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Using forty years of research to view Bahía Almirante on the caribbean coast of Panama as an integrated social-ecological system☆

Rachel Collin[a,*], Anne E. Adelson[b], Andrew H. Altieri[a,c], Kasey E. Clark[a,d], Kristen Davis[e], Sarah N. Giddings[b], Samuel Kastner[f], Leon Mach[g], Geno Pawlak[b,h], Sofie Sjögersten[i], Mark Torres[j], Cinda P. Scott[g]

[a] Smithsonian Tropical Research Institute, Balboa, Ancon, Panama
[b] Scripps Institution of Oceanography, University of California San Diego, La Jolla, CA, 92093, USA
[c] Department of Environmental Engineering Sciences, University of Florida, Gainesville, FL, 32611, USA
[d] Department of Geography & Planning, University of Liverpool, Roxby Building, Liverpool, L69 7ZT, UK
[e] Department of Civil & Environmental Engineering, University of California, Irvine, CA, 92697, USA
[f] Environmental Sciences, Western Washington University, Bellingham, WA, 98225, USA
[g] The School for Field Studies, Isla Colon, Bocas del Toro, Panama
[h] Mechanical and Aerospace Engineering, University of California San Diego, La Jolla, CA, 92093, USA
[i] University University of Nottingham, UK
[j] Department of Earth, Environmental, and Planetary Sciences, Rice University, Houston, TX, 77005, USA

A R T I C L E I N F O

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A B S T R A C T

Tropical coastal systems play a vital role in sustaining biodiversity, performing ecological functions, and providing ecosystem services. They are also home to 75% of people in the tropics. Given that coasts face intense anthropogenic pressures including climate change, human population growth, and land-use change, it is critical to develop an understanding of the linkages between physical processes, biological interactions, and social dynamics in the complex environment where land and sea meet. Here, we review and synthesize 40 years of research from the Bahía Almirante region on the Caribbean coast of Panama, summarizing the large knowledge base of marine ecology, paleontology, ecosystem science and social science and adding newer information on physical processes. We describe how the system experiences both global and local drivers that are common to many tropical coastal systems and examine the crosscutting linkages that shape the system's response to change. To accomplish this, we utilized the Press-Pulse Dynamics framework as a lens to organize the many strands of research and to allow the interdisciplinary research team to generate explicit illustrative hypotheses about important socioecological linkages related to stressors such as the variability in precipitation and increased migration and tourism. The goal for this review and synthesis is to encourage researchers in Bahía Almirante and other estuarine systems to consider the landscape and seascape more broadly, to reach beyond their immediate field of expertise, and to consider both social and environmental aspects as they seek to increase system understanding in ways that can enable more productive public discourse surrounding policy, infrastructural change, and conservation.

Resumen: Los sistemas costeros tropical juegan un rol vital en el mantenimiento de la biodiversidad, cumpliendo funciones ecológicas y previendo servicios ecosistémicos. Estos también representan el hogar para el 75% de las personas en los Trópicos. Dado que las costas enfrentan intensas presiones antropogénicas, incluido el cambio climático, el crecimiento de la población humana y el cambio en el uso de la tierra, es fundamental desarrollar una comprensión de los vínculos entre los procesos físicos, las interacciones biológicas y la dinámica social en el complejo entorno donde se encuentran la tierra y el mar. Aquí, revisamos y sintetizamos 40 años de investigación en la región de la Bahía de Almirante en la costa Caribeña de Panamá. Resumimos la gran base de conocimientos principalmente de ecología marina, paleontología y ciencias sociales y reunimos información más reciente sobre procesos físicos. Describimos cómo el sistema experimenta impulsores tanto globales como locales que son comunes a muchos sistemas costeros tropicales y examinamos los vínculos transversales que dan forma a

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* Corresponding author.
E-mail address: Collinr@si.edu (R. Collin).

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la respuesta del sistema al cambio. Para lograr esto, se utilizó el marco Press-Pulse Dynamics como lente para organizar las muchas líneas de investigación y permitir que el equipo de investigación interdisciplinario genere hipótesis ilustrativas explícitas sobre importantes vínculos socioecológicos relacionados con factores estresantes como la variabilidad en las precipitaciones y el aumento de la migración. Y turismo. El objetivo de esta revisión y síntesis es alentar a los investigadores de Bahía Almirante y otros sistemas estuarinos a considerar el paisaje y el paisaje marino de manera más amplia, ir más allá de su campo inmediato de especialización y considerar aspectos sociales y ambientales mientras buscan aumentar el sistema. Comprensión de manera que pueda permitir un discurso público más productivo en torno a las políticas, el cambio infraestructural y la conservación.

1. Introduction

Tropical marine ecosystems are vital to global ecological functions and provide important ecosystem services, yet they face common threats, including: (1) global change factors including warming, deoxygenation, acidification, and invasive species, (2) local stressors such as over extraction and increasing terrestrial inputs including sediment and nutrients, (3) rapidly growing human population with associated coastal development and scaling of local stressors, and (4) the challenges of meeting imposed external expectations and demands while constrained by limited resources for management and enforcement. Studies conducted in these interconnected social and ecological systems have historically viewed them through the lens of a single discipline or research question. These approaches generate important basic knowledge, which once accumulated can be synthesized into a more holistic view. This is reflected in a recent paradigm shift in environmental research towards holistic perspectives including the use of transdisciplinary research approaches (See Mauser et al., 2013; Pohl et al., 2021), and application of social-ecological frameworks like the PPD (Press-Pulse Dynamics) framework applied here (Collins et al., 2011; Díaz et al., 2015; de Vos et al., 2019). These approaches have seen a recent increase in popularity because considering the feedback between the social and ecological sub-systems helps to develop understanding of whole system resiliencies and vulnerabilities (Dick et al., 2018).

Application of holistic perspectives to the physical and ecological components of tropical coastal environments requires investment in long-term data and continuous monitoring of diverse biophysical aspects of the marine and terrestrial systems on relevant timescales, as well as mechanistic understanding. This includes monitoring meteorological conditions, water quality and circulation, and the diverse dynamics of organisms and ecosystems. There are few tropical coastal systems where appreciable datasets from diverse marine and terrestrial systems have been collected in a coordinated manner with the exception of coastal LTER (Long-Term Ecological Research) sites which

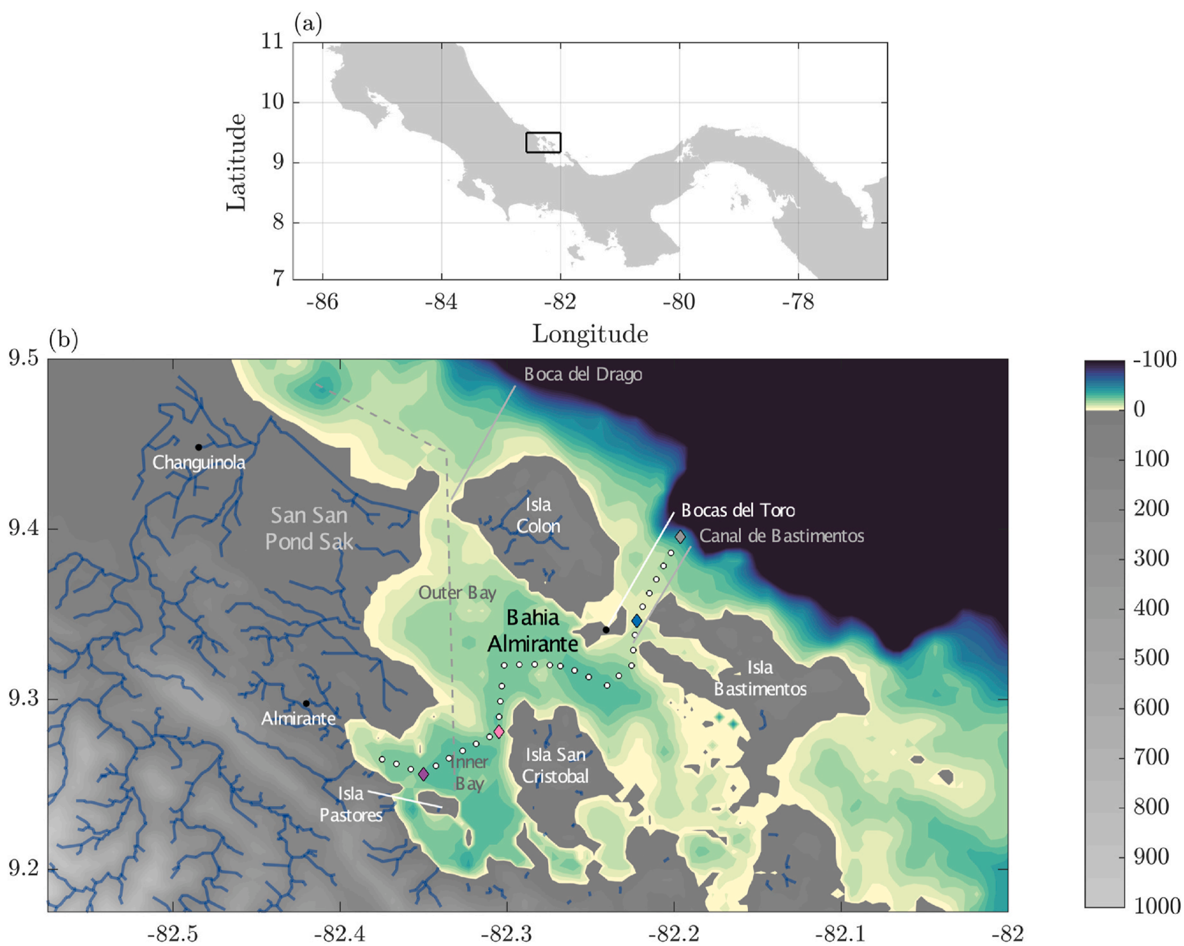

Fig. 1. A map of Bahía Almirante and surroundings, showing terrestrial topography (grayscale) and nearshore bathymetery (color). Rivers are marked in blue, and locations of interest are labeled. Dashed line shows the orientation of the edge of the breakaway illustrated in Fig. 2. Dotted line with colored diamonds shows the location of the transect illustrated in Fig. 7. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

demonstrate the power of this approach to understanding ecosystem dynamics (Kratz et al., 2003; Gosz et al., 2010). Likewise, the social component requires cultural information encompassing a range of communities and segments of the population viewed through the lenses of history, economics, culture, religion, policy, and the dynamics of civil society. Literature reviews demonstrate the rapid increase in publications using this integrated social-ecological approach (Colding and Barthel, 2019; Fischer et al., 2015; Herrero-Jáuregui et al., 2018; de Vos et al., 2019), and LTER sites have expanded their scope to include and integrate social factors across international sites (Haberl et al., 2006; Ohl et al., 2007; Dick et al., 2018). These international LTSER (Long-Term Socio-Ecological Research) sites exemplify how this can be planned in a systematic way. However, recent reviews of research outcomes illustrate their concentration in the northern hemisphere, and the preponderance of land-locked sites (Dick et al., 2018; Angelstam et al., 2019). Moreover, they highlight challenges faced in applying social ecological approaches (Dick et al., 2018; Angelstam et al., 2019). There is thus a need to apply this powerful approach to more tropical coastal regions.

