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Author(s): B. D. Dudley, R. A. MacKenzie, T. S. Sakihara, H. Dulaiova, C. A. Waters, R. F. Hughes, and R. Ostertag

Source: Pacific Science, 68(4):509-523. 2014.

Published By: University of Hawai'i Press

DOI: <http://dx.doi.org/10.2984/68.4.5>

URL: <http://www.bioone.org/doi/full/10.2984/68.4.5>

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Influences of N-Fixing and Non-N-Fixing Vegetation and Invasive Fish on Water Chemistry of Hawaiian Anchialine Ponds¹

B. D. Dudley,^{2,3,5} R. A. MacKenzie,³ T. S. Sakihara,² H. Dulaiova,⁴ C. A. Waters,⁴ R. F. Hughes,³ and R. Ostertag²

Abstract: In coastal waters, it remains unclear how terrestrial invasive species might alter nutrient availability and thus affect bottom-up control of primary production. Anchialine ponds are tidal- and groundwater-fed coastal water bodies without surface connections that provide convenient model systems in which to examine terrestrial to aquatic nutrient flow. To investigate how N-fixing and non-N-fixing terrestrial vegetation and invasive consumers affect water quality, we compared dissolved nutrient concentrations and physicochemical parameters among Hawaiian anchialine ponds surrounded by: (1) the non-nitrogen (N)-fixing tree *Thespesia populnea* (milo), (2) the exotic N-fixing tree *Prosopis pallida* (kiawe), (3) no tree cover, and (4) no tree cover but containing populations of invasive poeciliid fish. Average (± 1 SE) concentration of dissolved inorganic nitrogen (DIN) across all ponds ($51.15 \mu\text{M} \pm 3.1$; $n = 17$) was high, but there was no discernible pattern among pond types. Model results suggest that leaf litter breakdown from the exotic N-fixing tree contributed $<0.02\%$ of total dissolved nitrogen (TDN) in the water column at high tide. However, additions of phosphorus (P), especially from litter of non-N-fixing *T. populnea*, resulted in ratios of DIN to soluble reactive phosphorus (SRP) that varied between 4.5:1 and 35:1 across pond types. Our study suggests that: (1) DIN concentrations were more dependent on watershed-scale N inputs than local tree cover or the presence of poeciliids, (2) low water residence times in these ponds reduce effects of local biota on water nutrient chemistry, and (3) P from anthropogenic inputs and/or biota cause alterations to DIN:SRP ratios in anchialine pond water that may potentially alter primary production rates in these coastal ecosystems.

¹ This research was made possible by funding from NSF-Hawai'i Experimental Program to Stimulate Competitive Research (EPSCoR) Grant No. EPS-0903833. Manuscript accepted 21 February 2014.

² Department of Biology and Tropical Conservation Biology and Environmental Science, University of Hawai'i at Hilo, 200 West Kāwili, Hilo, Hawai'i 96720-4091.

³ U.S. Department of Agriculture Forest Service, Pacific Southwest Research Station, Institute of Pacific Islands Forestry, 60 Nowelo Street, Hilo, Hawai'i 96720.

⁴ Department of Geology and Geophysics, University of Hawai'i at Mānoa, 1680 East-West Road, Honolulu, Hawai'i 96822.

⁵ Corresponding author (e-mail: bruce.dudley@niwa.co.nz).

COASTAL AND MARINE ecosystems across the globe have been impacted by anthropogenic alterations to nitrogen and phosphorus availability (Vitousek et al. 1997, Diaz and Rosenberg 2008). Because primary production is often limited by one or both of these nutrients, increases in their availability tend to increase growth and biomass of primary producers (Valiela et al. 1997) and may alter benthic and planktonic primary producer community structure (Cloern 2001, Karez et al. 2004). Higher trophic levels may be affected by resultant changes to food source availability (National Research Council 2000), reductions in oxygen availability (Diaz and Rosenberg 2008), and increased toxic algal blooms (National Research Council 2000). The impacts of anthropogenic nutrient additions have been well documented

(Galloway et al. 2003), but nutrient contributions of invasive species to coastal waters have been somewhat overlooked despite recent evidence that introductions of invasive species may affect nutrient availability in aquatic ecosystems (Mineau et al. 2011, MacKenzie and Bruland 2012, Wiegner et al. 2013). In response to human-driven homogenization of global biota (McKinney and Lockwood 1999) and large human populations in coastal areas (Halpern et al. 2009), situations are now arising where introductions of invasive species may affect nutrient availability and bottom-up regulation of primary production in coastal aquatic ecosystems.

Hawaiian anchialine ponds are aquatic ecosystems that have in many instances been altered by invasive plant and animal species (Bailey-Brock and Brock 1993, MacKenzie and Bruland 2012). Anchialine ponds typically form in coastal areas of porous bedrock, such as limestone deposits (e.g., the Yucatán Peninsula of southern Mexico) or depressions in recent lava flows, as found on the younger Hawaiian Islands (Holthuis 1973, Schmitter-Soto et al. 2002). These landlocked brackish-water bodies experience dampened tidal fluctuations via subsurface inputs of ground and oceanic water flows, creating hydrologic environments that are quite distinct from both terrestrial ponds and marine tidal pools (Holthuis 1973, Brock et al. 1987). In Hawai'i, where the global majority of documented anchialine ponds occur (>600) (Brock et al. 1987), ponds found along the leeward coasts of islands typically are surrounded either by dense stands of *Thespesia populnea* (milo) trees, exotic nitrogen (N)-fixing *Prosopis pallida* (kiawe) trees, or bare basalt. These leeward coastal environments receive much less rainfall than the windward coasts (Giambelluca et al. 2013). This low rainfall, coupled with the highly fractured nature of lava flows, results in ephemeral stream systems that contain surface flow only after major rainfall events (Oki 1999). The bulk of leeward rainfall occurs in high-elevation cloud forests, where groundwater recharge amounts to more than 250 mm per year (Oki 1999). There is abundant groundwater flow toward the coastline, which is the major hydrologic

