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Article

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Columbia River plume intrusions drive episodic transport of larval Dungeness crab into the Salish Sea

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Abstract

Connectivity between estuaries and the coastal ocean plays a key role in shaping population dynamics for many marine organisms with planktonic larvae, yet the processes driving larval exchange remain difficult to observe and quantify. Previous studies have suggested that larvae of the commercially valuable Dungeness crab in the Northeast Pacific Ocean are occasionally advected into the estuarine Salish Sea. However, the transport mechanism and frequency of occurrence have not been resolved. Here, we use 6 years of observations and a process-based modeling approach to develop and test the hypothesis that buoyant plumes from the Columbia River, entering the ocean as turbulent gravity currents, entrain and transport coastal crab larvae ~400 km into the eastern Salish Sea during spring storms. Periods of persistent poleward winds that coincide with high river discharge predict the occurrence and timing of substantial coastal larval influx, and occur in approximately half the years studied. We demonstrate that the characteristic temporal pattern of resulting larval recruitment episodes reflects the tidally-modulated entrainment process. Our findings indicate that a wind- and tide-influenced river plume is a dominant larval transport pathway, with potential implications for fisheries management and for both monitoring and modeling river plume intrusions into estuaries.

Keywords: larval transport, river plume, *Metacarcinus magister*, Salish Sea, California Current System, basal and frontal mixing

047 1 Introduction

048
049 Despite long-standing evidence that recruitment success drives variation in abundance
050 of the Dungeness crab (*Metacarcinus (Cancer) magister*) [1–3], the most valuable
051 single-species commercial fishery on the U.S. west coast [4], the physical mechanisms
052 underlying interannual variability in recruitment remain poorly understood. Like many
053 benthic marine invertebrates, *Metacarcinus magister* has a bi-phasic life cycle with a
054 dispersive planktonic larval phase. Annual larval recruitment, defined as the delivery
055 of competent larvae to nearshore settlement sites, is a key determinant of “year-class
056 strength” [5, 6] through its influence on the number of larvae that settle and enter the
057 juvenile benthic population. Environmentally-driven variation in larval dispersal and
058 subsequent recruitment may control fluctuations in commercial catch throughout the
059 species’ range from central California to the Aleutian Islands [6].

060
061 In the northern California Current System (CCS), *M. magister*’s long pelagic larval
062 duration (130–150 d) consisting of five zoeal stages and a final megalopa stage before
063 settlement [7], together with evidence of high genetic connectivity [8, 9], suggests a
064 metapopulation linked by dispersal over broad spatial scales [8, 10]. Despite intense
065 fishing pressure, Pacific coast populations in the CCS have remained relatively stable
066 [3, 11]. However, at the northern extent of the CCS, fishery closures prompted by
067 unexplained declines in Washington state waters of the Salish Sea [12] highlight key
068 gaps in our understanding of the major drivers of *M. magister* population dynamics
069 and connectivity within partially enclosed waters.

070
071 Population connectivity in the CCS is regulated by seasonal and interannual vari-
072 ability in ocean circulation that governs large-scale transport [8]. While the California
073 Current (~ 500 km wide) flows equatorward year-round from Vancouver Island to
074 Baja California and dominates offshore circulation in the upper 100–300 m [13], surface
075 flow over the continental shelf undergoes seasonal changes in direction. *Metacarcinus*

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magister larvae hatch in coastal waters in mid-winter (January–March) [7], when pre- dominantly poleward, downwelling-favorable winds generate the poleward Davidson Current ($\sim 15 \text{ cm s}^{-1}$) over the shelf and slope [13]. Zoeae are carried northward and likely retained near the shelf by the onshore components of surface circulation [7, 14]. After the seasonal shift in prevailing winds known as the spring transition (usually in March–April), equatorward winds produce upwelling-favorable conditions, weaken and reverse the Davidson Current, and late-stage zoeae and megalopae are transported in the southward flow [15].

Climate variability in the North Pacific on interannual to decadal timescales is dominated by effects of the El Niño–Southern Oscillation (ENSO) and the Pacific Decadal Oscillation (PDO). Atmospheric teleconnections associated with these climate modes influence the strength and position of the wintertime Aleutian low pressure system, which modulates the intensity of poleward winds in the CCS [16]. Positive (warm) phases of the PDO are associated with a deepened Aleutian Low and alongshore winds that weaken equatorward transport in the CCS, whereas negative (cool) phases with a weaker Aleutian Low promote enhanced equatorward transport. ENSO shifts can produce broadly similar CCS responses, with El Niño (La Niña) conditions comparable to those associated with positive (negative) PDO phases [17]. Higher returns of *M. magister* megalopae in Oregon during the negative phase of the PDO have been attributed to greater southward transport in the CCS [15]. Conversely, years with low juvenile settlement on the Washington coast are associated with extensive northward transport during the pelagic larval phase, probably as a result of advective loss [10, 14], which occurs more frequently during strong El Niño events.

While a larger proportion of coastal megalopae settle and metamorphose into benthic juveniles on the continental shelf, physically protected estuaries are critical nursery habitats that promote greater juvenile survival and growth [18, 19], and may contribute disproportionately to fishery production. The Salish Sea is a large estuarine

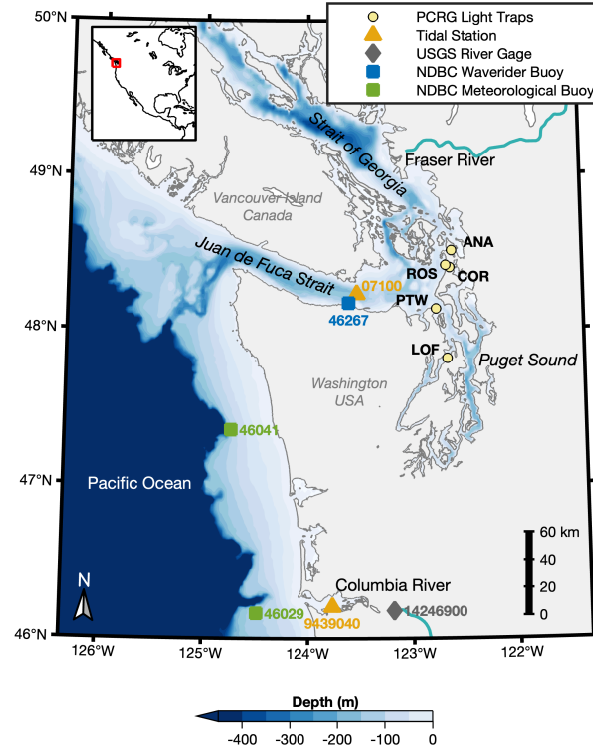


Fig. 1 The Salish Sea (Strait of Georgia, Juan de Fuca Strait (JDF), and Puget Sound) and Pacific coast of Washington state with locations of observational data sources used in this study. The two major rivers in this region are the Columbia at the Washington-Oregon border, USA (average discharge $7,300 \text{ m}^3 \text{ s}^{-1}$), and the Fraser in British Columbia, Canada (average discharge $3,475 \text{ m}^3 \text{ s}^{-1}$). Estuarine exchange flow through JDF, characterized by a lower density seaward surface flow ($20 - 40 \text{ cm s}^{-1}$) in the upper 50-60 m and intermediate and deep landward flow ($5 - 15 \text{ cm s}^{-1}$), is strongest in summer when increased freshwater discharge strengthens the surface outflow and coastal upwelling increases the density difference between oceanic and inland waters.

system spanning the US-Canada border with three major regions: the Juan de Fuca Strait (JDF), the Strait of Georgia, and Puget Sound, a network of interconnected basins (Figure 1). The Puget Sound management region produces a substantial proportion of the total Washington statewide *M. magister* harvest (8.3 to 11.9 million pounds were harvested from inland waters annually from 2009-2020) [12]. A seasonally varying estuarine exchange flow through JDF, the primary connection between the

Salish Sea and the Pacific Ocean, is characterized by landward transport of intermediate (60-125 m) and deep (≥ 125 m) oceanic waters and seaward transport of relatively low-salinity surface waters, modulated by tides and wind [20, 21]. The greater depth of megalopal diel vertical migration (> 100 m compared to 25 m off the outer coast) [22] and predominant seaward surface flow in JDF have led to the widely accepted conclusion that Salish Sea *M. magister* larvae are mostly retained in semi-enclosed basins, and input from the ocean is limited [3, 22].

However, juvenile settlement observed in North Puget Sound in 3 of 7 years between 1982-1988 was attributed to influxes of coastal larvae based on the juveniles' large size and early settlement timing [23-25]. Coastal megalopae recruit to estuaries primarily from April through June and attain a larger carapace size ($\sim 5 - 7$ mm length) than those that develop in inland waters of the Salish Sea ($\sim 4 - 5$ mm) [26], which settle later in the season, from June to September [23, 24]. Despite evidence of probable coastal-origin settlement, a mechanism for larval accumulation and transport [27] into the Salish Sea has not been resolved. Researchers hypothesize that coastal larvae are occasionally advected into JDF during episodic reversals to the estuarine circulation [14, 22, 24] caused by strong poleward winds that produce coastal downwelling [28, 29]. This "transient" flow regime is characterized by strong, surface-intensified inflows ($25 - 30 \text{ cm s}^{-1}$) confined along the 6-km wide slope on the Washington side of JDF [30]. Intrusions of buoyant plume water from the tidally-dominated Columbia River (CR), located ~ 250 km south of JDF and the largest source of freshwater to the Pacific Ocean in North America, form part of the inflow during major transient events [31-33].

