Marine intrusions in a microtidal coastal lagoon and their influence on the entry of meroplankton

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Abstract

It is essential for the functioning of intermittently closed/open lagoons and lakes (ICOLLs) to maintain a connection with the adjacent sea. This connectivity allows larval stages, like planktonic larvae, of marine estuarine-related species to move between environments by relying on water flows when the sandbar is open. This study aims to research the dynamics of marine intrusions into a microtidal coastal lagoon - Laguna de Rocha, Uruguay as a case study - during the open state of the sandbar. A 2-D hydrodynamic model was constructed, and model results were calibrated and validated with *in situ* data. A seawater tracer was used to determine the frequency, duration and intensity of marine intrusion under different wind, sea level and tributary discharge scenarios. Results showed that under calm conditions (light wind and basal discharge) at least one marine intrusion per day occurred in the vicinity of the inlet channel due to high tide. The sea level was essentially the main determinant of the duration of marine intrusions. Sea level rise has led to an increase in the duration (up to 22 hours per day) and spatial extent of marine intrusions. Conversely, tributary discharge primarily determined the intensity of marine intrusions attenuating them under high discharge

ICOLLs: intermittently closed/open lagoons and lakes
LR: Laguna de Rocha

scenarios. Strong SE (onshore) winds increased the duration of marine intrusions in all scenarios and the intensity of intrusions in the low sea level scenarios. Results about the importance of sea level for marine intrusions in Laguna de Rocha broaden the possible mechanism by which meroplankton can enter these microtidal systems. For instance, it could involve a combination of forces that overlap to raise the sea level above the lagoon water level (e.g. onshore winds, spring tides). Results suggest that the main force triggering seawater and larval entry may vary over time in the same lagoon. Therefore, in the microtidal Laguna de Rocha, we propose a mechanism for selecting incoming currents for the entry of estuarine-related larvae that, unlike other proposed mechanisms, may not be solely due to the effect of flood tide.

Keywords: hydrodynamic model; Delft3D; ICOLL; estuarine-dependent species; meroplankton; Laguna de Rocha

1 Introduction

The connectivity between estuaries and the adjacent sea is relevant for the ecological functioning of both ecosystems. The exchange of water between the sea and estuaries is influenced by factors such as tributary discharge, tidal amplitude, wind action and geomorphology (Valle-Levinson 2010). In meso- to macro tidal environments, tidal currents play a significant role on hydrodynamics (Dias et al. 2021), generating seawater, macromolecules and organisms of marine origin inflows, while low tides export these elements of fluvial and terrestrial origin from the estuaries to the sea (Amaral et al. 2020). In meso- to microtidal estuaries, wind and tributary discharge are more influential, affecting the hydrodynamics and organisms of these systems (Martins et al. 2007, Bruno and Acha 2015, Tuchkovenko et al. 2019). Coastal lagoons belonging to intermittently closed/open lagoons and lakes type (ICOLLs) (Roy et al. 2001) are environments that typically originate in mid-latitudes where the tidal range is low, and wave action allows a sandbar to form along the coast (Mc Sweeney et al. 2017). Seawater intrusion into these environments also depends on the morphology of the lagoons and the channel connecting them to the sea (Fiandrino et al. 2017, Tuchkovenko et al. 2019).

Some species in coastal lagoons are estuarine-dependent or opportunistic species, including croakers (e.g. *Micropogonias furnieri*), mullets (e.g. *Mugil lisa*) and shrimps (e.g. *Penaeus paulensis*), which are of economic importance (e.g. Fabiano and Santana 2006). Similarly, some crabs, such as the blue crab (e.g. *Callinectes sapidus*) or the burrowing crab (e.g. *Neohelice granulata*), play an essential role as target species for fishing or as ecosystem engineers due to their role of bioturbation in the sediments, and have larval export strategies (Bas et al. 2009, Epifanio 2019). These species need to enter the estuary during their larval stage (estuarine-related), and it is therefore essential to know the potential mechanisms involved. It is known that larvae are planktonic and that their swimming ability is limited, so they must develop strategies that allow them to take advantage of currents to move between environments (Joyeux 1998, Pineda et al. 2007). The combined influence of physical and behavioural factors determines the transport of larvae from breeding to nursery areas (Tankersley 2001, Queiroga and Blanton 2005). The success of the transport during the larval stage is largely dependent on the correct coupling of these factors (Iles and Sinclair 1982, Pineda et al. 2007).

The process by which larvae adapt their behaviour to tidal currents has been extensively studied and has been termed selective tidal stream transport (STST) (e.g. Tankersley 2001). Several studies showed the importance of tidal currents for the entry of larval stages of estuarine-dependent species of shrimp (Ogburn et al. 2013) and fish (Jager 1999, Hale and Targett 2018) or for the re-entry of crab larvae with larval export strategy (Queiroga et al. 2006, Epifanio 2019). The effect of wind on sea level and circulation can modulate the impact of STST and influence larval transport, particularly in coastal lagoons (Joyeux 1998, Queiroga et al. 2006). In addition, a combination of tidal and wind intensity has been observed as a driving force for the entry of estuarine-dependent larvae in a microtidal lagoon estuary (Bruno and Acha 2015, Bruno et al. 2018). Conversely, prolonged periods of intense rainfall have been shown to impede the recruitment of estuarine-dependent species in other microtidal coastal lagoon (Möller et al. 2009).

Due to the high variability of the forcings, field studies to determine the mechanisms of larvae movements into and out of coastal lagoons are usually very complex to implement. It is required a significant sampling effort both spatially and temporally, and some key processes may not be represented as those during storms. Considering these limitations, hydrodynamic modelling is a powerful and effective tool for understanding complex spatio-temporal processes that require high spatial and temporal resolution, to adequately follow the effects of poorly predictable forcing (e.g. non-astronomical forcing). This type of tool has been used to determine larval transport to breeding areas (Martins et al. 2007, Dickey-Collas et al. 2009). For example, the importance of wind direction and intensity on larval circulation and transport has been highlighted (Simionato et al. 2008, Franzen et al. 2019). Similarly, modelling can be utilized to simulate various scenarios and observe how different forcings change estuarine hydrodynamics or larval transport (Martins et al. 2007, Simionato et al. 2008, Dias et al. 2021).

Despite previous studies in microtidal estuaries and particularly in coastal lagoons (e.g. Whitfield et al. 2023), there are still unanswered questions regarding the entry of estuarine-related species larvae: i) How frequently do marine intrusions that enable the entry of larvae occur? ii) What are the duration and intensity of these intrusions? iii) How do sea level, tributary discharge and wind influence the duration and intensity of marine intrusions? iv) What is the spatial extent of the impact of the intrusions?

This study aims to understand the marine intrusions into a coastal lagoon, using hydrodynamic modelling to answer the abovementioned questions in Laguna de Rocha (Uruguay). A 2-D hydrodynamic model (Delft3D) was implemented, and *in situ* data was used to calibrate and validate the model and interpreted the results. Then, several numerical simulations were carried out to include scenarios that could occur based on the combination of different climatic and hydrological drivers, using the FLOW module of Delft3D. These simulations have enabled the analysis of the inflow of seawater under a variety of environmental conditions. Finally, the mechanisms through which estuarine-related meroplankton larvae gain access to estuaries, as well as the inherent natural challenges posed by climatological variations were discussed.

2 Study area

Laguna de Rocha (LR) and the adjacent coastal waters (CW) are located on the Southwestern Atlantic Ocean coast (34° 38' S - 54° 17' W, Uruguay, Fig. 1). This area is characterised by a subtropical climate with maximum air temperature in summer (average = 21°C) and minimum in winter (average = 11°C) (Barreiro et al. 2019). The region exhibits two semidiurnal tides with diurnal inequalities, the main one being the M_2 (main semidiurnal lunar component) accounting for 65% of the total tidal energy (D'Onofrio et al. 1999). The tidal range is about 40 cm, categorizing it as microtidal. However, atmospheric disturbances, particularly from wind, often surpass astronomical effects, resulting in sea level variations of up to 3 m above the expected astronomical tide (Alonso et al. 2017). Sea level variations on the Patagonian shelf are crucial in determining sea level changes in Uruguayan marine and estuarine waters, where the signal can be amplified or reduced by local conditions (Alonso et al. 2017). On the coast of Uruguay, NE winds are predominant year-round and are more frequent in spring and summer, leading to the generation of upwelling in these seasons (Piola et al. 2008, de Mello et al. 2022). East winds are also significant (Manta 2017). At the same time, the dynamics of the sea breeze, an air circulation generated by the differential heating between land and sea, are essential in the study area. Generally, the sea breeze starts at 11:00 on the seacoast, has a southeast direction and reaches a maximum speed of

7.1 m s^{-1} around 16:00 (Manta et al. 2021). This phenomenon is more frequent in summer. Precipitation in the study area is 1122 mm per year, showing no seasonal variations (Uruguayan Institute of Meteorology [INUMET]), although evapotranspiration is highly seasonal.