connection of land to sea on this coast and the major freshwater input to these ponds (Holthuis 1973). Hawaiian anchialine ponds are not only hydrologically unique, they are also home to a diverse assemblage of aquatic invertebrates, fish, algae, and microbes (Maciulek 1986, Sakihara 2012a), including several invertebrate species endemic to Hawai'i (De Grave and Sakihara 2011, Ng 2011). However, the biological structure and functioning of many of these ponds are changing as a result of the presence of invasive fish and possibly from increases in water nutrient concentrations (Bailey-Brock and Brock 1993, Wiegner et al. 2006, Capps et al. 2009, Carey et al. 2010, MacKenzie and Bruland 2012, Dalton et al. 2013).

Benthic primary production in many Hawaiian anchialine ponds is released from bottom-up controls primarily though high nutrient availability, to the extent that top-down controls such as grazing pressure by the dominant and endemic atyid shrimp *Halo-caridina rubra* may not be sufficient to control benthic algal growth (Dalton et al. 2013). Urbanization, resort development, and human population size on the Kona coast of Hawai'i, the location of ca. 70% of Hawai'i's >600 ponds, are increasing rapidly (State of Hawai'i Department of Business, Economic Development, and Tourism 2007). Such changes are typically associated with increased nutrient additions to groundwater (Dollar and Atkinson 1992, Savage et al. 2010). However, high nutrient concentrations can also be found in anchialine ponds downslope from undeveloped watersheds along these coasts (Street et al. 2008, Knee et al. 2010). Nutrients derived from invasions of N-fixing plants have been identified as potential causal agents of this observation (Brock et al. 1987, Street et al. 2008). Nitrogen-fixing trees contribute to nitrogen loading in streams in a variety of ecosystems (Compton et al. 2003, Atwood et al. 2010, Mineau et al. 2011, Wiegner et al. 2013), and in coastal dry shrublands of leeward Hawai'i cattle grazing has led to replacement of many assemblages of native species by invasive grasses and exotic nitrogen-fixing tree species, particularly *Leucaena leucocephala* and *Prosopis pallida* (Cuddihy and Stone 1990,

D'Antonio and Vitousek 1992, Wagner et al. 1999). *Prosopis pallida* was first introduced to the island of O'ahu as an ornamental plant in the 1800s (Nelson and Wheeler 1963) and has since been planted throughout the main islands, growing most prolifically on the dry leeward coasts (Gallaher and Merlin 2010). The Hawai'i Gap Analysis Program (GAP) survey of satellite images taken between 1999 and 2004 estimated the land area covered by *Prosopis* forests and shrubland within the state at 58,766 ha, ca. 3.55% of the total land area of the Hawaiian Islands (Gon et al. 2006). A phreatophyte, *P. pallida* grows substantially larger in coastal areas where it is able to access groundwater, compared to upland areas (B.D.D., unpubl. data), and it forms dense monospecific stands around anchialine ponds. Trees of the genus *Prosopis* can add large quantities of fixed N to soils (Rundel et al. 1982), hence this species has the potential to alter nutrient availability and productivity in anchialine pond habitats through direct additions of nitrogen-rich litter.

Within aquatic systems, high densities of invasive fauna such as poeciliid fish may also increase water column nutrient concentrations (Angeler et al. 2002, Rowe 2007). *Poecilia reticulata* is a poeciliid species that was first introduced to Hawai'i for mosquito control in the early 1900s (Brock 1960) and has since continued to be introduced to aquatic ecosystems, where densities may be 10–30 × greater than those of native fish (MacKenzie and Bruland 2012, Holitzki et al. 2013). Such high densities can increase nutrient loading in coastal and fresh waters by remineralizing refractory benthic organic material into more labile and bioavailable dissolved forms (MacKenzie and Bruland 2012, Holitzki et al. 2013). Invasions of poeciliids have been identified as a global problem (Lowe et al. 2000, Alemadi and Jenkins 2008), especially in the western Pacific (Maciolek 1984, Rowe 2007).

Alone or in concert, invasive plants and fish may be responsible for changes in pond water chemistry and the benthic accumulations of organic material replacing epilithic algal communities in many anchialine ponds in Hawai'i (Bailey-Brock and Brock 1993,

Wiegner et al. 2006, Dalton et al. 2013). Here, we examined the effects of canopy trees (either N-fixing or non-N-fixing) and poeciliid fish on anchialine pond water chemistry. To calculate nutrient residence times and leaf litter-derived nutrient flushing rates in the ponds we used a radon mass-balance method in combination with water level measurements in a subset of ponds. We hypothesized that: (1) inputs of N-rich leaf litter would increase total dissolved nitrogen (TDN) relative to other pools; (2) poeciliid populations would elevate N levels due to sediment biomineralization; and (3) the presence of non-N-fixing and N-fixing vegetation would lower dissolved oxygen (DO) and pH values due to breakdown of leaf litter.

MATERIALS AND METHODS

Pond Classification

We examined effects of the invasive N-fixing tree *P. pallida*, non-N-fixing tree *T. populnea*, and invasive poeciliid fish communities on water quality of Hawaiian anchialine ponds spread along a ~45 km stretch of Hawai'i's leeward coast (Figure 1, Table 1). We compared water from ponds encircled by: (1) canopies of *T. populnea* (i.e., "Non-N-fixing"), (2) canopies of *P. pallida* (i.e., "N-fixing"), (3) no vegetative canopy cover (i.e., "open," typically surrounded by either bare lava or sparse grasses and where inputs of plant material were likely to be negligible), and (4) no vegetative canopy cover but where ponds contained populations of *P. reticulata* (i.e., "open with fish"). Non-N-fixing and N-fixing ponds were selected that had monospecific tree cover of either *T. populnea* or *P. pallida*, respectively. Water residence times were assessed for two further ponds not included in water sampling due to mixed-species canopy cover (i.e., "Radon").