Plumes from the CR emerge as stratified pulses from an estuary with a narrow entrance at the Oregon-Washington border into the coastal ocean during ebb tide, where they detach from the bottom and spread across shelf waters as turbulent gravity currents [34]. Along the southern Washington coast, *M. magister* megalopae are

231 abundant and widely distributed in surface waters across the shelf between April and
232 June, forming contiguous patches that are 2–13 km in extent [35, 36]. Megalopae are
233 observed both within CR plume waters and concentrated along plume fronts [36, 37].
234
235 Roegner et al. [35] suggest that *M. magister* megalopae concentrated by the plume
236 front were transported into Willapa Bay, a large coastal estuary 50 km north of the
237 river, following an intrusion of the CR plume. While intrusions of Columbia plume
238 water into JDF are more common during the winter, they also occur in spring under
239 conditions of high riverflow and strong or persistent downwelling wind stress when the
240 coastally-trapped plume is advected north [38, 39]. The wind- and tide-influenced river
241 plume therefore offers a potential mechanism for the concentration of surface-oriented
242 coastal organisms and their transport into the Salish Sea [33].
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246 In this study, we use six years of nearshore megalopae size and abundance data to
247 investigate the drivers and degree of connectivity between coastal Pacific and inland
248 *M. magister* populations by analyzing the timing and characteristics of larval recruit-
249 ment at five sites in the Salish Sea. We address three central questions: 1) What is the
250 contribution of coastal megalopae to annual recruitment at each site? 2) Does inter-
251 annual climate variability affect the likelihood of larval transport into the Salish Sea?
252 3) Do coastal megalopae arrive in the Salish Sea following intrusions of the CR plume
253 that occur during wind-induced reversals to the estuarine circulation?
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256 We observe the early arrival of large numbers of phenotypically distinct coastal *M.*
257 *magister* megalopae following reversals in JDF surface flow in 3 of 6 years between
258 2019-2024, accounting for up to 86% of the annual larval returns at a site. Coastal
259 recruitment events can be predicted to occur 2–3 weeks after sustained periods of
260 poleward winds in April and May coincident with high CR discharge (probability of
261 occurrence = 0.83). Consequently, we develop a conceptual model for larval entrain-
262 ment in plumes from the CR and their northward transport into the Salish Sea. Using
263 a simple box model, we demonstrate that the characteristic temporal structure of
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coastal larval recruitment events reflects the entrainment of larvae into spreading, tidally-modulated CR plumes, modified by losses related to strong winds or dilution in JDF. Our results suggest that the timing and magnitude of coastal *M. magister* recruitment is governed partly by predictable mixing properties of strong CR plume outflows.

2 Results

2.1 Distinct patterns of coastal larval recruitment.

Nearshore records of *M. magister* megalopae abundance and carapace size measurements can provide insight into larval origin and transport processes when sampling occurs at a rate that resolves individual recruitment episodes [40]. To quantify the frequency and spatiotemporal patterns of Pacific coast larval recruitment in the Salish Sea, we analyze the timing and size distribution of *M. magister* megalopae captured in nearshore light traps at five sites (Figure 1) over six years from April to September, 2019–2024. Time series of the near-daily megalopae catch records show two distinct recruitment patterns: (1) pulsed ‘recruitment events’ that occur over several days to a week where daily catch increases by at least an order of magnitude, and (2) relatively prolonged periods of quasi-steady daily catch extending for several weeks, typically during the months of June and July (Figure 2).

“Early” recruitment events in late April 2019 and May 2019, 2020, and 2022 occurred synchronously at the three central sites adjacent to JDF, Rosario Head (ROS), Cornet Bay (COR), and Point Wilson (PTW), with peak catch dates within days of one another (Figure 3a). Events are typically characterized by a single peak at ROS and COR and multiple closely spaced peaks at PTW. The ratio of peak to integrated event catch is remarkably consistent across these sites and events (0.24 ± 0.06 , mean $\pm$ SD). The events also share similar temporal patterns with a linear increase to peak abundance at a normalized rate of $0.21 \pm 0.04 \text{ d}^{-1}$, and an approximately

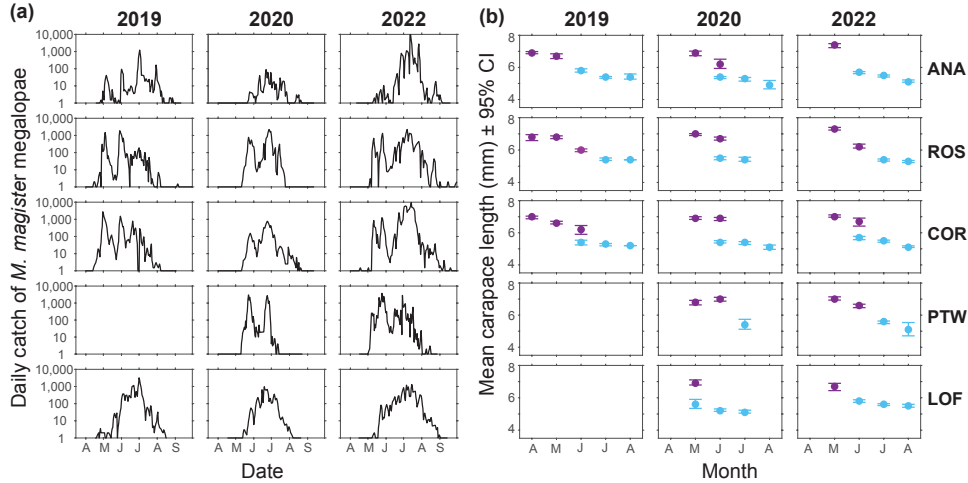


Fig. 2 Timing of larval arrival and size cohorts measured at five sites in the Salish Sea in 2019, 2020, and 2022. a) Daily time series of *M. magister* megalopae catch at light traps from April to September. Each subplot corresponds to a site-year combination. Sites are arranged in order of latitude: Anacortes (ANA), Rosario Head (ROS), Cornet Bay (COR), Point Wilson (PTW), and Lofall (LOF). b) Bootstrap estimates of mean megalopae carapace length (CL) $\pm$ 95% CI for mixture components identified by Gaussian mixture models fit to monthly size distributions at each site. Points are colored according to whether the component mean falls above or below the 6 mm size threshold (> 6 mm in purple, < 6 mm in blue). Size estimates are consistent with those reported by DeBrosse et al. [26], including the relative size differences observed between coastal and inland populations (mean 6.2 ± 0.03 mm in coastal Grays Harbor, WA, and 4.7 ± 0.05 mm at Anacortes, northern Puget Sound).

exponential decay with an e-folding time of $3.2 \pm 1.5 \text{ d}^{-1}$ (Figure 3b). Concurrent early events at Anacortes (ANA) and Lofall (LOF) follow a similar pattern with much smaller magnitudes. “Late” June–July events show greater variance, and are generally characterized by a steeper rise and a longer decay, likely due to the elevated background catch ($0.26 \pm 0.18 \text{ d}^{-1}$ increase and $3.7 \pm 3.4 \text{ d}^{-1}$ e-folding time). June–July recruitment patterns in most years are otherwise relatively prolonged and approximately Gaussian in shape (Figure 3a).

We distinguish recruitment cohorts of *M. magister* using Gaussian mixture models fit to monthly size distributions of megalopae carapace length (CL). The inverse variance weighted mean $\pm$ SE for the larger early cohort ranges from 6.2 ± 0.5 mm (May 2021) to 7.2 ± 0.2 mm (Apr 2023), whereas the small cohort ranges from 5 ± 0.2 mm

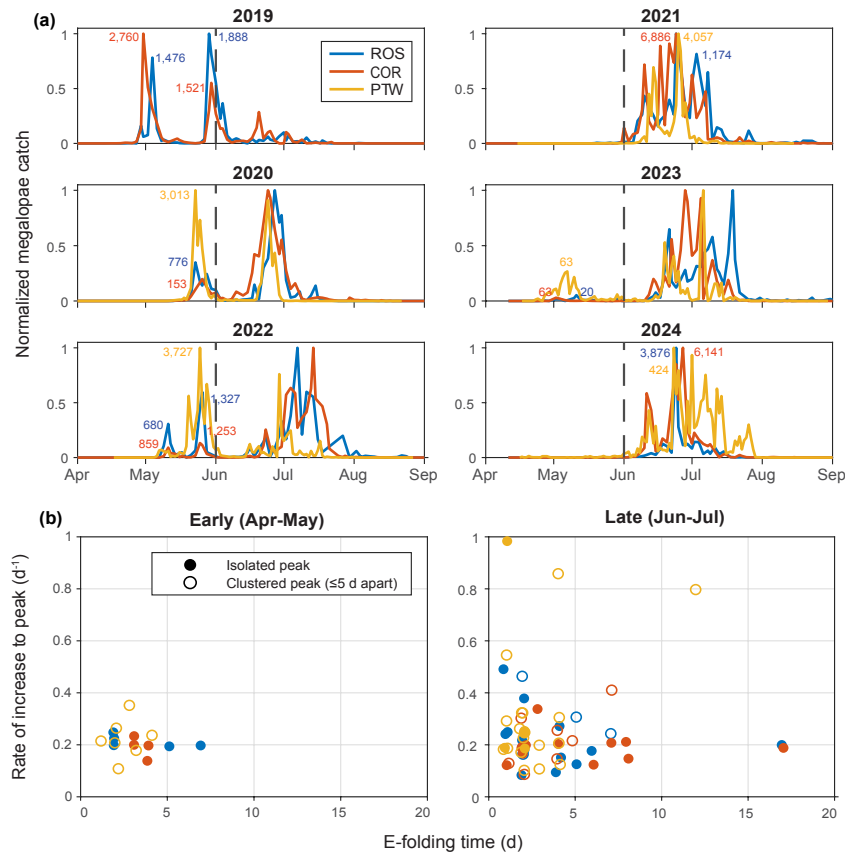


Fig. 3 Early- and late-season larval recruitment patterns at the three sites closest to Juan de Fuca Strait (JDF): Rosario Head (ROS), Cornet Bay (COR), and Point Wilson (PTW). (a) Normalized daily *M. magister* megalopae catch to light traps at each site. Daily catch was smoothed with a centered 3-day Gaussian filter and scaled by the maximum catch observed at each site that year (values range from 0 - 1). The dashed line at June 1 distinguishes ‘early’ and ‘late’ recruitment periods for the Salish Sea. Early peaks are labeled with catch magnitude (2021 and 2024 have no early events; late peak catch is labeled for reference). (b) Normalized slopes and approximate e-folding times for early (April and May) and late (June and July) season recruitment peaks in the time series. Events with a singular peak in catch are represented with solid circles (isolated peak), while events with multiple peaks occurring within 3-5 days of one another are distinguished with open circles (clustered peak).

(Aug 2021) to 5.7 ± 0.3 mm (Jun 2022), consistent with the previously described biomodal recruitment pattern of *M. magister* in North Puget Sound [23, 24]. The distinctive > 6 mm coastal cohort was observed in all years at the three central sites in April or May, and sometimes June (no data at PTW in 2019), and at the sites to the north and south in 2019 (no size data at LOF in 2019), 2020, and 2022, while

the < 6 mm Puget Sound cohort was recorded at all sites from June through July or August (Figure 2).

