UNIVERSIDAD AUTÓNOMA DE BAJA CALIFORNIA
FACULTAD DE CIENCIAS MARINAS
INSTITUTO DE INVESTIGACIONES OCEANOLÓGICAS

.

INTRUSIÓN DE SURGENCIAS Y MOVIMIENTOS DE PECES EN UNA BAHÍA TROPICAL

T E S I S

QUE PARA OBTENER EL GRADO DE
MAESTRO EN CIENCIAS EN OCEANOGRAFÍA COSTERA

PRESENTA

ALEXANDRE TISSEAUX NAVARRO

ENSENADA, BAJA CALIFORNIA, AGOSTO 2023

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Dedicatoria y agradecimientos

Agradezco a mi comité de tesis por su tiempo y guía. A los familiares que están y los que ya no están por el apoyo brindado durante estos dos años lejos de casa. A los viejos amigos que me brindaron su apoyo desde Costa Rica y a los nuevos que hice durante mi estancia en Ensenada.

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Resumen general

Esta tesis investiga la conexión entre los procesos físicos que se dan en la interfaz océano-atmosfera y su influencia en los procesos de intercambio de agua y movimiento de organismos dentro de una bahía tropical. El estudio se realizó en la bahía tropical Bahía Santa Elena que se encuentra en el Golfo de Santa Elena en la costa del Pacífico Norte de Costa Rica. Los principales hallazgos de la tesis son dos y se presentan en dos capítulos. El Capítulo 1 se centró en la ocurrencia de eventos de surgencia durante el veranillo y su influencia en el enfriamiento de la columna de agua dentro del área de estudio. Las observaciones revelan intrusiones de agua subsuperficial durante condiciones de viento favorables a surgencias produciendo enfriamiento de la columna de agua dentro de la bahía. Estos eventos de intrusión de surgencia tienen implicaciones socioecológicas en la región, especialmente en términos de productividad pesquera. El Capítulo 2 mostró la relación que existe entre los procesos oceánicos y meteorológicos con el movimiento de dos peces de importancia comercial en el área de estudio. Los datos de telemetría acústica, que abarcan dos meses, revelaron oscilaciones en la abundancia de peces relacionadas con el nivel del agua y la luz solar. Este estudio brinda información valiosa para el uso sostenible y la conservación de los recursos marinos en el área al considerar las variaciones ambientales y sus impactos en los organismos marinos. El desarrollo de investigación en bahías tropicales como Bahía Santa Elena aporta a un mejor entendimiento de estos ecosistemas y de esta forma mejorar actividades enfocadas a su conservación y manejo de los recursos naturales.

Introducción general

Los ecosistemas costeros son hábitats críticos para los organismos marinos al ser utilizados como áreas de crianza, refugios, áreas de alimentación y reproducción para numerosas especies de peces (Elliott et al., 2007; Rountree and Able, 2007). La presencia de organismos marinos en los ecosistemas costeros está influenciada por las condiciones fisicoquímicas, incluidas las variaciones cíclicas en los movimientos del agua, como las mareas y las olas (Rountree and Able, 2007), y la concentración de oxígeno (Duque et al., 2020; Gallo et al., 2020). Por lo tanto, el estudio de los procesos físicas que ocurren en los ecosistemas costeros puede ayudar a comprender el comportamiento de las especies recreativas y comerciales, lo que es crucial para desarrollar enfoques de gestión y conservación de especies amenazadas y explotadas.

La marea es el principal forzante físico de los ecosistemas costeros en comunicación directa con el océano. Las mareas son el resultado de un equilibrio entre la atracción gravitacional entre dos cuerpos y la fuerza centrípeta producida por la rotación de la Tierra (Valle-Levinson, 2022). La Luna y el Sol ejercen las mayores atracciones gravitatorias sobre la Tierra, lo que da como resultado la superposición de oscilaciones conocidas como constituyentes armónicos de marea. Al analizar la variación del nivel de agua producida por la marea como una suma de armónicos, como M_2, S_2, N_2, O_1, K_1, podemos comprender la complejidad de las mareas en sitios de estudio específicos (Valle-Levinson, 2022). Las mareas dominan el intercambio de agua en periodos cortos de tiempo (relativos a un ciclo de marea), por lo tanto, influyen en la disponibilidad de nutrientes y la estructura del hábitat, lo que puede impactar la distribución, el comportamiento y los ciclos de vida de los organismos marinos (Rountree and Able, 2007).

El viento es otra forzante física que puede producir un movimiento en las capas de aguas superficiales. Cuando el patrón de viento dominante sopla paralelo a la costa produce un desplazamiento de aguas superficiales hacia mar adentro a través del transporte de Ekman (Stewart, 2008). Este movimiento da como resultado el reemplazo de aguas superficiales cálidas con aguas de afloramiento de fondo frías, saladas y ricas en nutrientes (Stewart, 2008). A este movimiento vertical o afloramiento de aguas frías se le conoce como surgencias. El flujo ascendente de las aguas profundas hacia la zona eufótica crea un suministro continuo de nutrientes, lo que promueve la fotosíntesis y sustenta altos niveles de productividad (Largier, 2020). Las bahías, que están conectadas al océano costero, exhiben características y procesos distintos en las regiones de surgencia costera debido a su interacción con el océano (Largier, 2020). El término “Upwelling bay” se refiere a estas bahías que están influenciadas física, química y biológicamente por el afloramiento costero en el océano adyacente (Largier, 2020).

Adicionalmente, en measoamérica se puede observar una reducción de las precipitaciones e intensificación de los vientos durante los meses de julio y agosto, denominada veranillo (Magaña et al., 1999). Existen tres hipótesis principales para explicar el momento y la fuerza del veranillo en Mesoamérica (García-Franco et al., 2023): un mecanismo de retroalimentación de las temperaturas de la superficie del mar y los efectos de radiación de las nubes (Magaña et al., 1999), la hipótesis del ángulo de declinación solar (Karnauskas et al., 2013), y el chorro de bajo nivel del Caribe como modulador del transporte de humedad y la actividad convectiva (Amador et al., 2016;

Durán-Quesada et al., 2017). Recientemente García Franco et al. (2023), revisó estas teorías y concluyó que la teoría del chorro de bajo nivel del Caribe explica mejor las características del veranillo. El chorro de bajo nivel del Caribe representa un viento zonal máximo del este de 925 hPa en la región del Caribe (Wang, 2007). Sin embargo, no está claro si esta intensificación de los vientos durante el veranillo provoca surgencia costera.

Esta tesis presenta dos casos de estudio en los cuales se pretende analizar los procesos físicos que ocurren dentro de una bahía tropical y como influyen en la biología y ecologia del sistema. El área de estudio es la Bahía de Santa Elena, la cual es un sitio importante para las comunidades cercanas debido a su potencial turístico y pesquero (Villalobos-Rojas et al., 2014). En junio de 2018, la Bahía de Santa Elena fue designada como Área de Manejo Marino, con el objetivo de conservar y brindar un uso sostenible de los recursos marinos (MINAE, 2018). Comprender la dinámica de las mareas y la ocurrencia de eventos de surgencia es crucial para entender los patrones y procesos ecológicos que ocurren dentro de la bahía y garantizar el manejo adecuado de los recursos marinos en esta área. En el Capítulo 1, presentamos evidencia de eventos de intrusión de aguas de surgencia en Bahía Santa Elena durante junio y julio de 2021 y 2022. En el Capítulo 2, investigamos la relación entre las mareas y el ciclo día-noche con los movimientos diurnos y semidiurnos de los pargos colorado (*Lutjanus colorado*) y dientón (*Lutjanus novemfasciatus*) en Bahía Santa Elena. El Capítulo 1 será sometido a la revista Estuarine, Coastal and Shelf Science, y el Capítulo 2 será enviado a la revista Marine Biology.

Capítulo 1

Upwelling intrusion in a tropical bay during mid-summer drought

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Abstract

Bahía Santa Elena is a tropical bay located in the northern Pacific region of Costa Rica. This region experiences a period of reduced precipitation from July to August, known as mid-summer drought, induced by the intensification of northeastern winds from the Caribbean Low-Level Jet. Intensification of upwelling-favorable winds can cool surface waters adjacent to the bay, leading to an intrusion into the bay that alters the biological dynamics of coastal habitats. This study aimed to analyze the intrusions of upwelled waters into a tropical bay during a mid-summer drought month. We conducted two measuring campaigns from June to July in 2021 and in 2022. The first campaign consisted of a single acoustic Doppler current profiler (ADCP) moored inside the bay. The second campaign consisted of two mooring deployments: an ADCP with a thermistor chain inside the bay and an ADCP installed at the inlet. Each campaign presented five distinct intrusions, of upwelled water into the bay promoted by an offshore Ekman transport. Upwelling-favorable wind peaks were followed by a decrease in temperature of the water column. When the upwelling-favorable wind relaxed, a warm water jet entered the bay. These events may play an important role in biological process in tropical bays adjacent to upwelling zones during mid-summer.

Keywords: Tropical Bay, upwelling, Ekman, temperature, wind relaxation.

1. Introduction

Upwelled water intrusions to coastal bodies can play a key role in biogeochemical processes (Largier, 2020; Valentin et al., 2021). Upwelling occurs when a predominant wind blows parallel to the shore moving the upper layer of water column offshore due to the Ekman transport (Stewart, 2008). Surface warm waters are then replaced by cold, salty, and nutrient-rich bottom upwelled waters (Stewart, 2008). Upwelling events stimulate primary productivity and support the growth of phytoplankton communities. This, in turn, triggers a cascade of trophic interactions that benefit marine organisms, from zooplankton to commercially important fish species, to humans (Barlow et al., 2021; Kämpf and Chapman, 2016).

In the Central American Pacific coastal upwelling occur due to the presence of wind jets formed from the interaction with the topography. Those wind jets are produced by a pressure gradient between the Caribbean and Pacific induced by North America cold air masses that move to the tropics from November to May. The wind jets travel over a topographic gap generated by the Nicaragua Lake in northern Cost Rica and southern Nicaragua (Chelton et al., 2000; Clarke, 1988; Steenburgh et al., 1998). The funneling through the topographic gap induce strong winds in the Northern Pacific area of Costa Rica called *Papagayos* with an average speed of 10 ms-1, wind gusts up to 27.78 ms^{-1} and lasting in average four days in the northeasterly direction (Chelton et al., 2000; Clarke, 1988; Escoto-Murillo and Alfaro, 2021; Steenburgh et al., 1998). Papagayos wind jet leads to the upwelling of cold and nutrient-rich waters in the surface layer (Ballestero and Coen, 2004; McCreary et al., 1989; Vargas, 2002). The influence of the oceanic upwelling in the internal conditions of the coastal bodies along the central American Pacific area remains poorly studied (Escoto-Murillo and Alfaro, 2021).

Moreover, an intensification of wind can be observed in the Northern Pacific of Costa Rica during July and August, which is influenced by the Caribbean Low-Level Jet with a maximum easterly zonal wind at 925 hPa in the Caribbean region (Wang, 2007). The Caribbean Low-Level Jet's easterly winds varies semi-annually, with a peak occurring during boreal summer and another during boreal winter (Wang, 2007). The rainy season in Central America lasts from June to October. However, there is a mid-summer drought between July and August caused by reduced precipitation due to the presence of boreal summer peak of the Caribbean Low-Level jet (García-Franco et al., 2023; Herrera et al., 2015; Lizano and Alfaro, 2014; Magaña et al., 1999; Magaña and Caetano, 2005; Wang, 2007; Zhao et al., 2020). Mid-summer intensification in the wind should cause upwelling, cooling and enriching the surface waters as it does with the *Papagayo* Wind Jet during the dry season. This mechanism could increase the primary productivity in the area which benefits the fisheries and to local communities (Villalobos-Rojas et al., 2014).

This research aims to investigate the intrusion of upwelled waters into a tropical bay: Bahía Santa Elena. The study of cooling periods during mid-summer and the upwelling intrusion into a tropical bay in northern Pacific area of Costa Rica holds significance within the context of the study area being a Marine Management Area (MINAE, 2018) adjacent to an upwelling zone.

2. Materials and Methods

2.1. Study area

Bahia Santa Elena (Santa Elena Bay) is a semi-enclosed coastal system adjacent to the Gulf of Santa Elena and located in the northern Pacific area of Costa Rica (Figure 1). The bay is relevant for the nearby communities due to its tourism and fishing potential (Villalobos-Rojas et al., 2014). The bay has an average depth of 15 m and a channel extending east to west in the northern section (Tisseaux-Navarro et al., 2021). The tide that enters the system propagates from the Pacific towards the Gulf of Santa Elena and shows an average tidal range of 2.3 m and 2.7 in syzygies (Lizano R., 2006).

