle, B) Temperature, and C) Habitat Type. The blue line in A) indicates the mean across every Cycle. Bars indicate interaction between treatment levels. Stars indicate the level of significance of differences based on a Tukey post-hoc test (* ≤ 0.05, ** ≤ 0.01, *** ≤ 0.001, **** ≤ 0.0001, ns = not significant).

Figure 4: Three-Way Interaction of Temperature, Habitat and Date on Fertilization Success of *Fucus distichus*

Visualization of the three-way interaction of temperature, habitat, and cycle on the fertilization success of *Fucus distichus*. Solid colored lines represent the average fertilization success of the 12ºC treatments and dashed colored lines represent the fertilization success output of the 15ºC treatments. Red lines represent the average fertilization success of the Inner Coast Low-Salinity (ICLS) sites (n = 3), green lines represent the average fertilization success of the Inner Coast Full-Salinity (ICFS) sites (n = 3), and blue lines represent the average fertilization success of the Outer Coast (OC) sites (n = 3). The relationship between Habitat and Temperature was affected by the Cycle, with the Habitat-Temperature interaction differing during Cycle 2 from all other cycles (Cycle 1: $p<0.001$, Cycle 3: $p<0.001$, Cycle 4: $p<0.001$, Cycle 5: $p<0.001$, Cycle 6: $p<0.001$, Cycle 7: $p<0.001$). Comparisons between cycles marked with the same letter (i.e., a or b) are not significantly different from each other.

Figure 5: Fertilization Success Treatment Comparisons

Mean *Fucus distichus* fertilization success (Ratio of fertilized embryos to all (fertilized and unfertilized) eggs of 4 receptacles from a single individual) of each A) Cycle, B) Temperature, and C) Habitat Type. The blue line in A) indicates the mean across every Cycle. Bars indicate interaction between treatment levels. Stars indicate the level of significance of differences based on a Tukey post-hoc test (* ≤ 0.05, ** ≤ 0.01, *** ≤ 0.001, **** ≤ 0.0001, ns = not significant). NS indicates no significant difference between treatment levels.