We use the total number of megalopae caught at each site during the settlement season as an index of abundance. Accordingly, we divide the season into early (before June 1) and late (after June 1) periods and use the mixture model results to estimate the relative abundance of the coastal cohort during the early period and its contribution to total annual catch at each site. In 2019, estimated catch of the coastal cohort accounts for 86% and 79% of total annual catch at ROS and COR, respectively. Peak catch in May 2020 is an order of magnitude smaller and estimated returns make up a smaller proportion of overall catch (12% and 6%) due to late season returns of the Puget Sound cohort. At PTW, however, peak daily catch in May 2020 is $(O)10^3$ and the coastal cohort makes up 50% of overall catch. The highest daily catch of the coastal cohort occurs at PTW in late May 2022 (Figure 3b); the estimated proportion this year is much larger at PTW (62%) than at either ROS (21%) or COR (6%). The coastal cohort is also detected at ANA and LOF, but daily catch is $(O)10^1$ and does not contribute significantly to total catch at either site. In 2021, 2023, and 2024, returns of the coastal cohort at PTW, COR, and ROS are minimal and do not appear with the distinct early recruitment event shape observed in the other three years (Figure 3a).

2.2 Climate variability influences recruitment likelihood.

Interannual variability in atmospheric and oceanographic conditions influences both alongshore transport and the temperature regime experienced by coastal crab larvae during their pelagic development period, affecting their spatial distribution and growth rate [3]. We hypothesize that climate variability influences the likelihood of coastal *M. magister* larval recruitment in the Salish Sea in two ways: (1) by regulating megalopal abundance in coastal Washington waters in April and May; and (2)

through effects on the duration of poleward winds that ultimately drive their transport into the Salish Sea. Coastal recruitment in the Salish Sea is most likely to occur during conditions associated with the positive phase of the PDO, when warmer SST shortens the pelagic larval duration of *M. magister*, southern-sourced larvae are carried north to Washington by the Davidson Current, and a deepened Aleutian Low delays the spring transition to upwelling-favorable winds. Similar patterns associated with the El Niño phase of the ENSO are typically strong and consistent only during the positive phase of the PDO [17].

To develop this hypothesis in the absence of a multi-decadal record of larval recruitment that is required to resolve the effects of PDO variability, we examine trends in time series of the Oceanic Niño Index (ONI), coastal SST, winter and spring cumulative wind stress, and the timing of the spring transition over the 2019-2024 period (Figure 4). The PDO shifted from a positive to negative phase in 2019, reaching its most negative values since the mid-1950s in October 2021 (see Supplementary Fig. 1). Weak El Niño conditions in 2019 became neutral by the spring of 2020, shifting to sustained La Niña conditions from mid-2020 through early 2023. Strong El Niño conditions that began in the summer of 2023 persisted into the spring of 2024.

January–March coastal Washington SST (Figure 4a) does not consistently reflect ENSO variability except that the El Niño years correspond to the highest mean temperatures. We use the time-integrated January-March poleward wind stress as a proxy for the interannual variability of cumulative winter northward coastal transport. Cumulative wind stresses were highest in 2021, 2023, and 2024, and substantially lower in 2019, 2020, and 2022. Interestingly, spring (April-June) cumulative wind stress was generally inversely correlated with winter wind stress (Figure 4b). The latest spring transitions took place in 2022 (June 10) and 2020 (May 16), while 2019 (April 18) and the other three years had more typical spring transition timing between late March and late April (Figure 4).

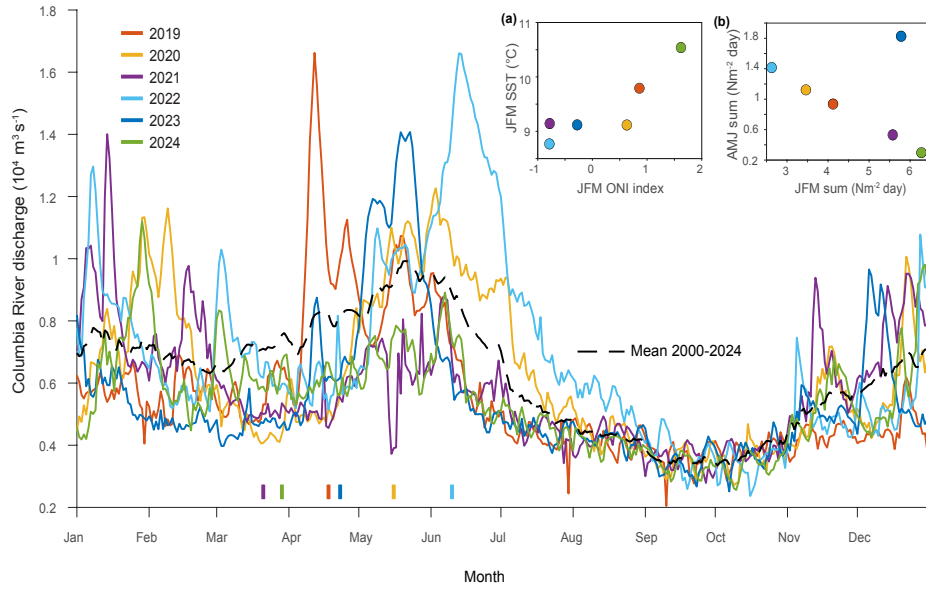


Fig. 4 Seasonal Columbia River discharge near Quincy, OR from 2019-2024 and indices of ocean-atmosphere variability. The estimated spring transition date for each year is indicated by a vertical bar above the x-axis. a) Three-month averaged January-March (JFM) Oceanic Niño Index (ONI) and mean JFM sea surface temperature (SST) ~ 30 km offshore of the southern Washington coast. b) Time-integrated poleward wind stress ($\text{N m}^{-2} \text{ day}$) for JFM, the coastal *M. magister* pelagic larval development period, and April-June (AMJ), the larval recruitment period. With the exception of 2023, JFM and AMJ cumulative wind stress are negatively correlated for these years ($r = -0.4$, without 2023 $r = -1$, Pearson correlation coefficient).

Interannual climate variability also affects regional hydrology. CR discharge often peaks earlier in the season and with reduced magnitude during El Niño and during the positive phase of the PDO [41]. However, the timing and magnitude of the peak spring flows from 2019-2024 did not consistently follow the ENSO pattern. The highest peak flow of $16,620 \text{ m}^3 \text{ s}^{-1}$ also occurred the earliest in April 2019, where discharge increased by more than a factor of 2 in one week following a high-intensity atmospheric river (Figure 4). River flow peaked around $12,000 \text{ m}^3 \text{ s}^{-1}$ in early June 2020, but the mean spring flow was similar in both years ($8,400 \text{ m}^3 \text{ s}^{-1}$). The highest mean discharge and largest spring freshet by volume occurred in 2022 with a peak in late June. Daily river

discharge exceeded the 25-year daily average in April-June for > 50 days in 2020 and 2022, 34 days in 2019 and 29 days in 2023; by contrast, spring discharge was below average in 2021 and 2024, with the lowest mean spring discharge of $6,073 \text{ m}^3 \text{ s}^{-1}$ in 2021.

2.3 Event-scale forcing predicts biological response.

While interannual climate variability establishes the background oceanographic setting in the Northeast Pacific, the northern CCS experiences substantial short-term “event” scale variability in alongshore winds and coastal hydrography. During the early upwelling season, frequent synoptic-scale wind reversals (2–10 days) generate downwelling conditions with northward flow over the shelf, and onshore Ekman transport which can weaken or reverse the exchange flow in JDF. Responding within hours to consequent changes in wind stress [31, 42], shallow, stratified CR plumes generated during periods of high discharge form confined northward coastal currents. Although salinity is the most reliable tracer of CR plume water (see Supplementary Fig. 2), measurements in this region are spatially sparse and intermittent. In the absence of salinity data, we use SST in JDF as a proxy for plume intrusions, which is effective in late spring and summer when CR water is warmer than ambient coastal waters [38] (see Supplementary Fig. 3).

From 2019-2024, at least one extended downwelling-favorable wind event occurred between April and June each year. While most events lasted around 8 days, downwelling winds in April 2020, 2022, and 2023 persisted for several weeks (19 to 28 days) (Figure 5a). Maximum daily wind stresses were $\approx 0.1 \text{ N m}^{-2}$ across all events, with the exception of April 2023, when maximum wind stress was nearly three times higher. Cross-correlation analysis identifies a consistent 3 day lagged relationship ($r = 0.4 - 0.7$) between daily wind stress and JDF current velocity at Angeles Point,

599 consistent with other observations of the lag time between the onset of coastal wind
600 events and reversals to surface currents ~ 70 km from the mouth of JDF [28, 43].
601

602 Two periods of moderate intensity surface inflows were observed in JDF in 2020,
603 2023, and 2024 and four in 2022 following wind events (no data in 2019) (Figure 5c).
604 Mean inflow velocity ranged from $17 - 31$ cm s $^{-1}$. The May 2020 inflow periods lasted
605 for a mean of 6.9 ± 2.6 d with SST anomaly $1.9 \pm 1.01^\circ\text{C}$. In 2022, inflows occurred
606 in every month from April-June for a total of 45 days, with an average duration of
607 11.2 ± 4.5 d and SST anomaly $0.48 \pm 0.82^\circ\text{C}$. Significant correlations between current
608 velocity and SST anomaly occur only in 2020 and 2022, with a lag of 0 days in 2020
609 ($r = 0.57$) and 1 day in 2022 ($r = 0.59$). By contrast, in 2023 and 2024 all surface
610 inflows occurred in April, generally with a weaker or negative SST anomaly (Figure 5c).
611

612 To investigate whether early coastal larval recruitment events (the biological
613 response) are predicted by periods of poleward winds with high CR outflow (the
614 physical forcing) (Figure 5), we calculate an event-based conditional probability:
615

$$622 \quad P(R | F) = \frac{N(R \cap F)}{N(F)}. \quad (1)$$

623 Here, F is the occurrence of a forcing event, R is the occurrence of a response event,
624 $N(F)$ is the total number of forcing events, and $N(R \cap F)$ is the number of forcing
625 events followed by the response. We define the biological response as a distinct larval
626 recruitment event of the coastal cohort that occurred simultaneously at the three
627 central sites in April or May, and the physical forcing as a period with above average
628 river flow that occurred at least five days before the end of a poleward wind event.
629