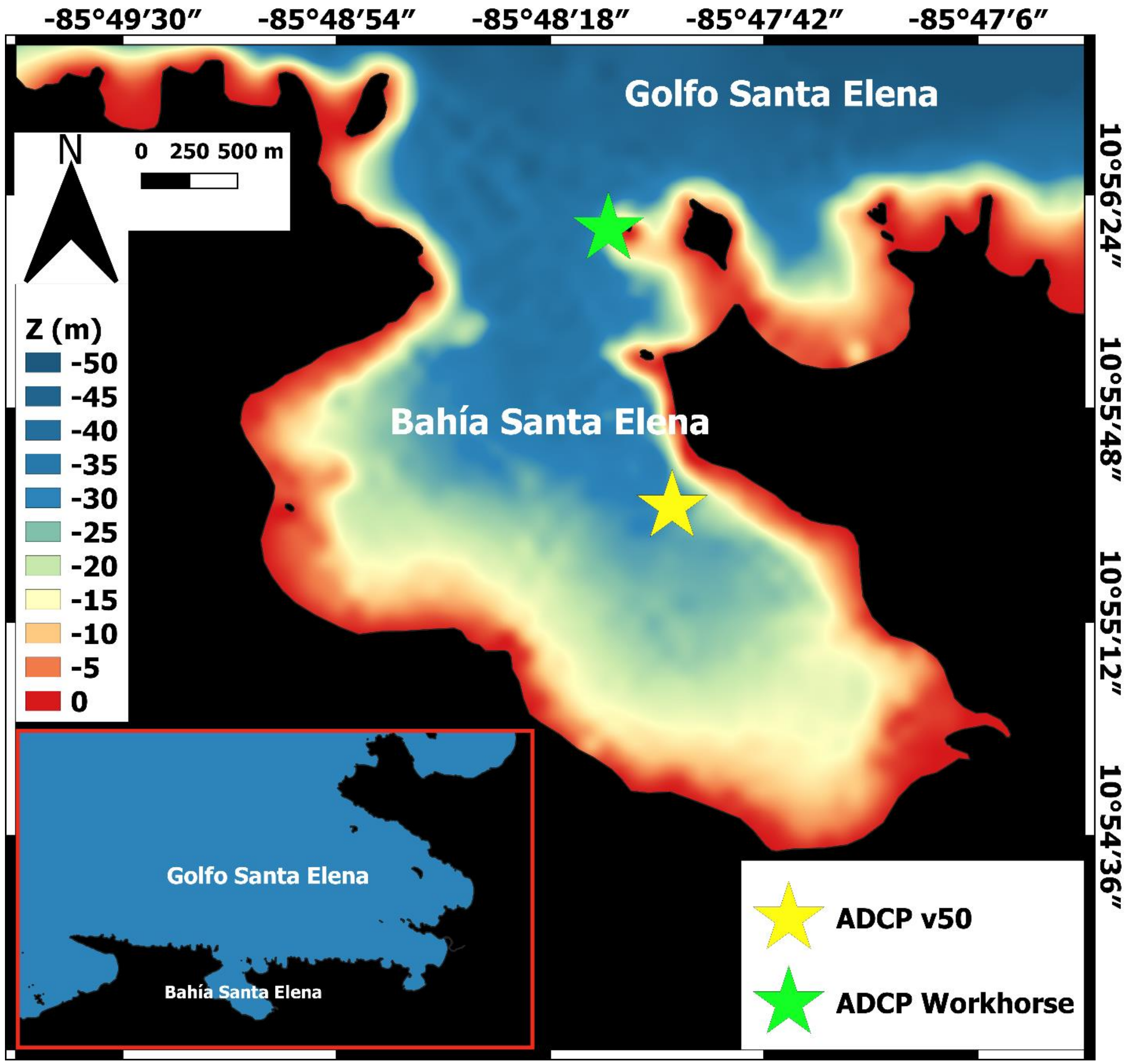

Figure 1. Bathymetry (colored map) of the study area; stars indicate the moorings positions. Yellow star corresponds to station 1 and green star to station 2. In the bottom left corner, map of the Golfo Santa Elena.

2.2. Data collection

Two month-long measuring campaigns were performed in Bahía Santa Elena. The first campaign, from June 15th, to July 13th, 2021, consisted of a Teledyne ADCP v50 installed at station 1 (10°55'31.4"N, 85°47'57.5"W, Figure 1) to measure current and water level data at a frequency of 1 ensemble per hour. Current data for 2021 were collected using 58 vertical bins with a 0.5 m resolution and a blanking distance of 1 m. The second campaign, from June 16th, 2022, to July 20th, 2022, consisted of two moorings deployed inside (same as station 1) and at the entrance of the bay (station 2, 10°56'18.2"N 85°48'08.2"W, Figure 1). At station 1, a Teledyne ADCP v50 recorded current and water level data at a frequency of 2 ensembles per hour, using 30 vertical bins with a 1 m resolution and a blanking distance of 1 m. Water temperature was recorded at station 1 using a chain of five thermistors placed at 2, 7, 12, 17, and 22 meters from the bottom, at a frequency of 60 samples per hour. At station 2, a Teledyne ADCP Workhorse Sentinel 1200 recorded current and water level data until July 10th; we only reported depth average velocity from this mooring. All data was averaged to hourly data for analysis.

Wind data of meteorological reanalysis were obtained from ERA5 to analyze the wind influence on the circulation of the system. ERA5 is the fifth generation ECMWF (European Center for Medium-Range Weather Forecasts) atmospheric reanalysis of global climate and is available at Copernicus Climate Change Service Information (Hersbach et al., 2022) (https:// cds.climate.copernicus.eu/).

2.3. Data analysis

Flow velocity components were rotated to align them to the axis of maximum variance: streamwise velocity component. Positive flow indicates outflow and negative flow represented inflow. Temperature anomaly was calculated by linear detrending, fitting a straight line to the dataset and subtracting it from the original values. The subtidal signal was obtained by removing diurnal and semidiurnal tidal variations to the streamwise velocity component, water temperature, and wind data using a Lanczos low-pass filter (Emery and Thomson, 2014) with period centered at 30 hours. Main modes of temporal and spatial variability of the flow and temperature profiles were obtained using an Empirical Orthogonal Functions (EOF, Kaihatu et al., 1998) analysis applied to the subtidal signal. The EOF main modes amplitude were cross correlated to wind velocity to explore the relationship between atmospheric forcing and water velocity and temperature.

Ekman transport, an upwelling indicator, was estimated using wind data following the method proposed by (Bakun, 1973). These calculations were made with Climate Data Toolbox (Greene et al., 2019). Firstly, wind magnitude (W) and wind stress (τ) where estimated:

$$W = \sqrt{(u^2 + v^2)}$$

$$\tau = \rho_{air}\ Cd\ (u^2 + v^2)$$

where ρ_{air} is a reference air density, 1.225 kg m^{-3}, Cd is the drag coefficient, 1.25×10^{-3}, u and v are then zonal and meridional wind components respectively from the ERA5 wind data. Then zonal ($\tau_x = \frac{\tau u}{W}$) and meridional ($\tau_y = \frac{\tau v}{W}$) components of wind stress where estimated. Finally, we obtained the zonal, $UE = \frac{\tau_y}{\rho f}$, and meridional, $VE = \frac{-\tau_x}{\rho f}$ components of Ekman transport; where ρ is a reference water density, 1025 kg m^{-3}, and f is the Coriolis frequency at a latitude of 11° N.

3. Results

Results are presented as follows. First, subtidal signal results are shown to highlight periods of low frequency outflows. Second, wind speed, Ekman transport, temperature anomaly, and depth-averaged velocity data depict a temporal variability that suggests an intrusion of upwelled waters from the adjacent sea. Finally, results from the EOF analysis illustrate the cooling from the upwelling intrusion to the bay and a correlation confirms its relation with upwelling-favorable wind conditions.

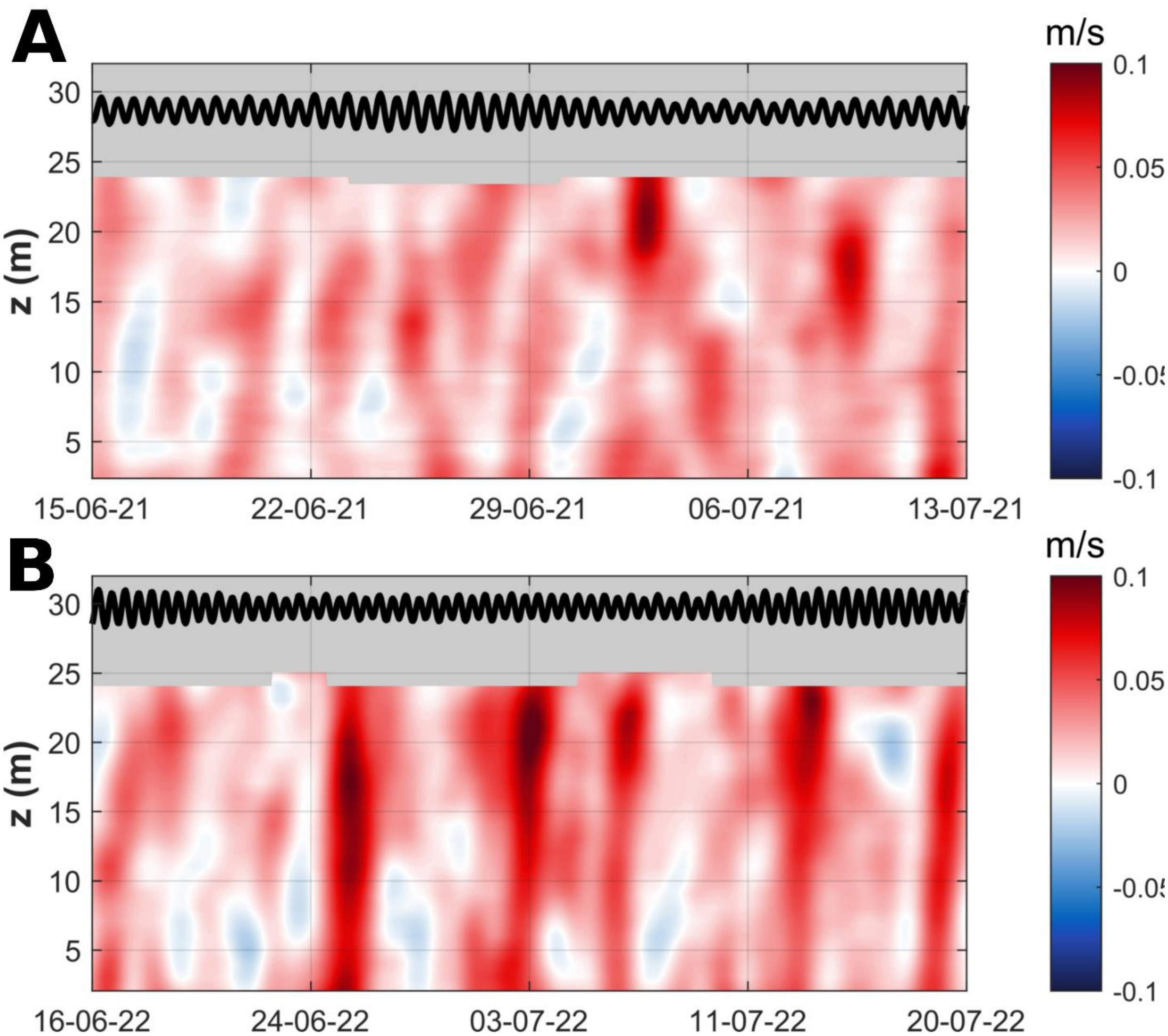

Figure 2. Subtidal streamwise velocity collected at Station 1 for the (A) first measuring campaign in 2021, and for the (B) second measuring campaign in 2022. Red and blue colors indicate outflow (or seaward), and inflow (landward) velocities, respectively.

3.1.Subtidal signal results

The subtidal streamwise velocity at station1 shows six outflow jets during the 2021 campaign (Fig. 2A) and five during the 2022 campaign (Fig. 2B). In both campaigns, higher outflow values were predominantly observed near the surface, and higher values (>0.1 m s^{-1}) occurred in 2022 than in 2021. Subtidal circulation shows a predominant weak outflow across the whole water column before and after these events, interrupted on some occasions by a vertically sheared flow.

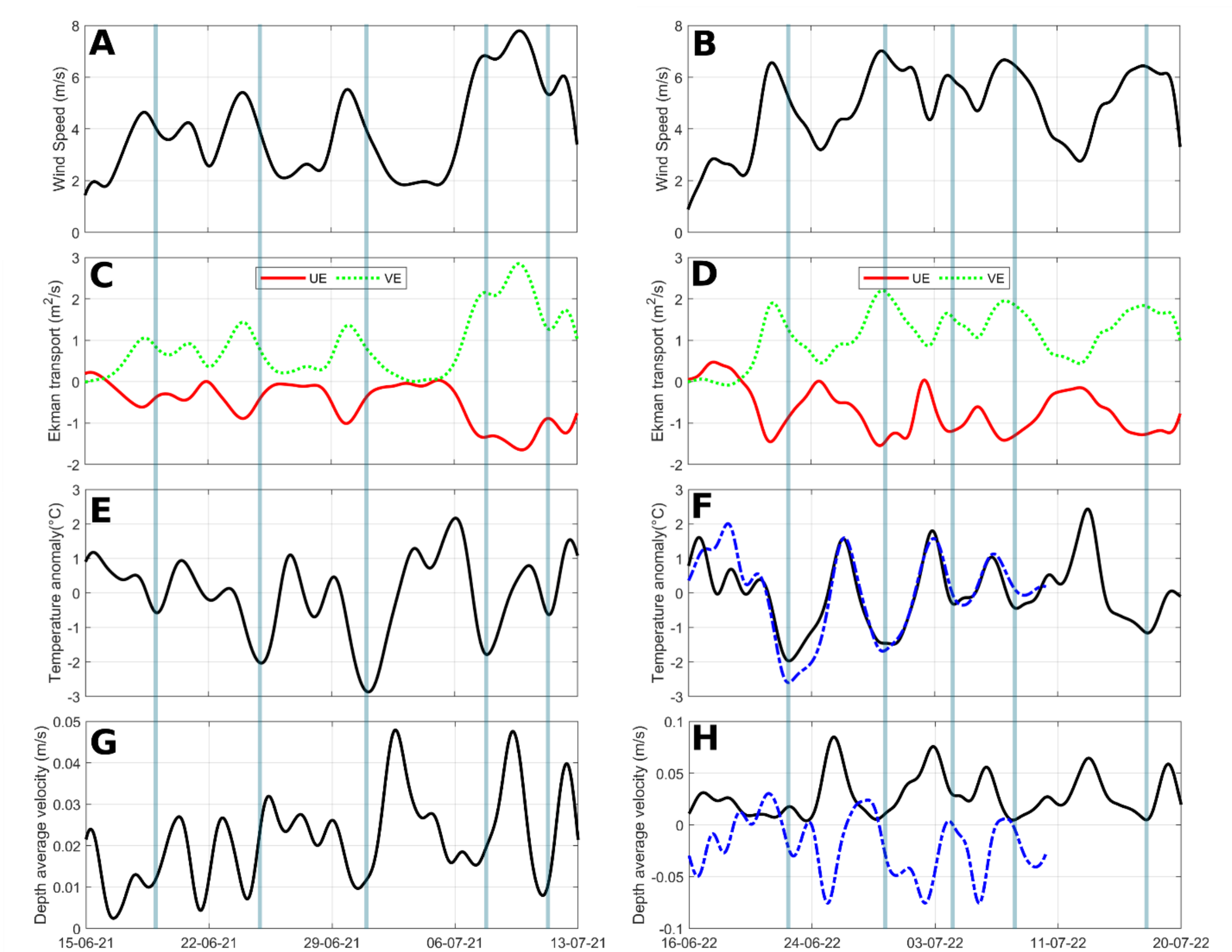

Figure 3. Subtidal time series of wind speed (A, and B), Ekman transport (C, and D), temperature anomaly (E, and F), and depth averaged velocity (G, and H) for the 2021 (left), and 2022 (right) measuring campaigns. Red continuous line in C, and D denotes zonal Ekman transport and green dotted line denotes meridional Ekman transport. Black line in E, and F indicates temperature anomaly, and in G, and H velocity at Station 1. Blue dashed line denotes temperature anomaly in F, and depth average velocity in H at Station 2. Grey lines mark when the lowest temperature was collected in each event.