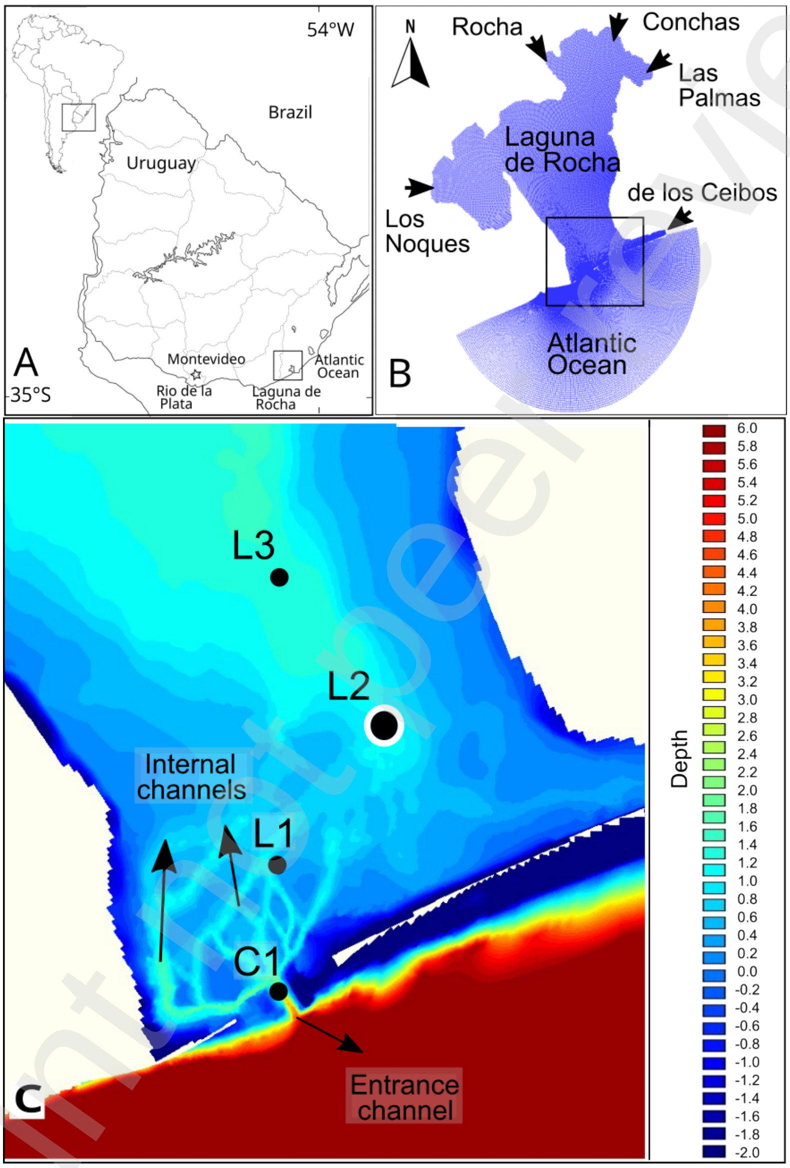


Figure 1. A) Location of the study area on the Atlantic coast of Uruguay. B) Irregular curvilinear grid used for the hydrodynamic modelling of the Rocha Lagoon and the adjacent sea. The black arrows indicate the location of the five tributary discharge sites included in the model. The curved area indicates the open oceanic boundary. C) Detail of the bathymetry of the channel area (colour gradient) and location of the model grid cells where the model output data were observed (black circles) and of the buoy where the field sensors were anchored (white circle).

LR is a very shallow lagoon with a mean depth of 0.6 m. The lagoon covers an area of 72 km^2 and has a catchment area of 1214 km^2 with an intermittent connection to the sea (ICOLL type according to Roy et al. 2001) (Fig. 1). The average daily flow received by the lagoon from its tributaries is 17.7 m^3 s^{-1}. The connection to the sea is through a channel that opens over the sand barrier (Rodríguez-Gallego et al. 2017). When LR is disconnected from the sea, the discharges of the tributaries raise the water level inside the lagoon until the sandbar breaks and a channel is established, which can last several months. After lagoon discharge, a seawater intrusion occurs, and the exchange continues as long as the channel remains open until the dynamics of sediment transport rebuild the sandbar (Conde et al. 2019). The inlet opens at least once a year, either naturally or artificially by the Municipality to reduce field floods and last several months. The exchange between the lagoon and the sea during the open sandbar period generates highly dynamic processes in the environment (e.g. of salinity and turbidity) and biological conditions within the lagoon (Rodríguez-Gallego et al. 2017; Espinosa et al. 2019, Machado et al. 2021).

LR and CW have been declared protected areas by Uruguayan national regulations and international conventions (e.g. Ramsar) due to their landscape value and the ecosystem services they provide. Some key species in these environments, such as the crabs *N. granulata* and *C. sapidus*, the shrimp *P. paulensis* and fish such as *M. furnieri*, *Symphurus plagiusa* (tonguefish) and *Paralichthys orbignyanus* (flounder), are estuarine-dependent or opportunistic species. These species move between the sea and the lagoon, generally entering at advanced larval stages and eventually recruiting into the lagoon (Santana et al. 2015, Machado et al. 2021). lthough the entry of these larvae through overwash events has been observed, the exchange is usually more significant during the open sandbar state (Machado et al. 2021).

3 Hydrodynamic model implementation

3.1 Hydrodynamic model

Delft3D-FLOW module is an open-source hydrodynamic modelling software developed by Deltares Institute in cooperation with Delft University of Technology. The model solves the baroclinic Navier-Stokes equation and the Boussinesq transport equation in 2D or 3D. The FLOW module performs water level calculations. A detailed description of this model can be found in Lesser et al. (2004). A seawater tracer included in the FLOW module was used to assess the dynamics of seawater intrusion into LR under different forcing conditions. This Delf3D-FLOW module has been widely used in estuarine systems in various regions, such as Portugal (e.g. Sousa et al., 2018), and Spain (e.g. Carballo et al. 2009), among others.

3.2 Model configuration

The area used for the hydrodynamic calculations includes LR and CW and corresponds to an open sandbar state (Fig. 1, Table 1). A two-dimensional model implementation was developed to simulate the LR dynamics. The Delft3D-FLOW module was configured with a curvilinear irregular grid (327 x 453 cells), with a resolution ranging from ~200 m at sea and up to ~9 - 30 m in the channel zone connecting the lagoon and the ocean. Within the lagoon, resolution gradually increases to 120 m in the north of the lagoon and at the open sea boundary (Fig. 1 B). The numerical bathymetry assumes an open sandbar state and that the shape of the channel does not change with time. The model configurations developed consider that the fluid is Newtonian, and that its density is constant. Bottom roughness was assumed to be uniform over the study area and not time-varying. Viscosity and horizontal eddy diffusivity were assumed to be constant. The model was implemented with open boundary conditions from September to October 2016. The first month was considered as the time when the model reached equilibrium (spin-up) and the variables were balanced. Table 1 summarises the main features of the simulation, including resolution and parameterisations.

Table 1. Main characteristics and parameters used in the Delft3D numerical simulations.

Parameter	**Specification**
Domain	54º 22 ' 00 ''W to 54º 10 '00 ''W 34º 32' 00 ''S to 34º 50' 00 ''S
Resolution	~200 m in the sea, ~9 – 30 m in the inlet between the lagoon and sea, increasing gradually to 120 m in the north of the lagoon
Gravity	9,81 m s^{-2}
Water and air density	1000 kg m^{-3} and 1 kg m^{-3}
Oceanic boundary Forcing	Hourly water level
Transport condition	Wáter level
Discharge	Daily discharge of 5 streams, calculations based on measured rainfall in the study area
Bottom roughness	Constant Manning's roughness coefficient of 0.024 Chezy formula with 500 to 4000 µm sediment diameters
Horizontal eddy Viscosity	0.5 m^2 s^{-1}
Horizontal Eddy Diffusivity	10 m^2 s^{-1}
Wind	Hourly data from station located on the coast, 40 km from the study area
Time period	01/08/16 to 31/10/16
Time step	15 seconds

The bathymetry of the entire area was assembled from different sets of available data taken at different times, including the lagoon body, the inundation area, and the channel area connecting the sea, the lagoon, and the coastal area. Most of the data comes from measurements obtained by the Universidad de la República and the Uruguayan National Navy (e.g. nautical charts). To assign a bathymetric value to each grid node, the averaging function and the triangular interpolation function were used first. Several bathymetries were carried out, considering the different shapes of the access channel (depth and width) and the internal channels of the estuary, using satellite images of the study area (using true colour analysis, RGB) as a guide. The different bathymetries were part of the model calibration adjustments.

Thirteen main tidal harmonic constants (M_2, S_2, N_2, K_2, K_1, O_1, P_1, Q_1, Msf, Mm, M_4, MS_4 and MN_4) from global data from the TPXO 7.2 TOPEX/Poseidon Altimetry model (http:volkov.oce.orst.edu./tides/global), with a spatial resolution of ~25 km, were used as astronomical forcing at the oceanic open boundary. In addition, hourly sea level data for the study area were obtained from the Copernicus Global Reanalysis (PHY_001_024) (https://resources.marine.copernicus.eu/products). The sea level corresponding to the sum of the astronomical tidal amplitude (calculated based on harmonics) and the sea level amplitude obtained from the Copernicus sea level base was used, which correctly described the data observed *in situ* at the port of La Paloma (SHOMA), located 13 km to the east of the lagoon mouth.

The location of the discharges was defined according to the main tributaries of LR, four in the north of the lagoon and one in the southeast (Fig. 1 B). Daily discharge estimates ($m^3\ s^{-1}$) generated by IMFIA-UdelaR using the GR4J model (Perrin et al. 2003), adapted for Uruguay (Narbondo et al. 2020), were used. This model was based on rainfall and potential evapotranspiration data obtained from the INUMET Rocha meteorological station, located 20 km from the study area, within LR watershed. The most significant discharge to the lagoon is from Rocha (60% of the total tributary discharge), followed by Las Conchas (17.5%), Las Palmas (10%), and Los Noques streams (9.4%), and De los Ceibos creek (3.1%) (Rodó 2013).

Surface boundary conditions were established using hourly wind data from a coastal weather station near the study area located in José Ignacio, approximately 40 km away (Manta et al. 2021). Spatially uniform wind was considered.

The model was calibrated by adjusting the bottom friction coefficient, the viscosity and the bathymetry of the internal channels connecting the main channel and the centre of the lagoon (Fig. 1 C). Bottom roughness was assumed to be uniform over the study area and without temporal variation. Several simulations were carried out varying the bottom roughness, on the one hand using the Manning coefficient (0.024, for u and v) and, on the other hand, changing the mean sediment grain size in the Chezy coefficient between 500 and 4000 μm.

The model validation was performed by comparing the temporal evolution of the simulated water level inside the lagoon at L2 and the data measured *in situ* with a tide gauge (EMAC-IADO) located at the same site (Fig. 1 B) during September 2016. Due to an existing referencing problem of the lagoon level data measured *in situ*, the data were compared by removing the mean (RM). To determine the performance of each model configuration on the water level in the lagoon, the root mean square error (RMSE) and its associated error (Skill) were estimated (Dias et al. 2009). RMSE and Skill can have values between 0 and 1; an RMSE of 0 and a Skill of 1 represents an excellent agreement between the model results and observed surface elevation.

3.3 Marine intrusion scenarios

The frequency, duration and intensity of marine intrusions under different environmental conditions or scenarios were studied for spring, the main period when larvae of estuarine-related species enter the lagoon. Ten days of unchanged conditions (wind, tributary discharge, and sea level) were used for training (spin-up), and then the conditions were adjusted according to the proposed scenarios for three days (72 h). The entry of seawater into the lagoon (a necessary condition for the entry of planktonic larvae) was evaluated by monitoring a seawater tracer simulating neutral particles (density 1000 kg m^{-3}), with an arbitrary initial concentration in the sea of 1 kg m^{-3}. The concentration of the tracer was estimated in the entrance channel (C1) and at three sites within the lagoon (L1, L2 and L3), located at increasing distances from the main channel (approximately 0.5, 1.5 and 3 km) (Fig. 1 C). The Delft3D-FLOW module was also used for tracer tracking. A total of 30 scenarios were analysed. The construction of these scenarios involved the combination of the three forcings (factors) with the most significant expected effect on the hydrodynamics of the system: wind (five conditions), tributary discharge (two conditions) and sea level (three conditions).