630 We estimate the expected time lag between forcing and response to be 14-21 days
631 on the basis of consistent results from observational data, our cross correlation results,
632 and scaling theory: 5-7 d for the plume to travel from the CR mouth to JDF under
633 moderate wind stress (~ 250 km, traveling $\sim 35 - 55$ km d $^{-1}$) [38]; 3-6 d to reach
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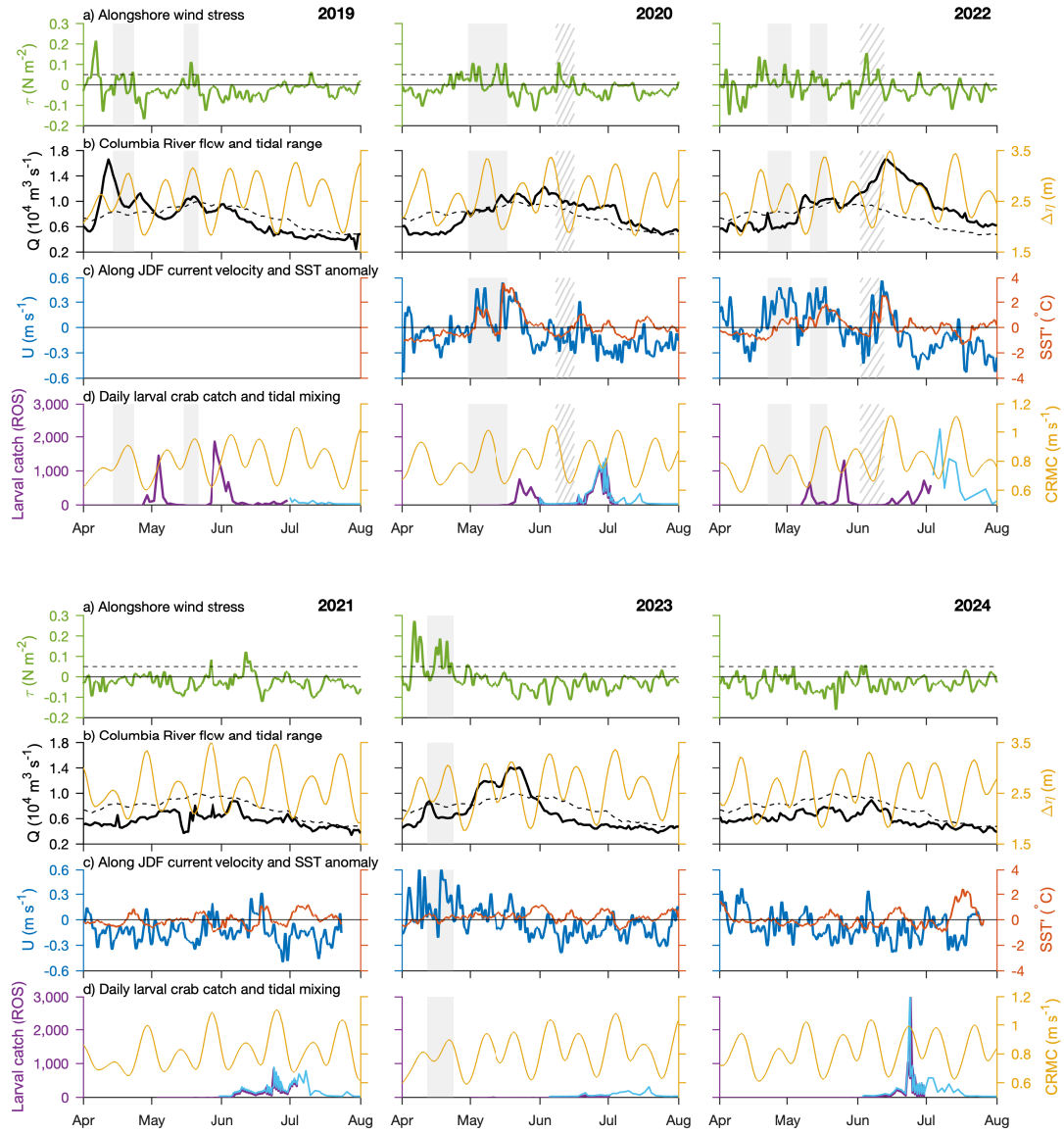


Fig. 5 Physical forcing imparted by the tidally-modulated Columbia River (CR) outflow and wind stress along the Washington coast along with the physical and biological response in the Salish Sea, for years with (2019, 2020, 2022) and without (2021, 2023, 2024) a biological response. The physical response is surface inflow in Juan de Fuca Strait (JDF), and the biological response is a coastal larval recruitment event. Grey shading indicates physical forcing “events”: periods of downwelling-favorable winds persisting for more than five days that coincided with above average CR discharge in April and May. Grey hatching indicates forcing events that occurred in June. a) Alongshore wind stress on the Washington coast (positive poleward, downwelling-favorable indicated by a dashed black line at 0.05 N m^{-2}). b) Daily mean CR flow rate and tidal range near the river mouth (25-yr daily mean flow rate shown as a dashed line). c) Along-strait current velocity and SST anomaly (positive eastward, into the strait). d) Daily catch of *M. magister* megalopae at Rosario Head (ROS) with the $> 6 \text{ mm}$ coastal cohort in purple and $< 6 \text{ mm}$ Puget Sound cohort in blue, and CRMC (a tidal mixing parameter) in JDF.

Angeles Point in JDF ($\sim 100\text{km}$, traveling $\sim 15 - 25 \text{ km d}^{-1}$); and 6-8 d for larvae
 carried by the inflow to reach ROS and COR ($\sim 60 \text{ km}$ at $\sim 7 - 10 \text{ km d}^{-1}$, based
 on the mean speed of landward flow). Out of the six forcing events we identified
 (Figure 5), five were followed by simultaneous recruitment events at ROS, COR, and
 PTW ($P = 0.83$) in 2019, 2020, and 2022. Using the date of peak catch at ROS
 because it has the most complete time series, we find that every early peak ($n = 6$)
 can be predicted by at least one and up to five possible forcing dates 14-20 days prior,
 including the peak in 2023 that is an order of magnitude smaller and lacks the distinct
 early recruitment event shape. Possible forcing dates occurred between 5 and 14 days
 before the end of a wind event; daily river flow ranged from $8,165 \text{ m}^3 \text{ s}^{-1}$ (April 2022)
 to $14,190 \text{ m}^3 \text{ s}^{-1}$ (April 2019).

3 A model for plume-mediated larval transport.

3.0.1 Conceptual overview and box model design

The strong conditional relationship between event-scale forcing and response supports
 a hypothesis for the major controls over conditions leading to the entrainment of *M.*
magister megalopae into tidally pulsed CR plumes and their subsequent northward
 transport into the Salish Sea (Figure 6). Rapid increases in CR outflow associated
 with snow melt and precipitation events, along with strong tidal currents, generate
 turbulent river plumes of relatively fresh water that enter the ocean with near-surface
 velocities of order $2 - 3 \text{ m s}^{-1}$ [44]. Broadly consistent with our observations, cal-
 culations show that when outflows exceed instantaneous river discharges of around
 $6,000 \text{ m}^3 \text{ s}^{-1}$ (much lower than typical flow rates during spring freshets), they carry
 sufficient mechanical energy to generate waves and jets that penetrate, deform, and
 overturn stabilizing density interfaces bounding river plume fronts and bases. Con-
 sequently, the progressive entrainment of seawater and near-surface megalopae into
 marginal mixing layers (Figure 6, panel 1) causes the density difference defining the

river plume to decline, while the concentration of megalopae increases to produce the signals intermittently evident in Figure 5.

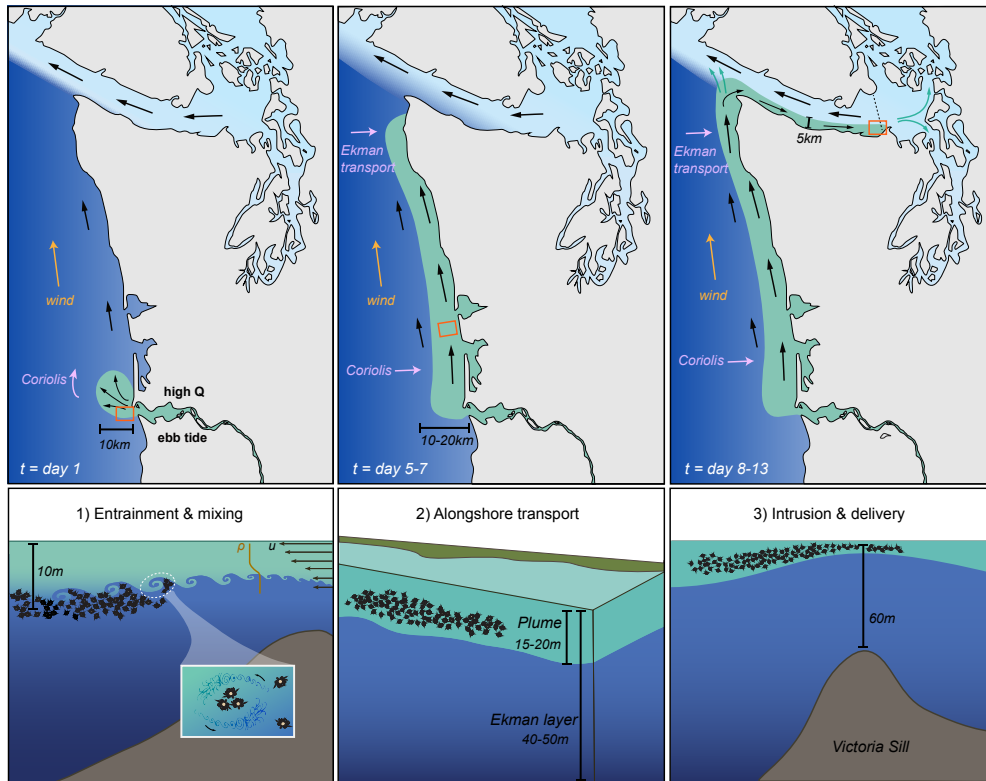


Fig. 6 Conceptual model depicting the physical processes involved in entrainment and transport of *M. magister* megalopae by the tidally-influenced Columbia River (CR) plume in spring during a period of southerly winds and high river flow. The top panels depict the evolution of the plume, spreading initially as a gravity current, then carried north by wind and buoyancy stresses as a coastal current in approximate geostrophic balance, and finally entering Juan de Fuca Strait (JDF). The bottom panels depict a cross section of the plume at each stage (indicated with a red box on the top panels). 1) In addition to stirring, entrainment and “frontal mixing” by overturning motions forming the head of a spreading CR plume (not shown), intense shear and turbulent “basal mixing” entrains coastal water and crab larvae concentrated in the upper 5-10 m of the water column. 2) During downwelling events, buoyancy and wind stresses drive the plume ~ 250 km north along the Washington coastline, with little entrainment of shelf water into the plume. 3) Buoyancy forces and onshore Ekman transport drive the plume into JDF, where it travels ~ 100 km along the southern margin of the strait before reaching Victoria Sill. At the east end of JDF, the inflow passes over shallow, complex bathymetry that disperses the inflow and entrained larvae.