Subtidal wind speed, Ekman transport components, depth averaged velocity, and temperature anomaly showed a qualitatively similar temporal variability at the two stations, and for both campaigns (Fig. 3). Subtidal wind speed varied in magnitude from 2 to 8 m $s^{-1}$and showed five wind peaks for each campaign where the wind speed (Fig. 3A, B) was higher than 4 m s^{-1}. Wind events also vary in duration, between 3 and 9 days. These wind peaks coincided with the northwestward Ekman transport peaks (Fig. 3C, D), meaning a seaward upper layer of water transported off the Gulf of Santa Elena. There was a cooling, after the wind peaks, and Ekman transport peaks, illustrated by a negative temperature anomaly in both campaigns (see grey lines in Fig. 3E, F). Wind relaxation induced warm water inflow denoted by a positive temperature anomaly. Depth-averaged outflow (Fig. 3G, H) at station 1 showed peaks that coincided with an increment of temperature anomaly (Fig. 3E, 4F). The 2022 campaign with two ADCP stations captured the entrance of water at station 2 (near the mouth) illustrated by a negative subtidal depth-average velocity (blue line Fig. 3H). The negative peaks of ~-0.07 m s^{-1} at station 2 occurred from 9 h. to 17 h. before each positive peak at station 1 (black line Fig. 3H).

These events occurred in both campaigns and repeated the same pattern. For example, in the 2021 campaign, the wind speed increases from 28^{th} of June and maintained high values to 4^{th} of July (Fig. 3A). Wind high values coincided with northwestward water transport (Fig. 3C), accompanied by a drop in water temperature (minimum value at night of 4^{th} of July, Fig. 3E). Then wind started drops on the 4^{th} of July below 4 m s^{-1}, when depth-average velocities increased (maximum value at night of the 6^{th} of July, Fig. 3G), and the temperature increases reaching highest values in the morning of the 7^{th} of July (Fig. 3E). The same happened in the mooring of 2022. For instance, the first event in this campaign occurred between the 21^{st} and 28^{th} of June, wind speed started increasing around the 21^{st} of June (Fig. 3B), which produces northwestern Ekman transport (Fig. 3D) and temperature drops to the lowest by 23^{rd} of June (Fig. 3D). The wind speed reached a relaxation point by the 26^{th} of June, depth-average velocities outside the bay (station 2) showed an inflow peak before the outflow peak within the bay (station 1) (Fig. 3F); and the bay depicted positive temperature anomalies on the 27^{th} of June (Fig. 3D).

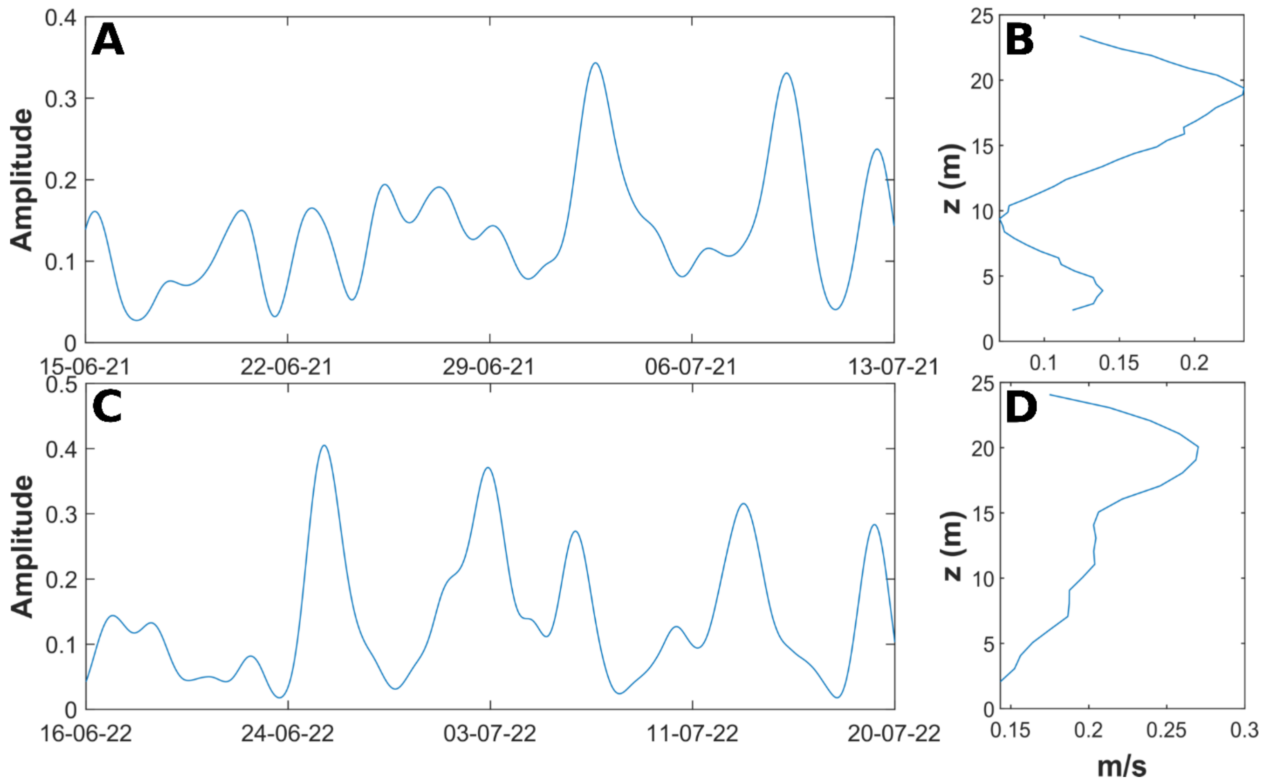

Figure 4. Upper panel: Temporal variation (A) and eigenvector (B) of EOF Mode 1 of subtidal streamwise velocity collected at Station 1 for the first measuring campaign in 2021. Bottom panel: Temporal variation (A) and eigenvector (B) of EOF Mode 1 of subtidal streamwise velocity collected at Station 1 for the second measuring campaign in 2022.

3.2.Empirical Orthogonal Functions and wind correlations

Mode 1 from the analysis of the Empirical Orthogonal Functions (EOF1) accounts for 47% of total variance for the 2021 campaign, and 75% of the total variance for 2022 (Fig. 4). EOF1 explains an outflow profile with a maximum speed at subsurface, ~20 m above the bottom, during both campaigns, with some speed increases at specific instants (Fig. 4) like the first days of July 2021 (0.08 m s^{-1}) and just after the 25th of June in 2022 (0.1 m s^{-1}). EOF1 was related with wind magnitude in both campaigns with a significant ($p<0.05$) cross correlation of 0.31 at a lag of 54 hours, and 0.60 at a lag of 98 hours for 2021, and 2022, respectively. Data from the thermistor chain revealed rapid temperature drops (maximum: -0.14 °C h^{-1}) and rises (maximum: -0.11 °C h^{-1}) in June and July 2022 (Fig. 5). This behavior was captured by the EOF1 temperature anomaly amplitude (Fig. 5B). Temperature anomaly EOF1 accounted for 86 % of total variance and was significant ($p<0.05$) inversely correlated with the wind speed with a maximum coefficient of -0.5460 at a lag of 21 hours (not shown). The temperature anomaly for EOF1 was the lowest 21 h after the wind speed peak, and the eigenvectors displayed a parabolic profile with maximum values at mid-depths, denoting depths of maximum temperature occurrence (Fig. 5C).

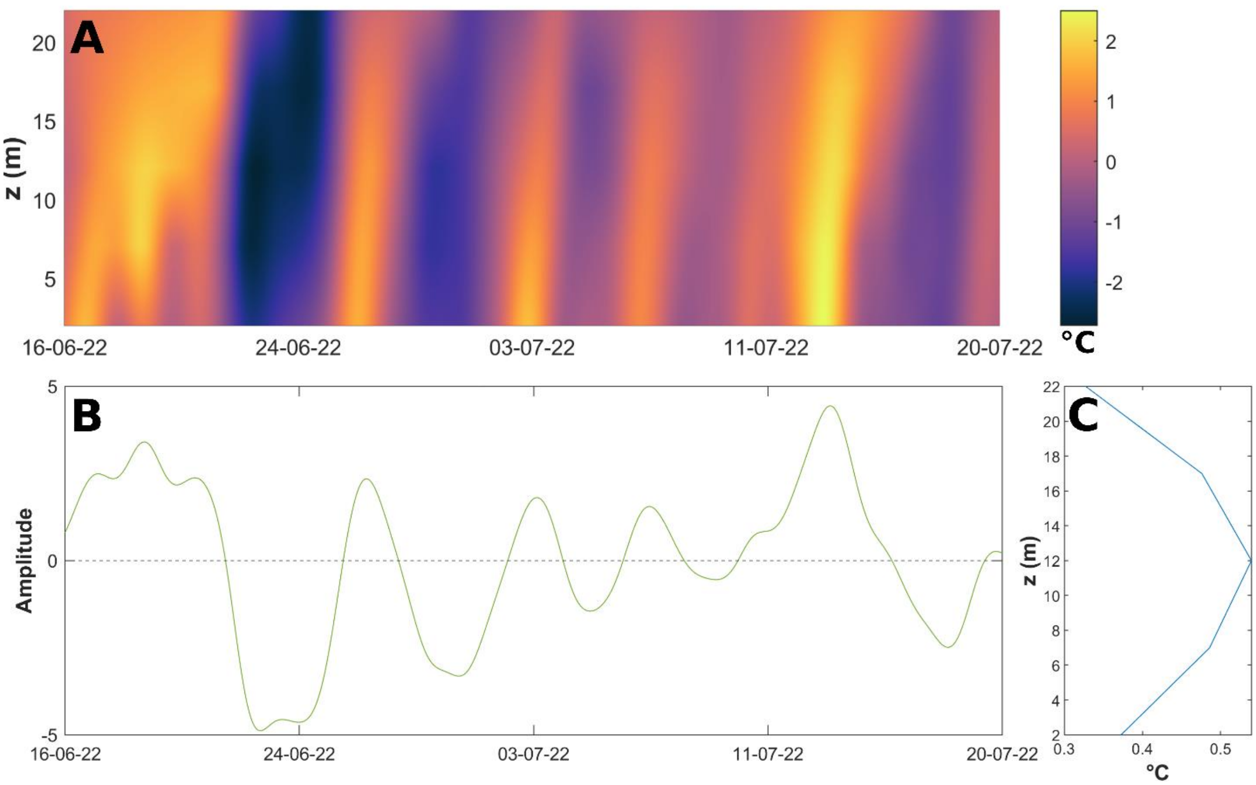

Figure 5. Upper panel: subtidal temperature profile (A) collected at Station 1 for the second measuring campaign in 2022. Bottom panel: Temporal variation (B) and eigenvector (C) of EOF Mode 1 of subtidal temperature collected at Station 1 for the second measuring campaign in 2022.

Based on the data collected during the study periods in 2021 and 2022, our findings revealed cooling periods during mid-summer, coinciding with the intensification of Northeastern winds. Specifically, we observed a significant decrease in water temperature in the bay following the onset of wind. After the wind intensity weakens, depth-averaged velocity increments were observed, and the water temperature increased again.

4. Discussion

Largier (2020) uses the term *upwelling bay* to define those bays which are driven physically and fueled chemically and biologically by the coastal upwelling in the contiguous ocean. Wind- driven coastal upwelling can be yearly present as brief anomalous events or as a seasonal phenomenon (Largier, 2020). The significance of upwelling bays lies in the diverse and thriving ecosystems they sustain. These habitats provide an ideal environment for primary and secondary consumers to thrive, creating a rich web of marine life that extends to higher trophic levels mammals (Croll et al., 2005; Kämpf and Chapman, 2016; Largier, 2020). Inhabitants of upwelling bays include a variety of species, from small microorganisms to big marine mammals (Croll et al., 2005). Coastal communities greatly benefit from the presence of upwelling bays. The availability of nutrient-rich waters, brought to the surface through upwelling, supports an abundance of small primary producers, fueling the entire food chain and enabling the proliferation of marine organisms (Croll et al., 2005; Kämpf and Chapman, 2016; Largier, 2020).

4.1. *Upwelling intrusion*

Cooling events observed between June and July of 2021 and 2022 may be attributed to upwelling. The Papagayos Wind Jet typically induces coastal upwelling in the northern Pacific coast of Costa Rica between November and May (Ballestero and Coen, 2004; McCreary et al., 1989; Vargas, 2002). Coastal upwelling has been poorly documented in the study area from June to October. Alfaro and Cortés (2021) highlighted a cooling event in mid-summer, with a marked drop in water temperature in Baha Salinas, north of the Gulf of Santa Elena. This event lasted up to 24 days due to possible upwelling produced by northeasterly winds. The upwelling events in the present work lasted less than six days following the period of wind intensification.

We show that upwelling events occur frequently during mid-summer; at least five events in a month. Northeasterly winds that cause mid-summer drought (MSD) are present every year, varying in magnitude (Magaña et al., 1999; Zhao et al., 2022, 2020, 2019) So upwelling events in Costa Rica's North Pacific may be present every year from June to August along the shelf of the Gulf of Santa Elena. Upwelled waters intrude adjacent bays as Santa Elena Bay and diminish the temperature of the water column.