For wind, the five conditions considered were the most frequent combinations of direction and intensity in the study area during spring and the breeze cycle (Manta 2017) (Table 2). The two discharge conditions were defined based on the study of total estimated discharges (from 1983 to 2017) in LR during spring (Narbondo et al. 2020). Based on these criteria, a basal and high discharge corresponding to the 50 and 95- percentile were selected, defined as 5 m^3 s^{-1} and 75 m^3 s^{-1}, respectively. Based on the analysis of the water level boundary conditions in the adjacent coast during spring 2016, three periods with different sea level were selected:.a low period (from 2 to 4 October), a medium period (from 21 to 23 October), and a high period (15-17 November), characterized by a mean sea level of -0.1, 0.1 and 0.3 m, respectively. Table 2 summarises the proposed scenarios (n= 5 × 2 × 3 = 30).

Table 2. Scenarios (n=30) to evaluate the duration and intensity of marine intrusions using a tracer. The table shows the three forcings with their respective categories: 1) wind (m s^{-1}): 5 categories, four fixed and one variable. 2) sea level (m): 3 categories. 3) tributary discharge (m3 s^{-1}): 2 categories.

	Wind (m s^{-1}, degree)	**Low Sea Level (LSL: average= -0.3 m)**		**Medium Sea Level (MSL: average= -0.1 m)**		**High Sea Level (HSL: average= 0.1 m)**	
FIXED	Light NE (S-NE: 2 m s^{-1}, 45 degree)	Basal discharge (5 m^3 s^{-1})	High discharge (75 m^3 s^{-1})	Basal discharge (5 m^3 s^{-1})	High discharge (75 m^3 s^{-1})	Basal discharge (5 m^3 s^{-1})	High discharge (75 m^3 s^{-1})
	Moderate NE (M-NE: 6 m s^{-1}, 45 degree)	Basal discharge (5 m^3 s^{-1})	High discharge (75 m^3 s^{-1})	Basal discharge (5 m^3 s^{-1})	High discharge (75 m^3 s^{-1})	Basal discharge (5 m^3 s^{-1})	High discharge (75 m^3 s^{-1})
	Moderate SEE (M-SEE: 6 m s^{-1}), 129 degree)	Basal discharge (5 m^3 s^{-1})	High discharge (75 m^3 s^{-1})	Basal discharge (5 m^3 s^{-1})	High discharge (75 m^3 s^{-1})	Basal discharge (5 m^3 s^{-1})	High discharge (75 m^3 s^{-1})
	Strong SE (F-SE: 12 m s^{-1}, 135 degree)	Basal discharge (5 m^3 s^{-1})	High discharge (75 m^3 s^{-1})	Basal discharge (5 m^3 s^{-1})	High discharge (75 m^3 s^{-1})	Basal discharge (5 m^3 s^{-1})	High discharge (75 m^3 s^{-1})
CHANGING	Sea breeze cycle (BM)	Basal discharge (5 m^3 s^{-1})	High discharge (75 m^3 s^{-1})	Basal discharge (5 m^3 s^{-1})	High discharge (75 m^3 s^{-1})	Basal discharge (5 m^3 s^{-1})	High discharge (75 m^3 s^{-1})

3.4 Marine intrusion assessment methodology

Marine intrusions into the lagoon in each scenario were characterised by number, duration and intensity, estimated from changes in tracer concentration at the four model observation sites (C1, L1 to L3). Marine intrusions were defined as periods when the tracer concentration increased above threshold values. The thresholds were determined as 0.70 and 0.80 kg m^{-3}, twice the baseline concentration in the calm scenarios (light wind and no rain) corresponding to low and medium sea levels, respectively. The frequency was determined as the number of times the tracer exceeded these thresholds during the simulation period (72 h). The duration of intrusion was calculated by measuring the periods during which the tracer exceeded the predefined thresholds on each simulation day (24 h). The average peak widths over the three days were calculated (72 h). Intensity was calculated by averaging the maximum height of each simulation day. These daily averages are referred to as cases in the subsequent data analysis.

The sea level at the ocean boundary conditions was compared with the tracer concentration at the channel (C1). The time difference between the moment the maximum sea level peak occurs at the boundary (highest high tide) and the moment when the maximum tracer peak is recorded in the channel was determined. The relationship between the two variables was examined using the Spearman correlation.

Patterns in the duration and intensity of channel intrusions (site C1) and the importance of different forcings were determined using a Classification and Regression Tree (CART) model. CART models are easy to interpret and provide "yes or no" decisions on the thresholds of the main variables involved in branch divisions (e.g. De'ath and Fabricius 2000). The CART was performed by dividing the cases (n=90, one per simulation day, i.e. 3 for each scenario) into 2/3 (n=60) and 1/3 (n=30), both for duration and intensity. The set with the highest number of cases was used to construct the models, using rpart v. 4.1.15 (Therneau et al. 2022) and partykit v. 1.2.6 (Hothorn and Zeileis 2015). A complexity coefficient (cp) of 0.001 and a minimum of 5 cases were considered before each partition to construct and build the trees. The resulting trees (one based on response duration and another based on intensity) were pruned according to the 1-SE rule, resulting in the tree with the best performance in terms of cost-complexity. The accuracy of the trees was evaluated using the set with the lowest number of cases (1/3). The number of misclassified cases divided by the total number of cases was used to calculate the error of each model. The final trees were presented graphically. All analyses were performed using R 3.5.3 (R Core Team 2019).

The extent, duration, and intensity of marine intrusions within the lagoon were compared in the four observation sites in the wind scenarios with the highest probabilities of occurrence: moderate SEE and strong SE. The average concentration and the deviation of the tracer during the three days of modelling in the study area were also determined.

4 Results

4.1 Model validation

The validation of the model was carried out with data from September 2016. During this period, the water level measured *in situ* showed three prominent peaks, and the maximum amplitude of the peaks recorded was 1.15 m (Fig. 2). The root mean square error (RMSE) between observations and model results ranged from 9.5 to 17.5% of the local amplitude, which means that the model performance can be classified from good to very good (Dias et al. 2009). The model configuration with the best performance was selected to simulate the dispersion of the tracer in marine waters (model 4, RMSE = 0.12 m, skill of 0.90, Table 3).

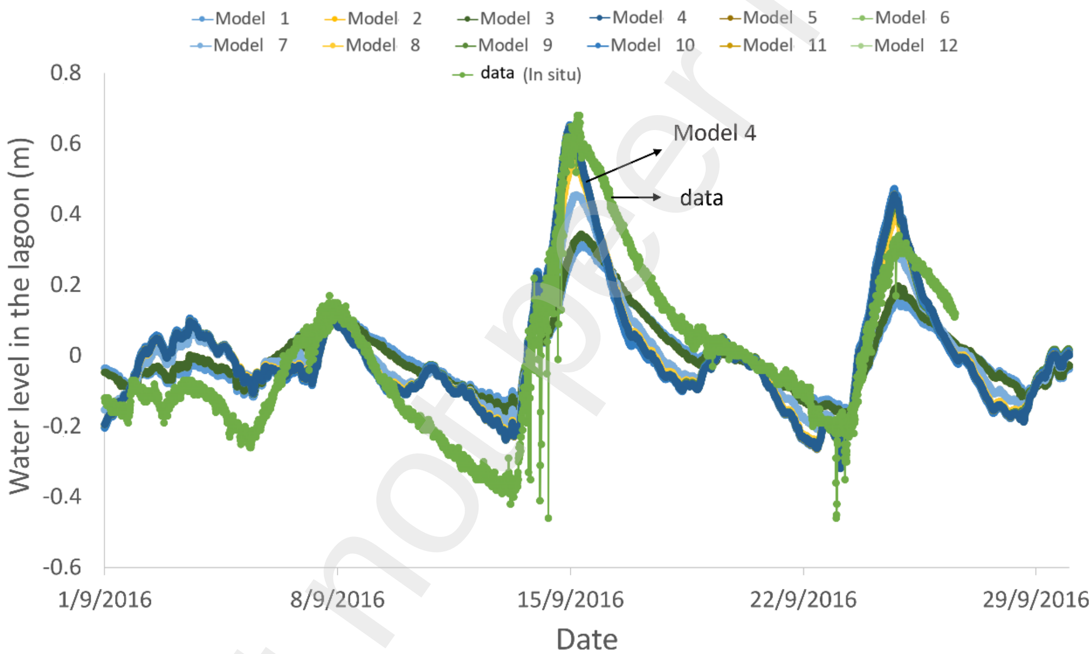


Figure 2. Water levels measured in situ in the lagoon (buoy = L2) and those simulated by the different model configurations. The plot indicates the series corresponding to the in situ data (light green) and the model configuration with the best performance (dark green, Model 4).

Table 3. Summary of the configurations implemented in Delft3D, with the respective root mean square error (RMSE) and Skill. The model configuration selected for its best performance (model 4) is shown in bold.