Mechanical entrainment and mixing across marginal density interfaces is complex [45–47]. At a basic level, the process is driven through the combined actions

of two mechanisms with relative contributions that evolve as newly-formed tidal plumes spread offshore. Ageostrophic “frontal mixing” arises from the collapse of oversteepened river plume fronts, generating powerful downward flows that drive large entraining eddies with turnover speeds proportional to the front height $h(t)^{1/2}$ (see Supplementary Table 2). Larvae entrained from underlying seawater by mechanical stirring accumulate within and behind the heads of propagating river plumes, consistent with the results of more detailed modeling studies that also consider important effects related to larval locomotion [27] (see Section 5.6). By contrast, the rate of “basal mixing” is modulated by the intensity of flow- and wind-driven turbulent shear concentrated at the gravity current base and is proportional to a shear velocity u_*^3 , where $u_* = \sqrt{C_d} |V_{CR} + V_{wind}|$ and C_d is a typical basal drag coefficient that is of order 10^{-3} (section 5.6, Supplementary Tables 2 and 3). Depending on the relative strength of southerly winds and the Coriolis force that turns the current northward as it approaches the Rossby radius $L_{R,CR} \sim 15$ km (see Supplementary Table 2) [48], an initially dominant frontal entrainment mechanism is overwhelmed by contributions from basal mixing as the vertical frontal area $\propto r(t)h_{CR}$ becomes much smaller than the basal area $\propto r(t)^2$ for a semi-circular plume spreading outward from the CR mouth.

Under downwelling conditions, the northward advection of the gravity current is driven by a combination of buoyancy forces and southerly wind stresses. Critically, the current is confined to the coast as a channelized flow by motions related to onshore Ekman transport that also inhibit seawater entrainment, preserving the structure of the larval “pickup” signal during transport toward JDF (Figure 6, panel 2). Retention of this signal past Victoria Sill ~ 100 km inland from the mouth of JDF depends, however, on the extent to which the advected plume and entrained larvae are transported beyond the inlet by strong winds or diluted through entrainment into surface outflows leaving the strait (Figure 6, panel 3).

We construct a simple 3-box model to test our hypothesis that the coastal larval recruitment signal in the Salish Sea reflects the predominantly tide- and wind-modulated pickup of *M. magister* megalopae during periods of elevated spring river flow (see Section 5.6). The first goal is to identify the processes underlying the consistent form of the recruitment signal in terms of the mechanics of entrainment into spreading CR tidal plumes. A second goal is to examine how the signal is modified by varying conditions of river discharge, tidal forcing, and wind stress over the 2019-2024 period. The box model consists of a semi-circular fixed volume box 0 which represents the near-surface larval source reservoir, consistent with a source region extending seaward from the CR mouth; box 1, the radially spreading CR plume; and box 2, which represents the JDF inflow. When the instantaneous discharge is sufficiently strong to drive frontal and/or basal mixing during plume spreading, the surface area-weighted contributions from these two mixing mechanisms draw larvae from a source box 0 with initial concentration C_0 into the overlying CR plume box 1 (see Supplementary Table 2). An evolution equation for the "pickup" of larvae from box 0 is:

$$\frac{dC_0}{dt} = -\frac{Q_{01}}{V_0}C_0. \quad (2)$$

Here, the source volume V_0 is fixed with an initial concentration $C_0 = 1$. The instantaneous exchange flux is

$$Q_{01} = \Gamma_b V_{\text{mix}} A_{\text{ent}}, \quad (3)$$

where $A_{\text{ent}} = \frac{1}{2}\pi R_{\text{mix}}^2$ is the semi-circular plume footprint and $\Gamma_b = d_{\text{mix}}/h_t$ (bounded between 0 and 1) tracks the fraction of the plume thickness penetrated by the growing mixed layer. Thus V_{mix} describes the instantaneous vigor of frontal and basal mixing,

875 whereas Γ_b describes how completely that mixing has penetrated the larval source
 876 layer (Figure 6, panel 1).
 877

878 The resulting increase in larval concentration in box 1 $C_1(t)$ depends on the influx
 879 from box 0, the rate at which larvae leave the spreading plume through northward
 880 export, and the concentration of larvae available for entrainment. A pickup event
 881 evolves over a maximum time that is typically tens of hours, ultimately limited by
 882 depletion of the source concentration $C_0(t)$. The characteristic box-1 filling time scale
 883
 884

$$887 \tau_{01} = \frac{V_{\text{eff}}}{Q_{01}}, \quad (4)$$

891 where the instantaneous volume of box 1 $V_{\text{eff}}(t)$ depends on the evolving mixing layer
 892 thickness and the time-dependent exchange flux $Q_{01}(t)$ is governed by time-varying
 893 CR outflow. This calculation incorporates the evolving river discharge, tidal modula-
 894 tion of the outflow, plume spreading, and the resulting frontal and basal mixing. We
 895 parameterize the competing export of larvae from box 1 using the dimensionless ratio
 896
 897
 898
 899

$$901 \Pi_{CR} = \frac{\tau_{01}}{\tau_{1,\text{out}}}, \quad (5)$$

904 so that the spreading-plume concentration evolves as
 905
 906

$$907 \frac{dC_1}{dt} = \frac{1}{\tau_{01}(t)} (C_0 - \Pi_{CR} C_1). \quad (6)$$

911 Thus the event-scale and tidal variability in larval input to box 1 is contained in
 912 $Q_{01}(t)$ and hence in $\tau_{01}(t)$, whereas Π_{CR} controls the strength of export relative to
 913 this time-dependent replenishment. The associated export time scale is $\tau_{1,\text{out}}(t) =$
 914 $\tau_{01}(t)/\Pi_{CR}$. Small Π_{CR} , thus, corresponds to rapid replenishment relative to export,
 915 whereas large Π_{CR} corresponds to rapid export relative to replenishment. The export
 916
 917
 918
 919
 920

itself represents the combined effects of wind stress, gravity-current spreading, and the active cross-sectional area through which entrained larvae are carried northward, and can be modified by onshore Ekman transport and internal circulation arising from Coriolis effects [48].

The eastward transport of entrained crab larvae into and along JDF in a narrow coastal counter-current (Figure 6, panel 3) is driven by the buoyancy of the intruding gravity current, the speed of onshore Ekman transport, and the amplitude of local tidal forcing, modulated by wind-related losses to the north. Combining these effects into a characteristic time scale for the inflow of larvae towards Victoria Sill τ_{12} , and introducing the time scale $\tau_{2,out}$ for the buoyancy- and tide-controlled propagation of the gravity current past the sill into eastern JDF, an evolution equation for the time-dependent larval concentration (C_2) expected to arrive in box 2 is:

$$\frac{dC_2}{dt} = \frac{1}{\tau_{12}} (C_1 - \Pi_{JDF} C_2). \quad (7)$$

Here, the control over the retention of the pickup signal upon arrival is the ratio of time scales $\Pi_{JDF} = \tau_{12}/\tau_{2,out}$, which is less than 1 except where strong southerly winds at the mouth of JDF cause the time scale τ_{12} to increase.

3.0.2 A larval entrainment signal modulated by river discharge, tides, and wind.

Using discharge data from Quincy, OR and parameters summarized in Supplementary Tables 2 and 3, we solve equations 2, 23 and 31 numerically using an explicit Euler scheme (see Section 5.6). We assume that during periods of high discharge, the CR outflow enters the ocean initially as a buoyant jet focused through the dredged navigation channel at the river mouth maintained at a width of 185 m and depth of 13 m, and then quickly evolves to spread as a gravity current. Following Horner-Devine

et al. [49] we assume that after lift-off from the bottom, the river plume thickness at its effective source is approximately half the channel depth (6.5 m).

With this plume thickness fixed and considering a reasonable lateral extent of entraining turbulent motions at the jet margins near the source to be comparable to the channel half-width, we take a dynamically active source outflow width to be 300 m for most calculations. This effective width yields mean velocities of a few meters per second, consistent with constraints from drifter observations [44], and we explore the sensitivity of the results to this choice below. Although initial plume salinity depends on the extent of mixing within the estuary [34] we note that when powerful outflows are driven by both inertial and buoyancy forces, most seawater–plume mixing occurs through frontal and basal mixing during plume spreading.

We identify three forcing scenarios that produce distinct larval pickup patterns, depending on whether entrainment is controlled predominantly by the time-varying (non-stationary) magnitude of the mean river discharge, by the superposed tidal outflows which can be strongly asymmetric, or by approximately equal contributions from both controls over the river outflow. Representative examples of these distinct forcing styles are captured in the 2019 and 2022 forcing events, which span regimes involving: (1) an increasing discharge over tens of hours and large tidal amplitudes (May 2019); (2) a decreasing discharge over hours and comparatively moderate tidal amplitudes (April 2019 and May 2022); and (3) a relatively steady discharge with large tidal amplitude (April 2022) (Figure 7).