Physical Pond Characteristics and Fish Densities

We measured pond surface area and depth within 1 hr of high tide. Pond depth was measured to the nearest centimeter at five points, across the long axis of each pond using a

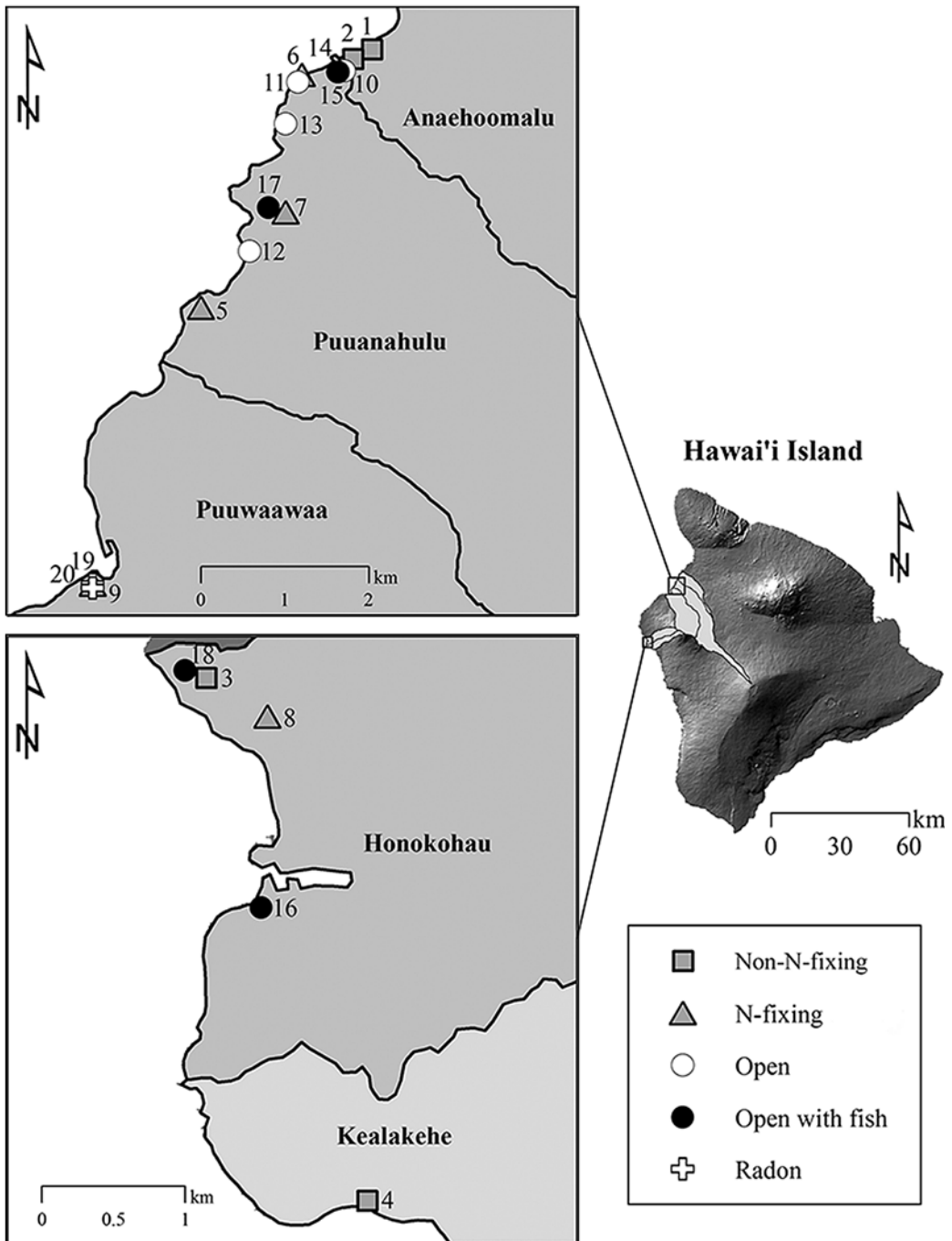


FIGURE 1. Study location with pond types in their respective watersheds on Hawai'i Island. Pond categories "Non-N-fixing" and "N-fixing" had monospecific tree cover of either *Thespesia populnea* or the invasive N-fixing tree *Prosopis pallida*, respectively. Ponds in the "Open" and "Open with fish" categories lacked overhanging vegetation and were typically surrounded by either bare lava or sparse grasses; ponds in the latter category contained populations of poeciliids. Ponds in the category "Radon" were sampled to assess water residence times.