Winds during MSD are also related to three significant upwelling stations located between southern Mexico and Panama, and known as Tehuantepec, Panama, and Papagayo (Legeckis, 1988; Magaña and Caetano, 2005; McCreary et al., 1989; Xie et al., 2005). These areas are exposed to boreal winter upwelling events due to increases of northeastern wind speeds (Chelton et al., 2000; Legeckis, 1988; Magaña and Caetano, 2005; McCreary et al., 1989; Salazar-Ceciliano et al., 2018; Xie et al., 2005). Wind speed increases were observed from July to August at the Tehuantepec and Papagayo areas using six years of data (Romero-Centeno et al., 2007). These wind speed increases are the main cause for coastal upwelling in Tehuantepec mid-summer (Santiago-García et al., 2019), which coincide with our results that indicate upwelling events in the Papagayo area during the same period.

The 2022 campaign demonstrated the occurrence of an inflow near the inlet, which was followed by an outflow observed within the bay ~13 h later. These circulation patterns are likely related to the morphology of the system. Tisseaux-Navarro et al., (2021) observed that the subtidal circulation exhibited lateral shear, with the outflow taking place in the northern and deepest side of the bay, while inflow occurred over the southern shoal. When the wind relaxed, an inflow jet occurred as the barotropic gradient shifted from landward to seaward, resulting in onshore water transport to restore the pressure balance (Carmack and Kulikov, 1998). In our data, inflow jets were observed after wind relaxations. Inflow jets have also been observed in Bodega Bay, California. Wind peaks were followed by the intrusion of cold water and wind relaxation by intrusion of warm water (Morgan et al., 2012; Wing et al., 2003). Upwelling events in Bodega Bay generated an equatorward cold flow, and warmer poleward flow during relaxation periods. Thus, wind relaxation resulted in rapid sea surface warming. The warm flow in Bodega Bay resulted from solar heating and advection of warmer offshore water into the area (Morgan et al., 2012; Wing et al., 2003). Suanda et al., (2016) also described a poleward propagating flow that led to an increase of water temperature by approximately 5°C in the Punta Concepción area in Southern California. In addition, Washburn et al., (2011) found that thermal fronts associated with the propagating warm flows in South Central California coast produced a temperature increase of 1-4 °C in a span from 2.9 h and 44.6 h; as warm water approached the moorings, poleward current speeds increased by 0.1–0.2 m s−1 and typically reached maxima after the arrival of warmer water.

Coastal systems in upwelling zones can be classified based on their shape. Elongated systems are defined as systems where the length is more than twice the width of the mouth (Largier, 2020). In such elongated systems, the influence of upwelling may vary spatially. For example, in the case of Ria de Vigo elongated system, the circulation patterns are associated with the upwelling/downwelling cycle in the mid-system (Barton et al., 2015). During upwelling conditions, cool, salty, and dense bottom water enters the ria, while warmer, low salinity and less dense surface water enter the ria during downwelling conditions (Barton et al., 2015). At the mouth of the system the circulation is influenced by the intrusion of wind-driven alongshore flow from the external continental shelf (Barton et al., 2015). In our study area, which can be classified as an elongated system, with a width of 1.5 km and a length of 4 km, the upwelling influence varies spatially. The influence of wind-driven currents is observed near the mouth of the Bahía Santa Elena, where outflows occur during upwelling-favorable wind conditions, and inflows are observed when wind ceases. In the inner bay, the influence of currents is only evident when warm water intrudes due to a weaking of the wind.

4.2. Impacts on biota

Upwelling events in the area during the dry season have been associated with higher fishing productivity (Villalobos-Rojas et al., 2014). The midsummer upwelling events described in this study are also suggested to play a key role in the productivity of the study area, and in other bays of similar characteristics adjacent to upwelling zones. During prolonged upwelling events, the bay can serve as a thermal refugee for fauna, due to the timing of temperature changes. The temperature variations typically manifest outside the bay first. Additionally, the shallow areas and the inner zones of the bay are expected to be warmer than deep areas outside the bay.

Furthermore, in areas with seasonal upwelling, the presence of nutrient-rich cold waters have an effect in species abundance and composition (Benoit-Bird et al., 2019; Du and Peterson, 2014; McIlwain et al., 2011; Rueda-Roa et al., 2017). In Northern Pacific of Costa Rica, including Bahía Santa Elena, fish abundance is influenced by upwelling events of the dry season (between January to march), including commercial fish species (Eisele et al., 2020; Espinoza et al., 2022; Farías-Tafolla et al., 2022). Hence, it is important to investigate the role of mid-summer upwelling events in the presence or absence of species.

It has been noticed that warm water transport generated by wind relaxation in upwelling areas can aid in the dispersal of larvae (Queiroga et al., 2007; Shanks et al., 2000; Wing et al., 1995). Furthermore, short-term temporal alternation from upwelling to relaxation is more productive than long-term variability (Lathlean et al., 2019; Menge and Menge, 2013). Upwelling transport nutrients to the upper layers of the water column, while during relaxation processes may transport oxygen to the lower layers. This heightens interest of upwelling/relaxation events during mid-summer in tropical bays adjacent to upwelling zones, and its effects and potential importance in biological process in the area.

5. Conclusion

Coastal upwelling is observed along the North Pacific coast of Costa Rica, induced by wind during mid-summer drought season. This upwelling phenomenon leads to a cooling of the water in Gulf of Santa Elena, which subsequently intrude into Bahia Santa Elena, an adjacent tropical bay. When upwelling-favorable winds cease, a warm flow jet moves towards the shore and enters the bay. In our study, we have demonstrated the influence of this warm inflow jet on the circulation patterns within the bay, resulting in increased water velocity values. These events, occurring during the mid-summer period in tropical bays adjacent to upwelling zones, are likely to have a significant influence on biological process in the area. To gain a deeper understanding of the dynamics at play, further monitoring is necessary to investigate the interaction between remote wind forcing, water density gradients and wind waves that enter the bay.

Acknowledgements

This research was funded by Consejo Nacional de Ciencia y Tecnologia (CONACyT), México, under grant given to Alexandre Tisseaux-Navarro (CVU: 1147800). Also, data collection of this research was supported by the 2021 and 2022 Environmental Observatory grant program of Vicerrectoría de Investigación, Universidad Nacional. Field support by Lara Family in Cuajiniquil is also acknowledge.

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Capítulo 2

Diurnal and semidiurnal movements of two commercially important fish in a tropical bay

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Abstract

Biological data collection and examination often overlooks short-term environmental variations and their influence on organisms. For example, when quantifying the abundance of a nocturnal fish species through discrete observations (i.e., a single sample during day and night) spatial disparities in abundance may arise due to sampling strategies. This bias can lead to errors in estimating abundance of particular species, potentially resulting in fishing regulations that harm their populations. This study investigated the relationship between oceanic and meteorological processes associated with the movement of two commercially important fish species in Bahia Santa Elena; a tropical bay located along the north Pacific coast of Costa Rica. Acoustic telemetry data spanning for two months was utilized to track the presence of 14 Colorado snappers (*Lutjanus colorado*) and 16 Pacific dog snappers (*Lutjanus novemfasciatus*) at different zones of the study area. A wavelet analysis showed dominant diurnal and semidiurnal frequencies and their temporal variability. The oscillations in fish data exhibited semi-diurnal and diurnal periodicity correlated with water level and sunlight that may be related to food access, and shelter. Oceanic and meteorological conditions are crucial to understand the dynamics of marine organisms in coastal environments and avoid detrimental management policies.

Keywords: Snapper/Lutjanidae, Tide, Wavelet, Mangrove, Tropical.

Acknowledgements

This research was funded by Consejo Nacional de Ciencia y Tecnología (CONACyT), México, under grant given to Alexandre Tisseaux-Navarro (CVU: 1147800). Also, water level data collection of this research was supported by the 2021 Environmental Observatory grant program of Vicerrectoría de Investigación, Universidad Nacional. Field support by Lara Family in Cuajiniquil is also acknowledge.

1. Introduction

Estuaries are critical habitats for marine organisms as they serve as nursery areas, shelter, feeding and reproductive grounds for a wide range of species (Elliott et al. 2007; Rountree and Able 2007). The presence of marine organisms in estuaries is influenced by physicochemical conditions, such as cyclical variations in water movement (Rountree and Able 2007) and oxygen concentration (Duque et al. 2020; Gallo et al. 2020). Studies that neglect the influence of tides on fishes, for example, may yield to misinterpretation of population size, occurrence, community structure, and biodiversity (Blauw et al. 2012), which can have significant ecological, social and economic implications for the management of aquatic resources.

Coastal fishes are known to exhibit semidiurnal or diurnal patterns influenced by variations in tide and sunlight (Alós et al. 2012; Pagès et al. 2013; Ramirez-Martínez et al. 2016; Aguzzi et al. 2020; Burke et al. 2020). Commercial and recreational fishing often target specific species or areas (Marchal et al. 2014; Hunt et al. 2019; Birdsong et al. 2021). Knowledge on the relation between movement patterns of fishes with sunlight and tides can help to improve fishing regulations, such as seasonal closures or restricted area use, which can minimize negative impacts on fish populations during vulnerable life stages or critical periods (McKinley et al. 2011).

The utility of wavelet and wavelet coherence analysis in examining complex behavioral patterns in aquatic organisms and its relation to environmental variables has been demonstrated in previous studies (Rodríguez et al. 2014; Viehman and Zydlewski 2017; Boswell et al. 2019). Wavelet transforms expand time series into time-frequency space and can therefore find localized intermittent periodicities (Grinsted et al. 2004). These analyses have been successfully applied in telemetry studies with fish, identifying semidiurnal and/or diurnal patterns and its variation in time for different species (March et al. 2010; Alós et al. 2012; Pagès et al. 2013; Zhang et al. 2020; Burke et al. 2020; Ulvund et al. 2021).

Tides impact feeding activity and predator-prey interactions of aquatic organisms as they experience alternating periods of high and low water level due to the tidal cycle (Sheaves 2005; IJsseldijk et al. 2015; Sheaves et al. 2017; Checon et al. 2020). Additionally, the day-night cycle plays a crucial role in the presence of aquatic organisms in coastal ecosystems, due to feeding strategies of predators and the avoidance strategies of preys (Zagars et al. 2012; Ramirez-Martínez et al. 2016).

The snapper family, *Lutjanidae*, encompasses some of the most highly sought-after fish species worldwide in both commercial and recreational fishing (Coleman et al. 2000; Amador and Aggrey-Fynn 2021; Engle et al. 2023). Along the North Pacific coast of Costa Rica, the Pacific dog (*Lutjanus novemfasciatus*) and Colorado (*Lutjanus. colorado*) snappers are two species that are typically targeted by artisanal and recreational fishers (Villalobos-Rojas et al. 2014). Juveniles of both species are frequently found in mangroves and estuaries (Fischer et al. 1995), while adults can be found in a wide range of coastal habitats, including rocky and coral reefs (Angulo et al. 2013;

Nelson et al. 2016). However, our understanding of habitat uses during different life-stages and the influence of environmental factors on movement patterns of these species remain limited.

It is important to study how the behavior of commercially and recreationally important fishes, as snappers, is related to the tidal variations or other external factors like wind, and sunlight. Knowledge of such relationships will facilitate unbiased sampling and abundance estimates. In this study, we used wavelet analysis on fish presence, sea level (tides), and sunlight data to establish correlations between these parameters. Our results provide new insights into the factors that influence the presence and abundance of snappers (*Lutjanidae)*, which can aid in the effective management and conservation of commercially and recreational species elsewhere, but also identify critical habitats and processes involved in their survival/persistence.

2. Materials and Methods

We constructed time-series using acoustic telemetry data of the Colorado (*Lutjanus colorado*) and Pacific dog (*Lutjanus novemfasciatus*) snappers. A wavelet analysis and wavelet coherence analysis were conducted to identify cyclical movement patterns and relate them with water level and sunlight data.

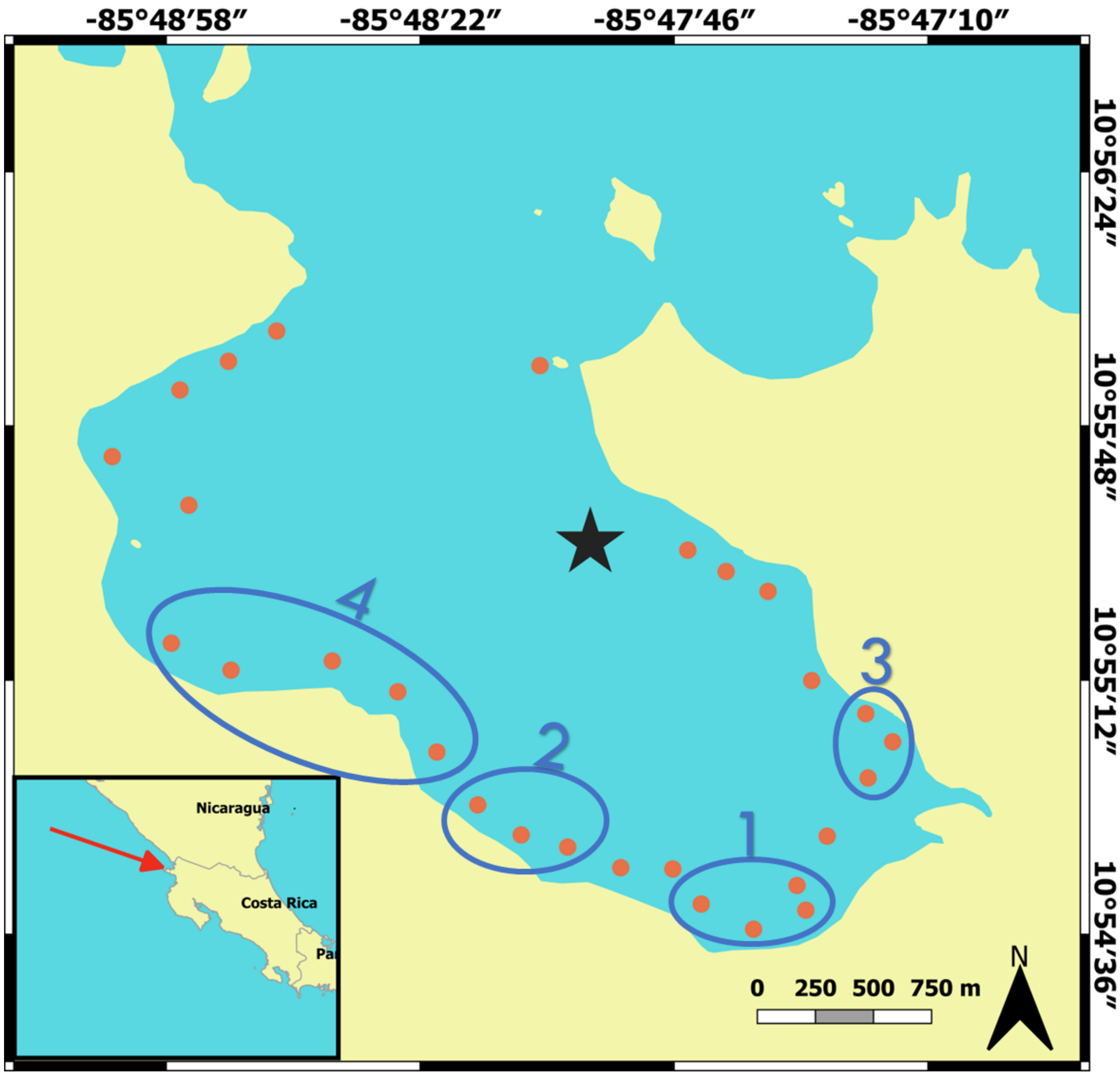

Fig. 1. Map of Bahía Santa Elena. Black star indicates the ADCP location. The orange dots denote the stations of acoustic receivers, and blue circles enclose the four zones with its identification number.