Bahía Almirante (Figs. 1 and 2), its catchment, and the surrounding islands on the Caribbean coast of Panama, is a tropical social-ecological system for which significant research effort has produced extensive discipline-specific knowledge. By bringing together in one place and summarizing decades of academic research describing the physical, biological, and social components of the system we highlight linkages and interactions between components. This synthesis is derived from an inter-disciplinary symposium held in celebration of 20 years since the inauguration of the Smithsonian Tropical Research Institute's (STRI's) Bocas del Toro Research Station. Following the symposium a 3-day workshop brought together academics with currently active, long-running research programs in and around Bahía Almirante, representing different fields, but by no means an exhaustive representation of researchers working in the area.

Here, existing peer-reviewed social and ecological research outcomes were drawn together and discussed in an interdisciplinary context. Our own unpublished results and observations were included when no published data were yet available on a topic. Through this exercise, our interdisciplinary team engaged in an iterative discussion processes to achieve a consensus to select two subsystems in the coastal environment that could best illustrate the utility of PPD framework to generate hypotheses about linkages within this particular geographical context. We decided to focus on (1) how the water cycle and particularly increased aridity and periodic shortages could mediate climate change impacts and, consequently, affect biodiversity and human well-being and (2) on how external pressures from the demand for tourism and migration impacts the environment and the equity, wellbeing, and quality of life of local people. Our goal is to illustrate how the PPD approach, or others like it, could help organize a vast amount of information, make explicit the connections between different components of the system, and propose testable hypotheses about the social-ecological mechanisms driving change in a productive, comprehensive, and interdisciplinary way. The limitations regarding this process mostly lie at the effort to intersect and cross disciplinary boundaries where the methodological terrain is not currently well formulated. We also acknowledge that the themes we selected were not the only options and numerous others could have been selected. But after careful consideration and collaboration we feel that they are strong points of entry for this transboundary work. Although the scope of this review is mainly limited to peer-reviewed, academic literature, the goal is for the hypotheses gathered to help structure future research in ways that might provide meaningful and useful information for diverse stakeholders in the archipelago navigating coevolving ecological and social changes.

The Bahía Almirante region has four attributes that make it an appropriate system to apply this approach and to offer broadly generalizable findings applicable to other tropical coastal systems.

- The setting amplifies the effects of natural and anthropogenic factors. Bahía Almirante is a semi-enclosed tropical embayment bounded by relatively small but steep watersheds and with limited open ocean exchange. Islands partition the bay into sub-basins lengthening water residence times in a way that amplifies climate

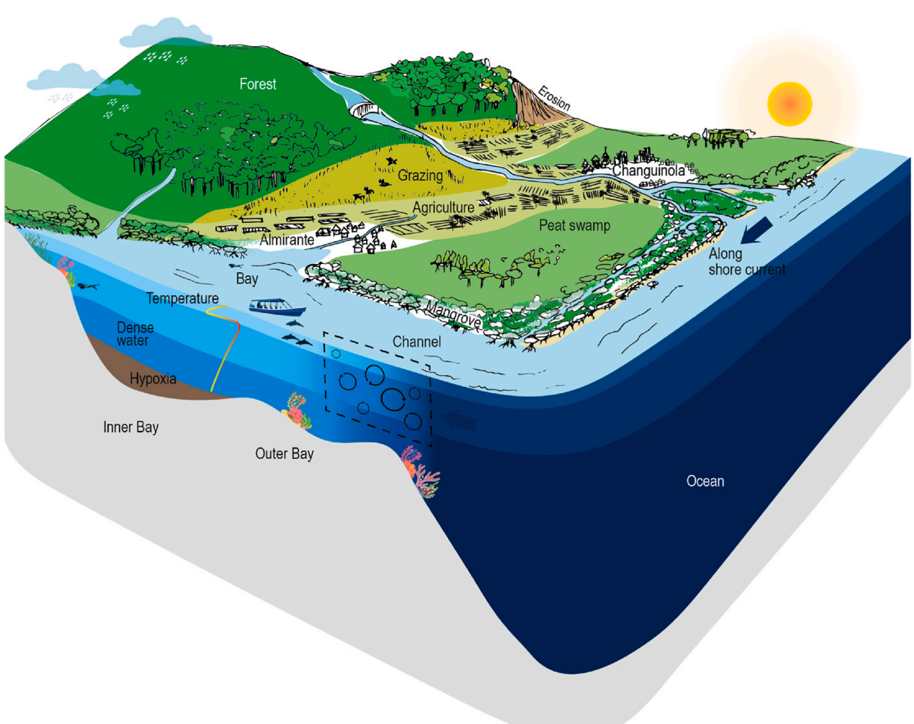

Fig. 2. Schematic cross-section showing the components of the landscape and seascape of Bahía Almirante.The open coast in front of the town of Changuinola is shown in the right-hand cut away, and a transect through the bay from Boca del Drago to the inner bay is shown in the left-hand cutaway.

influences, retains riverine and point-source inputs, and creates strong environmental gradients. This naturally creates a bounded system at a scale that is accessible to research.

- Bahía Almirante has experienced waves of documented socio-economic transitions that have brought change in how the system is viewed and used. This region is representative of many tropical coastal regions that have been subjected to colonialism thus leading to the displacement of traditional activities and cultural practices.
- The region is an example of recent explosive population growth and a transition from agricultural to tourist dominated economies coupled with external demands associated with international and national governance of natural spaces.
- A concentration of diverse research efforts provides a baseline of regional geological, ecological, and social scientific understanding.

The knowledge base of peer-reviewed publications, the focus of this review, is primarily the result of work by national and international researchers working at international organizations based in Panama (Smithsonian Tropical Research Institute (STRI) and The School for Field Studies (SFS)), as well as those based in the national university system (Universidad de Panama; Universidad Technológica de Panama; Universidad Marítima Internacional de Panamá). Much additional information is generated by NGOs (Sea Turtle Conservancy; Mar Viva; Audubon Panama, Give and Surf) and national entities (Instituto Nacional de Estadística y Censos (INEC)), Ministerio de Ambiente (MiAmbiente) and Autoridad de los Recursos Acuáticos (ARAP)), which is disseminated via reports and web pages which may or may not be widely accessible or permanently archived. Institutions based in Bocas del Toro host hundreds of students and scientists yearly (Scott and Mach, 2018). STRI alone has supported research resulting in hundreds of peer-reviewed publications since the construction of the main laboratory 20 years ago, and data from Smithsonian expeditions extends back a further 20 years. This manuscript is part of an effort to seek productive pathways for combining existing social and ecological research efforts and to promote interdisciplinary collaborations and research outcomes to guide the next 20 years of research.

1.1. *Application of Press-Pulse Dynamics (PPD) framework to Bahía Almirante*

The rapid growth of social-ecological system approaches to understanding the environment (Colding and Barthel, 2019; Fischer et al., 2015; Herrero-Jáuregui et al., 2018; de Vos et al., 2019) has shifted the paradigm of how ecosystems are studied, helped to formalize how we view the interactions between ecosystems and social systems, and how we predict their responses, resiliencies, and vulnerabilities. However, implementing such a research agenda can be challenging (Dick et al., 2018; Holzer et al., 2019), and the number of approaches and frameworks applied are as diverse and the systems studied (de Vos et al., 2019). Here we use the PPD framework (Collins et al., 2011) as it is an iterative, hypothesis-driven and scalable approach, which highlights the linkages between social and ecological systems through emphasis on discrete events (pulses) and continuous pressures (pushes) internal to the system, as well as external stressors (Collins et al., 2011). The structure is intuitive and approachable for marine scientists and ecologists, and it highlights the role of ecosystem services as a linkage between the ecological and social systems. We view the social-ecological system of Bahía Almirante through the PPD lens, describing the different components, the interdisciplinary linkages, feedbacks, and hypotheses of causal connections derived from traditional single-discipline studies. The framework shown in Fig. 3 provides a conceptualization of the fundamental relationships between the components in the system. The components are linked by hypotheses about causal relationships H1–H6 with the following characteristics: **H1**: How pulses and presses directly

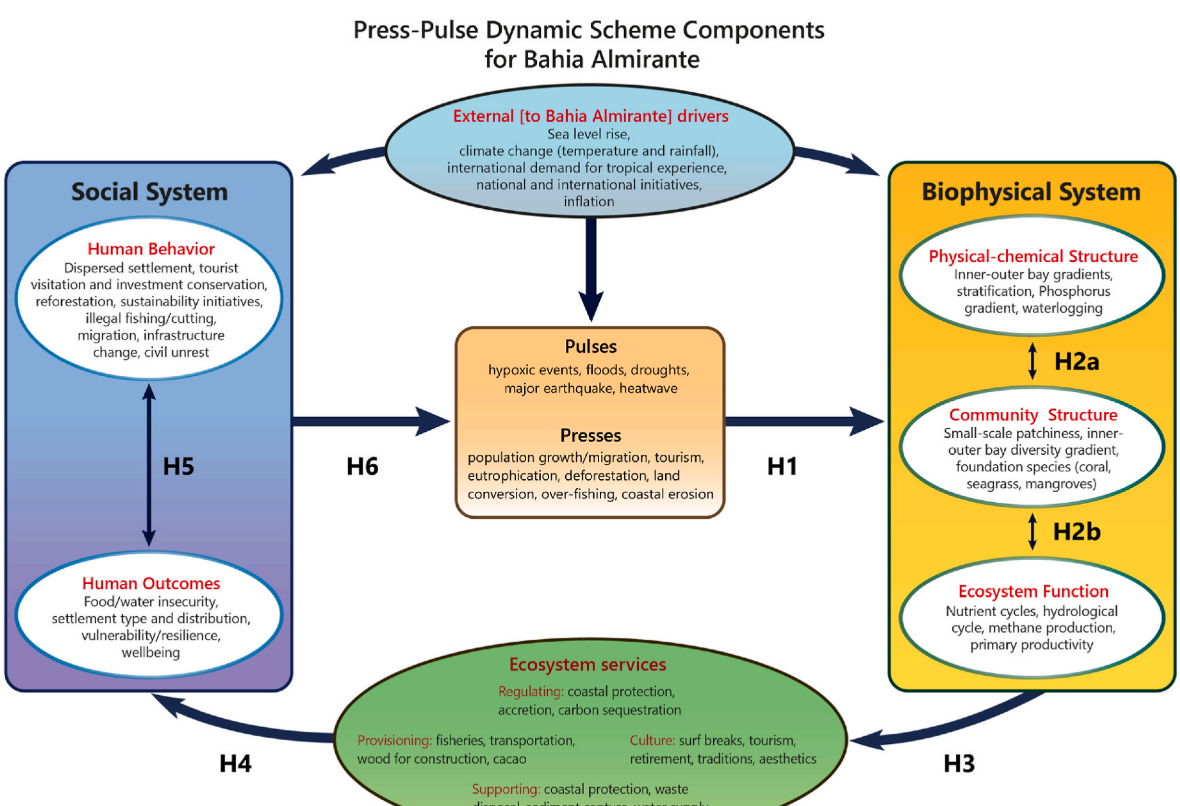

Fig. 3. Schematic diagram of the PPD framework (from Collins et al., 2011), with examples of each component drawn from the Bahía Almirante Social Ecological System. The causal hypotheses to be derived from the review of current knowledge are listed as H1–H6 (see text for details).

impact the biophysical system. **H2**: Linkages within the biophysical system showing how environmental conditions impact species occurrences, or how community structure impacts ecosystem function **H3**: How community structure and ecosystem function impact ecosystem services. **H4:** How ecosystem services impact humans. **H5:** Linkages within the social system, showing how impacts on humans and human behavior interact. **H6:** How human behavior can change the presses and pulses experienced within the system (Fig. 3).