Model code	Bottom roughness	Bathymetry	RMSE (m)	Skill
Model 1	Manning u, v=0.024	entrance channel, no internal channels at the mouth	0.12	0.83
Model 2	Manning u, v=0.024	entrance channel, with internal channels at the mouth	0.20	0.86
Model 3	Chezy SD_{50}=3500µm	entrance channel, with internal channels at the mouth	0.12	0.86
Model 4	**Chezy** **SD_{50}=500µm**	**entrance channel,** **With deep internal channels at the mouth** **overtopping**	**0.12**	**0.90**
Model 5	Chezy SD_{50}=500µm	entrance channel, with internal channels at the mouth	0.11	0.89
Model 6	Chezy SD_{50}=4000µm	entrance channel, with deep internal channels at the mouth	0.12	0.90
Model 7	Chezy SD_{50}=3000µm	entrance channel, with internal channels at the mouth	0.11	0.89
Model 8	Chezy SD_{50}=3500µm	entrance channel, with deep internal channels at the mouth	0.11	0.89
Model 9	Chezy SD_{50}=3500µm	Deep entrance channel, with deep internal channels at the mouth	0.11	0.89
Model 10	Chezy SD_{50}=3500µm	Deep entrance channel, with deep internal channels at the mouth overtopping	0.11	0.89
Model 11	Chezy SD_{50}=3500µm	wide entrance channel, with internal channels at the mouth overtopping	0.12	0.90
Model 12	Chezy SD_{50}=3500µm	wide entrance channel, with shallow internal channels at the mouth overtopping	0.12	0.90

4.2 Number, duration, and intensity of marine intrusions under different conditions

Three intrusion events were observed in the entrance channel under calm weather conditions (light wind and basal discharge) and low or medium sea level. These intrusions occurred every 24 hours. The concentration of the tracer was related to the variations in sea level in the boundary conditions (Spearman, rho=0.55 and 0.59; $p<0.01$), especially with the highest peak at high tide (Fig. 3 A and B). Under calm conditions and at high sea level (HSL), two intrusions were observed, and the concentration of the tracer showed a higher correlation with the sea level at the boundary compared to the other sea level scenarios (Spearman. rho=0.69; $p<0.01$). In this case, the daily lower peaks of water level also caused marine intrusions (Fig. 3 C). Intrusions in calm conditions had a longer mean duration with increasing sea level (from 3 to 18 h, Table 4). The intensity of marine intrusions was lower at low sea level (LSL) compared to the other two sea level conditions (Table 4). The time difference between the highest sea level peak at the ocean boundary and the peak of the tracer concentration in the channel also increased with the mean sea level (1.4, 3.4 and 4 h respectively, Table 4). These results indicate that even under calm conditions, there are daily inflows that can be favourable for larval entry and that conditions improve with the increase in sea level.

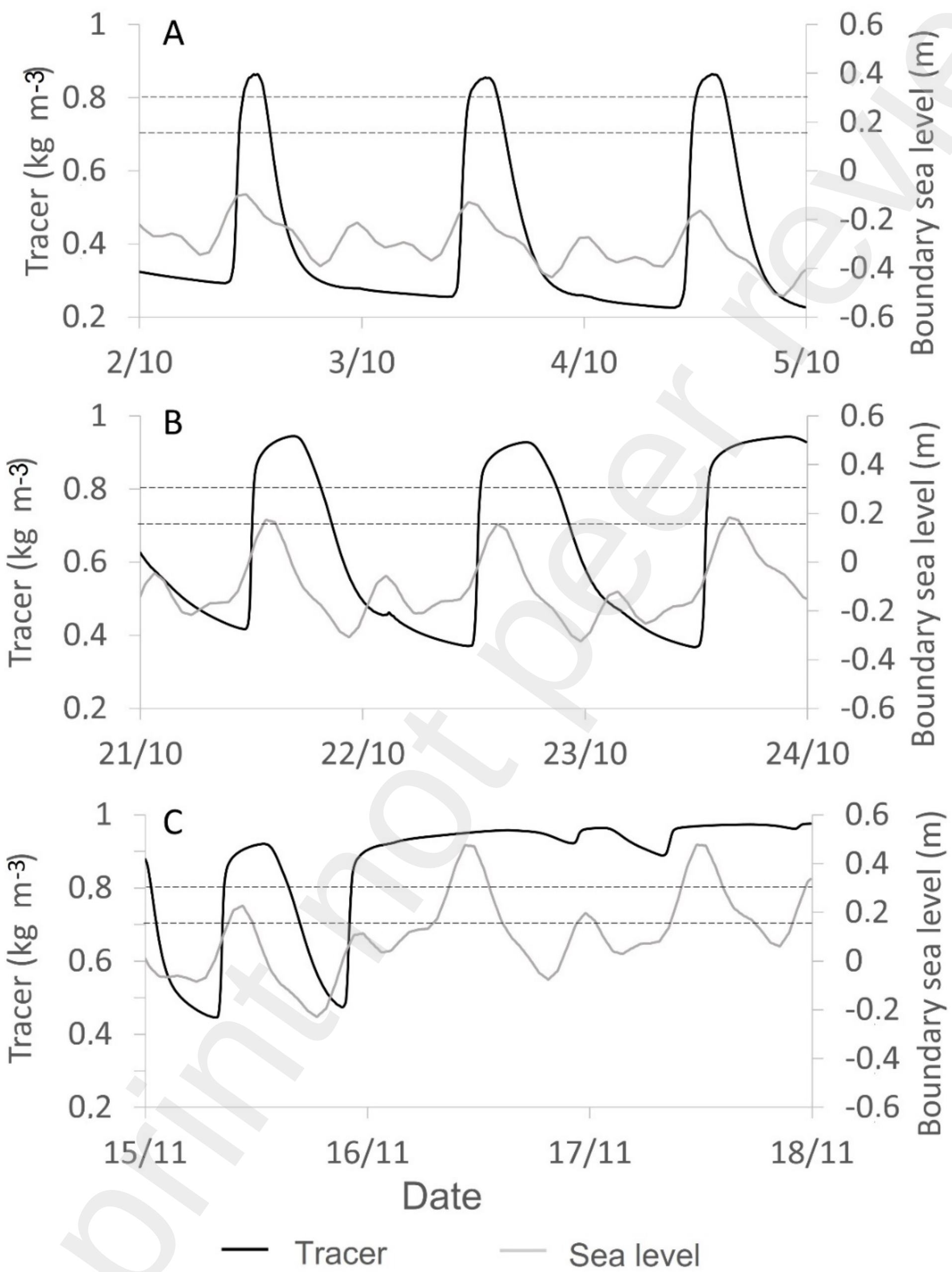


Figure 3. Temporal variation of the tracer (left axis) in the entrance channel (C1) and of the sea level at the sea boundary (right axis) under calm conditions (light NE wind and basal discharge). A) low sea level. B) medium sea level and C) high sea level. The horizontal lines indicate the 0.7 and 0.8 tracer thresholds.

Table 4. Comparison between tracer concentration and sea level at the ocean boundary under calm conditions (light NE wind and basal discharge) for the three sea level categories. The phase lag between the sea level peak at the boundary and the tracer peak in the lagoon, the correlation between these two variables and the average width and height ± standard deviation of the peaks in the channel (C1) are indicated. LSL: low sea level, MSL: medium sea level, HSL high sea level. *: statistically significant correlation ($p<0.01$).

Sea level	**Lag between water level peaks (min)**	**Spearman**	**Spearman (60 min lag)**	**Tracer peak width (h)**	**Tracer peak height (kg m^{-3})**
LSL	83	0.59 *	0.71 *	2.7 ± 0.4	0.86 ± 0.00
MSL	203	0.55 *	0.64 *	8.4 ± 1.6	0.94 ± 0.00
HSL	240	0.69 *	0.76 *	18.2 ± 9.8	0.95 ± 0.02

In the case of LSL and basal discharge, the number of intrusions remained at three events for all wind conditions except the strong SE wind scenario, where five events were recorded (Fig. 4 A). The duration and intensity were more significant in the strong wind scenario (10.7 h and 1.0 kg m^{-3} of tracer concentration, respectively) compared to the other wind conditions (2.6 to 4.2 h and 0.86 to 0.94 kg m^{-3}, respectively). The increase in tributary discharge reduced the number of intrusions to two in the strong SE wind and prevented them from occurring in the other wind scenarios. The increase in discharge also caused a considerable decrease in the duration (to 2.5 h) and average intensity (tracer concentration of 0.63 kg m^{-3}) of the intrusion under strong wind conditions (Fig. 4 A and B).

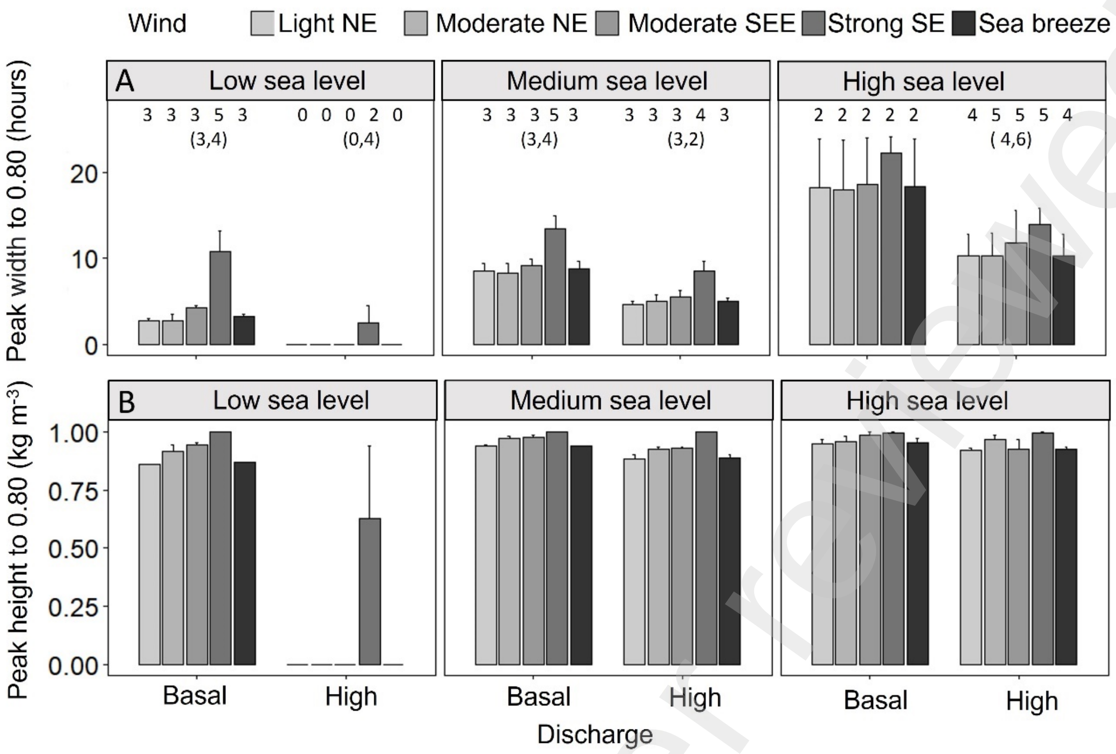


Figure 4. A) Duration (peak width > 0.80 kg m^{-3}) and B) Intensity (peak height > 0.80 kg m^{-3}) of marine intrusion in the channel (C1) in the different scenarios considered. The numbers in the upper panels indicate the number of intrusions in the simulation days (72 h) and in parentheses the average.

Regarding the mean sea level (MSL) and basal river discharge scenarios, the number of intrusions remained at three and reached five events under strong SE wind conditions. The two tributary discharge scenarios showed a similar pattern in the intrusions (Fig. 4 A). The intrusion duration in the basal discharge scenario was longer in strong wind conditions (13.4 h) than in other wind conditions (8.3 - 9.1 h). The intensity was also more significant in the high wind conditions, but the differences with the other wind scenarios were small, with all tracer concentrations > 0.94 kg m^{-3}. In the high discharge scenarios, the duration of intrusions decreased in all wind conditions (range: 4.6 - 8.4 h). The intensity slightly reduced except in the strong wind scenario (with an average tracer concentration of 1 kg m^{-3}).

