SPECIAL ISSUE-CURRENT EVIDENCE

Risk to native marine macroalgae from land-use and climate change-related modifications to groundwater discharge in Hawai'i

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Scientific Significance Statement

Coastal groundwater-dependent ecosystems and associated species, including native macroalgae, are highly adapted to the lowered salinity and nutrient subsidies of natural flows of submarine groundwater discharge (SGD). However, with climate and land-use change-induced shifts in SGD, invasive macroalgae are outcompeting native species, with drastic implications for these important ecosystems. This article contributes to a synthetic understanding of these processes by providing a salient case study from O'ahu, Hawai'i, and by reviewing evidence on the links between SGD and the composition of macroalgal communities. Results point to the critical importance of sound land, water, and wastewater management policies to reduce impacts on SGD and native coastal groundwater-dependent ecosystems, particularly in the context of climate change.

Abstract

Coastal groundwater-dependent ecosystems benefit from lowered salinity, nutrient-rich submarine groundwater discharge (SGD). Across Pacific islands marine macroalgae appear to have been challenged by and adapted to the stress of lowered salinity with a trade-off of nutrient subsidies delivered by SGD. Human alterations of groundwater resources and climate change-driven shifts brought modifications to the magnitude and composition of SGD. This paper discusses how native macroalgae have adapted to SGD nutrient and salinity gradients, but that invasive algae are outcompeting the natives near SGD with nutrient pollution. It is important to re-evaluate land and water use practices by modifying groundwater sustainable yields and improving wastewater infrastructure to keep SGD reductions minimal and nitrogen inputs in optimal ranges. This task may be particularly challenging amidst global sea level rise and reductions in groundwater recharge, which threaten coastal groundwater systems and ecosystems dependent on them.

Discharge of fresh and brackish groundwater along coastlines worldwide delivers a ceaseless supply of nutrient-rich water that sustains coastal groundwater dependent ecosystems (GDEs) (Kløve et al. 2014; Rohde et al. 2017). In unperturbed, natural watersheds, groundwater delivers ecologically optimal levels of nutrients from natural sources with a rate of groundwater discharge and salinity varying naturally with hydrological seasons and ocean levels. Human disturbed watersheds, particularly those with urban development and conventional agriculture, however, show a common theme of problems. Downstream of these areas, submarine groundwater discharge (SGD) can be polluted by nutrient-polluted wastewater (Dailer et al. 2010; Richardson et al. 2017a), agricultural fertilizer inputs (Valiela et al. 1997; Bishop et al. 2017), and even common-use pharmaceuticals (McKenzie et al. 2020) and pesticides (Welch et al. 2019). In addition, many springs in Hawai'i and elsewhere that were documented to be fresh in the past are now brackish as human withdrawals deplete coastal aquifers and changes in land use reduce recharge and groundwater flows, which contribute to seawater intrusion into coastal aquifers (Kelly et al. 2019). Furthermore, climate change-driven seasonal variation in precipitation directly influences recharge patterns and sea level rise amplifies seawater intrusion and salinization of coastal groundwater. SGD that supports precious coastal GDEs and cultural resources is therefore threatened on multiple fronts (Boulton 2020) (Fig 1).
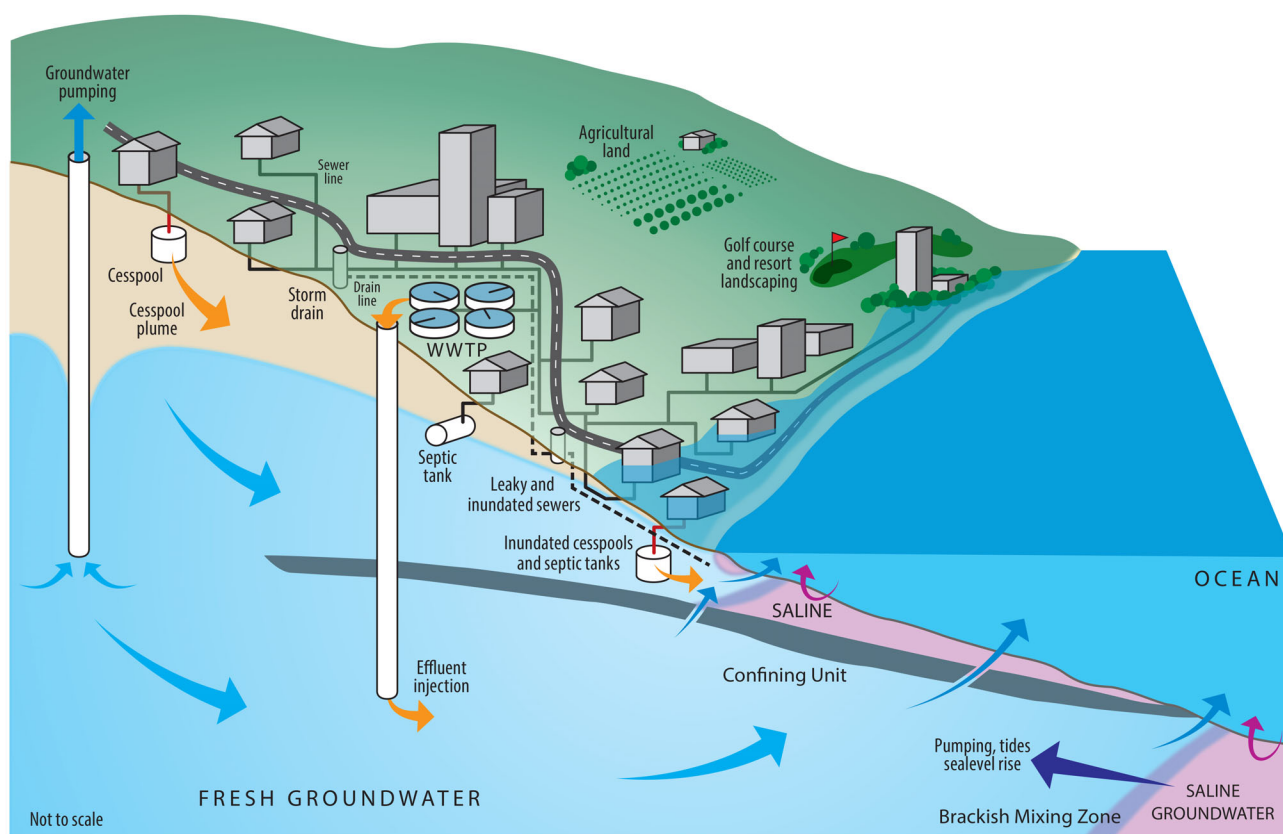