In the absence of significant wind-driven losses at either the CR mouth or JDF, when frontal and basal mixing are controlled mainly by accelerating river discharge, the resulting larval pickup and delivery signals are approximately symmetric (Figure 8). By contrast, tidal outflow-dominated mixing produces signals with a steady rise followed by a relatively slow decay, with a longevity related to sustained larval entrainment during several subsequent ebb tides (Figure 8). A strong tide combined with a

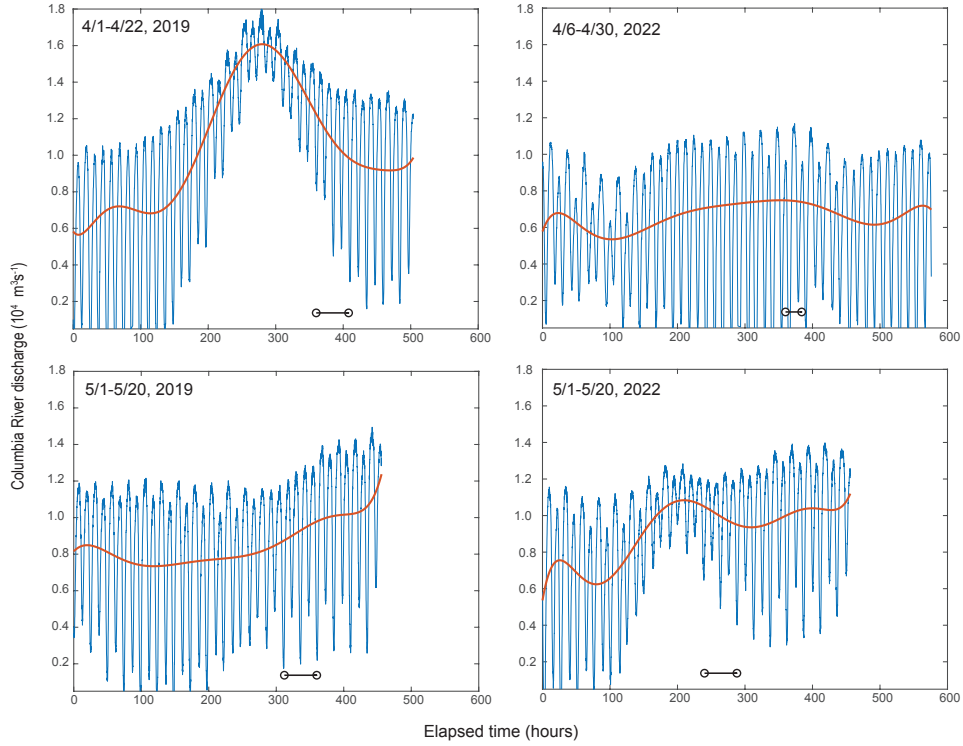


Fig. 7 Representative hydrographs of Columbia River (CR) discharge near Quincy, OR (87 km upstream of the river mouth) during four spring periods in 2019 and 2022. Blue lines show the tidally-modulated near-instantaneous discharge record, while the low-pass filtered discharge (red line) highlights changes in the underlying river flow. These periods were selected because they encompass identified forcing events (periods of persistent poleward winds with high CR discharge) that span varying regimes of steady or changing discharge with moderate or large tidal amplitude. Possible forcing dates, identified as days when forcing conditions were met 14-21 d prior to the peak in subsequent larval catch at Rosario Head (ROS), represent candidate dates for the initial entrainment of larvae into CR tidal plumes (indicated with a black line segment above the x-axis).

high but time-varying mean discharge produces an intermediate signal reflecting the influence of both forcing mechanisms (Figure 9).

There are two consistent features across all scenarios: the fractional peak in larval concentration in the pickup signal is 0.3-0.4, and pickup is governed primarily by the basal mixing mechanism. Frontal mixing alone drives an intense, short-lived period of entrainment over a few hours at most, leading to a sharp peak in larval concentration. Basal mixing, by contrast, results in relatively slower pickup that is intensified over

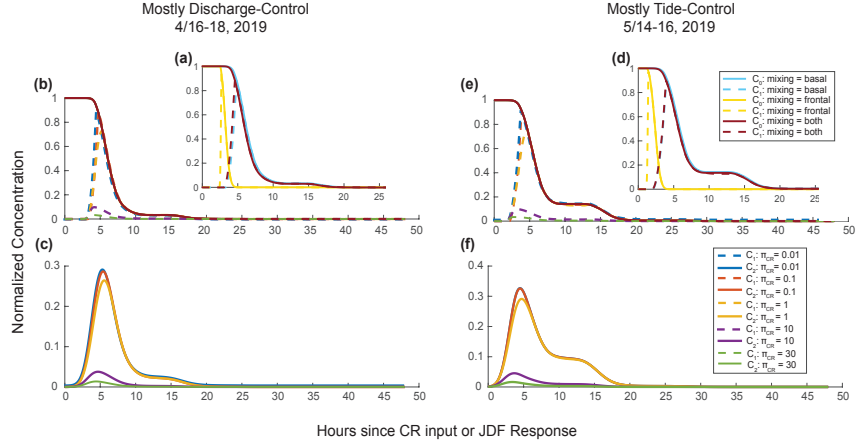


Fig. 8 Model predictions for larval entrainment into Columbia River (CR) tidal plumes during identified forcing dates in April and May 2019 and advection past Victoria Sill in Juan de Fuca Strait (JDF). a, d) Evolutions of larval concentration C_0 in the fixed volume source box 0 with progressive (mostly discharge-controlled) and/or punctuated (mostly tidally-controlled) losses to the spreading overlying plume box 1 via entrainment by frontal mixing, basal mixing, or combined mixing mechanisms. In general, larval pickup increases with high discharges and during tidal ebbs, and it declines or stalls during tidal floods. b, e) Dependence of larval concentration evolutions C_1 in box 1 to larval loss north ratios Π_{CR} assuming entrainment by both frontal and basal mixing (see text). c, f) Sensitivity of larval concentration in box 2 to wind effects at the mouth of JDF that flatten the delivered CR pickup signal as Π_{JDF} increases from 0. C_2 evolutions are smoothed with a 15-min moving Gaussian.

sequential ebb tides, resulting in a pickup period that can extend over tens of hours (Figure 8). The majority of larval entrainment occurs on the greater ebb when there is a strong diurnal inequality in tidal amplitude (Figure 9). Model results suggest that maximal larval pickup occurs when mixing is tidally-controlled with a steady river discharge of at least $8,000 \text{ m}^3 \text{ s}^{-1}$.

Strong export of entrained larvae from the spreading CR plume relative to their replenishment by mixing ($\Pi_{CR} \gg 1$), which can arise under strong wind-driven northward transport, or winds that advect some or all of the plume-carried larvae north past JDF ($\Pi_{JDF} \rightarrow 1$ or $\Pi_{JDF} > 1$), can flatten pickup and delivery signals or destroy them entirely. For example, if $\Pi_{CR} = 10$ during the May 2019 pickup event, larval losses related to the northward export of entrained larvae exceed inflows from mixing

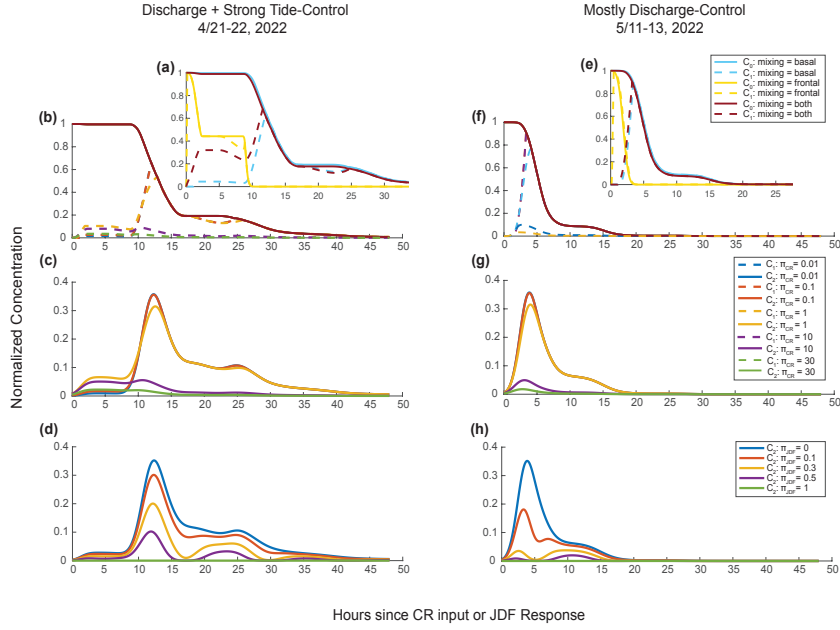


Fig. 9 Model predictions for larval entrainment into Columbia River (CR) tidal plumes during identified forcing dates in April and May 2022 and advection past Victoria Sill in Juan de Fuca Strait (JDF). a, e) Evolutions of larval concentration C_0 in the fixed volume source box 0 with progressive (mostly discharge-controlled) and/or punctuated (mostly tidally-controlled) losses to the spreading overlying plume box 1 via entrainment by frontal mixing, basal mixing, or combined mixing mechanisms. b, f) Sensitivity of larval concentration evolutions C_1 in box 1 to larval loss north ratios Π_{CR} assuming entrainment by both frontal and basal mixing. As with the 2019 results in Figure 8, larval entrainment is intensified with strong discharges and during tidal ebbs, and it weakens or stalls during tidal floods. c, g) Dependence of larval concentration in box 2 on wind effects at the mouth of JDF that flatten the delivered CR pickup signal as Π_{JDF} increases from 0 (compare with Figure 8). d, h) Sensitivity of larval concentration in box 2 to wind effects at the mouth of JDF that flatten the delivered CR pickup signal as Π_{JDF} increases from 0. C_2 evolutions are smoothed with a 15-min moving Gaussian.

processes, leading to a sevenfold decrease in the peak amplitude of the signal delivered to JDF.

The effects of wind at the entrance to JDF can be relatively subtle by comparison. In April 2022, with a ratio of northward to eastward current speed of 0.5, the increase in Π_{JDF} is sufficient to reduce the larval concentration peak by 1/3, without affecting the rate of signal decay and the overall event structure (Figure 9). The structure of the May 2022 signal is more sensitive to this advective loss of larvae: under the same conditions, the signal is lost entirely.