In the HSL and basal tributary discharge, two marine intrusions were recorded under all wind conditions. Their mean duration was very long (range: 18.2 to 22.1 h), and the intensity was more significant under strong wind conditions, with little variation compared to the other wind conditions (all tracer concentrations > 0.96 kg m^{-3}) (Fig. 4). In this case, the high tributary discharge increased the number of intrusions in all wind conditions, reaching the maximum values recorded, however, the duration of intrusions decreased in all cases (10.3 to 13.4 h). As with the MSL case, the intrusion intensity slightly decreased, except for the strong wind, which remained at 1 kg m^{-3}.

Overall, as the sea level increased, the occurrences of intrusions tended to decrease but lasted longer and were more intense. Interestingly, high tributary discharges appeared to increase the number of intrusions but to decrease their duration and intensity at MSL and HS, and prevent them at LSL. Winds had a lower effect than expected, where only strong SE winds tended to increase the duration and intensity of intrusions in all scenarios.

4.3 Forcings relative importance in the duration and intensity of marine intrusions

The CART results provide a complementary viewpoint to the previous analysis. According to CART, the forcing with higher relative importance in the duration of the intrusions was sea level (83%), followed much below by tributary discharge (16%) and wind (1%). The best regression model showed an average duration of the intrusions of 19 h in the basal tributary discharge and 11 h in the high tributary discharge scenario under HSL conditions (Fig. 5 A). The duration of the intrusion was 7.7 h in MSL conditions and 2.5 h in LSL. The estimated prediction error for the model was 4.6 h. Wind was not considered as a forcing factor to differentiate between cases.

However, the intensity of the intrusions was mainly determined by the tributary discharge (46%), followed by sea level (40%) and much below wind (14%) as was shown by the CART model. The best regression model indicated an average intensity of the intrusions achieving 0.95 kg m^{-3} of tracer concentration under MSL or HSL conditions (Fig. 5 B). Values of tracer concentration of 0.91 kg m^{-3} were obtained in conditions of basal tributary discharge and 0 kg m^{-3} under LSL and high river discharge, showing a lower intensity of intrusions, except for strong SE winds that predicted an intensity average of 0.63 kg m^{-3}. The prediction error for this model was 0.034 kg m^{-3}.

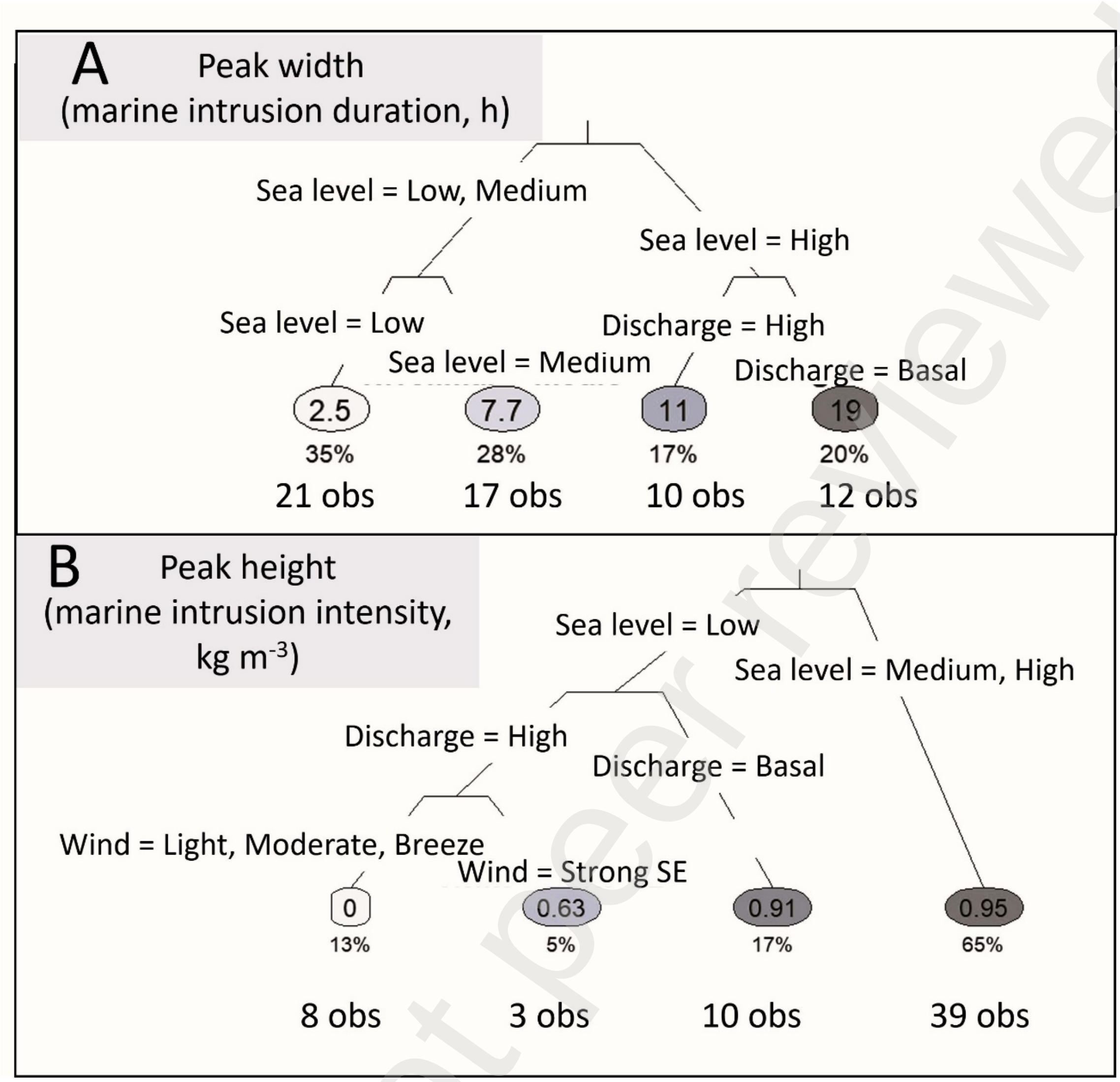


Figure 5. Regression tree diagram (CART) according to A) the duration and B) the intensity of marine intrusions. Each diagram indicates the average duration or intensity (light blue circles), the number of final observations of each terminal node and the corresponding percentage.

4.4 Marine intrusions extent

The marine intrusions reached the furthest observation site (L3) under HSL and basal tributary discharge (Fig. 6). Under LSL conditions, intrusions were only observed in the channel, except under strong SE wind and basal tributary discharge conditions (Fig. 6).

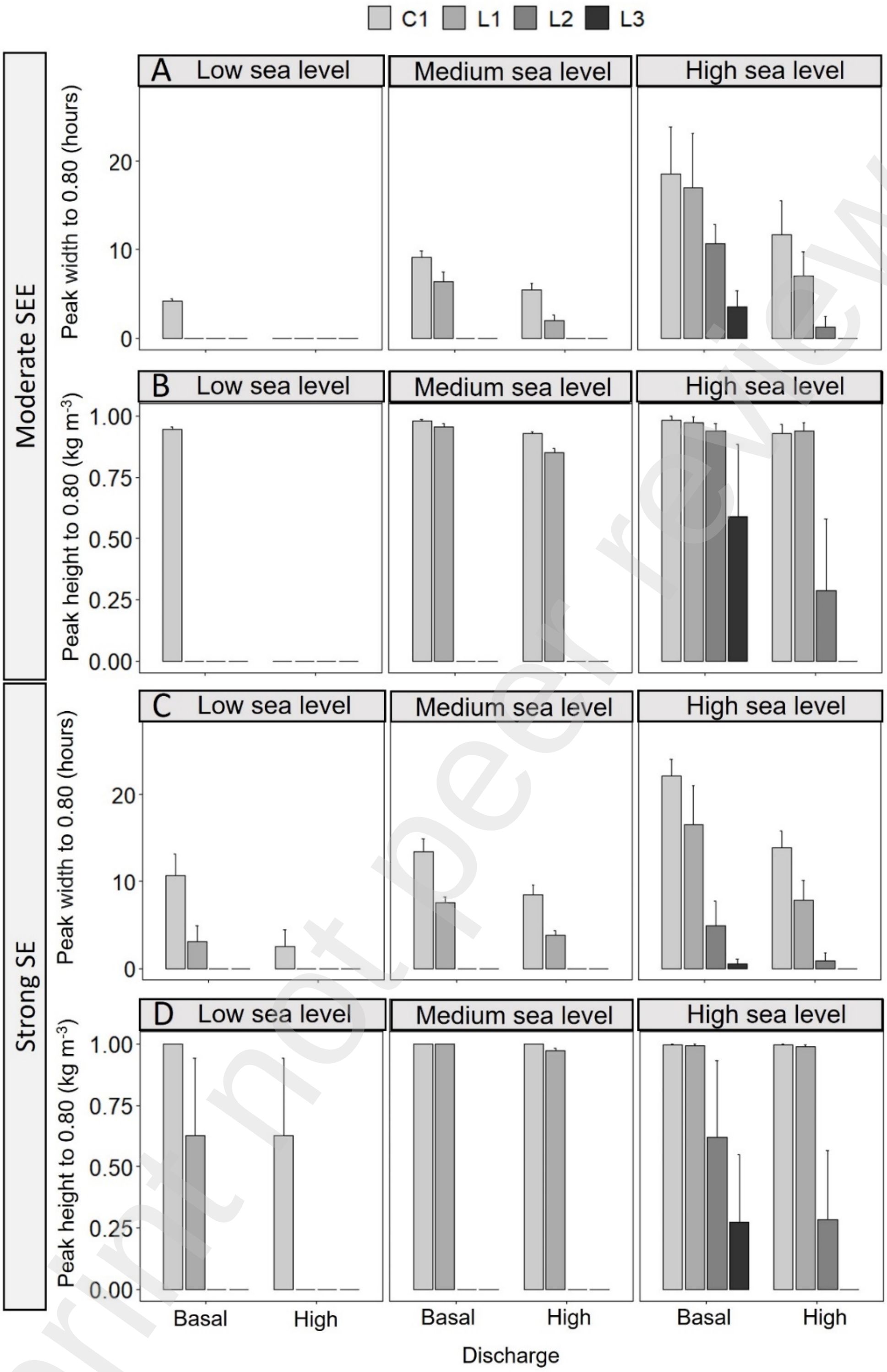


Figure 6. Duration (width of peaks > 0.80 kg m^{-3}) and intensity (height of peaks > 0.80 kg m^{-3}) of marine intrusions in the different observation sites of the lagoon (C1, L1 to L3) under moderate SEE wind (A and B panels) and strong SE wind (C and D panels) conditions.