TABLE 1
Physical Characteristics of Anchialine Ponds on Hawai'i's Leeward Coast

Pond	Classification	Area* (m ²)	Max. Depth* (m)	Max. Width* (m)	Average Time of Day Sampled (n = 6**)	Water Residence Time (hr)	Lat.	Long.
1	Non-N-fixing	11.73	0.4	3.0	1042 hours	—	19.91160	-155.89053
2	Non-N-fixing	9.1	0.45	4.2	1056 hours	—	19.91071	-155.89269
3	Non-N-fixing	17	0.55	5.0	1157 hours	—	Available on request	
4	Non-N-fixing	5.87	0.4	2.2	1144 hours	—	Available on request	
5	N-fixing	9.25	0.55	2.5	1043 hours	—	19.88416	-156.03055
6	N-fixing	2.59	0.68	2.3	1106 hours	—	19.90903	-155.89855
7	N-fixing	45.5	0.7	4.2	1021 hours	4.60	19.89428	-155.90067
8	N-fixing	8.84	0.65	3.5	1159 hours	—	Available on request	
9	N-fixing	0.91	0.7	1.3	1000 hours	1.90	19.85457	-155.92339
10	Open	9.8	0.45	1.5	1058 hours	—	19.90934	-155.89372
11	Open	7.65	0.95	1.7	1114 hours	—	19.90825	-155.899
12	Open	11.75	0.6	2.8	1121 hours	—	19.89015	-155.90485
13	Open	34.24	0.8	14.0	1158 hours	—	19.90379	-155.9005
14	Open with fish	104.1	0.88	7.9	1048 hours	—	19.90923	-155.89445
15	Open with fish	8.66	0.58	3.5	1102 hours	—	19.90923	-155.89438
16	Open with fish	73.33	0.8	19.4	1136 hours	5.47	19.66718	-156.02718
17	Open with fish	228	1.39	—	1108 hours	—	19.89478	-155.9026
18	Open with fish	7.63	0.55	4.3	1301 hours	—	Available on request	
19	Radon only	69.54	0.42	5.7	NA	1.73	19.85457	-155.92337
20	Radon only	3.59	0.66	2.8	NA	4.26	19.85423	-155.92337

Note: Maximum width was measured parallel to the coast. See text for methods used in canopy cover measurement. *, measured at high tide. **, n = 4 sampling periods for pond 9, n = 3 for pond 18.

meter stick, and surface area was estimated from approximate pond shape at high tide (e.g., circular, scalene triangle, etc.) and measured dimensions of the pond. Poeciliid densities were quantified using visual surveys according to Hankin and Reeves (1988), where a 0.25 m² quadrat was placed on the benthos for approximately 5 min, after which all fish within the quadrat were counted. After an additional 5 min, a second count was conducted and an average density value was calculated from the two counts. The anchialine ponds studied were shallow and had uniformly high water clarity and high densities of fish where they were present so that counts could be made accurately using this method.

Physicochemical and Nutrient Analyses

Physicochemical measurements were made on six occasions, at 2-month intervals, alternating between high and low tides over the sampling periods. Sampling was done within

1.5 hr of low/high tides over 2-day periods (low-tide samples: December 2011, April and August 2012; high-tide samples: February, June, and October 2012). At each sampling date, temperature (°C), salinity (ppt), dissolved oxygen (mg/liter), and pH measurements were made using a handheld probe (YSI 85, YSI Corp., Yellow Springs, Ohio) with the probe held approximately 10 cm above the benthic surface of each pond. We collected approximately 40 ml of water for nutrient analysis from each pond on the same sampling dates as YSI probe sampling described earlier. Water samples were collected using acid-washed syringes from ~10 cm above the benthic surface and filtered through precombusted 25 mm GF/F (Whatman) filters into acid-washed polyethylene vials. Collected samples were placed on ice in the field and during transport and immediately frozen when taken to the laboratory. Water samples were analyzed in the analytical laboratory at the University of Hawai'i at Hilo using

methods for nitrite and nitrate (ΣNO_3), ammonium (NH_4 ; $\text{NH}_3 + \text{NH}_4^+$), soluble reactive phosphorus (SRP), and TDN as described in Holitzki et al. (2013). Dissolved inorganic nitrogen (DIN) was the sum of ΣNO_3 and NH_4 . Dissolved organic nitrogen (DON) was calculated as the difference between TDN and DIN.

Pond Water Residence Time

To examine how pond water residence times might influence biotic effects on water quality, the residence times of five selected ponds were determined from pond volumes and total groundwater discharge to the ponds over a full tidal cycle. These ponds were selected across the coastal range of the study (Table 1, Figure 1). Groundwater discharge was the sole source of water to these ponds because there was no rainfall in the area during our residence time study. Pond water volumes were calculated from pond areas and depths measured using CTD-divers (Schlumberger, Inc.), and the average volume was determined for the deployment period. Groundwater discharge (Q_{GD}) to each pond was determined from a radon mass balance that accounted for radon inputs by groundwater discharge ($Q_{GD} \times \text{Rn}_{GW}$), diffusion from pond sediments (F_{DIF} , estimated according to Corbett et al. [1998]), and radon losses via atmospheric evasion (F_{EV} , calculated based on Schubert et al. [2012]), radioactive decay (F_{RD}), and recharge back to the aquifer ($Q_{GR} \times \text{Rn}_{SW}$). Groundwater radon activity (Rn_{GW}) was measured in wells located near the ponds using a radon detector (RAD-H2O manufactured by Durrige). Pond water radon (Rn_{SW}) was measured continuously over >20 hr to cover a full tidal cycle. A radon-in-air detector (RAD7 manufactured by Durrige) adapted to continuous water radon monitoring (Burnett and Dulaiova 2003) was deployed to measure pond water radon concentrations in 15-min intervals. For each measurement interval the radon and water mass balance was calculated and solved for groundwater discharge from the aquifer to the pond (Q_{GD}) and groundwater recharge from the pond to the aquifer (Q_{GR}) based on:

$$Q_{GD} - Q_{GR} = \frac{\Delta V}{T} \quad (1)$$

$$Q_{GD} * \text{Rn}_{GW} = Q_{GR} * \text{Rn}_{SW} + F_{EV} + F_{RD} - F_{DIF} \quad (2)$$

where ΔV is the change of pond volume over time T , here the length of one radon measurement cycle. The resulting groundwater discharges were then summed over the full tidal period and used for residence time calculations by dividing the volume of the pond by groundwater flux.