2.1. Study area

Bahía Santa Elena is a semi-enclosed bay located in the Gulf of Santa Elena, north Pacific coast of Costa Rica (Fig. 1). The bay has an average depth of 15 m and a channel extending east to west in the northern section (Tisseaux-Navarro et al. 2021). The tide that enters the system propagates from the Pacific towards the Gulf of Santa Elena, with an average tidal range of 2.3 m and 2.7 m in syzygies (Lizano 2006).

Wind and precipitation fluctuations are influenced by the Northern Pacific climatology of Costa Rica. Wind jets are generated by an atmospheric pressure gradient caused by North American cold air masses moving towards the tropics. The wind jets pass through a topographic gap created by the Nicaragua Lake, resulting in strong winds known as the Papagayos in the Northern Pacific region of Costa Rica (Clarke 1988; Steenburgh et al. 1998; Chelton et al. 2000). The Papagayos wind jet triggers the upwelling of cold, nutrient-rich waters that influence coastal ecosystems (McCreary et al. 1989; Vargas 2002; Ballestero and Coen 2004). From June to August, the intensification of wind produces Mid-Summer Drought in Central America (Wang 2007). Wind intensification during the mid-summer drought may result in coastal upwelling and an intrusion of upwelled waters into Bahía Santa Elena as observed from a thermistors chain by Tisseaux-Navarro et al. (*submitted/in-review*).

2.2.Data collection

Water level data

Hourly water-level data were obtained using a Teledyne v50 ADCP current meter. The instrument was moored on June 15th, 2021, in the main channel of Bahía Santa Elena (10°55'31.4"N, 85°47'57.5"W, Fig. 1) at 30 m depth, and it was retrieved on July 13th, 2021. The raw data were processed using Velocity software (Teledyne RDIntruments 2017).

Sunlight data

Top net solar radiation information was obtained from ERA5, which is the fifth generation ECMWF (European Center for Medium-Range Weather Forecasts) atmospheric reanalysis of global climate, and is available at Copernicus Climate Change Service Information (Hersbach et al. 2022) (https:// cds.climate.copernicus.eu/#!/home). A 13 h low-pass filter was applied to the top net solar radiation data to emphasize diurnal variations (day-night), resulting in a variable referred to as sunlight.

Telemetry data

Acoustic telemetry data collected from June 1st to July 31st, 2021 were analyzed for two common snappers (*L. novemfasciatus* and *L. colorado*) monitored inside Bahía Santa Elena, as part of an ongoing long-term behavior study. A total of 30 individuals (16 *L. novemfasciatus*; 14 *L. colorado*) were tagged internally with acoustic transmitters (V9-2x-180k-1, Innovasea®, Canada) in November 2020. Total length (TL) ranged from 28.8 to 44.6 cm in *L. colorado* (mean length, TL_{mean}: 33.6 cm) and from 22.5 to 49.3 cm *in L. novemfasciatus* (mean length, TL_{mean}: 34.9 cm). In addition, we deployed 28 acoustic receivers (VR2W-180 kHz, Innovasea®, Canada) around the study area to monitor the movement and residency of snappers (Fig. 1). The acoustic range of the receivers varied from 120 to 280 m across available habitats inside the bay based on a previous study (see Matley et al., 2022). Whenever a tagged fish swam within the detection radius of a receiver, the date and time of the detection were saved in its internal memory.

2.3. Data Analysis

The harmonic analysis applied to water level data determined the main tidal constituent amplitudes and phases using a least squares fit method, consisting in finding minimum root mean square errors between observed and theoretical harmonic model outputs (Lwiza et al. 1991; Valle-Levinson and Bosley 2003). The harmonic model represented the observed variable as a sum of sinusoidal harmonics of amplitudes (A) and phases (α):

$$A_T = A_0 + A_1 sen(\omega_1 t + \alpha_1) + A_2 sen(\omega_2 t + \alpha_2) + \cdots + A_n sen(\omega_n t + \alpha_n) \text{ (E1)}$$

where A_T is the observed water level, A_0 is the tidal residual, ω is the tidal wave frequency of the n constituent harmonics used in the analysis. The form factor of tide was estimated using harmonic amplitudes obtained from this analysis (Mustoe et al. 2005). We used the amplitudes and phases derived from the harmonic analysis to estimate the water level from the 1st of June to the 31st of July using Equation 1.

The goodness-of-fit (*Gf*) of the least squares fit was calculated using the following equation:

$$Gf = \frac{\sum(\bar{A} - A_{pred})^2}{\sum(\bar{A} - A_{obs})^2} \text{ (E2)}$$

Where $\bar{A}$ is the observations mean, A_{obs} is the observed value measured by the instrument, A_{pred} is the predicted value obtained from the least-squares analysis for the same time as the measured value. Goodness-of-fit provides a measure of the overall agreement between the harmonic model's predicted values and the actual data points.

A total of 11 *L. colorado* and 15 *L. novemfasciatus* were detected during June and July 2021, from the 30 fish originally tagged in November 2020. Fish that were monitored during this period were classified as large ($TL > TL_{mean}$) and small ($TL_{mean} < TL$) individuals. Receivers were grouped into four zones within Bahía Santa Elena based on their proximity and habitat type (Fig. 1). In Zone 1, receivers were near the entrance of a mangrove channel; this zone exhibits the presence of logs scattered around the receiver's area. In Zone 2, receivers were located in an area that had a combination of logs and rocks. In Zone 3, receivers were located adjacent to a mangrove channel, and this area also has a small rocky reef. In Zone 4, receivers were in the central coastline of the bay, relatively distant from the mangrove channels.

Telemetry data on *L. colorado* and *L. novemfasciatus* were used to create hourly time series in order to quantify the number of small and large individuals that were detected in each zone. Continuous wavelet transforms perform a local time-scale decomposition of a time series (Cazelles et al. 2008; Polansky et al. 2010). Wavelet transform and wavelet coherence analysis were performed using the MATLAB wavelet analysis toolbox developed by Grinsted et al. (2004) using the default *Morlet* wavelet function (for more information of this analysis, see Grinsted et al. 2004). Wavelet analysis allowed for the decomposition of temporal variability in dominant frequencies. Wavelet coherence was then calculated between the telemetry data and the sea level, and sunlight. The analysis of wavelet transformations was not performed on time series data for large and small *L. colorado* in Zone 3, and neither for large *L. novemfasciatus* in Zone 3 due to limited data.

3. Results

3.1. Water level

Water level data showed a maximum tidal range of 2.65 m (Fig. 2). Five harmonic constituents (M_2, S_2, N_2, O_1, and K_1) explained 99.3% of the water level variability in the bay during the mooring period. Therefore, the harmonic model hindcast generated for the study period using equation 1 was performed with a goodness of fit of ~99% calculated with the observed water level during the mooring period in the bay. The M_2 semidiurnal harmonic exhibited the highest amplitude of 0.88 m, followed by N_2 at 0.2 m and S_2 at 0.13 m. The diurnal harmonics showed the lower amplitudes, with K_1 at 0.13 m and O_1 at 0.05 m. These parameters yield to a form factor of 0.17.

Throughout the harmonic model predicted values for the study period, spring tides occurred fortnightly (every 15 days). Specifically, they were observed around the 13th and 25th of June, as well as around the 13th and 25th of July. Notably, a significant disparity in the water level range was observed between the days surrounding the 25th of June and 25th of July, compared to those around the 12th of June and 12th of July. The water level range during the former period was considerably larger (>0.8 m) than that of the latter period.

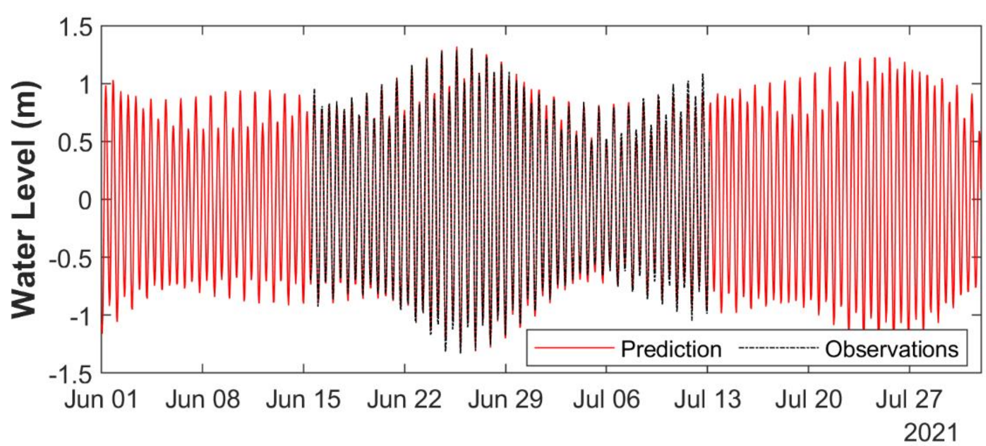

Fig. 2. Water level measured with the ADCP (black line) installed in Santa Elena Bay June 15th to July 13th, 2021, and modeled water level (red line) calculated applying the amplitudes and phases derived from the harmonic analysis into equation 1.

3.2.Wavelet transforms

The highest variability was observed in the diurnal band (24-hour) for both small and large *Lutjanus colorado* (Fig. 3, left and right panels, respectively). However, in Zone 1 (Fig. 3A and B), the semidiurnal (12-hour) band also displayed a sporadic significant variability, particularly for large *L. colorado* (Fig. 3 A-B). The diurnal and semidiurnal bands for large *L. colorado* in Zone 1, showed a near fortnightly periodicity. Movement of small *L. colorado* in Zone 2 (Fig. 3C) exhibited a predominant diurnal variability with an interruption in June 20 and 27. In contrast, large *L. colorado* of this species in Zone 2 only showed a significant diurnal variability during the first days recorded (Fig. 3D). Small *L. colorado* in Zone 4 (Fig. 3E) showed significant diurnal variability during the first half of June and during some periods around the 6th, 18th and 27th of July. Significant semidiurnal variability in small *L. colorado* in Zone 4 was only present around the 6th and 24th of July. For large *L. colorado* in Zone 4 (Fig. 3F), there was a significant diurnal variability observed around the 4th and 20th of July.

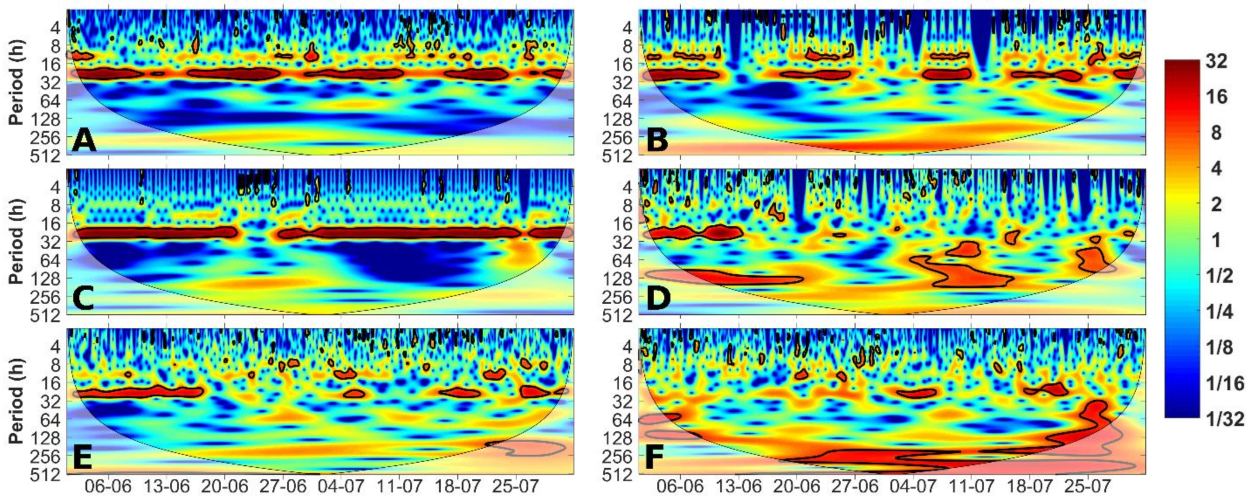

Fig. 3. Wavelet power spectra for time series of *Lutjanus colorado* abundance data in Bahía Santa Elena during June and July of 2021. The time series' periodicities are plotted on the y-axis, while their temporal evolution is shown on the x-axis. Wavelet power is color coded, going from low power in blue to high power in red. Significant regions in the wavelet power spectra are enclosed by red areas with black contour lines ($p < 0.05$). Pale shaded areas represent the cone of influence, where edge effects might distort the signal, these areas should not be interpreted for further analysis. Panels are for Zone 1 (A & B), Zone 2 (C & D), and Zone 4 (E & F). Left, and right panels are from small fish (A, C & E) and large fish (B, D & F), respectively.