2. Literature review

2.1. Climate of the Bahía Almirante area

Bahía Almirante is in the wet tropics on the Caribbean coast of Panama, with a Köppen-Geiger climate classification of Af (Tropical rainforest) (Beck et al., 2018) and relatively subtle seasonal changes in meteorological conditions (Fig. 4). Mean monthly air temperatures measured at the Bocas del Toro Research Station (BRS) meteorological station range between 25.3 °C and 27.3 °C and mean monthly relative humidity ranges from 88.3 % to 84.2 % in the wettest and driest months, respectively. Mean monthly rainfall ranges from 172 mm in October to 462 mm in July (Fig. 4), with an average annual rainfall over the last 20 years of 3629 ± 549 mm/yr (Paton, 2023).

There are two rainy seasons and two shorter dry seasons in the Bocas del Toro region (Fig. 4) (Paton, 2023; Kaufmann and Thompson, 2005). The first dry season lasts from January until April coincident with the dry season in the rest of the country. This period is wetter in Bocas del Toro compared to the rest of Panama, as the trade winds from the north hit the central Cordillera mountains, driving orographic precipitation. The first wet season is typically from April to August, with convective rainfall driven by the arrival of the Intertropical Convergence Zone (ITCZ) over Panama. During this first wet season, temperatures and precipitation are generally higher and wind speed, and solar radiation are lower than during the first dry season (Fig. 4). At the end of August, the second short dry season (Veranillo or mid-summer drought; Maurer et al., 2022) commences. During the Veranillo, there are high air temperatures, low and less variable precipitation, minimum wind speeds, and high solar radiation (Fig. 4). This is the season when water shortages and coral bleaching are most pronounced (R. Collin and C. Scott pers. obs.). The second wet season, in November and December, is distinct from the first wet season as the air temperature is lower, precipitation is higher, wind speeds are the highest of the year, and solar radiation is the lowest (Fig. 4). This is the season when road washouts and flooding are most common (Salvensen, 2023).

It is difficult to predict extreme rainfall events in Panama due to complexities in the local atmospheric circulation resulting from the influence of the two oceans, and the orography of a long and narrow mountainous landscape (Bezanillia-Morlot et al., 2020). Unstable convective rainfall over short periods in localized areas contributes to the disconnect of the Bocas del Toro climate from the rest of Panama

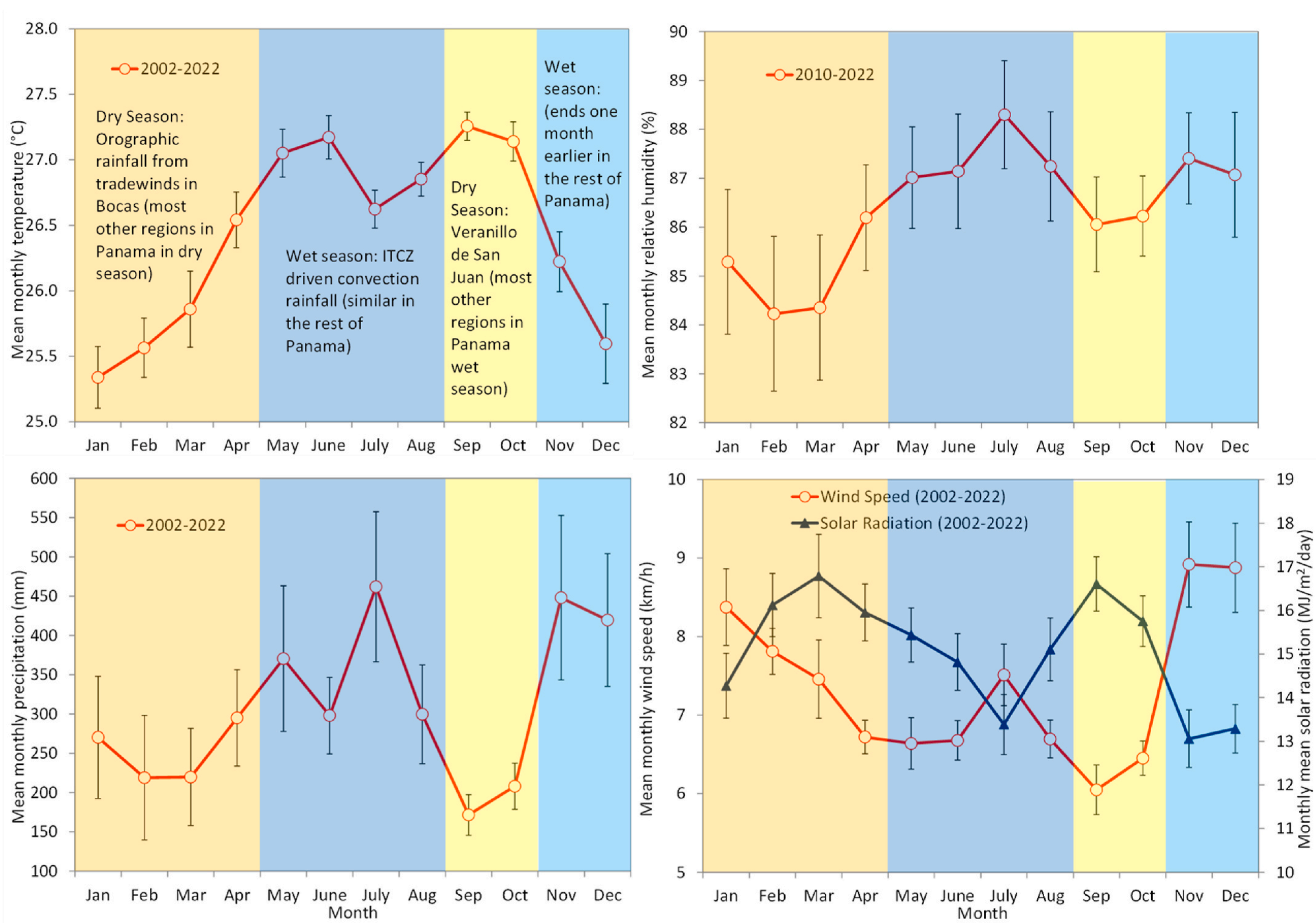

Fig. 4. Monthly averages of climatological variables as measured at the Bocas del Toro Research Station on Isla Colon (generated from Paton, 2019; 2021 for 2002–2022). The four seasons (Kaufmann and Thompson, 2005) are highlighted: Two wet seasons (blue shading), dry season (orange shading), and Veranillo (yellow shading). Panels show mean monthly a) air temperature, b) relative humidity, c) precipitation, and d) wind speed and solar radiation. Error bars are one standard error above and one below the mean. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

(Bezanilla-Morlort et al., 2020). For example, La Purisima 2010 and Hurricane Otto in 2016, both heavily impacted central Panama (ACP, 2014; Murphy et al., 2014), without high rainfall measured on Isla Colon (Paton, 2023). Panama has not experienced a hurricane in the last 150 years (NOAA, 2023). However, hurricanes and tropical storms passing north of Panama can disrupt the ITCZ, resulting in days of heavy rain from feeder arms that extend across the country and/or extended periods of very dry conditions (i.e., Hurricane Otto in 2016 and Hurricane Mitch in 1998) (Murphy et al., 2014), altering the general patterns described above.

2.2. Geology, land-use, land cover, and hydrology

The Bocas del Toro region around Bahía Almirante is underlain by sedimentary rocks that record the uplift and formation of the Isthmus of Panama (Coates et al., 2005). The northern part of the Bocas del Toro Basin and Islas Colon, Pastores, San Cristobal, Carenero, and Bastimentos, as well as the Zapatillas are made up of late Pliocene-Pleistocene shallow-water sediments, especially coral reef deposits. On Isla Bastimentos these overlie middle Miocene volcanic arc basalt and on Isla Colon a late Pliocene siliciclastic shale (Coates et al., 2005). The southern part of the bay and the Laguna de Chiriquí including Islas Popa, Cayo Agua, Escudo de Veraguas, and the Peninsula Valiente are made up of a Miocene and Pliocene, marine, transgressive/regressive shelf sequence overlying middle Miocene volcanic and sedimentary rocks (Coates et al., 2005).

Secondary forest and agricultural land types intermixed with secondary forest are the primary land cover throughout the Bahía Almirante catchment (Clark et al., 2022a, b). Agricultural land is used for small-scale agroforestry focused on cacao and cattle pasture. The largest urban areas are the towns of Bocas del Toro on Isla Colon (pop. 10,042), Old Bank (pop. 2679) on Isla Bastimentos, and on the mainland Almirante (pop. 19,646) and Changuinola (pop. 43,864) (INEC, 2021). San Pond Sak, a peat swamp forest with an ombrotrophic peat dome lies in the northwestern part of the Bahía Almirante catchment. This forest contains seven distinct swamp plant communities following bands from the coast toward the dome (Phillips et al., 1997). This distribution mirrors a significant phosphorous gradient in the underlying soil (Troxler, 2007; Cheesman et al., 2012) and peat deposits underlying the swamp forest can be 6–8 m thick (Phillips and Bustin, 1996a). Smaller peat swamp patches occur in low-lying parts of the islands, and there are extensive coastal swamps between Bahía Almirante and the Costa Rican border. Peat deposits extend under Bahía Almirante where tectonic subsistence has resulted in carbonate sediments overlaying them (Phillips and Bustin, 1996a,b). It is estimated that the area subsided by as much as 50–70 cm after the 1991 7.5 Limon earthquake (Phillips and Bustin, 1996b). Radiocarbon dates suggest that the peat is up to ~4000–4500 years old (Phillips and Bustin, 1996b).

The peat swamp forms an important regional carbon store, storing ca. 1500–1900 Mg C ha-1 (Upton et al., 2018) highlighting its need for protection from development. Further, this stored carbon is vulnerable to droughts and water table draw down as the resulting oxygenation of the peat profile at depth increases the release of CO_2 from microbial respiration from peat decomposition (Wright et al., 2013; Sjögersten et al., 2018). In these swamps the different forest tree species interact with the soil microbial communities and this connectivity strongly regulates the greenhouse gas emissions. High methane emissions occur naturally in peat swamps and as methane emissions are highly sensitive to increased temperature, there are serious concerns that climate heating will cause increased methane emissions from the swamps (Wright et al., 2013; Sjögersten et al., 2014, 2018, 2020; Hoyos-Santillan et al., 2016, 2019; Girkin et al., 2018, 2019).