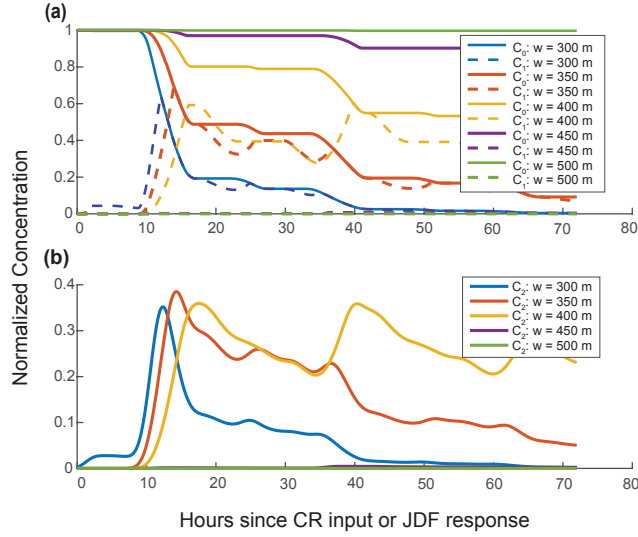


Fig. 10 Sensitivity of predicted evolutions of larval concentrations in boxes 0, 1 and 2 over April 21-22, 2022 (Figure 9) to variations in the dynamic plume source width.

For the specified plume thickness of 6.5 m, the characteristic dynamic plume source width strongly controls the shape and duration of the predicted larval pickup signal by setting the maximum outflow speed, a parameter to which frontal and basal mixing are highly sensitive (Figure 10). For example, the characteristic event shape (linear rise and exponential decay) we identify in our data analysis is preserved with increasing longevity if the width is increased by around 15% from 300 m (about 50 hours) to 350 m (>70 hours). However, the slower average outflow with a 33% increase to 400 m causes pickup to become entirely controlled by strong flows related to periodic tidal ebbs, and the exponential decay phase of the signal evident in the event data is lost. Virtually no pickup occurs at widths greater than about 450 m.

4 Discussion

Our results provide compelling evidence for a plume-mediated accumulation and transport mechanism driving the recruitment of Pacific coast *M. magister* megalopae in the Salish Sea. We find that seasonal atmospheric and hydrologic conditions provide

useful indicators for the overall likelihood of coastal larval recruitment in a given year, whereas event scale analyses can predict the occurrence and timing of individual recruitment events with reasonable confidence. Cumulative alongshore wind stress and average spring CR discharge most clearly distinguish years with and without coastal recruitment. Although coastal recruitment is more likely to occur in years with a late spring transition, the transition date alone is not a reliable indicator, since intermittent reversals to downwelling-favorable winds are relatively common in spring. Together, our conceptual and physical models provide a mechanistic framework that explains why these seasonal and event-scale relationships emerge over the 2019-2024 period.

Settlement of coastal-origin *M. magister* in North Puget Sound was first described in studies conducted between 1982–1988. Orensanz and Gallucci [23] report a large juvenile cohort that settled in May in 1982 and 1984, while Dinnel et al. [24] document comparable findings in 1984 and 1988. Patterns of interannual variability associated with coastal recruitment in the present study are also evident in these historical years. Oceanic transport indices calculated for a similar period (1983–1988) demonstrate that winter (January–March) northward transport over the shelf was relatively weak in 1984 and 1988, while spring (April–May) alongshore transport was northward only in those two years [14]. Late spring transitions occurred in 1984 (May 25) and 1988 (June 3), with a more typical transition date in 1982 (April 16). Spring discharge from the CR was generally higher than in the contemporary period, with exceptionally high flows in 1982 and 1984 (see Supplementary Fig. 4).

Consistent with our results, winter (January–March) ENSO conditions ranged from neutral in 1982 and 1984 to a weak El Niño in 1988, during a positive phase of the PDO. Notably, 2022 is the only year with substantial coastal recruitment during a strongly negative PDO. It is likely that relationships among the PDO, ENSO, and larval recruitment are complicated by pan-basin warming, which now overwhelms climate-oscillation driven changes in SST [50], as well as the increasing frequency and

intensity of large marine heatwaves in the Northeast Pacific (which occurred every year between 2019 and 2024) [51]. Over the last century, the timing of peak CR discharge has shifted from late June to late May, accompanied by substantial declines in average and freshet peak flows largely as a result of human management [52]. In future decades, climate change-associated warming may also result in earlier peak river flows dominated by rainfall rather than snow melt [53, 54]. The projected increase in the intensity and frequency of atmospheric rivers [55, 56] could cause precipitation-driven spring flows (as occurred in April 2019) to become more common, with associated southerly storms providing atmospheric forcing favorable for plume intrusions into JDF.

When interpreted alongside seasonal indicators of relative larval abundance, the results of our event-scale analysis demonstrate that the biological response is strongly constrained by physical forcing. Stormy winter and spring conditions (Figure 4b) likely reduced coastal larval supply through advective loss in 2023, potentially explaining the discrepancy between our conditional model prediction and observed recruitment in that year. The flattened shape of the larval recruitment signal (Figure 3) is consistent with model predictions from dilution by strong winds at the mouth of the CR or JDF, when $\Pi_{CR} \gg 1$ or $\Pi_{JDF} \geq 0.5$ (Figure 9). Major coastal recruitment events in 2019, 2020, and 2022 are associated with periods of poleward alongshore winds lasting more than 7 days, maximum daily wind stress of $\approx 0.1 \text{ Nm}^{-2}$, and daily river discharge that exceeds $8,000 \text{ m}^3 \text{ s}^{-1}$. These thresholds are broadly consistent with previous observations of conditions that lead to estuarine flow reversals [30] and springtime intrusions of the CR plume into JDF [39]. Similarly, the frequency of May-June plume intrusions identified in this study is comparable to that reported by Hickey et al. [39] for the mid-2000s.

Understanding plume intrusions that occur in June is complicated by summer ocean conditions, when stronger stratification and intermittent upwelling generate

highly variable nearshore circulation, and by the overlapping arrival of coastal and Puget Sound larval cohorts which prevents clear identification of a coastal recruitment signal. Prolonged downwelling-favorable wind events in June coincided with the decrease from peak CR flow in 2020 and the rapid increase to peak flow in 2022 (Figure 5). We expect that if coastal larvae were advected into JDF by plume intrusions in June in these years, the magnitude would have been reduced by enhanced dilution of plume waters under southward ambient coastal currents and by the effects of entrainment and mixing related to a stronger exchange flow in JDF.

For forcing events that occurred in April and May, the agreement between predicted and observed recruitment event structure is strongest at ROS. Events are characterized by a more symmetric shape in late April 2019 and late May 2022 (discharge-controlled entrainment), a linear rise and slow decay in late May 2019 and early May 2022 (tidally-modulated entrainment) (Figure 5), and by an average peak-to-total catch ratio of 0.26. Modeling results (Figure 9) suggest that the smaller magnitude of recruitment peaks in 2022 compared to 2019 (Figure 5) is potentially a consequence of greater dilution ($\Pi_{JDF} > 0$) by winds at the mouth of JDF (early May 2022) or entrainment into JDF outflows during a period of enhanced tidal mixing (late May 2022). The characteristic signal of steep rise and slow decay is also evident in observations of *M. magister* larval recruitment to light traps in Willapa Bay on the outer Washington coast following an intrusion of the CR plume in early June 1999 [35]. The duration of that recruitment event was around 4 days, similar to observations in the present study, where the majority of larval arrival during coastal recruitment events typically occurs over 4-7 days.

The model closely reproduces the shape of these events when parameterized with a fixed plume source thickness of 6.5 m and width in the range 300-350 m. An increase in plume width to around 375 m can easily reconcile a 4 day event longevity and preserve the linear rise-exponential decay structure. However, a duration of 7 days likely reflects

contributions from other processes. One indication is the occurrence of multiple peaks in larval catch during the May 2020 event at ROS and during several early events at PTW. Given the relatively short duration of downwelling periods compared to the timescale required to replenish the larval source near the river mouth, it is unlikely that multiple peaks represent a superposition of distinct CR pickup events. Instead, they may be related to recirculation in the eastern strait where inflowing and outflowing surface waters, steered by shallow and complex bathymetry, interact to produce an additional short-period variability in the recruitment signal (see Supplementary Fig. 5). Such recirculation would also increase event longevity, potentially contributing to the longer duration of observed recruitment events compared to model predictions.

Additionally, variation in settlement timing could result in a prolonged recruitment signal [35]. *M. magister* megalopae are strong swimmers, with a mean in-situ swimming speed of 11.1 cm s^{-1} [57] and laboratory-reported swimming speed up to 44.8 cm s^{-1} [58], allowing them to actively select shallow settlement habitat in estuaries when they are physiologically competent to settle [36]. Larval swimming behavior may also be important for accumulation and transport [27, 40, 59], yet our results suggest that the recruitment signal is dominated by physical rather than biological processes. The physical framework we develop to interpret the coastal *M. magister* recruitment signal may therefore have potential application for dispersion modeling. Hydrodynamic model simulations support JDF flow reversals as a plausible larval transport pathway into the Salish Sea [60, 61]. However, they typically track the fate of individual particles, and therefore do not represent the processes that aggregate larvae into the high concentrations associated with the recruitment events we observe in this study.

In recent years, the shift toward fisheries management approaches that account for changing environmental conditions has increased the need for mechanistic models to forecast changes to fishery resources and support more adaptive management

strategies [62]. In Washington state, fisheries are co-managed by the state and federally recognized Treaty Tribes, who reserved the right to harvest half of the fish and shellfish in their traditional fishing grounds in the Stevens Treaties [63, 64]. The Puget Sound Dungeness crab fishery is divided into numerous discrete management areas. Fishing access is determined by Tribes' usual and accustomed fishing areas and co-management agreements. In addition to the size, sex, and season-based regulations used in the coastal fishery, the Puget Sound fishery is managed using area-specific catch quotas [12].

Effective management therefore critically depends on understanding the drivers of population dynamics in different regions of Puget Sound. Most of the commercial *M. magister* harvest occurs in North Puget Sound [12], where influence from the coastal ocean appears to be significant. Evidence from the Oregon coast shows that *M. magister* larval recruitment is strongly linked to environmental conditions and can predict regional commercial catch four years later, when the new recruits reach a harvestable size [2, 15]. Whether the same relationship between larval recruitment and fisheries production holds true in the Salish Sea remains unknown. Nevertheless, our results show that larvae arriving from the coast make a predictable contribution to local populations and may be far more important than previously recognized.