The duration of marine intrusions within the lagoon decreased as distance from the channel increased for all sea level scenarios and both moderate SEE and strong SE wind conditions (Fig. 6). Similarly, an increase in the duration of intrusions with increasing sea level was observed for both wind and tributary discharge conditions (Fig. 6).

The intensity of the intrusions was generally higher in C1 and L1, with tracer concentrations ranging from 0.62 to 1 kg m^{-3}, and differed markedly from L2 and L3, with much lower concentrations (0.28 to 0.61 and 0.27 to 0.59 kg m^{-3}, respectively) (Fig. 6). In L3, the duration and intensity of the marine intrusion was higher under conditions of moderate SEE wind, even exceeding that under strong SE wind (Fig. 6).

During LSL and basal tributary discharge, very low tracer concentrations (0.2 to 0.4 kg m^{-3}) were observed over most of the lagoon surface. The highest concentrations were observed at the closed bpundaries within the lagoon and the entrance channel zone. The standard deviation was higher in the vicinity of the channel and more significant during strong SE wind conditions (Fig. 7). The tracer concentration was even attenuated when the tributary discharge was high (< 0.2 kg m^{-3}, Fig. 7).

Under MSL and basal tributary discharge, the influence of the tracer was observed in the middle zone of the lagoon (approx. 0.4 kg m^{-3}). Nevertheless, it concentrated more in the channel zone (concentration > 0.6 kg m^{-3}). The strong SE wind increased the average and deviation of the tracer concentration in the south-west part of the lagoon (Fig. 8). At high tributary discharge, the same spatial pattern as for basal tributary discharge was observed, but with a weakening of the tracer concentration throughout the study area. In this case, the standard deviation was higher in the channel zone compared to the standard deviation of the basal river discharge scenarios.

In the case of HSL and basal tributary discharge, the tracer concentration reached very high concentrations (approx. 0.8 – 1 kg m^{-3}) and considerable deviations (. 0.4 – 0.6 kg m^{-3}) in the central-southern part of the lagoon (Fig. 9). The moderate SEE and strong SE wind scenarios showed the highest concentrations of the tracer and also a ´´V´´ spatial distribution (higher concentrations at closed bpundaries), which was more pronounced in the second scenario. This spatial distribution differs from the other wind scenarios where the concentration gradient was more homogeneous in the E-W direction or even showed an inverted ´´V´´ shape (lower concentrations at the edges) (Fig. 9). A similar pattern occurred for the tracer concentration in the high tributary discharge scenario, except that the concentrations were lower, and the deviations were higher (Fig. 9).

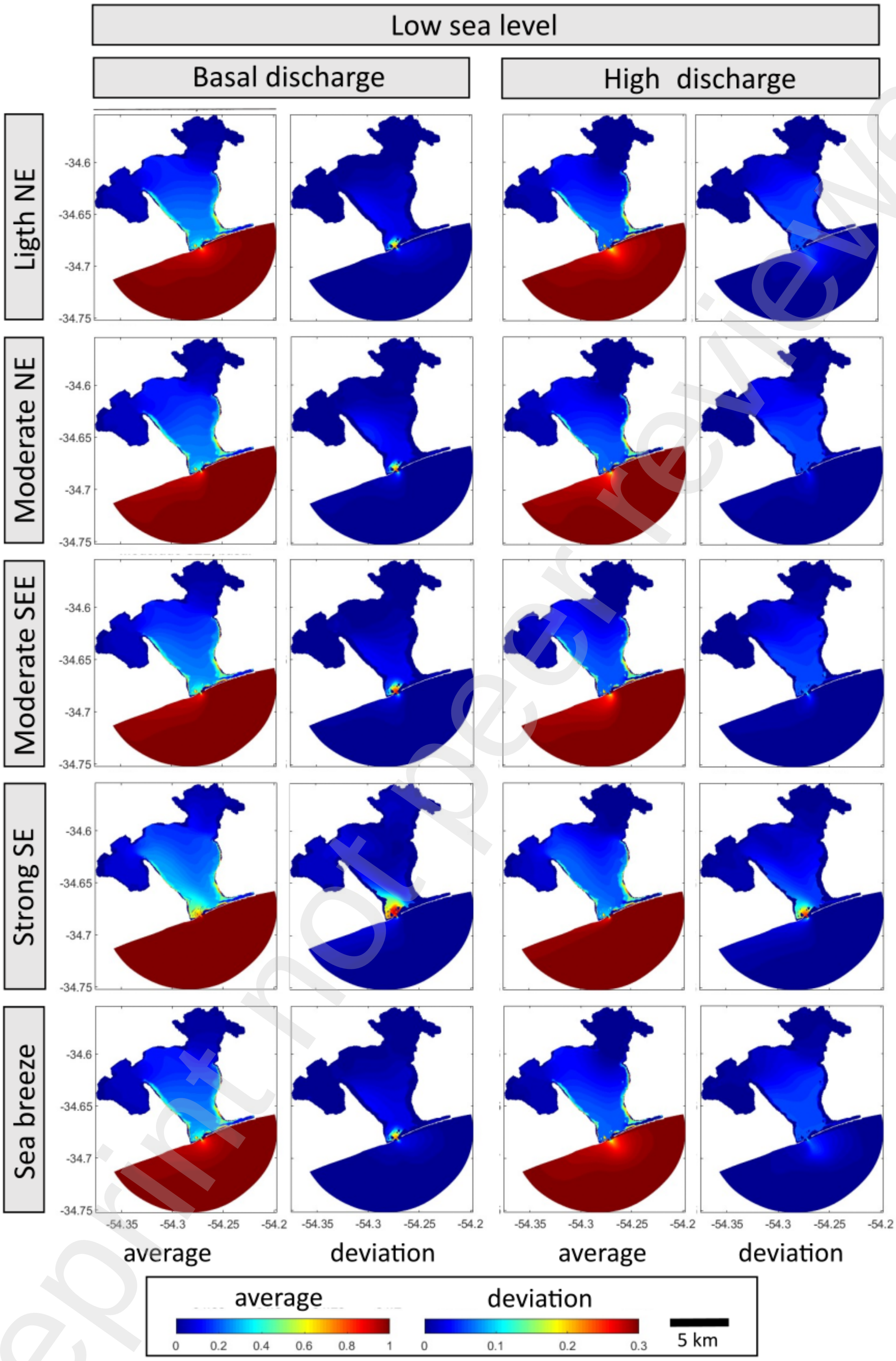


Figure 7. Average and standard deviation (kg m^{-3}) of the tracer concentration for low-sea level scenarios, under different wind (upper to lower panels) and discharge (left to right panels) conditions.