On the mainland, to the northwest of Bahía Almirante, two major rivers, the Río Changuinola and Río Sixaola drain a large area of the primary and secondary forest of the Cordillera Central. These rivers discharge along the open coast, close to Bahía Almirante, and under certain conditions, freshwater from these rivers flows along the coast and enters the bay indirectly through the channel at Boca del Drago (Fig. 5). Historically, banana plantations existed throughout the region but, today, they are restricted to the Rio Changuinola floodplain. An artificial canal linking the Rio Changuinola to Bahía Almirante was constructed through the swamp forest for banana transportation.

The catchments that drain directly into Bahía Almirante are, roughly, a similar size to the bay surface area, ~500 km^2 each (Adelson et al., 2022; Kaufmann and Thompson, 2005; Clark et al., 2022a, b). Rainfall is highest on the islands, with less rain along the coastal lowlands of the mainland and inner bay, including San Pond Sak, Almirante, and Isla Pastores (Clark et al., unpublished). Freshwater inputs, from direct and indirect river discharge and direct rainfall significantly influence the bay's physical oceanography (see below). Like other tropical systems with high intensity rainfall events, steep slopes and small catchments, the rivers draining the foothills into Bahía Almirante are "flashy" in that they rapidly respond to rainfall events (Clark et al., 2022b; Clark et al. unpublished) (Fig. 6). This flashy behavior is evident for the mainland mountainous rivers that flow into the inner bay (Fig. 6). There is often overbank flow, temporarily flooding the low-lying areas adjacent to the rivers. The rivers draining the peat swamps have a longer lag time between the start of rainfall and the river discharge, delaying peak flow into the bay by several days (Fig. 6). In the low-lying areas at baseflow, tides influence river stage and discharge, making it difficult to determine discharge (Clark et al. unpublished). While the rivers are fresh most of

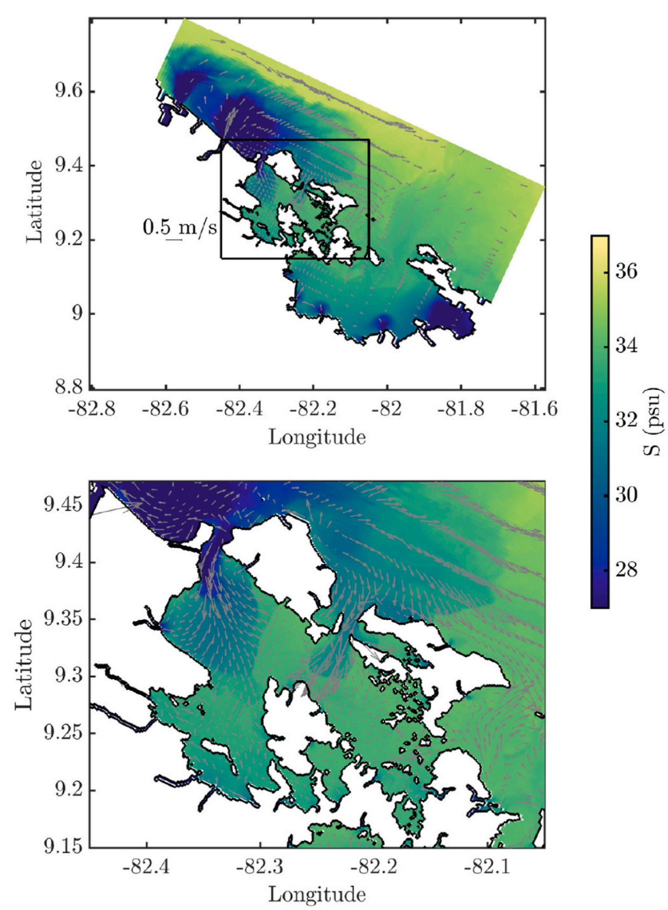

Fig. 5. Surface salinity (color scale) and velocity fields (arrows) from a realistic hydrodynamic simulation of the Bahía Almirante from the MAR Bocas model, a Regional Ocean Modelling System (ROMS) model. Results show a snapshot of model predictions on October 19, 2019, highlighting a common occurrence – freshwater from the Changuinola and Sixaola River plumes entering the bay through Boca del Drago. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

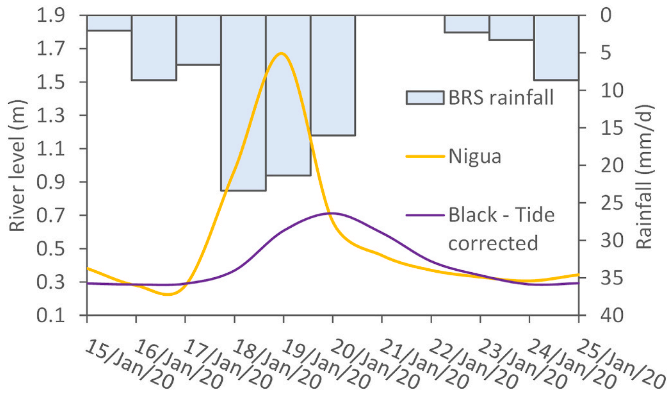

Fig. 6. Example hydrograph from two mainland rivers that flow directly into Bahía Almirante. The lines show the levels of the Nigua River and Black River (with the tide influence removed), and blue bars show the rainfall over the same 10 day period at the Bocas del Toro Research Station (BRS) (Clark, unpublished). (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

the year, saltwater wedges or intrusions extending several km from the river mouths into low-lying coastal areas are common during low discharge and low rainfall periods.

Water quality also differs between rivers entering the bay from mountain catchments and the swamp (Clark et al., 2022a, b). In the peat swamp, the typical blackwater rivers are frequently hypoxic and have generally acidic (mean pH = 5.8) but variable pH (4.5–7.5 pH) (Clark et al., 2022a, b). The clear dark brown color of the peat swamp rivers suggests high humic acid and low particulate load. The rivers draining the mountainous catchments are well-oxygenated with pH ranging from 6.4 to 8.4 (Clark et al., 2022a, b), characteristics typical of such streams. Phosphate and nitrate + nitrite concentrations are generally low, with higher values occurring in rivers that flow through the towns (i.e., Rio Nigua in Almirante) (Clark et al., 2022a, b). There is minimal wastewater treatment, which drains either directly or through septic systems into the bay. These point sources from towns and settlements, mostly clustered along the coast around river mouths, likely contribute to locally higher organic matter load and nutrients, especially in the inner bay near Almirante where water residence times are high (see below).

2.3. *Physical conditions, hydrography and circulation of Bahía Almirante*

Bahía Almirante is a shallow (~20 m), microtidal estuary with maximum depths of ~30 m. The mean daily tidal amplitude is 0.35 m (maximum 0.6 m). Three major channels (Boca del Drago, Canal de Bastimentos, Cayo Coral, Fig. 1), which are shallower than the middle and inner bay, connect the bay to the ocean. Bay water properties are influenced by oceanic, atmospheric, and riverine forcing (Kaufmann and Thompson, 2005; Adelson et al., 2022). Offshore coastal currents and water properties are modulated by basin-scale dynamics such as the Panama-Colombia Gyre, a cyclonic recirculation feature in the Mosquito Gulf region (Mooers and Maul, 1998; Andrade et al., 2003; Kastner et al., 2024), and by seasonal winds driven by the migration of the Intertropical Convergence Zone (ITCZ) (Kaufmann and Thompson, 2005). Deeper regions of the inner bay are subject to seasonal hypoxia (Adelson et al., 2022) while intermittent hypoxic events have also been observed at shallower depths with associated acute ecological implications (Altieri et al., 2017; Lucey et al., 2020). A hydrodynamic model of the complex interplay of marine and riverine processes in Bahía Almirante (MAR--Bocas) is being developed and validated using a 3-dimensional implementation of the Regional Ocean Modelling System (Shchepetkin and McWilliams, 2005).

Freshwater fluxes into the bay from rivers and direct precipitation create strong vertical and horizontal salinity gradients. Often a 2–10 m thick brackish "cap" occurs over saltier bottom waters and depth-averaged salinity increases towards the ocean. Water temperatures generally range from 27 to 30 °C but can reach above 32 °C in shallow embayments (Lucey et al., 2020; Collin and Chan, 2016). Temperature and salinity transects extending from offshore to the inner bay from October 2019 (Fig. 7) illustrate the typical structure reflected in 10 years of weekly sampling data (Fig. 7) (Adelson et al., 2022) with a salty deep layer and a freshwater cap throughout the bay. High temperatures also occur in subsurface inversions (Fig. 7). These inversions, most evident in the inner bay, occur because the freshwater cap allows radiative heating to penetrate to saltier waters below, but insulates these bottom waters from atmospheric cooling. Thermal inversions are thus observed more frequently with increased salinity stratification. Seasonal averages show thermal inversions between 20 m and the surface in the inner bay near Almirante from June to August and again between November and January (Adelson et al., 2022).

There are regular seasonal hypoxic conditions at depth (>20 m) in the inner bay between July and December with intermittent refreshment events commonly occurring in September/October, during the Veranillo (Adelson et al., 2022). Similar to thermal inversions, hypoxia at depth is well-correlated with vertical density gradients, indicating that strong stratification isolates deep waters from surface oxygen sources (Adelson et al., 2022). Oxygen levels at depth are also strongly correlated with the magnitude of thermal inversions reflecting common isolation effects (Adelson et al., 2022). In general, temperature, oxygen concentration, and pH all covary across the bay (Lucey et al., 2020).

Environmental forcing determines the onset and termination of hypoxic events and temperature inversions, specifically through seasonal variation in precipitation and its influences on stratification and mixing. Increased precipitation in May and June results in increased stratification which serves as a barrier for vertical ventilation of deeper waters. Isolated, higher salinity water at depth warms due to radiative heating, while dissolved oxygen is diminished due to biological oxygen demand. Seasonal changes in wind stress are roughly coincident with seasonality in hypoxia, though analysis yields no significant direct relationship with deep oxygen levels indicating that wind stress is insufficient to overcome the strong vertical stratification (Adelson et al., 2022). Analysis of specific hypoxia events suggests that breakdown is related to lateral advection of high salinity, high oxygen water from offshore (Adelson et al., 2022). Areas near the ocean-connected channels are cooler, more saline, and have higher oxygen concentrations than the inner bay, consistent with an offshore reoxygenation source. Inner bay dissolved oxygen levels are correlated with near bottom outer bay salinity indicating that isolated deep water is refreshed when denser water enters the bay. Bahía Almirante thus functions as a tropical fjord where deep water in the inner bay is renewed intermittently when conditions offshore and in the channels are favorable (Farmer and Freeland, 1983; Adelson et al., 2022; in prep). The reduction in vertical salinity stratification during the Veranillo and later at the end of the rainy season in January allows for increased salinity in the channels and renewal of inner bay deep water (Adelson et al. in prep). The mixing processes in the channels and through the bay that set salinities for inflowing water remain poorly understood. The fjordal paradigm for seasonal hypoxia and thermal inversion formation, with isolation of deep water in the inner bay and intermittent advective refreshment, suggests that hypoxia would most likely occur without nutrient addition from terrestrial runoff, but these factors may exacerbate the problem. The drivers of interannual variation in the intensity, duration, and spatial extent of hypoxia have yet to be determined.