Fig. 1. A schematic representation of coastal hydrology highlighting prevalent groundwater flow (light blue arrows) and seawater intrusion (dark blue arrow), also indicating SGD, which is composed of terrestrial freshwater (light blue arrows) and saline groundwater discharge (pink arrows) across the land-ocean interface. The flow patterns are affected by natural recharge, but also by anthropogenic effects including groundwater withdrawal and altered recharge and flow patterns due to build infrastructure, as well as augmentation by wastewater effluent injection, leakage from wastewater infrastructure (sewer lines, cesspools, and septic tanks), and irrigation (agriculture and landscaping). Many of the latter also affect the nutrient budgets of groundwater. This paper explores the combined effects of salinity and elevated nitrogen, the major sources of which are wastewater and fertilizers, as well as manure and animal feedlots (not typical for Hawai'i but relevant for example in American Samoa; Shuler et al. 2017). Wastewater is gaining attention in Hawai'i as the state focuses on the upgrade of > 80,000 cesspools still in operation. Especially those along the shoreline are subject to subsurface inundation. In fact, subsurface inundation due to extreme tides and sea level rise already causes sunny-day flooding (represented by the blue hue along the shoreline), the significance of which for our purposes is that it floods streets, flushes sewer lines, storm drains, cesspools, and septic leach fields directly into groundwater which then readily delivers nitrogen and other contaminants via SGD to the coastline (McKenzie et al. 2021). Across multiple islands in Hawai'i, it has also been realized that treated wastewater effluent injected near the coastline also surfaces in the nearshore region—even in areas where the injection protrudes below confining layers, because of discontinuities in those layers (Fackrell et al. 2016; Amato et al. 2020). Illustration by Brooks Bays, SOEST Publication Services.

Submarine groundwater that discharges as coastal springs in considerable volumes affect coastal salinity and chemistry, driving bottom-up effects on ecosystems. Spring discharge is dynamic, and most importantly it is affected by seasonal precipitation patterns and sea level fluctuations (Gonneea et al. 2013) and by daily tides (Dulai et al. 2016). So, while discharge is continuous, its magnitude and composition vary. Because of the dynamic nature of SGD and significant dilution of groundwater plumes by flood tides and currents, coastal organisms near springs and diffuse benthic discharges are exposed to large shifts in water quality parameters. These may range from < 10% of ocean water to full ocean composition, from nutrients that are comparable to offshore levels to two-three orders of magnitude higher, and changes from negative to positive aragonite saturation levels, all with each low-to-high tide switch, roughly twice a day (Richardson et al. 2017b).

While SGD provides nutrients and moderate temperatures, reef plants and benthic animals are subject to and tolerate, if not thrive, in these twice-a-day tidal, large salinity and nutrient shifts. For example, native macroalgal species are likely to have evolved under conditions of natural SGD inputs throughout the Hawaiian Islands where coastal springs and seeps occur (Huisman et al. 2007). These fresh, nutrient-rich plumes provide a subsidy of nitrogen, while providing stress in the diurnal transition between salinities from fresh SGD influence at low tide to saline marine waters during high tide. For marine plants, there is a trade-off between salinity stress and nutrient availability. This is likely to have led to niche partitioning along the zone of SGD influence by marine plant species, with some taking full advantage of SGD borne nutrients with strong tolerance for variable salinity, and others hedging their bets with some intermediate salinity tolerance and weaker nutrient subsidies. In Hawai'i, native, brackish-water adapted species that are known to occur in SGD influenced systems include *Gracilaria coronopifolia*, *Gracilaria parvispora*, *Ulva lactuca*, tubular *Ulva* species, and *Cladophora* spp. (Huisman et al. 2007). Many more tropical native algae are also likely to favor SGD but remain unstudied.

Over the last century, in particular, anthropogenic land-use change has altered watershed function to a significant degree (Bunsen et al. 2021). One example of an extreme change is the Pearl Harbor or Pu'uloa aquifer located in O'ahu, the most populous island in Hawai'i. Irrigation water demands for agricultural activities such as sugarcane and pineapple cultivation since the turn of the 20th century have led to a diminishing number of artesian springs on land, decreasing stream flow (Oki 2005) and salinization of coastal springs (Engels et al. 2020). While sugar and pineapple are largely gone from O'ahu (with the last sugar plantation in 'Ewa closing in the 1990s), the Pu'uloa aquifer continues to be highly utilized as the main source of drinking water for the island of O'ahu. Recent work suggests that current sustainable yield estimates may be too high to adequately protect SGD and springs (Burnett et al. 2020), particularly under climate change

(Bremer et al. 2021). SGD at Pu'uloa was recently quantified at 250,000 m^3 d^{-1} (Kelly et al. 2019) in comparison to an estimated pre-development volume of 750,000 m^3 d^{-1} (Oki 2005). The harbor has undergone significant environmental degradation, with the decrease in freshwater flow, water contamination, and introduction of nonindigenous species being the largest threats (Coles et al. 1999).

Macroalgal community structure may change due to modifications to SGD volume, salinity, and nutrient concentrations but also with the introductions of non-native macroalgae. Native and invasive macroalgal species have been documented to reach bloom conditions in extensive areas near SGD seeps with nutrient pollution. In coastal Maui waters, invasive algal species, *Cladophora sericea*, *Ulva lactuca*, and *Hypnea musciformis* persistently bloomed in regions near wastewater treatment plants during the 1990s (Smith et al. 2005; Dailer et al. 2012). Native *Dictyosphaeria cavernosa* also bloomed extensively in Kāne'ohe Bay in the 1970s before the Kāne'ohe sewage diversion (Smith et al. 1981). Overall, blooms of invasive species occur in regions impacted with sewage or effluent discharges—*H. musciformis* in Maui, *Gracilaria salicornia* on several sites in O'ahu, or suspected discharges that could explain dominance of *Eucheuma denticulatum* and *Kappaphycus alvarezii* in Kāne'ohe Bay.

Despite such widespread evidence of SGD's bottom-up influence on GDEs, there is a limited number of studies that combine coastal hydrology and its change over time with the evolution of algae and their adaptation to changing coastal hydrological and chemical conditions. The objective of this study is to use Wailupe, O'ahu (HI, USA), as an example of a site where algal studies can be matched with SGD measurements to gauge plant responses to large ranges in salinity and nutrients, over relatively small distances. We discuss how native macroalgae have adapted to SGD nutrient and salinity gradients. We also look at reasons why native macroalgae are outcompeted by invasive ones near SGD sites with steep salinity gradients and nutrient pollution.