The wavelet analysis revealed that *Lutjanus novemfasciatus* primarily exhibited diurnal and semidiurnal variability (Fig. 4). In Zone 1, small *L. novemfasciatus* (Fig. 4A) displayed significant semidiurnal variability from the end of June until the end of July. Diurnal variability was also present in the first half of June. For large *L. novemfasciatus* in Zone 1 (Fig. 4B), significant semidiurnal variability was present on sporadic occasions from the start of June to July 10th, and significant diurnal variability was present from the 11–21st of June, and during June 27th. In Zone

2, small *L. novemfasciatus* (Fig. 4C) showed significant semidiurnal and diurnal variability during the same periods; the first days of June (from June 9–18th), from July 8–18th, and from July 27–31st). For large *L. novemfasciatus* in Zone 2 (Fig. 4D), significant diurnal variability was observed with a near fortnightly interruptions around June 6th, June 23rd, July 8th, and July 23rd. The same fortnightly interruptions were observed for small *L. novemfasciatus* in Zone 3 (Fig. 4E) that coincided with significant semidiurnal variability. Small *L. novemfasciatus* in Zone 4 (Fig. 4F) showed significant semidiurnal variability from June 19th to July 8th, and significant diurnal variability was present sporadically around the first days of June, on June 18th and 23rd, and on July 1st and 25th. For large *L. novemfasciatus* (Fig. 4G), significant diurnal variability was present mostly the entire record with an interruption around July 21st and 30th.

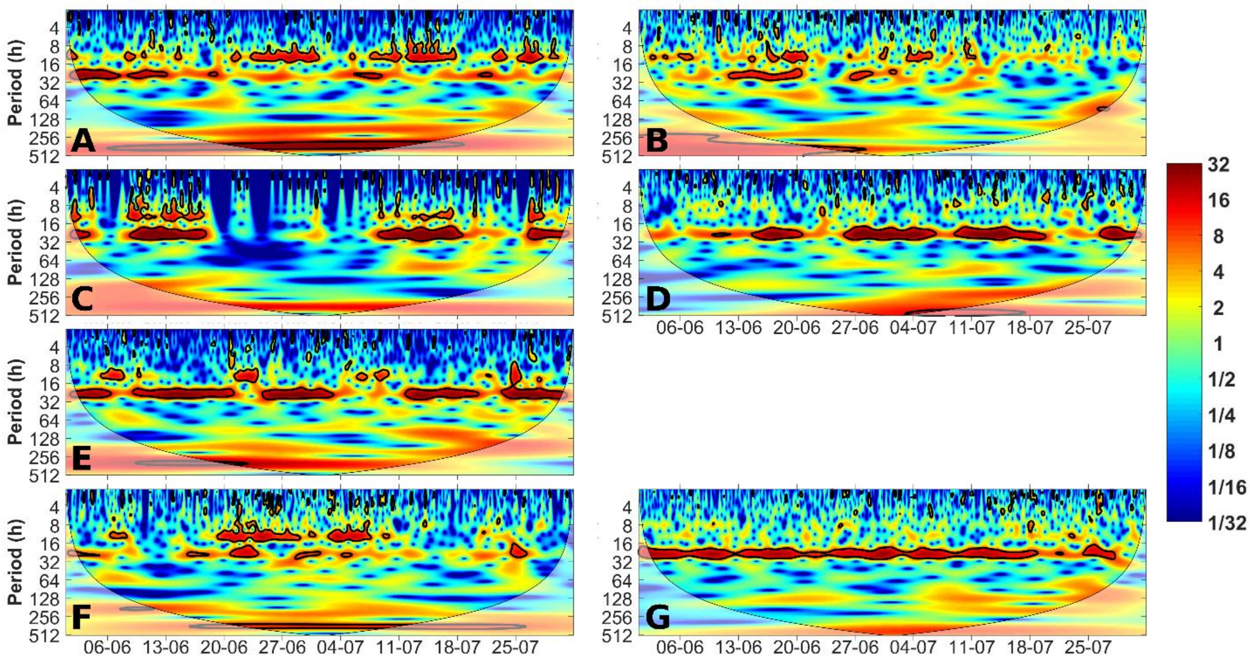

Fig. 4. Wavelet power spectra for time series of *Lutjanus novemfasciatus* abundance data in Bahía Santa Elena during June and July of 2021. Panels are for Zone 1 (A & B), Zone 2 (C & D), Zone 3 (E), and Zone 4 (F & G). Left, and right panels are from small fish (A, C, E & F) and large fish (B, D & G), respectively. For a description of wavelet power spectra see the legend of Fig. 3.

3.3. Wavelet coherence

Coherence with water level

Wavelet coherence analyses showed a strong relationship (> 0.9) between the abundance of both species and water level in the diurnal and semidiurnal bands. This relationship was consistent regardless of individual size (Fig 5 & Fig. 6). Moreover, the phase arrows pointed to the left, indicating an antiphase relationship This suggests that during low tide there were more *L. colorado* individuals detected close to the receivers in comparison to high tide.

In Zone 1, during June and July, small *L. colorado* (Fig. 5A) consistently showed significant coherence in the semidiurnal and diurnal bands, while large individuals (Fig. 5B) experienced interruptions in coherence every two weeks. In Zone 2, small *L. colorado* (Fig. 5C) displayed intermittent coherence in the semidiurnal band and continuous coherence in the diurnal band, except for an interruption around June 23rd. On the other hand, large *L. colorado* (Fig. 5D) occasionally exhibited coherence in both bands. In Zone 4, both small (Fig. 5E) and large (Fig. 5F) *L. colorado* exhibited significant coherence in the diurnal and semidiurnal bands, but with frequent interruptions.

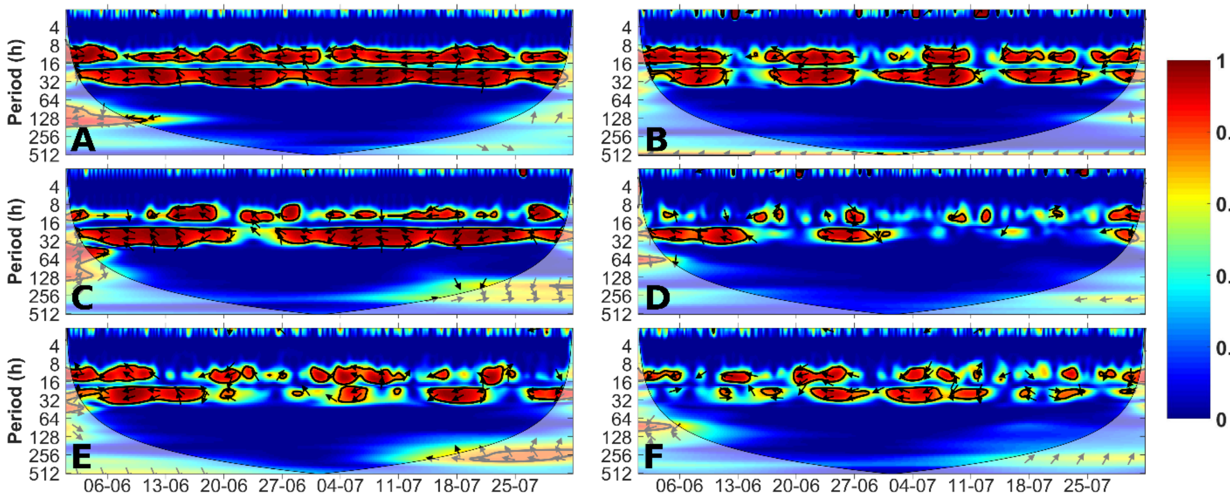

Fig. 5. Wavelet coherence between water level and *Lutjanus colorado* in Bahía Santa Elena in June-July of 2021. Panels are for Zone 1 (A & B), Zone 2 (C & D), and Zone 4 (E & F). Left panels are from small fish data (A, C, & E), right panels (B, D, & F) are from big fish data.

For *L. novemfasciatus* in Zone 1, both small and large individuals (Fig. 6A and Fig. 6B) exhibited significant coherence in the semidiurnal and diurnal bands during June and July, with slight interruptions around June 18th and July 18th. In Zone 2, small *L. novemfasciatus* (Fig. 6C) showed fortnightly interruptions in coherence for both the diurnal and semidiurnal bands. In contrast, large individuals (Fig. 6D) consistently maintained coherence in the diurnal band and showed shorter episodes of high coherence in the semidiurnal band.

In Zone 3, small *L. novemfasciatus* (Fig. 6E) exhibited significant coherence in both the diurnal and semidiurnal bands. However, intermittent interruptions indicated fluctuations in the species abundance-water level relationship during the study period. On the other hand, a similar behavior was found in Zone 4, where both small (Fig. 6F) and large *L. novemfasciatus* (Fig. 6G) demonstrated significant coherence in both the diurnal and semidiurnal bands. But for large *L. novemfasciatus* coherence was relatively stronger in the diurnal band, with two brief interruptions by the end of July.

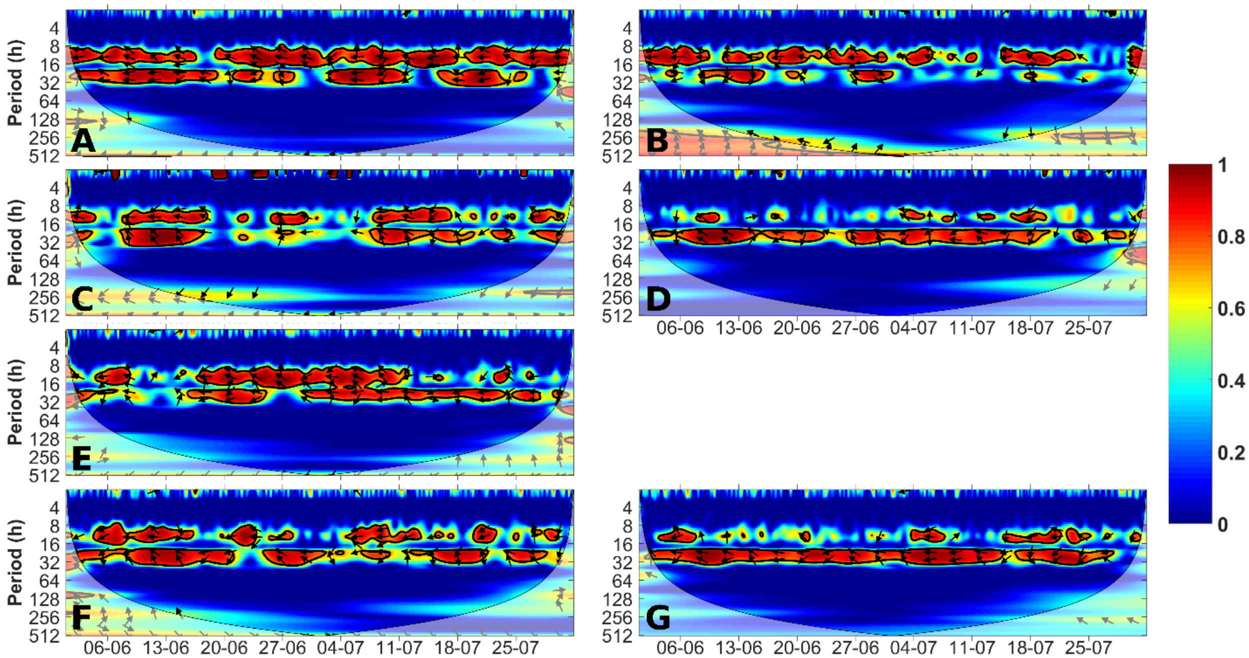

Fig. 6. Wavelet coherence between water level and *Lutjanus novemfasciatus* in Bahía Santa Elena in June-July of 2021. Zone 1 (panels A and B), zone 2 (panels C and D), and zone 3 (panel E). Left panels are for small individuals (A, C, E & F), right panels (B, D, & G) are for big individuals.

Coherence with sunlight

The wavelet coherence analysis revealed a strong correlation in the diurnal band between sunlight and fish movements across all zones for both species, notwithstanding their size (Fig. 7, and Fig. 8). The coherence arrows consistently pointed to the left, indicating an antiphase relationship, suggesting that snapper abundance was higher during periods of reduced sunlight.

In Zone 1, small *L. colorado* (Fig. 7A) showed a persistent coherence with sunlight in the diurnal band during the whole study period, while large (Fig. 7B) individuals depicted interruptions approximately every two weeks. Similar results were found in Zone 2, where small *L. colorado* (Fig. 7C) displayed coherence in the diurnal band, except for an interruption around June 23rd. Large *L. colorado* (Fig. 7D) showed high coherence mainly in the diurnal band from June 1st to 12th, and around June 26th and July 27th. In Zone 4, there were instances of coherence observed in the diurnal band between sunlight and both small (Fig. 7E) and large *L. colorado* (Fig. 7F).

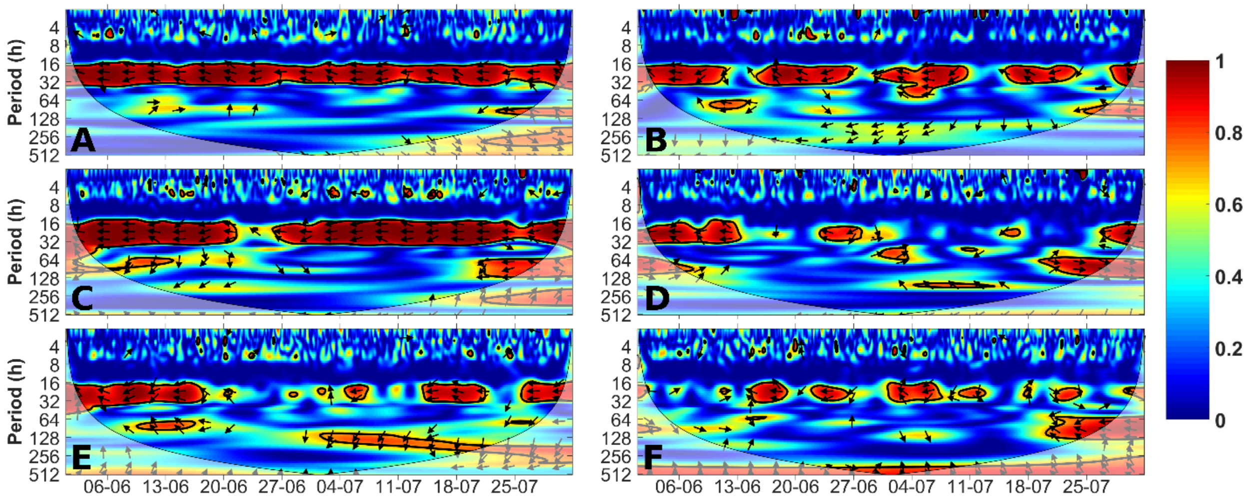

Fig. 7. Wavelet coherence between sunlight and *Lutjanus colorado* in Bahía Santa Elena in June-July of 2021. Panels are for Zone 1 (A & B), Zone 2 (C & D), and Zone 4 (E & F). Left panels are from small fish data (A, C, & E), right panels (B, D, & F) are from big fish data.