The large spatial gradients observed in hypoxia along the bay are also observed in other physical and biological water properties. Weekly monitoring data demonstrate gradients in chlorophyll and dissolved organic matter (DOM), with both reaching higher concentrations in the inner bay and at depth compared to more offshore sites and to surface waters (Weinstock et al., 2022). The distributions of water properties and hypoxia prevalence (e.g., more hypoxia in the inner bay) suggest

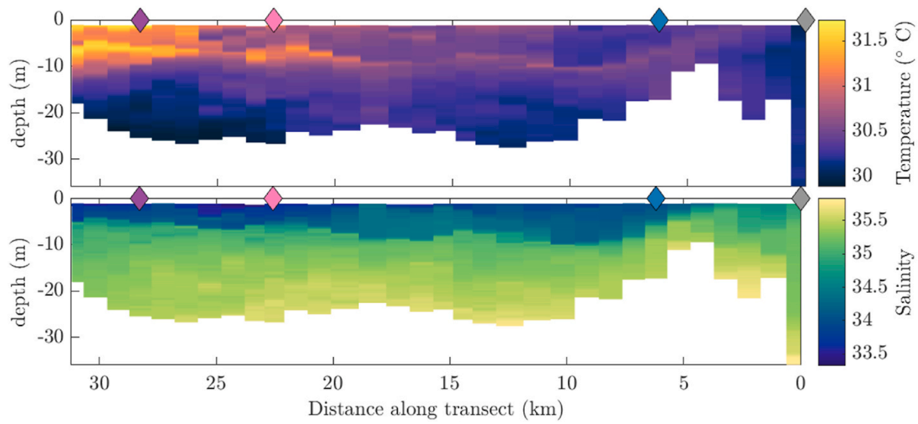

Fig. 7. Cross section of Bahía Almirante from a vessel-based profiling transect on October 19, 2019 showing water temperature (top) and salinity (bottom) following the track shown in Fig. 1 from offshore (gray diamond) through a pass (Canal de Bastimentos, blue diamond) to the inner bay (pink and purple diamonds). Notable features include a thermal inversion with maximum temperatures between 5 and 7 m depth (top) and a freshwater cap (bottom), most pronounced in the inner bay towards the mainland. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

that residence times are spatially variable across the bay. The residence time of water within the bay, estimated from a heat budget, ranges from 9 to 26 days for the full bay but are higher for the inner bay (17–45 days), consistent with the observed spatial variability of water properties (Adelson et al., 2022). Observations further indicate that temperature and oxygen concentration both serve as a measure of water 'age' or isolation time. This would suggest that time series of temperature at depth can be an effective metric for hypoxia for Bahía Almirante and for this type of system in general.

3. The biological seascape of Bahía Almirante

The striking geomorphology of Bahía Almirante, the complex coastline, and the archipelago fragment the bay into a complex seascape of microhabitats (Fig. 1). This is reflected in the patchy distribution of foundation species and the communities they support. The distribution differs from the paradigms of Caribbean community organization, which usually depict clear, linear zonation from the terrestrial margin to open ocean of mangrove stands, seagrass meadows, and coral reefs.

Most of the land-sea interface of Bahía Almirante is fringed with red mangroves (*Rhizophora mangle*). White mangroves (*Laguncularia racemosa*) and black mangroves (*Avicennia germinans*) can occur in patches, as can *Pelliciera* species. The distribution of the red mangrove stands is shaped by the mosaic of environmental conditions in the bay (Guzman et al., 2005; Lovelock et al., 2004, 2005, 2006). They create hundreds of mangrove keys and form fringes along the margins of the mainland and the large islands, with medium-sized trees on the seaward edge and nutrient-limited dwarf forests in the interior. Larger trees occur along river mouths and on the landward edge of these fringes (Lovelock et al., 2004, 2005). The prop roots of mangroves support diverse fouling communities and fishes (Seemann et al., 2018; MacDonald and Weis, 2013; MacDonald et al., 2008; Wulff, 2009). In Bahía Almirante mangroves are exporters of nutrients that are taken up by reef organisms (Granek et al., 2009) and their removal can drastically change the local benthic community (Granek and Ruttenberg, 2008; Granek & Frasier, 2007).

Dense seagrass meadows cover much of the shallow seafloor. Their ecology has largely been studied as part of broader-ranging regional or temperate tropical comparisons (e.g., van Tussenbroek et al., 2014; Freestone et al., 2020). The dominant species in Bahía Almirante is *Thalassia testudinum*, but *Syringodium filiforme*, *Halodule beaudettei* and *Halophila decipiens* also occur. Seagrass ecotypes (wetland, river, mangrove, and reef) are deliminated by sediment characteristics, which can include riverine sediment, reef-derived calcium carbonate sediments, or materials derived from wetlands and mangroves (Carruthers et al., 2005). In Bahía Almirante seagrasses may form dense beds but are also often found growing sparsely amongst corals and sponge gardens at shallow sites. Seagrass characteristics reflect high nutrient availability (Carruthers et al., 2005) and light and nutrient availability may jointly regulate seagrass cover and biomass (Gaubert-Boussarie et al., 2021).

Coral diversity is relatively high, with most of the Caribbean species represented (Guzmán and Guevara, 1998a,1998b; 1999, 2001). Many of the fringing reefs follow a relatively steep slope downward towards the soft sediment benthos that is typical of most of the deeper parts of the bay. At the deepest reef extent, individual coral colonies commonly sit untethered in sediments rather than in a consolidated reef framework. A widely accepted Caribbean paradigm is that ecosystems are encountered in onshore-offshore zones with mangroves fringing the land, leading to seagrass, and then to reefs. However, in Bahía Almirante the small mangrove keys foster entire coral communities that thrive in and amongst their roots (Stewart et al., 2021, 2022). Gardens of calcareous algae that contribute to calcareous sand deposits are also prominent in the shallows as are reefs dominated by sponges or by soft corals. In the shallows, many sites defy classification into a particular ecosystem with bottom cover exhibiting different combinations and proportions of coral colonies, zooanthids, calcareous algae, small clumps of seagrass, and encrusting and ropey sponges.

Due to the high rainfall and terrestrial influence, water clarity is lower than in many parts of the Caribbean, resulting in shallower depth distributions of photosynthetic foundational organisms like corals and seagrasses, whose distributions are often shaped by light. This shallow distribution of coral and seagrass communities is fortuitous as thermal inversions and hypoxia make the deeper parts of the bay marginal habitat at best (Neal et al., 2014; Lucey et al., 2021). It also results in higher diversity at shallower depths than observed in much of the Caribbean (Altieri et al., unpublished data). The spatial distribution of hypoxia also shapes biodiversity (Lucey et al., 2023; Weinstock et al., 2022). The most diverse and topographically complex reefs and most diverse fish communities occur in the outer bay with the highest mixing and greatest oceanic influence, such as around the Zapatillas, Cayo Agua, Isla Popa and near Crawl Cay (Guzmán and Guevara, 1998a, b; 1999, 2001; Dominici Arosemena and Wolff, 2005).

The overall diversity of marine life in the bay is similar to much of the Caribbean. Most of the corals, gorgonians, sponges, echinoderms and other invertebrates documented from the Caribbean also occur in Bocas del Toro (e.g., Collin et al., 2005; Diaz, 2005; Sanchez and Wirshing, 2005). Bahía Almirante has higher documented diversity of less-studied invertebrates due to the intensive taxonomic work, DNA barcoding and diversity surveys that have been conducted over the last 20 years (Rocha et al., 2005; Bonnet and Rocha, 2011; Collin et al., 2019a, b, 2020a,b;

2021; Ellison et al., 2022; Miglietta et al., 2018; Torati et al., 2011). In contrast, fish diversity and abundance are noticeably lower inside Bahía Almirante than at many other Caribbean sites, with somewhat more typical fish faunas evident at the shallowest sites and the exposed sites outside the bay, which also have the most intact reef (Dominici-Arosemena and Wolff, 2005). This could be due to the remoteness of the bay from other similar habitats. It is the only large area with a complex and protected coastline in ~1000 km of straight, exposed, sandy coastline from Bluefields in Nicaragua to Colon in central Panama. The lack of up-steam reefs and the location of Bocas in the Colombia-Panama Gyre may isolate this area from the rest of the Caribbean. The slow rate of water renewal in the inner bay may further isolate the biota from the greater Caribbean. Such isolation could make the bay uniquely vulnerable by reducing the rate of recolonization after local disturbances or extinctions.

The marine fauna of Bahía Almirante includes many of the charismatic megafauna and endangered fisheries species typical of the Caribbean. The only naturally occurring population of manatees in Panama reside in the large rivers in the peat swamps (Díaz-Ferguson et al., 2017; Guzman and Condit, 2017). Manatee has been exploited as a food source in the region for thousands of years and historical records show that it was still used as food into the 1600s (Wake et al., 2013). The coastal bottlenose dolphin populations in the bay have evolved a unique communication style and are genetically differentiated from other populations (May-Collado & Wartzok, 2008; Barragán-Barrera et al., 2017). They currently face threats from intensive interactions with boat tours and increasing boat engine noise (Kassamali-Fox et al., 2020; Barragán-Barrera et al., 2017; Perez-Ortega et al., 2021). Turtles were once numerous (Wake et al., 2013; Meylan et al., 2013) and globally significant fisheries in Panama, focused in the Bocas del Toro region, are estimated to have exported shell from over 150,000 turtles (Mortimer and Donnelly, 2008). Turtles face various threats from direct hunting and egg collecting, disruption of nesting beaches from sand mining, tourism activities and nest predation from feral dogs, yet hatchlings produced in the area are vital for Caribbean populations of hawksbill turtles (Meylan et al., 2013). Benthic communities in Bocas del Toro may reflect the impacts of significant declines in turtle abundances (Cannon et al., 2022; Łukowiak et al., 2018). Iconic Caribbean invertebrates like queen conch and spiny lobster are still sufficiently abundant that there is an artisanal fishery for them, and they routinely appear on restaurant menus, although Panama seasonally regulates conch, lobster, and sea cucumber, and participates in the regional lobster regulations set by the General Secretariat of the Central American Integration System (SICA) and the Organization of the Fisheries and Aquaculture Sector of Central America (OSPESCA).