In the case study of the reef at Wailupe, we have a remarkable opportunity to bring the hydrologic information collected about a spring-seep complex, to the issues of impacts on the marine plant community to derive broader conclusions about the impacts of SGD on benthic communities and food webs. While the evidence provided here is drawn from Hawai'i, the points deduced are relevant to coastal environments across the Pacific and beyond, where climate and human perturbations affect coastal aquifer salinities and nutrient levels. Also, because salinity and nutrient concentrations are interdependent in SGD affected sites, we explore their combined effects.

Case study of Wailupe as a polluted urban reef

Wailupe is one of the primary regions of SGD in the roughly 8-km long Maunalua Bay, O'ahu, Hawai'i (Fig. 2).
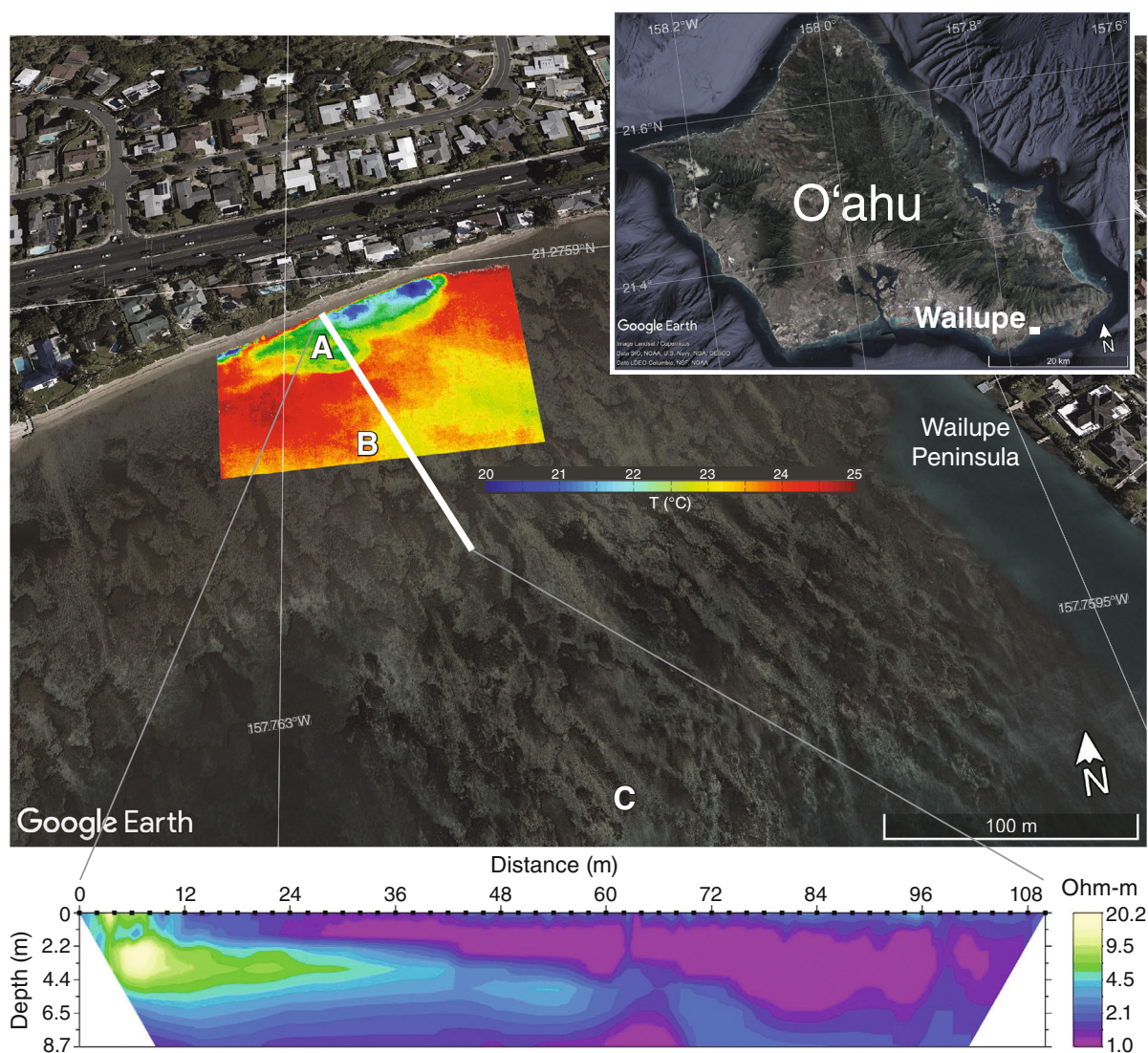
Fig. 2. At Wailupe, SGD has been mapped using thermal infrared imagery according to methods and using instrumentation of Lee et al. (2016). Data provided by Lee (pers. comm.; Lee and Dulai 2021). Temperatures are given in °C and warm ocean colors are indicated by red, and cool coastal springs and seepage by blue and green colors. Subsurface resistivity reveals freshening of the coastal aquifer out to at least 60 m offshore (Dimova et al. 2012) where the white to green colors indicate more resistive fresh/brackish water and the purple represents conductive salty pore water. The high resistivity in the nearshore region in the subsurface profile matches the location of the springs identified using temperatures in the surface water. For the algae growth experiments, site A is located immediately in the area affected by the springs, site B is located in the transition zone with intermittent, and significantly diluted SGD influence, and site C experiences no SGD inputs (Amato et al. 2018). Illustration by Brooks Bays, SOEST Publication Services.

The embayment is on the eroded southeastern flank of the Ko'olau Volcano shaped by stream erosion, secondary volcanic deposits, and higher stands of sea level. Groundwater discharges through regions where high-permeability volcanic rocks outcrop through otherwise low permeability Quaternary calcareous sediments (Eyre et al. 1986). At Wailupe, groundwater discharges through about five distinct major springs fed by preferential flow through subsurface conduits as well as a wider seepage face along the coastline at low tide line on top of a lower conductivity layer (Fig. 2). Tidally

averaged SGD within Wailupe amounts to 6500–13,000 m^3 d^{-1} (Dimova et al. 2012; Richardson et al. 2017a). The nearby Wailupe Stream only provides intermittent flow during periods of extended rainfall (Eyre et al. 1986); SGD is the major freshwater and nutrient runoff pathway that persists year-round.