Data Analysis

We used linear mixed effects models to test the effects of pond types and tide stages on dissolved oxygen, pH, temperature, and nutrient concentrations in anchialine ponds. Pond type (non-N-fixing, N-fixing, open, fish) and tide (high or low) were treated as fixed factors, and pond number was treated as a random factor. Post-hoc pairwise comparisons between the four pond types were performed using Tukey contrasts. Calculations were performed with the lme function of package “nlme,” and post-hoc pairwise comparisons with the ghl function of package “multcomp” using the statistical software R (R Development Core Team 2011). Values for Pond 16 were not included in analyses of the effects of pond cover and fish presence on dissolved oxygen, pH, and water column nutrients based on evidence of substantial sewage influence (see Discussion) but were included in water temperature analyses. Instead, values for Pond 18 (sampled on the last three sampling events) were used in analyses of dissolved oxygen, pH, and water column nutrient differences. Data were checked for normality using quantile-quantile plots (Wilk and Gnanadesikan 1968), and homogeneity of variances was assessed by plotting residuals against fitted values (Quinn and Keough 2002). Data conformed to these assumptions, except NH_4 , SRP, and DON, which were transformed (natural log) before analysis to improve homogeneity of variances. This analysis also assumes independence of the ponds sampled. Based on quantile-quantile plots

and the risk of contamination of this type of sample, two outlying values (one DON value and one NH_4 value) were removed from the data sets before final analysis. We interpreted P values $< .05$ as significant. Error terms for means are reported as ± 1 standard error (S.E.).

RESULTS

Total dissolved nitrogen concentrations in anchialine ponds did not depend on tree cover or fish presence and were dominated by DIN, largely ΣNO_3 (Table 2). TDN means for the four pond types were comparable, ranging from $59.5 \mu\text{M} \pm 9.29$ (non-N-fixing, $n = 4$) to $63.5 \mu\text{M} \pm 8.2$ (N-fixing, $n = 5$), and we did not detect significant effects of pond type on TDN. Similarly, DIN, and ΣNO_3 , did not differ among pond categories. We did see effects of pond type and tide on some nitrogen-containing compounds; both NH_4 ($F = 3.51$; $df = 3, 13$; $P = .042$) and DON ($F = 3.52$; $df = 3, 13$; $P = .046$) values were greater in non-N-fixing covered ponds relative to open ponds. Furthermore, SRP concentrations were greater in ponds with non-N-fixing canopy cover compared with N-fixing and open ponds ($F = 4.54$; $df = 3, 13$; $P = .022$), though not compared with fish ponds. Pond type in-

fluenced dissolved oxygen levels in anchialine pond water ($F = 9.96$; $df = 3, 13$; $P = .001$), with non-N-fixing canopy ponds exhibiting lower dissolved oxygen levels than all other pond types. Tree cover also affected pond water pH ($F = 9.43$; $df = 3, 13$; $P = .001$); pH was lower in non-N-fixing canopy ponds than in open ponds with or without fish, and pH was lower in ponds with N-fixing cover than in open ponds without fish. We found no effects of canopy cover on water temperature.

TDN, DIN, and ΣNO_3 did not differ between high- and low-tide sampling events. NH_4 was lower ($F = 9.56$; $df = 1, 77$; $P = .003$), DON higher ($F = 17.79$; $df = 1, 77$; $P > .001$), and SRP lower ($F = 6.11$; $df = 1, 78$; $P = .016$) at high tide than at low tide. Dissolved oxygen content ($F = 31.21$; $df = 1, 70$; $P < .001$), pH ($F = 4.37$; $df = 1, 75$; $P > .001$), and temperature ($F = 7.20$; $df = 1, 77$; $P = .009$) were greater during high tides than low tides. Salinity did not differ between high- and low-tide sampling events.

Water depth and radon concentrations in the ponds differed with respect to tidal cycle, and radon levels across all ponds ranged from 200 to 67,000 dpm m^{-3} . Calculated groundwater discharge also varied with tides, showing maximum fluxes during rising (dominated by discharge from the downstream coastal

TABLE 2
Physicochemical Characteristics of Anchialine Ponds on Hawai'i's Leeward Coast

Parameter	Classification of Ponds				
	Groundwater	Non-N-Fixing	N-Fixing	Open	Open with Fish
TDN (μM)	123.01 \pm 15.12	59.53 \pm 9.29	63.49 \pm 8.22	62.60 \pm 3.07	61.33 \pm 5.96
DIN (μM)	74.00 \pm 15.50	42.79 \pm 7.42	51.61 \pm 9.63	56.60 \pm 2.82	54.37 \pm 5.23
ΣNO_3 (μM)	73.75 \pm 15.12	35.82 \pm 7.50	48.98 \pm 10.43	55.89 \pm 2.9	53.02 \pm 5.28
NH_4 (μM)	0.30 \pm 0.13	6.96 \pm 3.07a	2.62 \pm 0.91ac	0.71 \pm 0.11b	1.35 \pm 0.33bc
DON (μM)	49.26 \pm 15.50	20.72 \pm 6.07a	11.50 \pm 1.58ab	6.42 \pm 0.63b	7.69 \pm 1.54ab
SRP (μM)	3.11 \pm 0.64	6.04 \pm 2.17a	1.57 \pm 0.20b	1.71 \pm 0.20b	2.06 \pm 0.24ab
DO	—	2.80 \pm 0.71a	5.78 \pm 0.59b	6.75 \pm 0.33b	6.78 \pm 0.48b
pH	7.58 \pm 0.38	7.43 \pm 0.11a	7.72 \pm 0.17ac	8.11 \pm 0.04b	7.98 \pm 0.05bc
Temp. ($^{\circ}\text{C}$)	20.5 \pm 1.18	22.19 \pm 0.55	23.46 \pm 0.39	23.45 \pm 0.30	23.62 \pm 0.83
Salinity	—	9.10 \pm 2.19	4.62 \pm 1.38	3.84 \pm 0.29	6.40 \pm 2.04