Due to a large body of work on the paleontology and historical ecology of the area, the current seascape can also be viewed through a historical lens. Fossils collected in Bocas del Toro play an important part in our understanding of faunal and environmental changes around the rise of the Isthmus of Panama (e.g., Collins, 1993; Coates et al., 1992, 2003, 2005; Smith and Jackson, 2009; Klaus et al., 2012; McNeill et al., 2013; O'Dea and Collins, 2013). There are ample observations that shifts in the bay ecology were underway well before the most recent human population boom. Ecological changes in the shallow Bahía Almirante reefs probably began over 1500 years ago when reef accretion in the deeper, currently hypoxic part of the bay slowed and then ceased (Figuerola et al., 2021). This was followed by reductions in relative abundances of herbivorous fish and epifaunal suspension feeding bivalves, and relative increases in infaunal bivalves and micropredatory fishes (Cramer et al., 2020). More recent shifts associated with changes in size and trophic structure of molluscs and decrease in acroporid corals appear to have begun in the 19th century (Cramer et al., 2012). There is further evidence of a recent phase shift from *Porites* dominated reefs to *Agaricia* dominated reefs associated with increases in terrigenous inputs in the 20th century (Aronson et al., 2014). While estimated timing of these shifts may depend on the dating methods and fauna surveyed (Cramer et al., 2020; Aronson et al., 2014), it is clear that the reefs have been undergoing phase shifts and that the timing of these shifts may vary across the seascape (Cramer et al., 2020).

3.1. History and culture of Bahía Almirante

Flows and migrations of people have occurred across the archipelago since the late Holocene (Guerrón-Montero, 2006; Spalding, 2013a, 2013b; Wake et al., 2013), and people in the region are reliant on the bay for both tangible and intangible ecosystem services including food and medicine, recreation, fisheries, transport, cultural well-being, and sense of place and identity (Scott et al., 2024). These ecosystem benefits are intertwined with other common-pool resources including wood, water, land, and areas for recreation (Manning, 2007; Scott and Mach, 2018), yet few empirical studies have directly linked ecological shifts to anthropogenic stressors (O'Dea et al., 2014; Spalding, 2013a) over this long history.

Prior to colonization, the Caribaro region (now Bahía Almirante) supported diverse cultures with settlements populated by the Dorasquez, Changuinas, Miskitos, Guaymies, Viceitas, Teribes, Terrabas, Borucas, Urinamas, Changuenas and Chalibas peoples (Molina Castillo, 2008). Artifacts recovered from Isla Toxar (now Isla Colon) (Molina Castillo, 2008) suggest that life in the archipelago was well-structured with socio-political hierarchies, social ranking, and extensive settlements (Wake et al., 2004, 2013). Radiometric dating suggests that the people occupying the region between AD690–1410 relied on domesticated root crops, wild tree crops, terrestrial vertebrates, offshore fish species, and inshore marine fish and molluscs (Wake et al., 2013; O'Dea et al., 2014). *Strombus pugilis* conch shells recovered from middens suggest that 1500 years of human-driven, low-intensity subsistence harvesting resulted in evolution of reduced size at maturity indicating that humans were actively engaged in changing the land and seascape well before modern times (O'Dea et al., 2014).

Despite enduring violence, disease, and displacement with the 1502 arrival of the Spanish to Bahía Almirante, the "Teribes" (now Naso), the Bribri, and the "Guaymies" (now Ngäbe), survived and still occupy the region (Stephens, 2008; Molina Castillo, 2008). Today, the Ngäbe are the most populous Indigenous group (INEC, 2014) and the Ngäbe-Buglé Comarca, a semi-autonomous Indigenous area designated by the Panamanian government in 1997 sits adjacent to Bahía Almirante. Of the approximate 22,000 people currently residing in Bocas del Toro archipelago, 65% are Indigenous, 26.5% are Mestizo and 9.9% are AfroPanameño (INEC, 2018). Recent estimates of foreign-born residents are not available, but in 2010 approximately 7% of the population was foreign-born and numbers of foreign migrants have continued to increase since then (Spalding, 2018). This ethnic and cultural diversity reflects a long history of regional colonization and migration.

The economic booms over the last 250 years have brought multiple waves of people of African, Indigenous, Chinese, European, and Panamanian Latino descent to the Bocas del Toro region which continues to shape society (Guerrón Montero, 2006, 2011; Spalding, 2013a). During the 18th and 19th century Bahía Almirante was a center for pirate activity (Howard, 2019). These multi-ethnic groups were provisioned by the British and encouraged to raid Spanish towns and ships. As piracy diminished, they settled in the area, and residents of Boca del Drago still strongly identify with this pirate heritage (Howard, 2019). In the 17th and 18th century the region was the site of conflicts between local indigenous groups and the Miskito Indians from Honduras and Nicaragua (Araúz, 2007). In the 1770s, the low-lying land in the province was reported to be deserted (Jaén Suárez, 1998) with the exception of British families who migrated from the Antilles with enslaved Afro-Antilleans (Heckadon Moreno, 1980; Waisome et al., 1981). As early as the 1830s, Ngäbe began to re-settle in the Bahía Almirante region (Guerrón Montero, 2006). Thousands of Afro-Antilleans migrated to Bocas del Toro from the 1890s onwards to work for the banana companies, and from central Panama upon completion of the Panama railway in 1855 and the Panama Canal in 1914 (Guerrón Montero, 2020). During this period Bocas Town was formed and soon became the third most economically important city in Panama. The legacy of colonization and the banana industry from the late 1800s to the mid-1950s culturally isolated the archipelago from the rest of Panamá due to its distance from the capital and the dominance of the English language (Guerrón Montero, 2006, 2011). The legacy is also evident in the alterations to the land and seascape via the clearing of forests for cultivation of bananas and cacao, and dredging of waterways to support ships transporting bananas to Europe and North America (Stephens, 2008). Following the economic boom in the 1800s and early 1900s the economy slumped after the 1930s as the banana industry suffered various setbacks. The 1991 Limon earthquake, which damaged a lot of vital infrastructure further worsened the region's economic decline.

Today, despite the most recent economic boom due to tourist development around Bahía Almirante, Bocas del Toro province and the Ngäbe-Bugle comarca have some of the poorest living conditions in the nation (Guerrón Montero, 2014). An unequal distribution of power and resources has persisted since the Spanish occupation (Marín Araya, 2012; Molina Castillo, 2008). For example, Ngäbe were excluded from working at the UFC due to a lack of English-speaking capacity thereby limiting their economic prosperity (Pleasant and Spalding, 2021). Today Ngäbe livelihoods are dependent upon subsistence fishing and agriculture, and coffee production via seasonal migration of some communities to neighboring Chiriquí province. Ngäbe living in urbanized areas lament the loss of connection to the land and try to keep their agricultural roots alive through a variety of cultural practices (Visser, 2021). In the archipelago, various Ngäbe communities are actively trying to promote artisanal crafts, eco-tours, and cultural experiences to visitors as tourism increases (Furnari et al., 2020).

The completion of a road to connect the coastal towns of Almirante and Changuinola directly to the rest of Panama in the early 2000s allowed for the settlement of more people and movement of goods into and out of the region. However Bocas del Toro remains somewhat isolated and remote from the center of the country despite the presence of a booming tourism industry. Local infrastructure has not kept pace with the increase in demand associated with the influx of tourists, lifestyle migrants, and associated businesses since the early 2000s. This is evidenced by frequent power outages, locally poor sanitation, insufficient road maintenance, limited availability of potable drinking water, and unreliable transport of goods and services to the island. The growth of the tourism industry and demand for natural resources for development have outpaced the ability of local governing agencies to provide quality infrastructure that meets tourism and immigrant demands. A shift from agricultural and fishing activities to service employment whereby local people are changing livelihood strategies away from traditional jobs to working at hotels and restaurants as well as the direct impacts of agricultural and fishing practices, tourism, and entrepreneurial endeavors all contribute to the perception that the culture and ecology of the Bahía Almirante and its surroundings are changing (Suman et al., 2018).

4. Hypotheses derived from PPD

Below we consider in more detail two specific pressures on the Bahía Almirante system in terms of the PPD framework. These were selected by the research team to most effectively convey the importance and potential utility of an interdisciplinary framing for developing future research questions and/or identifying potentially useful interventions. We describe the way the water cycle (with a focus on increased variability and associated periodic shortages) and pressures from tourism and migration influence the Bahía Almirante system as a whole. A set of specific hypotheses, corresponding to H1–H6 of the PPD framework (Fig. 3) are derived from these narratives as examples of potential causal linkages. Placing these in the graphical PPD framework illustrates how this can be used to organize the complex dynamics of these systems into discrete ideas that can be tested and refined through further research.

4.1. System responses to pulsed changes in freshwater availability

It is impossible to predict the impacts of climate change (an external driver) on environmental conditions in Bahía Almirante with certainty, but Fig. 8 and the following narrative explore the potential impacts of reduced rainfall as a pulse stressor on the interconnected human-ecological system. Regional climate models do not perform well on a local scale in Central America given the region's renowned diverse micro-climates (reviewed in Hannah et al., 2017; Hidalgo, 2021). Overall warming is likely, but the direction and magnitude of rainfall changes are less certain (Hannah et al., 2017; Seneviratne et al., 2021) and limited modelling studies suggested that Bocas del Toro will experience significantly drier summers by the end of the 21st century (Fabrega et al., 2013). Attempts to model river discharge in the region under climate change have also had limited success (Hidalgo et al., 2013; Varadarajan et al., 2022). The development of accurate regional climate and hydrology models and collecting the required validation datasets are major research challenges and an important knowledge gap. Until these models and datasets are available, climate-related presses and pulses will be difficult to predict. Even without predictive models, it is apparent to residents of the region that extreme rainfall events are resulting in more frequent flooding in towns and small settlements, while extended dry periods (referred to below as drought), especially in September and October, during the Veranillo, have resulted in water shortages (Collin, Mach, Scott, pers. obs.). The impacts of hydro-meteorological events have been reviewed for the region (Pérez-Briceño et al., 2016) and Changuinola was identified as the 7th most impacted municipality in Panama.

Drought is a pulse that can potentially impact coastal vegetation (**H1** & **H2;** Fig. 8). Swamp areas respond to drought via water table draw down which profoundly alters their biogeochemical functioning and long-term carbon storage. During dry periods fires occur in areas dominated by grassy vegetation (Sjogersten pers. obs.), a threat that would increase with increasing drought conditions. If dry periods become more intense, more frequent, and longer and sea level rises faster than peat swamp forest accretion, or another major subsidence event like the 1991 earthquake occurs, the regional swamps will be at risk of saltwater intrusion. Currently, the salt intolerant swamp vegetation is protected from high salinity water by a beach towards the open ocean and a mangrove fringe along the bay such that the lateral marine infiltration into the peat is ~2 m (Phillips et al., 1994). However, it is not uncommon to see a thin line of dead or leafless trees edging the onshore side of the mangrove forest. This ghost forests may be the result of intermittent saltwater intrusions. A larger die-off was observed after the subsidence caused by the 1991 earthquake (Phillips and Bustin, 1996a, b; Camacho and Víquez, 1994). If intrusion increases significantly vegetation will shift, with salt intolerant species replaced as mangroves encroach further inland, more of the peat deposit could be drowned in the ocean, and eventually be capped with carbonate sediment (Phillips and Bustin, 1996b). Climate warming and drought could also dry out and collapse the peat dome, resulting in burial of the peat under fluvial sediment (Phillips and Bustin, 1996b). Drought-driven hyper-saline conditions could also result in mangrove forest mortality, reducing vital nursery habitat for fishes (**H3**). These linking hypotheses highlight how additional research focused on drought periods could help provide a more nuanced understanding of the dynamic responses of coastal vegetation, which can ultimately impact carbon sequestration and greenhouse gas dynamics.