Currently, the Wailupe area is developed for residential use. As recently as the beginning of the 20th century, the characteristic land use was small-scale farming and the coastal plain was characterized by marsh areas, brackish springs, and

fishponds. These were filled in to make way to coastal urban development. While multiple aquifers on the island have experienced severe drawdown due to groundwater withdrawal for municipal and agricultural uses, there is very little withdrawal from the aquifer feeding SGD at Wailupe. Current and pre-development water budgets are suggesting unchanged groundwater budgets (Eyre et al. 1986). Coastal development, however, has resulted in modifications of subsurface groundwater conduits resulting in severe decrease or disappearance of coastal springs and drydown of coastal ponds (Erlens and Athens 1994). Coastal spring discharges have decreased and their salinities have increased. In the absence of actual measurements, anecdotal evidence and historic photographs from the turn of the 20th century show horses drinking from coastal springs wading in knee deep ocean water. The current higher salinities would prevent horses from drinking that spring water although dogs are still observed to drink from a few that preserved their low salinity.

Review of methods applied to map and quantify SGD and their relevance to algal studies

Several studies have advanced our understanding of the complexity of coastal hydrology in island settings. Thermal infrared (TIR) imagery works extremely well in tropical high island environments, where discharging cold groundwater can be distinguished from warm ocean surfaces. Johnson et al. (2008) revealed m-to-km scale groundwater plumes emanating from the young basaltic shoreline predominantly as coastal springs in West Hawai'i. In contrast, coastal discharge through caprock in O'ahu and Maui is often a mixture of diffuse seepage and spring discharge (Kelly et al. 2019). Although infrared thermal imagery provides a large-scale view of discharge to the ocean surface, it cannot determine if the buoyant brackish plumes directly influence benthic organisms. This can be assessed by measuring salinity and nutrients at depth or producing depth profiles to assess mixing conditions in the water column. Often groundwater emanates directly from the ocean floor allowing benthic organisms to differentially settle and grow around seep locations, based on the species' physiology. These seeps and springs are fed by subsurface conduits that can be imaged using electric resistivity imaging (Dimova et al. 2012). The images provide information on spatial distribution and temporal variability of fresh/brackish groundwater in the subsurface that can be matched with benthic algal maps. Salinity, silica, radon, radium, and other geochemical tracers have been applied to quantify SGD based on their coastal mass balances (Taniguchi et al. 2019). Because of the dynamic nature of SGD, the long-term observations are the most helpful in understanding the nuances of groundwater discharge and its effects on coastal geochemistry and ecosystems (Richardson et al. 2017a,b). Algae have been shown to integrate chemical signatures from the water over days, for example as has been shown for $\delta^{15}N$ values of algal tissue that

reveal surprising fine-scale detection of wastewater in coastal regions (Dailer et al. 2010, 2012; Amato et al. 2020). Predictable near-conservative mixing relationship between salinity and nutrients can be used to estimate nutrient concentrations from extended salinity measurements (Bishop et al. 2017; Richardson et al. 2017a; Amato et al. 2018).

Here, we report on SGD spatial distribution, as well as discharge rates and coastal salinity fluctuations observed over a 28-d tidal cycle around a major spring at Wailupe, O'ahu (Richardson et al. 2017a). We apply the hydrological and water chemistry observations to algal physiology and their expected/observed form and distribution.

Hydrological observations

Subsurface geophysical electrical resistivity imaging (Dimova et al. 2012) provided enhanced detail of coastal groundwater exchange and associated salinity distribution and fluxes at Wailupe (Fig. 2). The images taken in time steps over a tidal cycle show clear enhanced upward fresh groundwater flow at low tide and seawater intrusion at high tide, with the largest salinity changes in the subsurface extending beyond 10 m offshore. Despite tidally driven discharge and recharge patterns, the cores of the springs had a relatively constant salinity of 1–7 throughout the tidal cycle. SGD estimates from coastal geochemical budgets of radon (Richardson et al. 2017a) confirm this tidal discharge–recharge pattern. Discharge from one of the major springs fluctuates from 0 to 2000 m^3 d^{-1}, with a tidally averaged flow of 640 ± 360 m^3 d^{-1} over 28 d. SGD being the sole source of freshwater results in coastal salinities and nitrate concentration ranges of 13–35 and 0.3–40 μM, respectively. Temperature distribution shows the extent of spring plumes in the surface water and also the seepage line along the coastline (Fig. 2).

During the study period in August 2015, salinity was within the maximum growth range of some algae species of 18–28, as adapted and modified from Amato (2015; Amato et al. 2018, see below) for 2.6 ± 2.2 daylight hours per day, with some days having 0 and some as much as 8 h in that salinity range during daylight hours (Fig. 3). The spatial extent of the area experiencing these freshened conditions can be estimated from TIR images (Fig. 2), salinity and nutrient spatial surveys (Nelson et al. 2015; Richardson et al. 2017a), and spatially distributed salinity sensor deployments (Lubarsky et al. 2018). The area affected by the springs at low tide extends to about 10,000 m^2.

What does SGD mean for reef algae?

The majority of marine algae species are intolerant of freshwater or hyposaline conditions as shown by tissue death and species replacement along a gradient of freshwater to ocean salinities. In most cases, plant sizes are smaller at reduced salinity (Norton et al. 1981). Species tolerant of some

hyposalinity may modify osmotic relations within cells to acclimate to lowered salinities. Other studies have shown that some species alter their morphologies and apical tip formation in response to tolerated, but lowered salinities (*see* Supplemental Materials for detailed examples of salinity impacts on tolerant reef algae). Increased branching has been observed under hyposaline conditions in all of the major algal lineages, such as *Grateloupia filicina* (Zablackis 1987), *Chondrus crispus* (Mathieson and Burns 1975), *Fucus vesiculosus* (Jordan and Vadas 1972), and *Ulva intestinalis* (Reed and Russell 1978). Here, we discuss additional benefits of SGD accrued by native tropical algae in response to synergies in field conditions presented by SGD seeps: hyposaline osmotic pressures/increased nutrient availability/cooled water temperature combinations. Exposure to SGD promotes striking responses in physiology and ecology in recently studied species of *Gracilaria* in Hawai'i and may point to fascinating evolution of novel traits among algae of SGD-influenced ecosystems.

The ability to acquire major limiting factors ultimately governs the competitive abilities of almost every plant. Understanding the nitrogen budget of marine plants thus becomes key to understanding competitive interactions on reefs where there are clear winners and losers, the mechanism of impact

for some invasive species, as well as allowing us to project possible future impacts of climate change-associated alterations in sea level, rainfall, and aquifer recharge. For marine plants, the nitrogen budget has at least three important early components, despite knowing that the timing of these processes can vary substantially across macroalgal genera. Wheeler (1983) defines the three stages as *uptake*—removal of nitrate from the environment and physical transport into an alga; *assimilation*—the processes by which nitrate is used to form small organic molecules, such as amino acids; and ultimately *incorporation*—the processes by which nitrogen-containing organic molecules are combined to form macromolecules built of amino acids (Berges 1997).