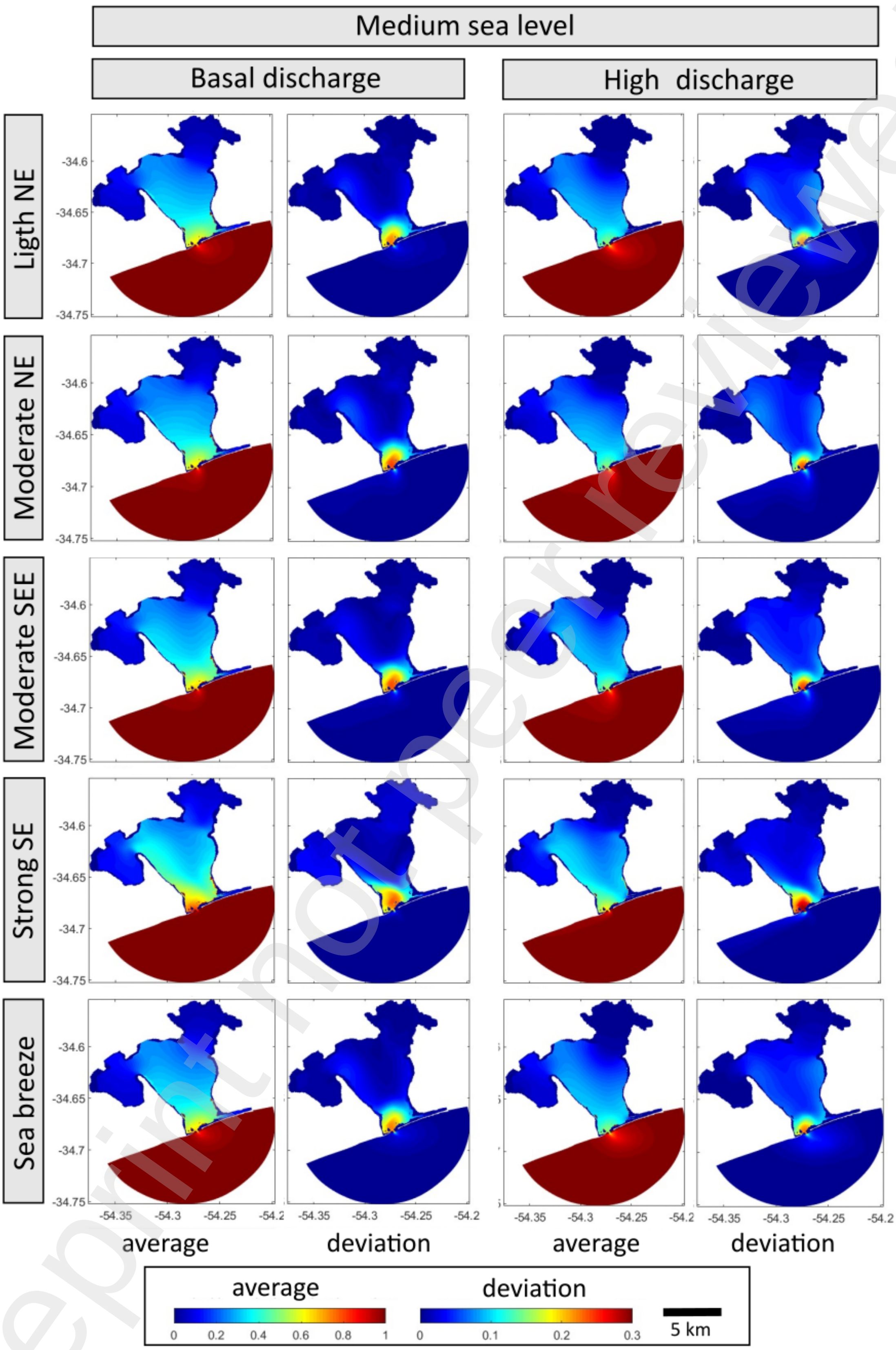
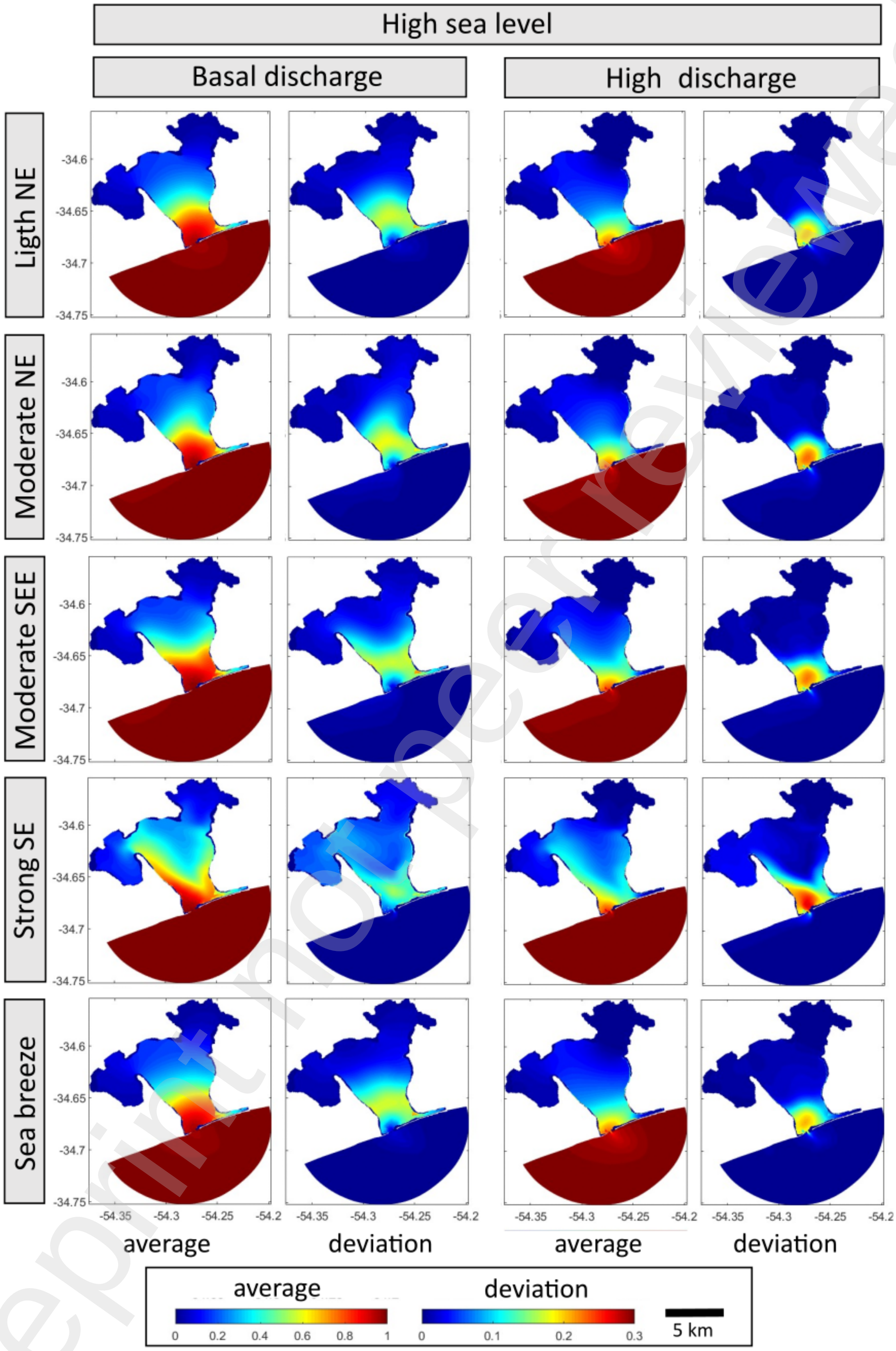


Figure 8. Average and standard deviation (kg m^{-3}) of the tracer concentration for medium-sea level scenarios, under different wind (upper to lower panels) and discharge (left to right panels) conditions.



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518 Figure 9. Average and standard deviation (Kg m^{-3}) of the tracer concentration for high-
519 sea level scenarios, under different wind (upper to lower panels) and discharge (left to
520 right panels) conditions.

5 Discussion

This study contributes to understanding the exchange process between a coastal lagoon and the adjacent sea and answers the questions established. The duration of marine intrusions was related to sea level; high sea levels and basal tributary discharge caused significantly longer intrusions (19 - 22 h). The intensity of the intrusions in the main channel was driven mainly by the tributary discharge and sea level. In conditions of low sea levels, short daily periods (2 - 4 h in duration) were favourable for the entry of seawater, mainly during the highest high tide, while marine intrusions were practically prevented or restricted to the channel zone when the sea level was low, and the tributary discharge was high. On the contrary, when the sea level was medium or high, the intrusions were observed in the central-southern area of the lagoon. The wind forcing had minor importance, reinforcing the intrusion processes in particular cases.

5.1 Model validation

The implemented model showed good performance in representing the water levels in LR. The RMSE values in this study were slightly above those reported in the modelling of the Laguna de los Patos (Martins et al. 2007) and the Ria de Aveiro (e.g. Vaz et al. 2019), large systems with a permanent connection to the ocean through a channel of approx. 300 and 600 m wide, respectively. Therefore, a higher difference between observed and simulated values by the model in this study may be related to the simplifications assumed i.e. bathymetry and geomorphology remained unchanged during the simulation. Based on this simplification and the general precision of the model (RMSE, sub-optimal but in an acceptable range), it can be considered that the general characteristics of the circulation in the lagoon - particularly in the southern part - are satisfactorily captured by the model. Therefore, this constitutes a valuable tool for assessing marine intrusion processes in this lagoon.

5.2 Marine intrusion dynamics

This study showed that the duration and intensity of marine intrusions are very sensitive to sea level. The relationship between marine intrusions in the channel and the currents induced by the sea level has already been observed in a microtidal bay on the Texas coast (USA) (Brown et al. 2000). This study demonstrate that even under basal tributary discharge and each of the sea level scenarios, the maximum high tide exceeds a sea level that ensures at least one marine intrusion per day, despite being in a microtidal regime. The CART analysis compared the impact of the three studied forcings and identified sea level as one of the most critical variables. However, this analysis also recognised the importance of tributary discharge and winds, the latter of lesser relative importance. This is crucial because these forcings, together with other variables, influence variations in sea levels (Teixeira 2019).

The main sea level variations on the Atlantic coast of Uruguay and the Río de la Plata respond to meteorological factors such as temperature, wind, and the Río de la Plata discharge, which combine differently depending on the spatio-temporal scale (D'Onofrio et al. 2008, Saraceno et al. 2014, Verocai et al. 2016). Regionally, higher sea levels in the study area are associated with strong SE (onshore) winds, storm surges originating from the Patagonian shelf, or a combination of both (Simionato et al. 2004, D'Onofrio et al. 2008, Verocai et al. 2016). On the contrary, lower sea levels along the Uruguayan coast occur under conditions of persistent northerly (offshore) winds (Verocai et al. 2016, Saraceno et al. 2014). Winds parallel to the coast also affect sea levels through Ekman transport. Winds from the SW, generally occurring in autumn-winter, tend to generate positive sea level anomalies on the Atlantic coast of Uruguay, while winds from the NE generate negative anomalies (Saraceno et al. 2014, Trinchín et al. 2019). Therefore, the sea level in the study area and regional wind dynamics are closely related, affecting the marine intrusions in LR. Nevertheless, local winds seem to be of minor importance, affecting the water exchange only at specific conditions.

According to the simulations, the most frequent winds in the study area (light NE, moderate NE, moderate SEE, sea breeze) did not directly generate marine intrusions, except for the strong SE wind. Despite being a less critical forcing, differences in the duration of the intrusion between winds of similar directions, such as moderate SEE and strong SE, indicate that wind intensity is a relevant parameter. On the other hand, studies in coastal lagoons have indicated that wind is the main factor in determining marine intrusions and larval ingress (Martins et al. 2007. Franzen et al. 2019). The main difference with our research was that those authors considered regional wind effects rather than local effects, such as local wind stress. To enhance our understanding of the impact of wind in marine intrusions into LR, it is of utmost importance to conduct further studies that consider a larger area for model implementation (e.g. nested models).

This study confirms that increasing the discharge from the lagoon during high tributary discharge conditions may prevent or limit the duration and intensity of marine intrusions with LSL. This is consistent with totally limnic conditions within a typical brackish lagoon (Laguna de los Patos, about 300 km north of LR) and evidence of large discharges into the adjacent sea during a period of high rainfall (El Niño event) (Möller et al. 2009, Bitencourt et al 2020). The CART found significant effects of tributary discharge on the intensity of intrusions showing its higher impact with LSL. However, the duration of intrusions decreased under HSL, but the frequency of intrusions increased. Moreover, at the highest tributary discharge, a general pattern of larger tracer variability was observed in the southern area and the entrance channel, under all wind and sea level conditions. This suggests a greater exchange between the lagoon and the ocean in both directions occurs, as previously identified by Fiandrino et al. (2017). Therefore, it can be concluded that tributary discharge affects the dynamics of marine intrusion in microtidal coastal lagoons with limited connection to the ocean.

The prevailing conditions in the study area are light to moderate NE to SE winds (2-6 m s^{-1}), a total tributary discharge < 18 m^3 s^{-1} and an average sea level of 0.1 m with irregular semi-diurnal oscillations. However, studies based on historical data have observed changes in the trends of some meteorological variables (D'Onofrio et al. 2008, Verocai et al. 2016). For example, an increasing trend in annual precipitation has been observed since 1970 (Bidegain et al. 2012). Trends have also shown an increase in the frequency of heavy precipitation (> 25 mm day^{-1}) and an increase in the frequency of droughts (e.g. Bidegain et al. 2012, Caorsi et al. 2018). Sea level rise (1 to 3 mm yr^{-1}, for the period 1955-2014), increased frequency of high sea level events and increasingly extreme sea level minima have also been observed (e.g. D'Onofrio et al. 2008, Verocai et al. 2016). These changes could affect the dynamics of marine intrusions in the coastal lagoons of Uruguay. For example, increased precipitation would tend to decrease the intensity and duration of marine intrusions. However, an increase in mean sea level would have the opposite effect, leading to a rise in the duration and intensity of intrusions. According to the results of this study, if these two opposing trends coincide, the result will be a higher frequency of intrusions and more significant variability of environmental conditions in the southern part of the lagoon and near the channel due to alternating marine intrusions and fluvial discharges (e.g. Fig. 4 A, 8 and 9). Nevertheless, different combinations of these climatic trends may raise the overall variability in the system, reducing predictability not only for managers but also for fishing resources and biodiversity as a whole.