Note: All values are presented as mean ± 1 SE; $n = 4$ ponds for each classification except "N-Fixing" ($n = 5$). Groundwater values are derived from Johnson et al. (2008) measurements from shallow wells along the Kona coast ($n = 17$). Values for each parameter that share the same lower-case letter do not differ significantly ($P > .05$) according to Tukey's HSD method for pairwise multiple comparisons. Where no lower-case letters are presented, no significant effect of pond type on that parameter was shown by ANOVA ($P > .05$).

side of the pond) and falling tides (dominated by upstream discharge) and minimum discharge at high and low tides. Average groundwater fluxes per ~20 hr of deployment were 0.15 to 7.9 m³ hr⁻¹ to each individual pond. The magnitude of groundwater discharge was correlated to pond cross-section areas because these draw more water from the aquifer. Pond water residence times ranged from 1.7 to 5.5 hr (Table 1).

Poecilia reticulata densities ranged from eight to 28 fish/m². The average number of fish observed was 14.7 ± 0.7 fish/m².

DISCUSSION

Influences of Canopy Cover and Invasive Fish

Vegetation cover influenced pond water quality characteristics but not in the ways we had hypothesized. We had predicted that ponds surrounded by exotic N-fixing *P. pallida* would be different in physicochemical parameters, but the non-N-fixing tree *T. populnea* appears to be a species that alters the functioning of anchialine ponds, and might be considered an ecosystem engineer (Jones et al. 1994). Non-N-fixing canopy ponds differed more substantially from open ponds in this study, and the N-fixing ponds were generally not greatly different from open ponds. Ponds with non-N-fixing canopies had increases in concentrations of DON and NH₄, which can be attributed to the breakdown of leaf litter leachate within these ponds (Herbert 1999). Leaf litter of *P. pallida* contains three to four times the nitrogen content by mass of *T. populnea*, so this effect may be due to the 2 × greater litterfall rates of *T. populnea* compared with *P. pallida* (Nelson-Kaula 2013). Furthermore, *T. populnea* leaves are large and fibrous, and slower to decompose than those of *P. pallida* (M. Riney, unpubl. data). As a result, non-N-fixing canopy ponds contained well-developed organic sediment layers and had lower pH and dissolved oxygen levels, compared with exotic N-fixing canopy or open pools (which typically lacked such sediment layers). This sediment probably plays a role in the ponds' physicochemical characteristics because it is rich in organic

matter and nutrients. Groundwater feeding the ponds is close to saturation state in oxygen (>80% oxygen saturation); this is due to the low organic matter content in the aquifer (Johnson et al. 2008). Reduction in DO content of water in ponds under canopies has been previously reported from inland ponds that do not experience the tidal fluctuations of these anchialine systems (Werner and Glennemeier 1999, Battle and Golladay 2001, Skelly et al. 2002). This is likely due to consumption of oxygen from decaying leaf litter at the bottom of ponds (Rubbo et al. 2006). Canopy cover may also decrease DO by reducing photosynthetic production of oxygen by continually resetting the benthic surface as falling leaf litter covers the base of the ponds (Nelson-Kaula 2013) or through shading. The lower pH in *T. populnea* canopy ponds may be related to increased release of humic acids and CO₂ during litter decomposition (Wetzel 2001, Batzer et al. 2004, Stoler and Relyea 2011). Reduction of light by canopies may reduce the photosynthetic removal of carbonic acid by periphyton communities, which would also reduce pH (Wetzel 2001, Stoler and Relyea 2011). Although ponds with *T. populnea* canopy tended to have higher salinity than other pond groups, this does not explain their relatively low pH. To the contrary, higher salinity has a higher pH buffering capacity that would moderate any photosynthesis/respiration-induced pH changes; central-North Pacific surface seawater has a pH very close to 8 (Nakano and Watanabe 2005), and pH measured in all ponds in this study was near or below that value.

The abundance of nitrogen in groundwater entering these ponds and nearshore waters affected by groundwater discharge (Street et al. 2008) raises the possibility that primary production in these areas is limited by the availability of phosphorus. Concentrations of SRP in purely marine Hawaiian waters are typically below 1 μM and around 2–5 μM in groundwater in this region (Johnson et al. 2008, Street et al. 2008, Knee et al. 2010). Comparison of salinity and DIN values from this study with regression lines from Street et al. (2008) suggests that these increases in NH₄ made little difference to total