For small *L. novemfasciatus* (Fig. 8A) in Zone 1, there was consistent coherence in the diurnal band with intermittent interruptions around the 27th of June, and the 13th and 26th of July. Large *L. novemfasciatus* (Fig. 8B) in Zone 1 showed sporadic coherence only in the diurnal band. In Zone 2, small *L. novemfasciatus* (Fig. 8C) had fortnightly interruptions in diurnal coherence, while large individuals (Fig. 8D) showed consistent coherence throughout June and July. Zone 3 demonstrated significant coherence in the diurnal band for small *L. novemfasciatus* (Fig. 8E), with interruptions around June 23rd and July 23rd. In Zone 4, there was intermittent coherence between sunlight and small *L. novemfasciatus* (Fig. 8F) in the diurnal band. Large *L. novemfasciatus* (Fig. 8G) in Zone 4 showed consistent coherence throughout June and July.

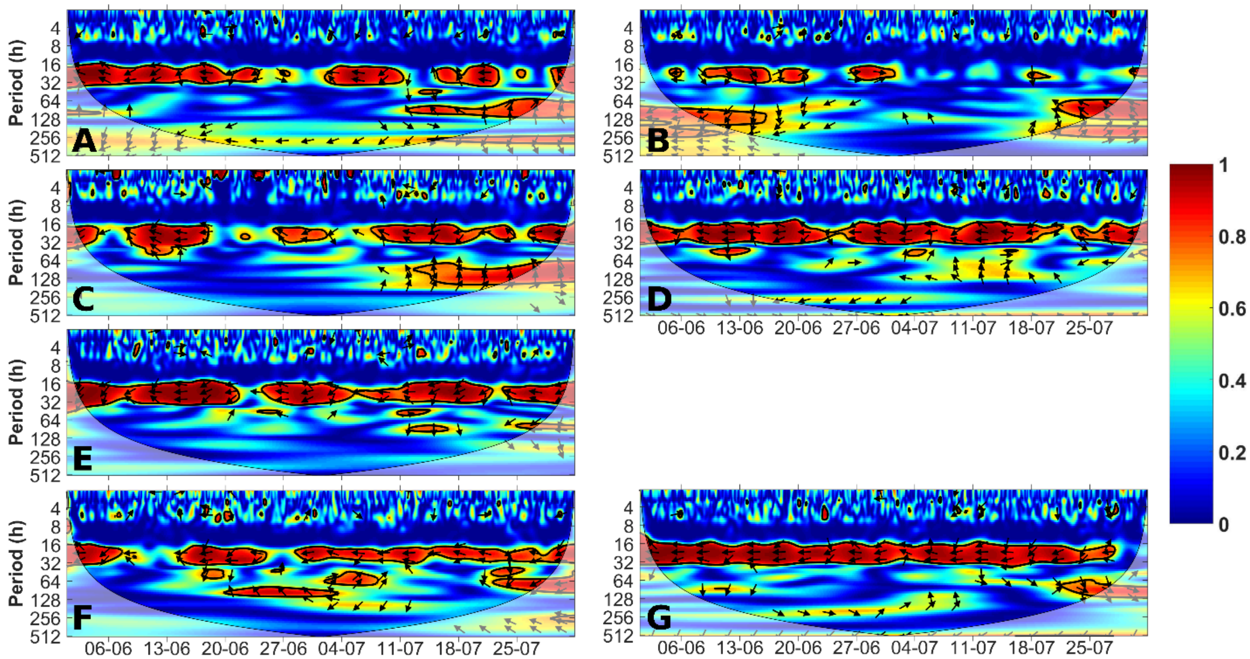

Fig. 8. Wavelet coherence between sunlight and *Lutjanus novemfasciatus* in Bahía Santa Elena in June-July of 2021. Panels are for Zone 1 (A & B), Zone 2 (C & D), Zone 3 (E), and Zone 4 (F & G). Left panels are from small fish data (A, C, E & F), right panels (B, D, & G) are from big fish data.

4. **Discussion**

We observed periodic oscillations in fish data within the semidiurnal and diurnal bands, which were associated with tidal and sunlight patterns. Understanding and accounting for these environmental conditions are crucial for comprehending the dynamics of marine organisms in coastal environments. Neglection of these factors in the monitoring of commercial fish populations could potentially result in detrimental management policies that may negatively impact their populations.

4.1. Tidal harmonics and water level hindcast

The water level showed a maximum tidal range of 2.67 m during spring tidal cycle, which is consistent with a mesotidal system (Davies 1964; Mustoe et al. 2005). The tide at Bahía Santa Elena is classified as semidiurnal based on the form factor of 0.17 (Mustoe et al. 2005). The larger lunar elliptic semidiurnal constituent N_2 was higher than the solar semidiurnal S_2. Some authors (i..e. Lizano R., 2006) neglected the N_2 component to forecast astronomical water level variations, leading to a potential error in water level predictions for Bahía Santa Elena. The error in the water level prediction occur since fortnightly astronomical water level variations should be different at any given month when $N_2 > S_2$ (Valle-Levinson 2022). This asymmetry in the fortnightly variations should be considered in future sampling strategies.

4.2. Tidal effects on organisms

The influence of semidiurnal tides was more evident in small *L. novemfasciatus,* which exhibited a dominant semidiurnal variability pattern. Sporadic diurnal variability was also observed, associated with tidal motion. There was a high coherence between small and large fish from both species and water levels, in diurnal and semidiurnal bands. The motion of small fish was closely linked to tides and their access to refuge provided by the estuary. Certain species of *Lutjanidae* family frequently inhabit bays and estuaries during their early life-stages as these habitats provide abundant resources and refuge from large predators (Sheaves 2005). As adults, snappers often undergo ontogenetic habitat shifts, moving from mangrove and estuarine habitats towards reefs and other coastal areas (Lyons and Schneider 1990; Fischer et al. 1995; Mendoza et al. 2009).

The internal zone of Bahía Santa Elena is characterized by extensive mangrove coverage. Mangroves are highly productive and structurally complex habitats that provide aquatic species, such as snappers, with temporary refuge with their root systems against predators (Sheaves 2005; Vega et al. 2015). In a recent study, the bay was found to harbor a diverse range of 140 fish species (Espinoza et al. 2022). Bahía Santa Elena holds great significance for the surrounding communities due to its tourism and fishing potential, leading to its designation as a Marine Management Area (Villalobos-Rojas et al. 2014; MINAE 2018). In this study, all the receivers were strategically placed near mangroves and other available habitats within Bahía Santa Elena that remained flooded regardless of the tidal phase. During low tides, snappers are likely to move to deeper areas or other areas outside the detection range of the receivers, as the tidal mangroves become completely exposed. As the water level rises during high tide, the snappers move back to the mangrove area.

Our findings indicate that large *Lutjanus novemfasciatus* and *Lutjanus colorado* exhibited a semidiurnal behavior in Zone 1. This behavior is likely attributed to their access to feeding areas within the mangroves, rather than being driven by anti-predator behaviors (Sheaves 2005; Aguilar-Betancourt et al. 2017). Small *L. colorado* (< 25 cm TL) showed a preference for feeding on small fish, but as they matured, they underwent an ontogenetic dietary shift, transitioning to a diet consisting primarily of crustaceans such as crabs and shrimps (Rojas 1997). Zone 1 is located near the entrance of a mangrove channel that experiences tidal flooding, and the availability of these sites during high tide likely present an opportunity for feeding.

The tidal movements observed in our study contribute to two ecological processes: (1) providing refuge from predators for small fish and (2) offering feeding opportunities for large fish. Sheaves (2005) extensively discusses how mangroves serve as productive feeding areas for fish due to the abundant invertebrate fauna. Moreover, the shallow waters and complex structures of mangroves offer a refugee from predators. It is worth noting that the availability of mangrove habitats for fish is limited in many regions worldwide, as these habitats undergo alternating inundation and exposure due to the tidal cycle (Sheaves 2005).

Tidal patterns can also affect benthic organisms that have limited mobility due to interactions with other species. A study conducted in sandy beaches in Brazil revealed that the feeding activity of gastropod *Olivella minuta* was higher during low tide, probably due to a lower risk of predation (Checon et al. 2020). Furthermore, larger organisms as marine mammals also may be influenced by tides. In the Netherlands, sightings of harbour porpoise (*Phocoena phocoena*) were found to be tide-dependent, likely associated with an increased abundance of preys during high tide (IJsseldijk et al. 2015). Even birds are not exempt from tidal influences, as observed in a study of wading birds in a salt marsh in Rhode Island, where their foraging behavior changed throughout the tidal cycle (Raposa et al. 2009). The effects of tides extend to all levels of the food chain within coastal ecosystems. Therefore, it is important to consider the influence of tides on the abundance and behavior of all aquatic organisms in these environments.

4.3. Day-night cycle effects on organisms

Fish must migrate in and out of the mangroves with tide and utilize alternative habitats when mangroves are inaccessible (Sheaves 2005). An example illustrating the influence of tides on fish behavior is evident in the migration patterns of juvenile mangrove jack, *Lutjanus argentimaculatus*, within a mangrove estuary in Thailand. These juveniles exhibited a movement pattern associated with tides, showing increased activity in the mangrove areas during nighttime and high tide periods (Zagars et al. 2012). This behavior is likely driven by higher availability of sought-after food items during these specific periods. In Australia, *L. argentimaculatus* primarily feeds on crabs that inhabit the forest floor of mangroves (Sheaves and Molony 2000; Zagars et al. 2012). Moreover, according to Rojas (1997), *L. colorado* adults in Golfo de Nicoya are described as nocturnal feeders based on capture times and analysis of their diet composition. This observation is consistent with our findings of increased nocturnal activity in both snapper species in Bahía Santa Elena. High wavelet coherence was found in the diurnal band between sunlight and the abundance of both species; sunlight was out of phase with respect to the abundance data, indicating that there were more snappers detected at night.

The behavior of *L. argentiventris*, in intertidal creeks has been observed to be influenced by both diurnal and spring-neap tidal patternes. A higher number of small fish was observed during the day at neap tides than during the night, while a greater number of larger fish was observed at night during both spring and neap tides (Ramirez-Martínez et al., 2016). Similarly, our data suggested an increased nocturnal activity and a fortnightly interruption in diurnal patterns in both species. This pattern of fortnightly interruptions may be associated with the spring-neap tidal cycle. To further explore this hypothesis, it would be beneficial to conduct wavelet coherence analysis using a longer time series of water level data in order to determine if there is coherence in the fortnightly frequency band.

4.4. Mangrove ecosystem importance

The importance of protecting mangrove ecosystems is underscored by our findings, which highlight the great importance for commercial fish species and the need for sustainable fishery development. Unfortunately, mangrove ecosystems are rapidly declining at a rate of 1 to 2% per year due to logging, coastal development, and aquaculture (Duke et al. 2007; Polidoro et al. 2010). Of particular concern are the Atlantic and Pacific coasts of Central America, where up to 40% of mangrove species are endangered (Polidoro et al. 2010). Historical evidence shows pre-Columbian tribes used mangroves for thousands of years, but deforestation intensified after the conquest (López-Angarita et al. 2016). Despite protective laws, expanding human activities have led to a continued decrease in mangrove cover since 1990, even within protected areas (López-Angarita et al. 2016). Although Costa Rica's overall mangrove loss may appear comparatively small when compared to other nations in the region, it is worth noting that between 1970 and 2000, a staggering 39.6% of mangroves were lost within the country (López-Angarita et al. 2016).

The preservation of mangroves as commercial fish habitats is not only important for ecological reasons but also for social and economic sustainability. Mangroves provide essential breeding, nursery, and feeding grounds for many commercially valuable fish species (Vega et al. 2015; Harborne et al. 2016; Jiang et al. 2022; Wanjiru et al. 2022). These habitats support the livelihoods of countless fishermen, as they rely on healthy fish populations for their economic well-being (Londoño et al. 2020; Yamamoto 2022).

4.5. Sampling implications

In our study, wavelet analysis was employed to reveal fish movement patterns and their correlation with environmental data. These findings carry significant implications for the monitoring of nekton species in coastal ecosystems.

The application of wavelet analysis extends to studying the influence of tide and sunlight variability in chlorophyll concentration in coastal systems (Blauw et al. 2012). In addition, Blauw et al. (2012) draw attention to potential errors that can rise from neglecting tide considerations in marine monitoring, emphasizing the significance of high-resolution monitoring. For example, daily measurements of phytoplankton concentration at noon could lead to biased conclusions due to different tidal phases. Also, bi-weekly sampling of phytoplankton concentration may show distorted variations and species composition over a period of several months, while these data reflect different phases of the spring-neap cycle (Blauw et al. 2012). Furthermore, when sampling from multiple sites, comparing two zones becomes challenging if measurements are conducted at different tidal or night-day phases. Discrepancies in abundance between locations could mistakenly be attributed to sampling time differences. Those errors can also arise when sampling fish species influenced by tides and sunlight in coastal ecosystems.