For a given individual plant anchored in and under the influence of the SGD flow such as illustrated in Fig. 3, we can anticipate that uptake kinetics for nitrate govern the extent of nitrate uptake and ultimately assimilation and incorporation (there is little ammonium in SGD flows; Fig. 3d).

By example, Liu et al. (2016) report that *Gracilaria lichenoides* has a particularly high rate for removing nitrate from the environment at a rate of over 60 μmol g^{-1} dry wt h^{-1} by the enzyme nitrate reductase (NR) as a first step. If typical dry weights for *Gracilaria* are 7.2% of the wet weight
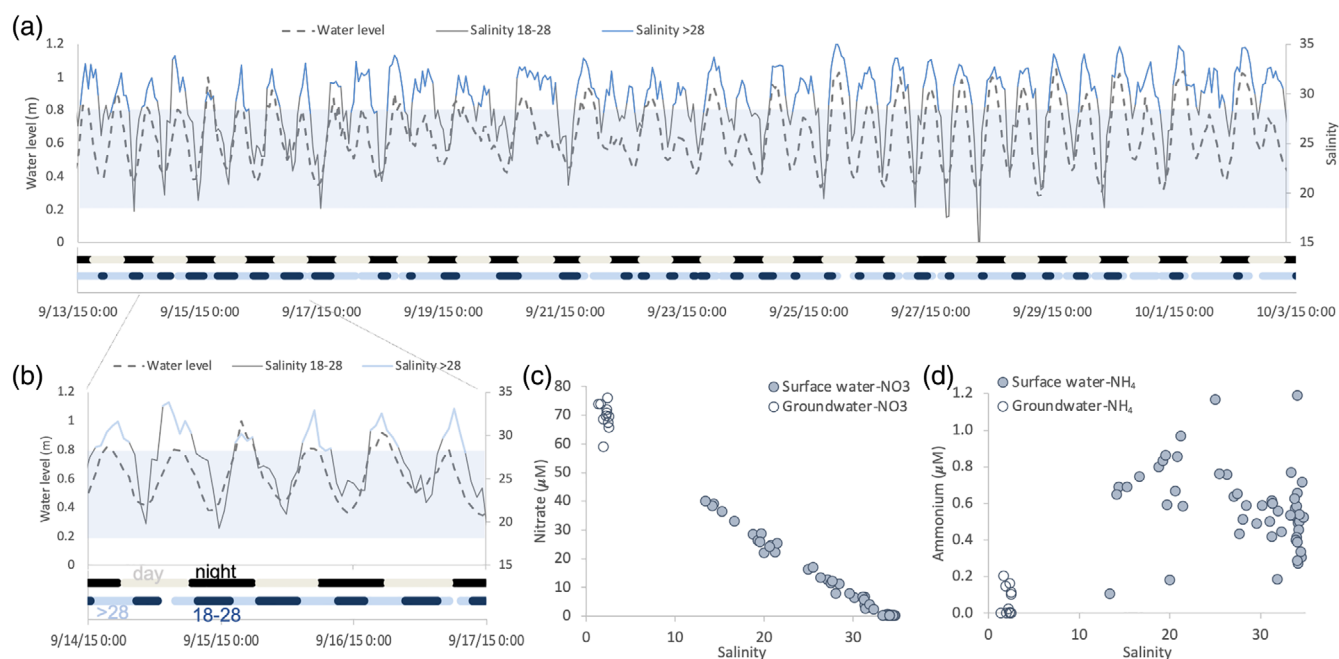

Fig. 3. Hourly salinity and water level data (Dulai 2021) measured 0.3 m below the surface and a 5 m lateral distance from a major spring at site A in Fig. 2 over (**a**) a 28-d tidal period and (**b**) a 4-d inset from that period at Wailupe, O'ahu. The dashed line shows water level, the darker sections of the salinity record indicate a salinity range of 18–28, and the light blue sections indicate salinity above 28. The bars at the bottom of panels (**a**) and (**b**) show daytime and nighttime hours as well as the duration of salinity intervals > 28 (light blue) and 18–28 (dark blue). These dark blue sections on panels (**a**) and (**b**) therefore represent maximum growth conditions for *Gracilaria* species at salinities of 18–28 and nitrate of 12–34 μM as defined by Amato et al. (2018)—they observed elevated growth rates between 19 and 27 (Fig. 5) and for the purpose of this analysis this range was simplified to 18–28 to capture the maximum growth range. Nitrate (**c**) is highly elevated in coastal springs and salinity is a good predictor of expected water column nitrate concentrations due to its almost conservative mixing with offshore waters (Richardson et al. 2017a). The coastal springs are not a major source of ammonium to the water column and there is no conservative mixing line of ammonium concentrations with salinity (**d**).

(Capo et al. 1999) and these hold for other species of *Gracilaria*, then the actual uptake expressed on a fresh weight basis in living tissues is understandably slower at ~ 4 μmol acquired g^{-1} wet wt h^{-1}. A typical plant or large branch of *G. coronopifolia* as collected by Amato in Amato et al. (2018), may weigh 3–4 or more grams of wet weight, the entire surface of which is metabolically active in acquiring NO_3^- via uptake and assimilation.

Putting these uptake patterns in an ecological context, we find that on a diurnal basis, plants on a reef in that period of SGD influence from salinities of 18–28, would be exposed to nitrate levels ranging from 12 to 34 μM flowing past anchored plants (Fig. 3). Thin boundary layers over tissues of that 4-g plant associated with flow could lead to delivery of a minimum of approximately 6 μmol over a 0.4-h daylight period to a maximum of over 76 μmol of assimilated nitrate acquired per day for the 4.8-h daylight conditions (derived from 2.6 ± 2.2 daylight hours per day; Fig. 3). For a typical 4-g plant, daily exposure to SGD for less than 1 h would lead to nutrient limitation. As the length of the SGD exposures increases during the day, then a 4-g living plant could assimilate as much as 76 μmol per plant in that exposure, until daylight is lost, the tide finally turns and/or the plant is saturated in all its uptake and nitrate tissue storage.