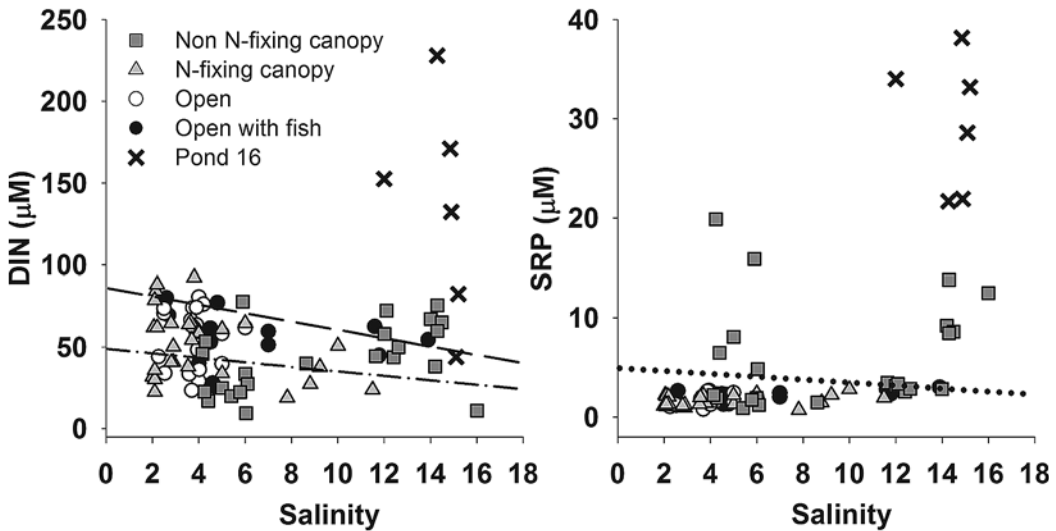


FIGURE 2. Anchialine pond nutrient concentrations compared with literature-derived mixing lines for salinity gradients on the Kona coast, Hawai'i Island. Lines on the left panel show the relationship between DIN and salinity in Hawai'i Island groundwater at central Kona locations (dashed line), and elsewhere on the leeward side of Hawai'i Island (dot-dashed line) from Street et al. (2008). The dotted line in the right panel shows the relationship between SRP and salinity for leeward Hawai'i groundwater from Knee et al. (2010). Pond 16 is plotted separately based on evidence of substantial inputs of DIN and SRP from sewage (see Discussion).

DIN in pond water (Figure 2). However, SRP concentrations in non-N-fixing *T. populnea* ponds were regularly above the mixing lines of Knee et al. (2010) (Figure 2, right). Water column DIN:SRP in individual non-N-fixing *T. populnea* ponds averaged 10:1, substantially lower than N-fixing *P. pallida* ponds (33:1), open ponds (35:1), and open ponds with fish (28:1, excluding pond 16). Ratios of DIN:SRP in open and N-fixing ponds are within the range for which P availability has been shown to limit epilithon growth in rivers, (Bowman et al. 2005) and marine benthic microalgal communities (Welker et al. 2002). In mixing zones on leeward Hawaiian coasts, DIN:SRP ratios > 35 are common but not ubiquitous (Knee et al. 2010). Changes in these ratios of available nutrients are only likely to alter growth rates of primary producers where N or P are not both available in excess; in many anchialine ponds on the Kona coast of Hawai'i it is possible that both N and P are available in sufficient quantities for maximum growth of epilithon (Sakihara 2012b). Nevertheless, high nutrient concentrations are not

ubiquitous among Hawaiian coastal waters (Wiegner 2006; R.A.M., unpubl. data), and canopy cover and invasive fish presence are common features of anchialine ponds and coastal water bodies (MacKenzie and Bruland 2012). Hence, reductions in N:P ratios such as those observed in this study following P additions from the *T. populnea* canopy cover and fish presence have the potential to alter primary production rates in these coastal ecosystems.

We predicted that water column TDN concentrations in anchialine pond waters would increase due to the presence of the N-fixing tree *P. pallida*, and poeciliid fish. These hypotheses were formulated based on previously documented effects of N-fixing plants and poeciliid fish on stream water (Compton et al. 2003, Holitzki et al. 2013, Wiegner et al. 2013) and coastal wetland ecosystems (MacKenzie and Bruland 2012) and the high densities of poeciliid fish and N-fixing trees around our study ponds. In contrast to results in prior studies, high inputs of N-rich leaf litter and the presence of

poeciliids had no discernible influence on TDN content of these waters. To explain these observed differences in the effects of N-fixing tree cover, we estimated potential contributions of TDN from *P. pallida* to pond water for five N-fixing ponds (pond nos. 5, 6, 7, 8, and 9) using:

$$TDN_{N\text{-fixing}} = M_{N\text{-fixing}} \times A_{\text{pond}} \times \%N_{N\text{-fixing}} \times k_N \times t \quad (3)$$

$$M_{N\text{-fixing}} = \frac{I_{N\text{-fixing}} \times A_{\text{pond}}}{k} \quad (4)$$

and

$$\%N_{\text{-fixing contribution}} = \frac{TDN_{N\text{-fixing}}}{TDN_{\text{pond}} \times V_{\text{pond}}} \times 100 \quad (5)$$

where $TDN_{N\text{-fixing}}$ is the amount of TDN released from *P. pallida* leaf litter breakdown (g), $M_{N\text{-fixing}}$ is the total standing stock of *P. pallida* leaf litter (g), A_{pond} is the pond area (m^2), $\%N_{N\text{-fixing}}$ is the percentage of N in *P. pallida* leaf litter, k_N is the N mineralization factor (day^{-1}), and t is the average residence time of water in the pond (days). We applied an average residence time to ponds 5, 6, and 8. The total standing stock of *P. pallida* leaves $M_{N\text{-fixing}}$ is equal to $I_{N\text{-fixing}}$ the daily leaf litter input of *P. pallida* leaves ($\text{g} \cdot \text{m}^{-2} \cdot \text{day}^{-1}$), the decomposition rate of *P. pallida* leaves, k (day^{-1}), and the area of the pond. Litterfall rates were estimated at $0.04\text{--}0.24 \text{ g m}^{-2} \text{ day}^{-1}$, based on rates from the five N-fixing ponds used in this study averaged from January to October 2012 (Nelson-Kaula 2013), and 0.02 day^{-1} for the litter decomposition rate based on in situ measurements using leaf litter transplants (M. Riney, unpubl. data). Contributions of N from *P. pallida* leaf litter were determined from $TDN_{N\text{-fixing}}$, TDN_{pond} (concentration of TDN in the water column [g m^{-3}]), and V_{pond} (pond volume [m^3]). Residence time is described earlier, and the N remineralization rate was taken as 0.01 day^{-1} , approximated from the relationship of remaining N to remaining ash-free dry biomass during breakdown of leaf litter from a related mimosoid legume, the invasive N-fixing tree *Falcataria moluccana* (MacKenzie et al. 2013). The