A total of 11 fish species showed a relationship between their abundance and the tides in a study in the Rookery Bay National Estuarine Research Reserve in Florida (Ellis and Bell, 2008). Certain species demonstrated higher abundance during high tide, while others were more abundant during low tide. The authors suggested a nekton sampling strategy that considers the tidal cycle; arguing that a comprehensive sampling effort is likely to yield a more accurate understanding of the intertidal ichthyofauna compared to studies that focus on a single tide interval. Finally, they conclude that data interpretation should be confined to the context of the sampled tide stage, and emphasized the importance of minimizing temporal deviations from the targeted tide stage when restricted sampling is necessary.

The results presented in this study support the recommendations mentioned above and suggest that they be incorporated into sampling designs for coastal ecosystems. Therefore, we strongly suggest to consider sunlight and tide when conducting studies in similar environments.

Conclusion

Our study highlights the significance of incorporating environmental factors, such as the tide, into species management strategies, emphasizing the crucial role of biological monitoring in coastal regions. To ensure the accuracy of measurements, we recommend conducting sampling with minimal time intervals between each sampling event. For instance, simultaneous samplings at two different zones, precisely timed with respect to tide and sunlight, can facilitate improved spatial and temporal comparison of abundance. In order to ensure the reliability of monitoring studies, it is essential to consider diurnal, semidiurnal, and fortnightly variations in commercially important species found in coastal areas, such as Lutjanidae family species. Neglecting these environmental factors can lead to biased sampling strategies and management decisions that may have a detrimental effect on valuable species populations. It is crucial to investigate whether similar behavioral patterns exist in other coastal regions to broaden the scope of monitoring efforts. Consideration of these environmental factors is critical for effective management of commercially important species and the long-term sustainability of coastal ecosystems.

Compliance with Ethical Standards

The authors declare that they have no conflict of interest. They also declare that all applicable international, national and/or institutional guidelines for sampling, care and experimental use of organisms for the study have been followed and all necessary approvals have been obtained.

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Conclusión general

Los principales hallazgos de la tesis fueron dos. Primero, una bahía tropical mostró períodos de enfriamiento en temporada de veranillo debido a la intensificación de los vientos favorables a surgencias. Estos eventos de surgencia coinciden con una disminución de la temperatura del agua, seguida de un aumento de temperatura después de que cesa el viento. El afloramiento ocurre fuera de la bahía e incursiona hacia dentro produciendo un enfriamiento. El viento mueve las aguas superficiales desde el área exterior, enfriando las aguas adyacentes a la bahía. Estos eventos de enfriamiento y calentamiento pueden tener un efecto en la dinámica biológica dentro de la bahía que debería explorarse en futuras investigaciones. Nuestros hallazgos resaltan la importancia del sistema de manglares dentro de bahías tropicales para las especies de peces estudiadas y enfatizan la necesidad de considerar factores ambientales, como las mareas, en el manejo de especies. El monitoreo preciso, incluidas las variaciones en el comportamiento de las especies, es crucial para evitar conclusiones sesgadas y garantizar ecosistemas costeros sostenibles. Se necesita más investigación para comprender las forzantes que rigen la dinámica de la bahía. En general, tener en cuenta estos factores ambientales es esencial para el manejo efectivo de las especies y la preservación del ecosistema costero.

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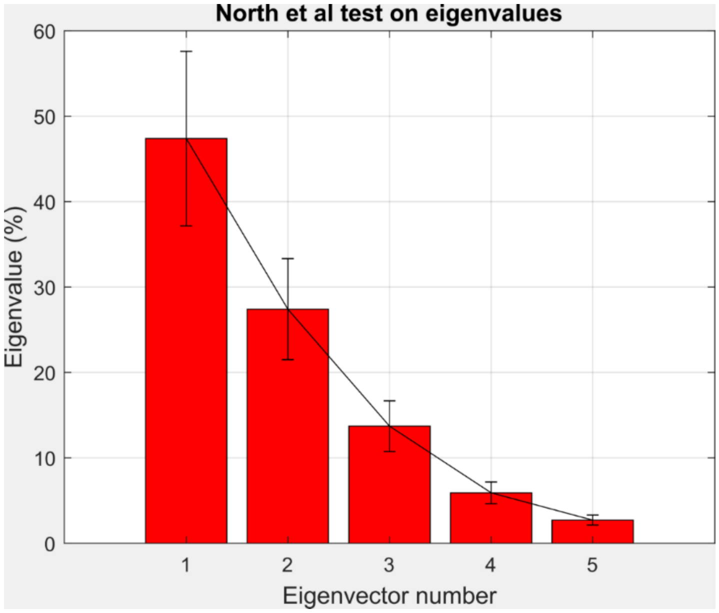
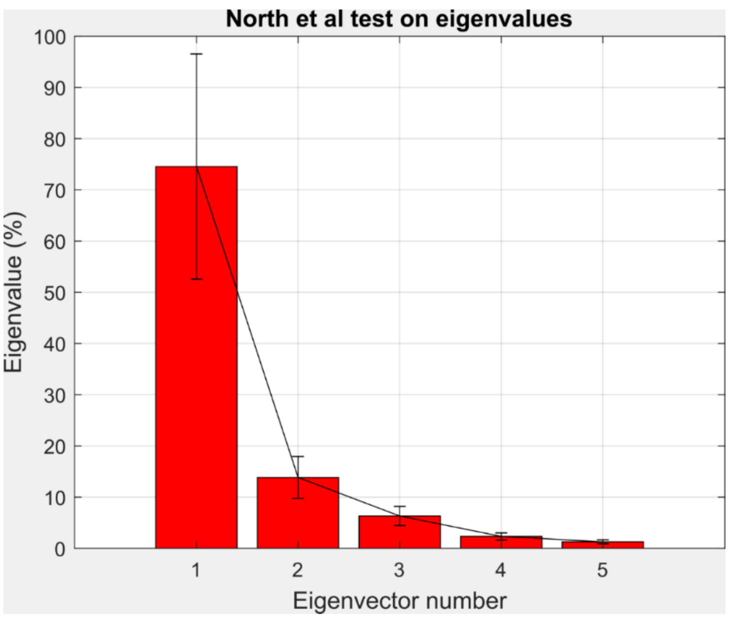
Suplementos generales

Los modos que se obtuvieron aplicando Funciones Empíricas Ortogonales a la velocidad de la corriente submareal recopilada en el sitio 1 para la campaña del 2021 (Suplemento 1) y la campaña del 2022 (Suplemento 2) resultaron ser independientes después de realizar la prueba de acoplamiento de modos descrita por North et al. (1982).

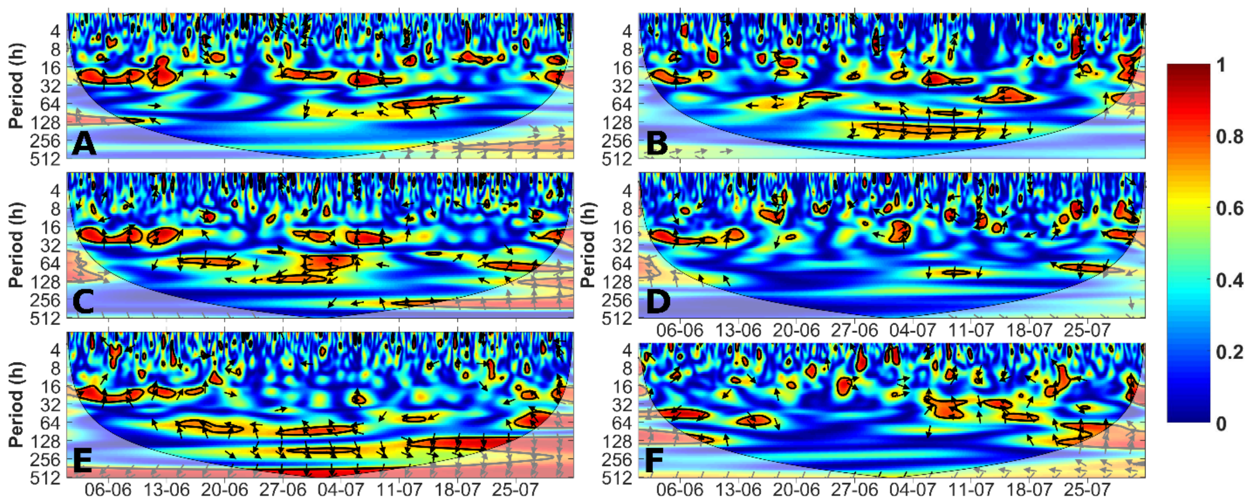


Suplemento general 1. Porcentaje explicado por cada modo del análisis EOF de la velocidad de la corriente submareal recopilada en el Sitio 1 para la primera campaña de medición en 2021. Las barras de error se basan en el criterio discutido por North et al. (1982).

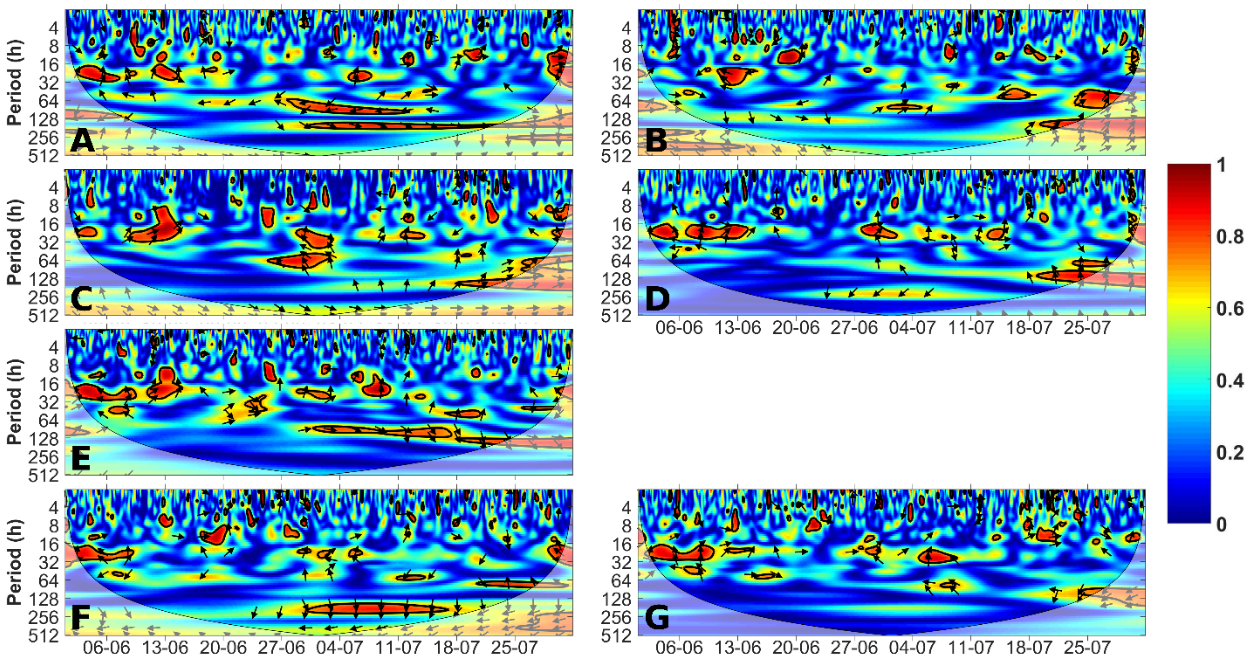


Suplemento general 2. Porcentaje explicado por cada modo del análisis EOF de la velocidad de la corriente submareal recopilada en el Sitio 1 para la primera campaña de medición en 2022. Las barras de error se basan en el criterio discutido por North et al. (1982).

Se obtuvieron datos horarios de temperatura medida por un termistor marca HOBO en el interior de Bahía Santa Elena (latitud: 10.91386°, longitud: -85.78997°). Y Se realizó un análisis de coherencia de ondículas entre los datos de temperatura y las series de tiempo de los pargos. Sólo se observó alta coherencia de manera esporádica (Suplemento general 3 y 4) en las bandas diurna y semidiurna sin embargo la coherencia fue muy baja en comparación a las obtenidas con el nivel de agua y Luz Solar. Cabe notar que se observó coherencia alta y significativa en periodos altos (más de 64 horas), por lo debería estudiarse la relación entre los peces y la temperatura con series de tiempo más largas.



Suplemento general 3. Coherencia ondículas entre temperatura y *Lutjanus colorado* en Bahía Santa Elena en junio-julio de 2021. Los paneles son para Zona 1 (A y B), Zona 2 (C y D) y Zona 4 (E y F). Los paneles de la izquierda son de datos de peces pequeños (A, C y E), los paneles de la derecha (B, D y F) son de datos de peces grandes.



Suplemento general 4. Coherencia de ondículas entre la luz solar y *Lutjanus novemfasciatus* en Bahía Santa Elena en junio-julio de 2021. Los paneles son para la Zona 1 (A y B), Zona 2 (C y D), Zona 3 (E) y Zona 4 (F y GRAMO). Los paneles de la izquierda son de datos de peces pequeños (A, C, E y F), los paneles de la derecha (B, D y G) son de datos de peces grandes.

Asunto: Voto aprobatorio sobre trabajo
de tesis de grado de Maestría

Dra. Adriana G. González Silvera
Coordinadora de Investigación y
Posgrado, F.C.M.
Presente

Después de haber efectuado una revisión minuciosa sobre el trabajo de tesis presentado por el estudiante **Alexandre Tisseaux Navarro,** para poder presentar la defensa de su examen y obtener el grado de **Maestro en Ciencias en Oceanografía Costera**, me permito comunicarle que he dado mi voto **Aprobatorio,** sobre su trabajo titulado:

INTRUSIÓN DE SURGENCIAS Y MOVIMIENTOS DE PECES EN UNA BAHÍA TROPICAL.

Esperando reciba el presente de conformidad, quedo de usted.

Ensenada, B. C., a 31 de julio de 2023

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Dr. Braulio Juárez Araiza
Director de tesis

c.c.p. Expediente

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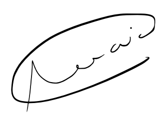

Dra. Amaia Ruiz de Alegría Arzaburu
Sinodal

c.c.p. Expediente

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Ensenada, B. C., a 31 de julio de 2023

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Dr. Mario Espinoza Mendiola
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