Additionally, as suggested above, some studies indicate that certain algae can acquire and store nitrate without sunlight until enzymatic activity can resume in daylight hours (Roleda and Hurd 2019). Thus, luxury levels of this essential plant nutrient could also be captured via night-time storage, in what may be a species-specific trait. Not surprisingly, the role of osmotic potentials within reef plant cells subjected to these salinity ranges are not well understood but may be important in moderating uptake. Yet, the near constant flow of elevated nitrate past anchored plants is likely to allow those plants to acquire and assimilate nitrate for storage to a point of such surplus that plants are then limited by other inorganic nutrients, for example, phosphate. Such seep/spring sourced SGD profoundly enhances nitrate availability, uptake, and/or storage as well as assimilation by NR. This surplus of nitrate is in marked contrast to growth conditions offshore in fully marine settings.

If plants are anchored offshore, far away from seep influence, then we might expect our same model plant at 4-g fresh weight to become almost immediately nitrate-limited as nitrate availability at salinity 35 is < 1 μM (site C, Fig. 2). Ammonium concentrations at < 1 μM could possibly supply some of the N budget, associated with lower energetic costs for acquiring ammonium, yet that low concentration is likely to also limit plant growth.

Thus, given the same kinetics for nitrate uptake, those plants at the outer reef region—under limiting nutrient conditions—would sustain two imbalances. The first imbalance would be much reduced rates for diurnal nitrate assimilation tied to very low nitrate concentrations surrounding the plants. The second would be the limitation of almost no nitrate uptake and storage at night, regardless of nitrate availability. It is possible that these offshore plants would use ammonium as a primary N source, despite ammonium's very low levels, as discussed above.

In a long-term view, SGD seeps in reefs could provide strong selective pressures for many reef plants to evolve highly efficient nutrient uptake mechanisms that can operate day and night based on SGD delivery of nitrate. Substantial variation is already known to occur among *Gracilaria* species uptake rates (Smit 2002; Liu et al. 2016). Alternatively, there could be strong selective pressures on growth rates to favor ammonium as preferred source of nitrogen in non-SGD regions.

Complexity of native algal responses

Only a few native algae have been studied for growth rate as a function of salinity, while holding other factors constant. More ecologically relevant and interesting are the increasing number of studies that examine growth of native and invasive algae under field relevant conditions—varying salinity and nutrient concentrations as a combination of factors that we have shown are influenced by SGD.

By setting parameters constant for 16-d growth experiments, Amato et al. (2018) directly documents the impact of salinity and nutrient ratios for Hawaii's endemic *Limu manauea* or *G. coronopifolia*. This scheme does not account for more complex interactions where tidal mixing drives conditions from full seep conditions to full oceanic conditions; however, this scheme does allow us to focus on the impacts of SGD combinations of temperature, nutrients, and low salinities. The only other study that comes close demonstrated increased branching while growing *G. filicina* under only hyposalinity treatments (Zablackis 1987; other examples in Supplemental Material Figs. S1, S2).

Thus, under the influence of simulating SGD conditions, the acclimation potential as estimated by growth rate, photosynthetic features, branching habit, or morphology (tip score—an index that tracks change in branching) were evaluated via field and laboratory studies (Amato et al. 2018). Representative plants were collected from coastal settings. Their growth after 16 d in simulated SGD conditions is shown in four panels in Fig. 4. At the start of these experimental runs, plants with similar initial tip scores (ratio of tips to mass) were selected, and randomly placed in one of four treatments. Strikingly, the plants with greatest extent of new branches (highlighted by black arrows) formed after the growth period were not the plants in full strength seawater treatment but rather at salinity 27 with nitrate concentration of 26.6 μM (Fig. 4c). Even grown in salinity 19 (Fig. 4b), plants were readily able to add new branches and branch tips (*see* black arrows), although to a lesser extent. At the highest nutrient concentration, however, plants cultured in a much lowered salinity resulted in loss of tissues revealing a physiological intolerance by these younger apical tissues to extreme
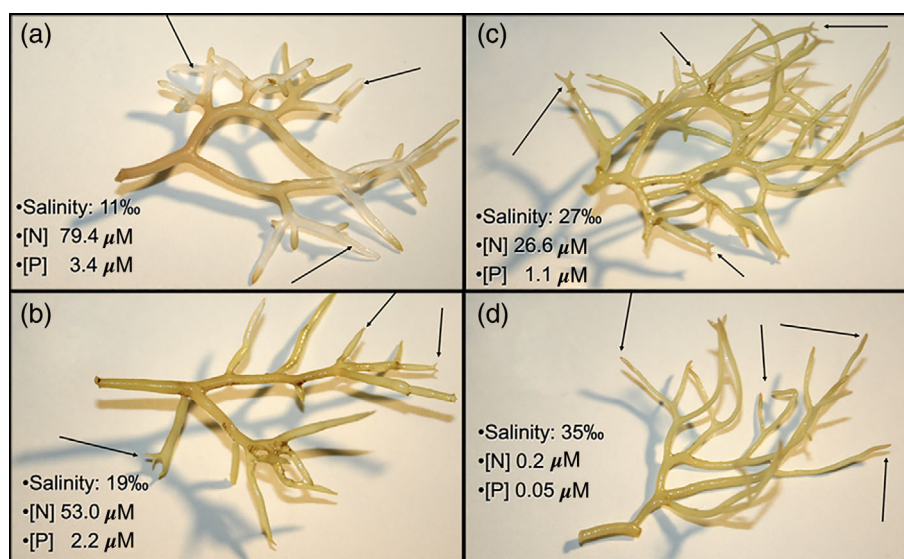
Fig. 4. Representative upper branches of *G. coronopifolia* after being grown for 16 d under simulated SGD conditions ranging from low salinity with elevated nutrient concentrations to oceanic conditions with limited nutrient availability. Initially, all plants were selected to have similar tip scores (Fig. 5) and were randomly placed in one of four treatments. (**a**) Representative plant grown in brackish water but elevated nutrient concentrations; (**b**) representative plant grown in 19 salinity but mid-range nutrient concentrations; (**c**) representative plant grown in 27 salinity but lower-range nutrient concentrations; and (**d**) representative plant grown in full seawater but minimal nutrient concentrations.

hyposalinity that could not be offset by 79.4 μM nitrate (Fig. 4a). Plants that came from the field and were randomly placed in full seawater at salinity 35 with appropriately very low levels of nutrients produced fewer new branches or were unable to grow at rates comparable to the plants grown in the 19–27 salinity range. These visual data reveal the extent to which SGD combinations had an unrecognized but significant effect on morphology of plants in this species. More branching leads to faster growth as well as more surface area for uptake of nutrients, both traits that are consistent with strong selective pressures by at least one species to favor SGD conditions.