Observed and anticipated climatic changes may also have implications for the bay's circulation (**H1** & **H2**; not shown in Fig. 8) and hypoxia. Reduced freshwater input during September and October, associated with the dry Veranillo period, appears to promote intermittent inner bay refreshment. This suggests that reduced rainfall could actually reduce hypoxia under certain conditions. Reduced sediment and solute inputs during dry periods could also help reduce eutrophic conditions conducive to hypoxia. On the other hand, the potential

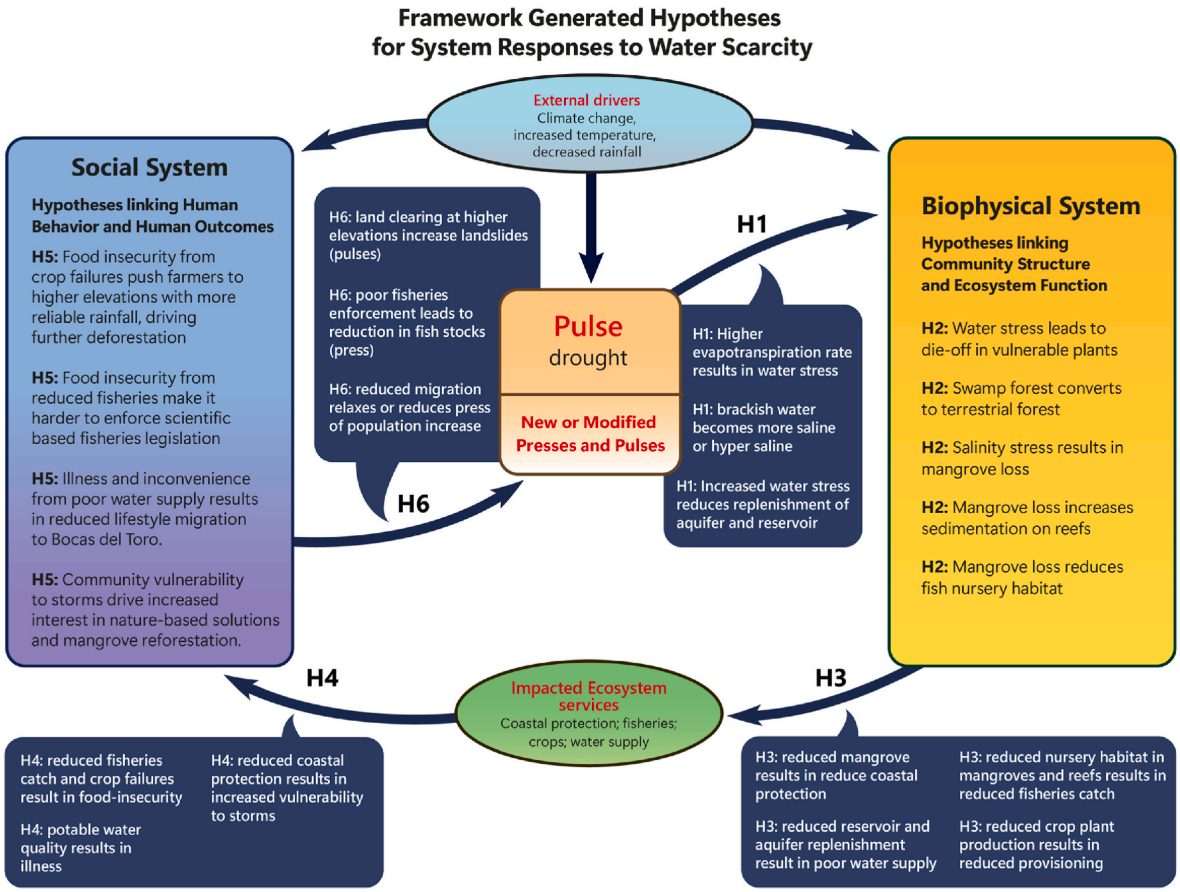

Fig. 8. PPD framework (Collins et al., 2011) for understanding the potential impacts of water scarcity on the Bahía Almirante Social Ecological system. Some of the numerous potential linking hypotheses show how the pulse of water scarcity could impact the system in various ways. Hypotheses that treat topics falling within traditional ecological research are presented in the yellow box and hypotheses falling within traditional social science are presented in the purple box. Hypotheses linking social and biological systems via ecosystem services and pulses and presses are shown in blue bubbles. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

dieback of vegetation in the catchments could increase soil and sediment erosion during rainfall events and may thus act to increase the sediment volume reaching the seagrass and reefs, while reducing aquifer replenishment. Moreover, if drought alternates with extreme rainfall events, higher sediment loads could increase eutrophication and reduce overall water quality and clarity as density gradients set up conditions for deep-water hypoxia during rainy periods. This could result in more widespread persistent hypoxia that may kill the vibrant shallow reefs and result in dead zones, as was observed in 2010 (Altieri et al., 2017). Thus the impact of drought on the physical circulation and hypoxia may depend on the intensity of intermittent rainfall events and the subsequent rainy season.

Clear waters and calm sunny days, typical of Veranillo drought periods, set up ideal conditions to promote thermally-induced coral bleaching. If this season continues to experience the decreasing rainfall and increasing temperatures apparent during the last few years, marine life will experience increased thermal stress. Warm, hypoxic water in the inner bay already limits the distribution of some animals (Lucey et al., 2023) thus it is likely that with increased heating, diversity in the bay will be further reduced, impacting fisheries species and subsistence and artisanal fisheries (**H3**) resulting in food insecurity (**H4**). Reef loss could also impact coastal protection as well as the tourist industry that is the basis for much of the regional economy (**H3** & **H4**).

In the Bahía Almirante catchment, the impacts of extreme climate events and climate change combined with population growth are going to exacerbate shortages and vulnerabilities stemming from economic water insecurity and poverty, where access to clean water is already precarious and where sanitation services are limited. Available rainfall should provide sufficient water available to meet human needs, but because of institutional, financial, and human capital limitations, potable water is often locally or seasonally scarce (Comité de Alto Nivel de Seguridad Hídrica, 2016). In Bocas del Toro province, 47% of households use the national public aqueduct system (Institute of Aqueducts and Sewers – IDAAN), 23% use a public community aqueduct, 11% use rainwater, 6.5 % use river water, the remaining 12% use other drinking water sources (Comité de Alto Nivel de Seguridad Hídrica, 2016). With increasing dry periods, rain capture for household water supply is no longer sufficient and increasing demand from rapidly expanding population and seasonal tourism has compounded the situation and resulted in shortages for those served by IDAAN on Isla Colon, even with the recent addition of several wells (**H5**) to augment the reservoir. In Bocas Town, shortages during the high season for tourism have resulted in closures of small businesses and reduced tourist revenue (**H4** & **H5**). These high season events have also exacerbated issues of water equity as businesses are able to pay premiums for water services limiting what is available for many local households. The tourism industry could also be negatively impacted if changing conditions and drought conditions result in biodiversity loss. Reduced biodiversity could impact the tourist economy either directly through reduced appeal for eco-tourism or potentially through indirect effects of reef mortality on surf break quality (Sadrpour and Reineman, 2023) (**H4**). Increased hardships due to fishing revenue loss could produce new presses on the system if this results in increased land clearing for agriculture (**H6**). Decreased tourism could result in less presses from population growth due to reduced demand and emigration or increased environmental activism of the local community (**H6**).

All parts of the PPD diagram should be viewed as hypotheses ripe for further investigation, refinement, and testing, either alone or in combination. Viewing the impacts of changes in precipitation through the PPD framework highlights a number of knowledge gaps and areas for further research. For example, knowing that there is a major regional knowledge gap with respect to predicted changes in rainfall patterns can help researchers frame their work in an appropriate climate change context. Stating explicitly how land-use change can interact with climate to impact well-being and livelihoods not only directly through water scarcity, but also potentially indirectly through changes to water-quality, turbidity and eutrophication in the bay impacting fisheries and tourism income highlights the current lack of water quality data for Bahia Almirante as well as sparse information on fisheries landings and how they relate to environmental conditions.

4.2. The press of tourism and migration on the Bahía Almirante system

Tropical coastal regions often have economies based on extractive traditions, providing food (fish, bananas, cacao), raw materials (tropical hardwoods, shells), and more recently relaxation, ecological and cultural experiences through tourism. Global and domestic demand for these goods and services is steadily increasing. The tensions between these external demands, local socio-economic, political and cultural factors, and local environmental and human wellbeing all play out in Bocas del Toro. In Fig. 9 (**H1–H6**) and the following narrative we describe the press of tourism and life-style migration on the Bahía Almirante system and the hypothesized connections between the impacts.

An estimated $20 billion, or 8.6% of all global travel and tourism expenditures was spent directly on wildlife tourism in Latin America in 2018 (WTTC, 2019). In Bocas del Toro, in 2021, direct expenditures on wildlife boat tours alone were estimated at $1.4 million (Mach et al., 2023). A high percentage of the local economy around Bahía Almirante is dependent on tourism, which is reliant upon a "pristine" image and the ability to be marketed as an island paradise. Some have gone so far as to try and label the archipelago as the Galapagos of the Caribbean (Guerrón Montero, 2020). With an estimated 154,000 visitors entering the archipelago each year (Scott and Mach, 2018), and a post-COVID boom in life-style migrants, it is anticipated that numbers of visitors, revenue, and benefits from tourism will continue to increase, as will the social pressures and natural resource impacts (**H1** in Fig. 9).