amount of standing stock of *P. pallida* leaves required to meet the observed TDN concentrations in ponds was determined by solving equation 1 for $Mass_{N\text{-fixing}}$ using $[TDN]_{\text{pond}}$. Based on this calculation we estimate that breakdown of *P. pallida* leaf litter contributes only 0.02%–0.1% of the TDN in anchialine ponds. The standing stock of daily *P. pallida* leaf litter needed to maintain TDN levels observed in anchialine ponds would be equivalent to $12,000\text{--}920,000 \text{ g m}^{-2}$ and would require $210\text{--}400 \text{ g m}^{-2} \text{ day}^{-1}$ in litter inputs. Thus, direct inputs of exotic N-fixing trees would not be expected to add considerably to the TDN in the water column of these pond ecosystems. We note first that these calculations are based on high-tide measurements, and at low tide litter decomposition effects on TDN may be greater. Second, residence times measured were lower than those of many coastal ponds and estuaries (Rasmussen and Josefson 2002, Hougham and Moran 2007). These low residence times are driven by high regional groundwater flow (Oki 1999), tide propagation into the coastal aquifer, and small pond volumes. Third, DIN concentrations in water bodies where effects of N-fixing flora have previously been found are comparatively low (e.g., $<5 \mu\text{M}$ [Mineau et al. 2011]). With lower background DIN, contributions from litter breakdown would form a larger proportion of the total N available. Nitrate makes up over 95% of the surprisingly high DIN concentrations in groundwater from these aquifers (Johnson et al. 2008, Street et al. 2008). High ΣNO_3 to NH_4 ratios in pond water sampled are a further indication that the majority of DIN present is groundwater-derived and not mineralized within ponds.

Similarly, the impacts of poeciliid fish on anchialine pond water quality were likely masked by high and variable background levels of dissolved N or P in all ponds. For example, the two- to eightfold increases in TDN ($4.1 \mu\text{M}$) and ΣNO_3 ($1.8 \mu\text{M}$) reported from poeciliid-invaded streams compared with poeciliid-free streams in Holitzki (2010) would likely have gone undetected in anchialine ponds where concentrations of these nutrients in “open” ponds varied from 28.9 to

88.4 μM and 29 to 80.5 μM , respectively. It is interesting that fish densities in the anchialine ponds studied were 4–10 \times higher (108.8 ± 24.0 fish/ m^2) than densities of poeciliids from comparative studies where the effects of invasive poeciliids on water nutrient content were found (12–25 fish/ m^2) (Holitzki 2010, MacKenzie and Bruland 2012). High nutrient concentrations and consistently low DIN:SRP (5:1) were observed in Pond 16, which contained a dense population of poeciliids. However, the presence of a sewage injection upslope from this pond (Johnson et al. 2008) and ^{15}N -enriched epilithon ($\delta^{15}\text{N} > 25\%$ [B.D.D., unpubl. data]) suggest that some portion of this difference is the result of sewage inputs (McClelland et al. 1997).

CONCLUSIONS

Water residence times of these small anchialine ponds were short in comparison with many coastal ponds and estuaries, including those with surface connections to the sea (Rasmussen and Josefson 2002, Schallenberg and Burns 2003, Hougham and Moran 2007). These residence times are driven by regional groundwater flow, which is amplified by tide propagation into the coastal aquifer in addition to small pond volumes; groundwater flow in this region is substantial, resulting in estimated submarine groundwater discharge between 2,500 and 15,000 $\text{m}^3 \text{km}^{-1} \text{day}^{-1}$ (Kay et al. 1977, Peterson et al. 2009). Low residence times of enclosed coastal water bodies tend to reduce the effect of biological processes that may remove or add nutrients to the water column (e.g., denitrification [Hougham and Moran 2007]) and, in the case of anchialine ponds in this study, leaf litter breakdown and remineralization of benthic organic material by fish. TDN concentrations found here were high in comparison with those of many studies of terrestrial pond and wetland systems (e.g., Battle and Golladay 2001, Hillebrand and Kahlert 2001), including coastal wetlands throughout Hawai'i (R.A.M., unpubl. data), and were high even in areas of the landscape with low human population density and development. However, based on our calculations, the mass of leaf litter from

N-fixing trees deposited directly into these anchialine ponds is four to five orders of magnitude less than that required to maintain the TDN concentrations observed, and we typically observed the large majority of TDN to be inorganic. Dissolved inorganic N concentrations (i.e., those available for uptake by aquatic primary producers in these ponds) depend on the concentration of DIN in water entering the ponds via the downhill flow of groundwater, inputs of organic N to the ponds, cycling processes within the ponds, and water residence times. In this case, high concentrations of DIN in groundwater entering the ponds and low water residence times likely reduced our ability to detect organic N inputs from invasive flora and biomineralization by invasive fauna within the ponds, and we did not have enough evidence to accept our hypotheses that these exotic species increase water column TDN concentrations. Nevertheless, tree canopy cover by the non-N-fixing *T. populnea* did affect SRP concentrations, DO, and pH of pond waters, and distributions of these trees may prove to play a part in controlling pond community structure and trophic dynamics.

ACKNOWLEDGMENTS

We thank Lucas Mead and Tara Holitzki at the EPSCoR laboratory at the University of Hawai'i at Hilo for their sample analysis work. T. Frauendorf, A. Korwin, M. Riney, and N. Wilhoite assisted us greatly in the field. D. Corbett provided technical assistance.

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