5.3 Conceptual model of LR hydrodynamics

The current conceptual model of the hydrodynamics of LR (Conde et al. 2000, 2019) proposes an alternating cycle of lagoon phases, dependent on the state of the sanbar. This alternation may occur more than once a year and is summarised as limnetic and uniform conditions in the closed sandbar phase versus a salinity gradient in the open sandbar phase (presence of an inlet), which in turn influences the lagoon biological communities (e.g Bonilla et al. 2005, Rodríguez-Gallego et al. 2015, Amaral et al. 2016, Machado et al. 2021). A conceptual model of the sandbar dynamic at shorter time scales has also been provided, describing the berm height and lagoon-ocean connectivity in relation to coastal (sediment accumulation, wave dynamics) and catchment (river discharge) processes (Conde et al. 2019). This study deepens the understanding of the short-term temporal and spatial variability resulting from the lagoon-ocean water exchange. The model highlights the high-frequency dynamic, with inflows and outflows of water occurring daily and sub-daily in the southern zone, in the vicinity of the channel. For example, seawater (with a salinity of greater than 70%) or brackish water (with a salinity of less than 70%) can be found in the vicinity of the channel, contingent on the time of day (Fig. 3). Variability increases during periods of high river discharge. Our results also demonstrated that sea level, tributary discharge and local winds are crucial in determining the frequency, duration, intensity and spatial extent of marine intrusions. In addition to the most evident south-north spatial gradient, lateral gradients in the lagoon (from west to east shore) have been previously proposed (Rodríguez-Graña et al. 2008, Espinosa et al. 2019) and were confirmed with our model.

5.4 Entry mechanism of estuarine-related meroplankton into microtidal coastal lagoons

The importance of sea level for the marine intrusion into LR shown in this study expands the possible conditions by which meroplankton may ingress into these microtidal systems (Whitfield et al. 2023). As has been shown, any arrangement of forcings that raise the sea level above the lagoon water level may allow the meroplankton to enter coastal lagoons. This explains why several studies conclude the importance of different factors in the influx of seawater and larvae into microtidal coastal lagoons, such as wind, tide, and sea breeze (Martins et al. 2007, Bruno and Acha 2015, Bruno et al. 2018). Moreover, even the main force that triggers the entry of seawater and larvae can vary over time in a single lagoon, as was shown in this study. Fish and decapod larvae without an endogenous cycle of vertical migration coupled to the tides detect incoming currents through changes in hydrostatic pressure, salinity, and temperature, among others (Rogers et al. 1993, Queiroga et al. 2006, Epifanio 2019). Larval behavioural responses include changes in swimming direction or swimming frequency and speed (kinesis) to accelerate the entry rate into the estuary (Epifanio 2019). Therefore, estuarine larvae on the seaward side or in the lagoon access channel could detect incoming currents and initiate active behaviour to enter the lagoon.

Overall, we proposed that on the adjacent coast and in the inlet, larvae attempting to enter LR can select the incoming currents for larval transport, which, unlike the STST, may not be solely due to the flood tide effect. In turn, some studies have observed that larvae of an estuarine-related species known to use the STST mechanism also take advantage of wind-generated onshore current pulses (Joyeux 1998, Queiroga et al. 2006). Even in environments where mesotidal amplitude and channel morphology (e.g. width, depth) are sufficient to generate tidal currents within estuaries, interannual variability in the maximum abundance of larval exporting portunid crabs has been linked to sporadic favourable wind-generated inflow events (e.g. Queiroga et al. 2006). The use of incoming currents by larvae, proposed for LR, may also be useful in other coastal lagoons, microtidal or mesotidal estuaries.

A possible mechanism for larval entrance in the microtidal LR is through the daily pulses generated by the highest tide every day, once larvae suitable for estuarine recruitment congregate in the adjacent marine zone. Meroplankton often show changes in activity associated with cyclical environmental factors such as day-night cycles and lunar phases (Wheeler and Epifanio 1978, Queiroga et al. 2006, Bruno et al. 2018). A common feature of most LR estuarine-related species or those phylogenetically related to them (e.g. megalopae of *C. sapidus* and *N. granulata*, decapodids of *Peaneus* spp. or peneids and larvae of *Micropogonias* spp. or croakers) is that larvae enter estuaries or bays during nighttime inflows (Olmi 1994. Cházaro-Olvera et al. 2009, Hale and Targett 2018). Additionally, the duration of these inflows impacts the abundance of the larvae, with higher numbers observed during longer inflows (e.g. Wenner et al. 2005, Biermann et al. 2016). Based on the model simulations, this indicates that the greatest numbers of larvae will enter LR when sea levels are medium to high (e.g. marine intrusions > 8 h) as a result of interactions between various forces that lead to sea level increases (e.g. moderate to strong SE and SW winds, spring tides).

In addition, low recruitment has been reported in certain situations in coastal lagoons, indicating a barrier to larval entry. For example, prolonged periods of high freshwater discharge impede shrimp larval entry in a nearby coastal lagoon (Möller et al. 2009). This is consistent with the results of this study, where the duration and, ultimately, the frequency of marine intrusions decreased under conditions of high river discharge and low sea level. The current results align with the advection of most estuarine fish and decapod larvae towards the coastal zone observed in LR during a period of high rainfall

(Machado et al. 2021, Machado et al. unpublished). Similarly, some studies have shown that winds favoring lagoon discharge (Martins et al. 2007, Franzen et al. 2019) or withdrawing water from the coastal zone (e.g. upwelling), limit larval invasion (Queiroga et al. 2006).

The estuarine outflow, in turn, provides the chemical (humic substances, salinity) or physical (temperature, hydrostatic pressure) signals for larvae to locate the microtidal estuaries along the coast and congregate in front of them (Wheeler and Epifanio 1978, Epifanio 2019). This process is critical, as the number of larvae entering the estuary depends partly on the initial concentration of organisms outside (Miller and Shanks 2004, Queiroga et al. 2006, Santana et al. 2015). Once the estuarine-related fish larvae locate the estuary, the behaviour is usually triggered to remain in place until the conditions necessary to enter the estuary are met (e.g. Strydom 2003). Prolonged periods of no discharge from the lagoon to the coastal zone can prevent larval concentration in the nearshore, creating a bottleneck for recruitment within estuaries (Strydom 2003). The alternation of inflow and outflow observed in this study may ensure the entry of larvae and the emission of these signals. In turn, early juveniles of estuarine-related fish species have been reported to enter during the outflow phase by actively swimming behaviour (Whitfield et al 2023 and citations herein). Therefore, calm to moderate meteorological conditions that maintain a sea level and river discharge that allow an alternation of water flows in both directions could be the optimal conditions to facilitate the entry of more species at different stages of development.

In ICOLLs such as several Uruguayan coastal lagoons, the presence of sandbars is one of the main factors impeding water and biological connectivity between lagoons and the ocean (Conde et al. 2000, 2019. Machado et al. 2021). In the case of the shrimp *P. paulensis*, the effect of the closed sandbar in preventing larval entry is very evident, with more frequent juvenile harvesting in lagoons with higher connectivity to the ocean (Fabiano and Santana 2006). Although the entry of estuarine-dependent larvae has been observed during overwash events, the exchange is usually lower than when the channel over the bar is opened (Tweddle and Froneman 2017, Machado et al 2021).

6 Summary and conclusion

The results of this study, which focused on the frequency, duration, intensity and extent of marine intrusions in the vicinity of LR channel, showed that conditions for larval influx occur daily during the analysed period and in the open inlet state. Sea level is highlighted as the main forcing determining the intrusions' duration. The higher the mean sea level, the more extensive the marine intrusions are. Strong SE winds also tended to increase the duration of intrusions in all scenarios. Tributary discharge followed by sea level determined the intensity of marine intrusions; higher discharge attenuates, and higher sea level intensifies the marine intrusions. The intensity of intrusions was generally higher near the channel but can achieve central zones of the lagoon as the sea level increases.

In order to enhance the relevance of the regional scale for some of the factors evaluated (e.g. wind) may be necessary to implement the model with a larger marine area (e.g. nested models). Furthermore, water level measurements at different lagoon locations should be available to investigate further the effects of forcing on the spatial variation of marine intrusion within the lagoon.

Knowing the importance of sea level for marine intrusion in LR allows us to extend the number of recognised mechanisms by which meroplankton may enter these systems. For example, it could be any arrangement of forcings whose overlapping effect is to raise the sea level above the lagoon water level, achieving the different spatial extent of the marine intrusion according to that combination of forcings. The results suggest that even the main force that triggers the entry of seawater and therefore larvae can vary largely over time in a single lagoon. Therefore, we propose in LR a mechanism based on the selection of incoming currents for larval transport that, unlike the STST, may not be solely due to the flood tide effect.

Previous studies highlighted that one of the main determinants of larval entry for estuarine-related species is the duration of marine intrusions and the time of day they occur. Specifically, these studies found that larval entry is maximised when there is a high abundance of entry-competent larvae in the marine zone, sea level rises at night, and small or moderate tributary flows allow prolonged marine intrusions. In the study area, sea level rise is caused by a combination of astronomical and atmospheric factors. For example, in cases where spring tides, remote tides or winds (e.g. onshore or SW parallel winds) cause sea level rise, the signal is coincident and amplified.

These results are relevant for understanding and managing of LR protected area. On the one hand, knowledge of processes at small temporal and spatial scales will be improved by developing more precise study methods. Field studies to assess short-term changes in water conditions and the abundance of estuarine-related larvae near the entrance channel as a function of incoming currents are required to verify the proposed mechanism. On the other hand, the protocol for the artificial opening of the sandbar is based only on conditions that influence the lagoon water level with watershed origin (e.g., rainfall forecast) (Conde et al. 2019). The results of this study showed the importance of other factors in the lagoon-ocean exchange, such as sea level, which should be included as criteria to complement future management decisions, if fisheries - other than water quality - are also intended to be preserved.

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