Fastest growth rates promoted by SGD

Not only did plants in the salinity range from 19 to 27 outperform the full salinity treatment as well as the hyposalinity treatment of 11, from the visual assessments in Fig. 4, the plants under moderate SGD conditions also quantitatively produced more new branches (tip score), became bushy and grew faster (Fig. 5). Plants in the lowest salinity condition showed continued signs of physiological intolerance of salinity 11 by the low growth per day and fewest new branch tips produced, consistent with the tissue damages shown in Fig. 4. Finally, plants grown under conditions of full salinity and trace nutrient concentrations were unable to accelerate growth and yet did not show signs of tissue loss (compare Fig. 4). The plants in marine conditions did not maintain

significant new tip production, a surprise given that the plants were in their supposed native habitat, as "marine algae."

In combination, we can see the potential this species has for physiological adjustments to lowered salinities with elevated nutrients as parameters in SGD-rich habitats. This native species appears to be fully adapted to conditions where SGD delivers rich plumes of nutrients to mix with near shore waters, leading to high levels of productivity by at least this alga. In sum, moderate levels of simulated SGD increase numbers of branches in a plant that can then grow faster in two ways: by having more branches and by having higher rates of photosynthesis.

Invasive algal blooms

SGD seeps are also well-known sites in Hawai'i for invasive algal blooms. A number of studies have linked land-based sources of pollution to coastal discharges that set up competition of Hawai'i's notable invasive algae against the native marine flora (Smith et al. 2002). Anthropogenic influences change SGD in profound ways such that nutrient concentrations ramp up to excessive levels (Hunt Jr. and Rosa 2009; Amato et al. 2020). In those cases, we have been able to document changes in macroalgal community structure in a transect from adjacent to the Wailupe seep to offshore setting, with limited SGD influence.

Invasive algae on Hawaiian reefs are by definition non-native competitive dominants although the mechanisms underlying that dominance are likely to change with each
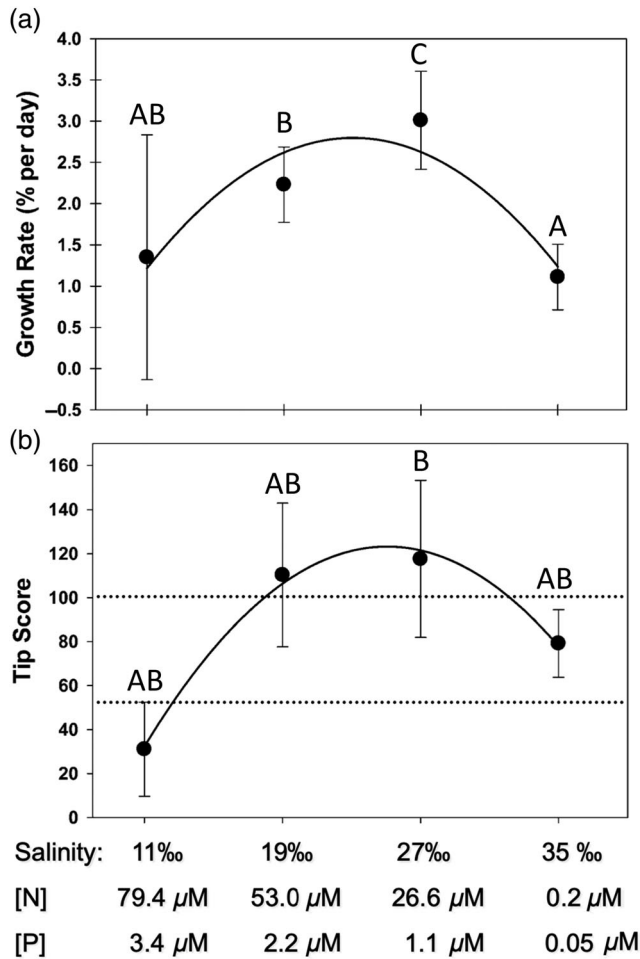
Fig. 5. Growth rate and tip score for *G. salicornia* under conditions of simulated SGD as indicated on the bottom of the figure (same as Fig. 4). Replicate plants were selected for growth for 16 d under controlled conditions that simulated SGD during two pooled trials. ANOVA results are added as letter categories above each point. (**a**) Shows mean growth rates by replicate plants under four simulated SGD conditions. (**b**) Shows tip scores of replicate plants under four simulated SGD conditions. Error bars indicate standard deviation of the mean at 1-sigma. The dotted lines indicate the starting range for tip scores of samples on day 0 of the trials. Data are from Amato et al. (2018).

Fig. 6. Benthic community analysis of the three sites at Wailupe, Oʻahu, from Amato et al. (2018). Transect ID letters refer to placement on an onshore offshore gradient matching sites A, B, and C as indicated on Fig.2 . Transect ID numbers relate to randomly chosen, 10 m transects positioned parallel to shore at each site. Site A transects A1–A5 were adjacent to the spring 25 m from shore. Site B transects B1–B5 were 81 m from shore. Site C transects C1–C5 were 337 m from shore and were relatively unimpacted by SGD. The proportion of dominant and other benthic categories is shown for each transect.

invasive species. In field settings, we find these invasive species close to seeps; their percent benthic covers tail off with offshore distance from SGD input(s). At Wailupe, the sites closest to the springs (Fig. 6) are dominated by two invasive species noted in red. Native turf algae and a native zoanthid follow to bring the cover to about 80% occupied by the living assemblage. These observations suggest that the two invasive algae, *G. salicornia* and *Acanthophora spicifera* are either superior competitors in nutrient acquisition, or possess broader tolerances to salinity ranges, or both states. Neither species has been investigated for these capacities.