Tourism in its many forms (residential, volunteer, surf, nature-based and party tourism) plays an ever-increasing role in regional social and economic hierarchies (Mach, 2021, 2022), especially through impacts on land use and land tenure. The region has been experiencing an influx of predominantly wealthy newcomers from other parts of Panama as well as Europe, North and South America with the economic capital to set up businesses and develop and promote the area to fit their definition of paradise (Spalding, 2013b). Significant tax breaks and neoliberal land reforms to privatize land have drawn foreigners to the region (**H5**), many of whom develop businesses related to tourism around Bahía Almirante (Guerrón Montero, 2014; Thampy, 2014; Spalding, 2017). In

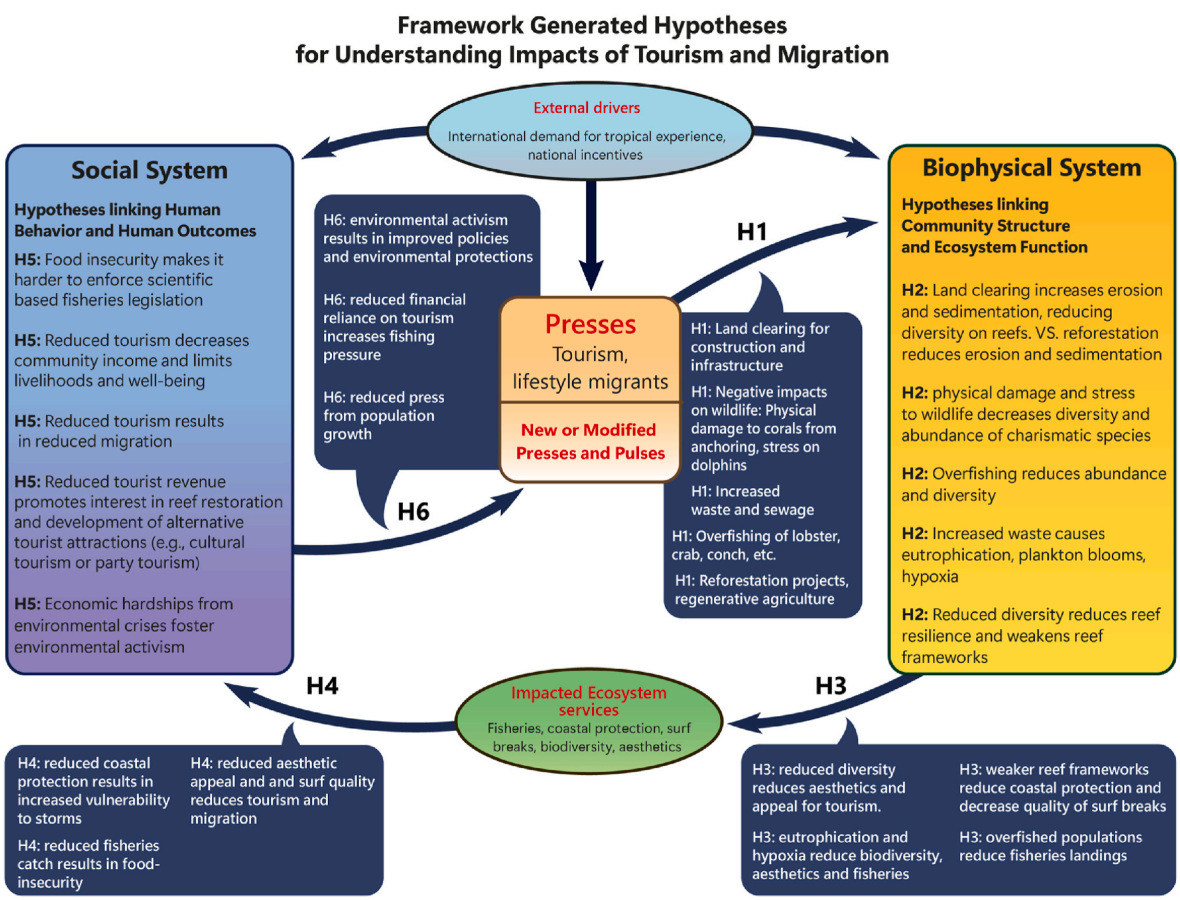

Fig. 9. PPD framework (Collins et al., 2011) for understanding the potential impacts of water scarcity on the Bahía Almirante Social Ecological system. Some of the numerous potential linking hypotheses show how the press of migration and tourism could impact the system in various ways. Hypotheses that treat topics falling within traditional ecological research are presented in the yellow box and hypotheses falling within traditional social science are presented in the blue-purple box. Hypotheses linking social and biological systems via ecosystem services and pulses and presses are shown in blue bubbles. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

Bocas del Toro this often creates land-use and land tenure disputes. Ngäbe and other long-standing Bocatoreño families may follow traditional land tenure practices and often lack clear land titles (Thampy, 2014; Howard, 2019). Institutions like the World Bank and Panamanian government continue to facilitate neoliberal land title reforms so that land may be more easily bought and sold to foment economic growth, and investment (Spalding, 2017; Suman and Spalding, 2018) in ways many indigenous communities have argued fail to secure their rights to collective self-ownership of land they have utilized for decades (Guerrón Montero, 2014; Thampy, 2014). As incomers buy untitled land for development or investment, local families are often displaced, removed or relocated (Finley-Brook and Thomas, 2010; Thampy, 2014) (**H5**).

Tourism also presents direct and indirect threats to the Bahía Almirante ecosystem. Some direct threats to ecosystems and organisms, such as chasing dolphins on tours, handling of starfish and sloths, visitors standing on top of corals, and noise pollution from motor-boat tours, are not only directly stressful to the biota (**H1**), but actively work against the industry and lend to decreased tourist satisfaction (Mach et al., 2023). Other direct threats to the local environment may be less immediately evident. For example, unregulated conversion of forest into settled or semi-urban areas with localized forest loss is partly driven by the short-term rental market to meet tourist demand (Mach, 2021). Investor occupation of prime ocean-front real estate and exclusive hotels in front of or on top of mangroves and coral reefs provide guests "eco" tourism experiences, but at a cost to the local environment that is not always evident to the tourists (**H1** & **H2**).

Increased demand from tourists who may not be aware of local conservation challenges also impacts the environment through increased fishing pressures. Seasonal fishing moratoriums on Caribbean spiny lobster (*Panulirus argus*), and total prohibition of conch and sea cucumber in combination with fishing regulations in the Isla Bastimentos National Marine Park (IBNMP), and mangrove removal prohibitions (**H5**), are the current management strategies for controlling over utilization of marine resources in the region (Guerrón Montero, 2005, Gaceta Oficial No 28397-C, 2017, Gaceta Oficial No 28681-B, 2018). However, many restaurants continue to highlight fresh lobster on their menus, and prohibitions have been walked back on several occasions due to economic hardships (**H4** & **H5**). The press and pulse dynamics related to lobster are thus emblematic of the wider socio-ecological issues linking both persistent and short-lived environmental stressors that reduce species size and abundance while at the same time making regulation more difficult due to the economic reliance of marginalized communities on the commercial value of the species.

Finally, overall population growth from permanent residents and short-term visitors in the face of poor infrastructure impact both the ecosystem and the well-being of local residents with the most marginalized groups at highest risk. The island infrastructure struggles and occasionally or frequently fails to keep up with the demands of a growing population with highly consumptive habits and lifestyles. As described above, and evident from our observations and lived experience in the area, increasing demand for water and energy resources compounds with variable weather patterns, aging infrastructure and deforestation to result in frequent and severe shortages in potable water. During prolonged dry spells, restaurants and hotels are not able to support tourists and have had to close during the peak season, with some of the wealthier residents temporarily leaving the area. Local people, especially those lacking the resources to install water storage at their homes, must rely on water trucked and ferried in from other parts of the country. Conversely, during high rainfall periods, frequent flooding, and a poor drainage system result in sewage overflow in urbanized areas, potentially leading to disease outbreaks and eutrophication of the bay. The impacts of unregulated tourism and growth could threaten the area's aesthetics (**H3** & **H4**) to the point where this may reduce future tourist revenue (**H5**), result in vocal responses from those involved in the tourist economy (**H6**), and further engender economic marginalization of Afro-Antillean and Ngäbe communities with limited ability to participate in and profit from the tourism economy (Guerrón Montero, 2014; Pleasant and Spalding, 2021).

The use of the PPD framework and the discussions surrounding its application to understanding the pressures of tourism and migration into the area have highlighted a number of potential areas for future collaborative work. For example, as a result of our work together on this manuscript, several of us are now collaborating to understand how the press of sea-level rise and resulting coastal erosion will interact with shoreline hardening and other infrastructure projects to impact the environment, livelihoods and recreation on Isla Colon. For example, recently proposed construction of a ring road around the island and a cruise ship dock are responses to demands for improved infrastructure to boost tourism visitation and increase access to beaches on Isla Colon. Not planned with climate change or best practices in coast erosion defenses or nature-based solutions in mind various sectors of the community are concerned that these projects will reduce the quality of visitor experiences and further disrupt ecologically sensitive areas of the island. This is just one case where data and projections based on physical or biological sciences can be merged with social science research to increase understanding and ultimately influence future infrastructure projects improving their resilience to changing conditions while increasing sensitivity to local demands for effective transportation, beach access, and ecological and surf-break integrity.

4.3. Looking forward

To reach a more holistic understanding of complex systems requires research approaches that explicitly analyze the system as an integrated whole. We illustrated here, how the PPD framework can be applied to organize information about Bahía Almirante and break this into explicit testable hypotheses about causal relationships. There are many different frameworks that can be productively applied (de Vos et al., 2019) and the best choice will depend on the ultimate study objectives. Our goal is that this review and synthesis will encourage researchers in Bahía Almirante and other estuarine systems to consider the landscape and seascape more broadly, to reach beyond their immediate field of expertise, and to consider both social and environmental aspects as they seek to increase system understanding.

The approach described here deals with the academic synthesis of information. To ultimately gain a full understanding and to help translate this understanding to actionable solutions, to use it as a basis to design science-based policies, and to effectively preserve the fragile human-natural system we must employ more transdisciplinary approaches. Beyond academic synthesis we must generate synergies between researchers, and local community and conservation efforts, as well as promote broader and more creative data sharing and dissemination (Holzer et al., 2019; de Vos et al., 2019; Diedrich et al., 2022; Bourgeron et al., 2018). Looking beyond single disciplinary work is the first step, but we hope that a more broadly synthetic academic understanding of Bahía Almirante will ultimately lead to work that actively includes transdisciplinary components, amplifies local voices, and involves local stakeholders resulting in greater sustainability and resilience for this very special system.

CRediT authorship contribution statement

Rachel Collin: Writing – review & editing, Writing – original draft, Visualization, Resources, Project administration, Funding acquisition, Formal analysis, Conceptualization. **Anne E. Adelson:** Writing – review & editing, Visualization, Formal analysis. **Andrew H. Altieri:** Writing – review & editing, Writing – original draft, Funding acquisition, Conceptualization. **Kasey E. Clark:** Writing – review & editing, Writing – original draft, Visualization, Formal analysis, Conceptualization. **Kristen Davis:** Writing – review & editing, Resources, Funding acquisition, Formal analysis, Conceptualization. **Sarah N. Giddings:** Writing – review & editing, Resources, Funding acquisition. **Samuel Kastner:**

Visualization, Formal analysis. **Leon Mach:** Writing – review & editing. **Geno Pawlak:** Writing – review & editing, Writing – original draft, Visualization, Resources, Funding acquisition, Formal analysis, Conceptualization. **Sofie Sjögersten:** Writing – review & editing, Writing – original draft. **Mark Torres:** Writing – review & editing, Conceptualization. **Cinda P. Scott:** Writing – review & editing, Writing – original draft, Conceptualization.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

No data was used for the research described in the article.

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