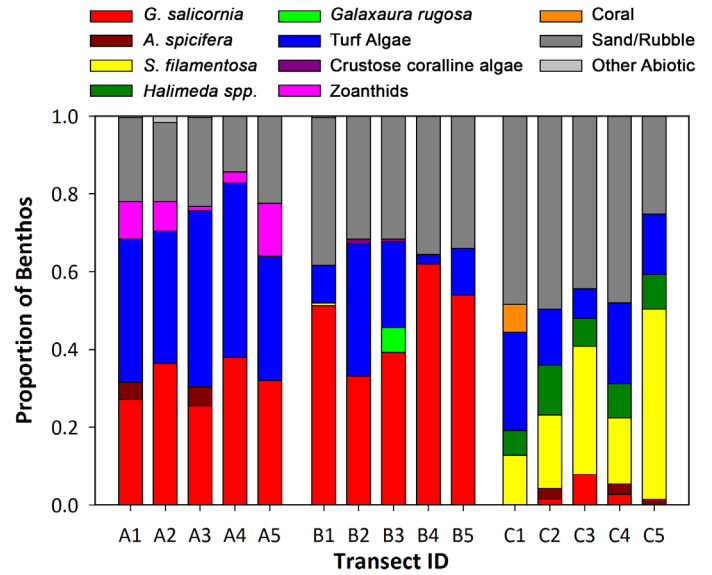Further offshore, where nutrient concentrations are at background levels, we find more diversity of native algae, and the near absence of invasive species and zoanthids. Ecologically, one can consider that the absence of SGD "levels the playing field," native species are not outcompeted by the non-natives and with that shift, we find greater species diversity (Fig. 6c) albeit, with lower growth rate due to nutrient limitations. In sum, moderate levels of wastewater in SGD at Wailupe illustrate how SGD appears to have changed the competitive interactions on this reef and allowed for increases in the invasive algae that outcompete native species, which are now found primarily in low productivity offshore locations.

Finally, our earlier *G. coronopifolia* discussion illustrates complexity of one species in physiological intolerance, branching, and growth rates. Other natives are not as well studied but the SGD influence on biomass is likely. Keeping SGD nutrient enrichment as close to pre-development levels as possible could minimize having communities dominated by competitively superior non-native species. From this single native species case study at Wailupe, the implications to our native flora are clear. Low-impact SGD is expected to lead to fewer invasive algal blooms and favor the return of native algae to on-shore parts of the reefs they likely once occupied.

Current status and future outlook

The various benefits of SGD to GDEs range from constrained muffled temperatures (Fujita et al. 2019), presence of

colder temperatures and lower salinities that have been linked to higher oxygen content that is beneficial and preferred by fish (Starke et al. 2020), and nutrient inputs that promote bottom-up regulation of food chains (Duarte et al. 2010; Starke et al. 2020).

This study delves deeper into the underlying effects of SGD. Algae integrate across a number of physical factors to live in a wide range of salinities, if that brackish water brings otherwise limiting nutrients. Yet, because these are pulsed deliveries but only available for a fraction of time each day, optimal conditions may exist for those few hours.

Unfortunately, there are multiple runaway effects resulting in changes in the magnitude, salinity, and nutrient content of SGD. Climatic effects are currently largely uncontrollable, sea level has been steadily rising, driving more seawater into coastal aquifers. Precipitation patterns have also changed resulting in lower recharge rates. But when we look at local factors, we recognize multiple ways how the deterioration of SGD could be reverted or prevented. Recharge can be improved by land-use choices through having more permeable urban surfaces and restoring native forests (Bremer et al. 2021). Lower groundwater withdrawal rates can be achieved by better management of water resources and water re-use (Burnett et al. 2020). SGD supports GDEs and hence SGD should be considered when establishing sustainable yields for coastal aquifers (Duarte et al. 2010) as required by the Hawai'i State Water Code and the public trust doctrine (Sproat 2009). Yet, sustainable yield in Hawai'i largely does not specifically incorporate springs, SGD, and streamflow, given the reliance on the simple Robust Analytical Model 2 (Burnett et al. 2020; Elshall et al. 2020), which does not explicitly consider ecological and public trust uses. Artificial recharge, although not yet applied in Hawai'i, has been used elsewhere to minimize seawater intrusion (Casanova et al. 2016).

A major local issue not just in Hawai'i and other Pacific Islands but also at continental coastal sites is that the aging and deteriorating wastewater infrastructure is becoming further compromised by sea level rise (Elmir 2018; McKenzie et al. 2021). There are numerous examples of inadequate wastewater treatment and effluent disposal practices (Hunt Jr. and Rosa 2009; Fackrell et al. 2016). Cesspools are a source of untreated wastewater and have been shown to contribute common ions that change groundwater salinity and excessive amounts of inorganic and organic dissolved nitrogen and phosphorus (Fig. 1). While centralized wastewater treatment systems are a huge step up from discharge of raw sewage from cesspools, they also need to be upgraded to meet increased demand and the need to eliminate not just nutrients but other contaminants of emerging concern. The highly conductive island hydrogeology is not ideal for onsite effluent disposal because of short distances to coastline and fast transport rates preventing proper bioremediation. Yet, where offshore effluent disposal is too expensive, the effluent is typically injected into the coastal aquifer leading to its discharge into nearshore shallow waters with drastic consequences (Dailer et al. 2010). While the treated effluent is lower in nutrients than raw wastewater, the effluent still elevates groundwater salinity and nutrient budgets, lowers pH and aragonite saturation levels, and increases coastal temperatures when it leaks into the nearshore areas (Hunt Jr. and Rosa 2009; Prouty et al. 2017; Richardson et al. 2017b; Amato et al. 2020).

Fresh SGD has been decreasing over time due to groundwater withdrawal. Excessive pumping creates saltier discharges, with lower nutrient concentrations to sustain plant production. This fundamental shift in SGD has the potential to limit food for herbivore grazing and ultimately food security for communities that rely on fishing for protein.

SGD provides lower salinity and optimal nutrient levels to coastal GDEs. Groundwater withdrawal and sea level rise causes salinization of coastal aquifers and a decrease in fresh- and brackish water discharge. While the lower discharge and resulting higher salinity in itself is a problem for some GDEs, the decrease in associated nutrient fluxes causes major disruptions to coastal food webs (Duarte et al. 2010). We may think then that for nutrient-polluted groundwater, the lowering of SGD improves coastal water quality, but does it? There is a fundamental ecosystem service provided by SGD in delivering optimal levels of nutrients to coastal communities. A complete elimination of any brackish groundwater carrying terrestrial nutrients will have a negative impact on GDEs, coastal primary productivity and species diversity. In addition, groundwater flow dilutes chemicals originating in wastewater in the coastal aquifer, and decreased flow will result in higher nutrient concentration in settings where attenuation within the aquifer is minimal. So, from the perspective of nutrient fluxes, this may be a zero-sum game: the product of concentration and discharge will result in the same amount of nutrients discharged into the coastal zone under high flow-high dilution and low flow-low dilution scenarios. The bottom line is that if we want to preserve native GDEs, we need to preserve SGD flow and keep associated nutrient loads in check. Keeping SGD as close to pristine as possible needs to be a goal, or we risk setting the stage for persistent, multi-year invasive algal dominance. We risk disruption of coral reefs and their food webs, loss of foods (fish, invertebrates, and macroalgae) for local residents, and a profound change in way of life.

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