4.1 Conclusions

The importance of river plumes to larval transport has often been inferred from their influence on coastal circulation and stratification, but rarely demonstrated. We present evidence that Columbia River plumes are an important transport pathway connecting coastal and inland Salish Sea Dungeness crab (*Metacarcinus magister*) populations. In contrast to existing models for behaviorally-mediated accumulation [27, 59] and cross-frontal transport [65, 66], we propose a model for the intermittent physical entrainment of larvae into energetic buoyant plumes through frontal and basal mixing processes

1427 that are intensified during periods of high river runoff and strong tidal outflows. We
1428 develop and test the hypothesis that the resulting distinctive temporal signal of this
1429 larval pickup mechanism can be carried northward into the Salish Sea by coastally-
1430 trapped plumes during periods of downwelling-favorable winds. Our results show that
1431 model predictions of the larval pickup signal are particularly sensitive to the strength
1432 of southerly winds and the geometry of the river mouth.

1433 Consequently, our work has important applications to both monitoring and mod-
1434 eling effects of Columbia River plume intrusions on larval transport into all estuaries
1435 north of the river mouth. We suggest that the physical forcing relevant for lar-
1436 val transport identified in this study (downwelling winds, a significant river plume)
1437 could be important to other upwelling systems around the world. Broader implica-
1438 tions for coastal regions include a framework for predicting the influence of wind- and
1439 tide-influenced river plumes on coastal connectivity and the transport of biological
1440 organisms, pollutants, and nutrients alongshore and into neighboring estuaries.

1441

1442 **5 Methods**

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1444 **5.1 Biological data**

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1446 Biological sampling was conducted at five sites within Washington state waters of the
1447 Salish Sea, with spatial coverage across three of five major basins of Puget Sound and
1448 the eastern JDF. Site locations were chosen for accessibility to a pier or dock and
1449 proximity to juvenile crab settlement habitat. Larval crab abundance and carapace
1450 measurements were collected by the Pacific Northwest Crab Research Group (PCRG),
1451 a collaborative research consortium that established a larval crab monitoring network
1452 in 2019 which allowed for simultaneous observation of larval dynamics at monitor-
1453 ing sites across the southern Salish Sea [67]. Network participants used light traps

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deployed from a dock or pier at each site to capture *M. magister* megalopae during their nearshore settlement period (April to September) following a standardized sampling protocol developed by the Swinomish Indian Tribal Community [68].

Light traps are passive sampling devices used to capture positively phototactic organisms; originally designed to capture aquatic insects, they have been modified for the study of larval fishes and invertebrate zooplankton that are attracted to light at night. The traps can be used in the nearshore coastal zone, capture organisms that are difficult to sample with nets [69], and have been found to be very effective for sampling *M. magister* megalopae [2]. Samples were collected daily at PTW from 2020–2024, and every 1–3 days at all other sites from 2019–2024. Due to the irregular sampling interval, linear interpolation was used to estimate larval abundance for missing dates and produce continuous daily time series. Carapace dimensions including width (widest point of the carapace) and length (rostral spine to base of carapace) of a subset of ~ 30 individual megalopae per trap were measured each week using a metric dial caliper with a precision of 0.1 mm.

5.2 Mixture models to distinguish larval cohorts

Gaussian mixture models (GMMs) were fit to larval size measurements to identify and characterize distinct larval cohorts by modeling underlying distributions within the data (see Supplementary Fig. 7). Carapace width (CW) and carapace length (CL) were strongly correlated ($r = 0.8$), and the distribution of the CL-to-CW ratio showed a single dominant mode, reflecting a conserved size ratio among larvae. Greater variance in CL measurements (0.56) than CW (0.17) indicated that CL was more effective in distinguishing larval phenotypes. For each unique site–month–year combination, a separate model was fit to CL measurements with the number of components (G) ranging from 1 to 3. Model selection was based on the Bayesian Information Criterion (BIC). If the best-fitting model had multiple components but one component contained

fewer than 20 individuals, or if ΔBIC indicated weak evidence ($\Delta\text{BIC} < 6$) for multiple components, the simpler model was selected. To estimate uncertainty in cluster means, bootstrap resampling ($n = 1000$) was performed for each selected model, and 95% confidence intervals were calculated from the resulting distribution of bootstrap means.

Two distinct size cohorts characterized by bootstrap mean CL ≥ 6 mm and < 6 mm were observed across years and sites where two model components were identified. To estimate the weekly catch of each size cohort, individuals were grouped by measurement week, and Monte Carlo simulations ($n = 1000$) were performed using the posterior cluster membership probabilities from the GMMs to generate weekly proportions of larvae in each cohort and associated 95% confidence intervals. Daily catch of each cohort was estimated using the weekly mean proportions applied to the daily light trap time series with the assumption that proportions remained constant throughout the week, incorporating uncertainty in cluster assignment into cohort recruitment estimates.

5.3 Event-shape analysis

Peaks in recruitment time series can indicate the shoreward transport of accumulated larvae resulting in sudden increases in larval abundance [40]. To characterize and compare early (prior to June 1) and late (after June 1) larval recruitment events, we analyzed event shape by estimating the geometric properties of the time series. Daily larval catch data were smoothed using a centered 3 day Gaussian filter to suppress high frequency variability while preserving event structure and timing. Peaks in larval catch were defined as local maxima in the smoothed time series and identified using minimum prominence of $0.75 \times \text{SD}$ of the catch time series, with a minimum separation of three days between peaks. For each event, the slope was calculated as the rate of increase from a baseline defined as the local minimum occurring within the 5 day period preceding the peak catch. Slopes were normalized by the peak catch and expressed

as a rate of increase per day. The decay from the peak of each recruitment event was quantified using the e-folding time, defined as the time required for catch to decline to $1/e$ ($\approx 37\%$) of the peak value.

5.4 Physical data

Hourly wind speed and direction from coastal meteorological buoys were obtained from the National Oceanic and Atmospheric Administration’s (NOAA) National Data Buoy Center (NDBC) for the Cape Elizabeth buoy (Station 46041) and the Columbia River Bar buoy (Station 46029) for the period 2019–2024. In 2022, almost no data were collected at Station 46041. To provide wind information on the Washington coast for April through July 2022, we performed a regression between data from 46041 and 46029 ($r^2 = 0.88$) using coefficients determined from linear regression over the same period in 2019, 2020, 2021 and 2023. Hourly wind data were used to calculate alongshore wind stress using the drag coefficient of Large and Pond (1981) and low-pass filtered using a 24-hr running mean. Alongshore winds at Cape Elizabeth are positive toward 320°T and well correlated with other buoys off the coast of Washington.

Upwelling-favorable periods are indicated by equatorward (northerly) winds, and downwelling-favorable periods by poleward (southerly) winds. Downwelling-favorable wind events were identified as sustained periods of poleward wind stress with a duration of at least 5 days where the daily average wind stress exceeded 0.05 N m^{-2} at least once. The start of each downwelling event was defined as the first day that wind stress became positive; the event ended on the first day winds became upwelling favorable (defined as $\leq -0.05 \text{ N m}^{-2}$) or if there were five consecutive days of very weak winds ($< 0.01 \text{ N m}^{-2}$).

Surface current speed, direction, and sea surface temperature (SST) data were obtained from the NDBC Waverider buoy at Angeles Point (Station 46267) moored $\sim 4 \text{ km}$ offshore in 75 m of water and located $\sim 80 \text{ km}$ from the mouth of JDF.

1611 Current speed and direction are recorded at 1 m depth and SST at 0.46 m depth
 1612 at 30-min intervals. Data collection at this buoy began in April 2020, and data were
 1613 retrieved for the period 2020–2024. Current speed and direction were converted to
 1614 eastward and northward components and rotated into an along-strait coordinate sys-
 1615 tem at that location (78°T). Along-strait current and sea surface temperature were
 1616 low-pass filtered with a cosine–Lanczos filter (33 h, zero-phase) to isolate the subtidal
 1617 components of the time series. SST anomalies were defined as residuals from a linear
 1618 fit to the filtered March–August SST record for each year. Surface inflow events in
 1619 JDF were defined as periods with an average velocity of at least 20 cm s^{−1} into the
 1620 strait for a duration of more than 48 hours. Inflow periods separated by less than 72
 1621 hours were considered a single event.

1629 Hourly tidal current predictions for the Juan de Fuca East station were retrieved
 1630 from the Canadian Hydrographic Service (CHS). The cube-root-mean-cubed current
 1631 speed or CRMC = $(u^3)^{1/3}$ was calculated as a proxy for tidally induced mixing in
 1632 the eastern strait. Hourly tide height predictions for Astoria, OR were retrieved from
 1633 NOAA and used to calculate daily tidal range. Both tidal indices were smoothed using
 1634 a 75-hr running mean to highlight spring-neap tidal variation.

1639 Columbia River discharge data were obtained from the U.S. Geological Survey
 1640 (USGS) station at Port Westward near Quincy, OR for the period 2000–2024. Flow
 1641 recorded at this site accounts for 97% of the average annual river flow at the CR
 1642 mouth [41]. Daily mean river discharge was calculated for each year 2019–2024. The
 1643 25-yr mean daily discharge was calculated to capture both interannual and decadal
 1644 scale variability in river flow.

1649 Upwelling indices at 48° N , 125° W were obtained from the NOAA National
 1650 Marine Fisheries Service to develop an estimate of the date of spring tran-
 1651 sition. The Bakun index values are a daily average of cross-shore transport
 1652 in units of cubic meters per second along 100 m of coastline. The physical
 1653

spring transition date was defined as the spring minimum in the cumulative upwelling index. The monthly Pacific Decadal Oscillation (PDO) index from 1950-2024 was retrieved from NOAA's National Centers for Environmental information (<https://www.ncei.noaa.gov/access/monitoring/pdo/>). The three-month averaged Oceanic Niño Index (ONI) from 1950-2024 was retrieved from NOAA's Climate Prediction Center (<https://www.cpc.ncep.noaa.gov/data/indices/oni.ascii.txt>). Coastal Washington SST data were obtained from NDBC OOI Westport Shelf (~ 30 km offshore) for the months of January-March in 2020-2024 and Westport Offshore (~ 60 km offshore) in 2019 and averaged to daily values.

5.5 Time series analysis

The effects of coastal alongshore wind stress on current velocity in JDF and the relationship between current velocity and SST anomaly were examined using cross-correlation analysis. Daily averages of the physical time series were used to capture relevant time scales associated with synoptic atmospheric forcing and to estimate lag times in days between forcing and response variables during the months of April through June each year. Time series were determined to be weakly stationary; for years when data exhibited a seasonal trend, a least squares linear regression was fit to the time series, and the residuals were used in subsequent analyses. Statistical significance was assessed using an approximate 95% confidence threshold based on an effective sample size adjusted for autocorrelation to account for serial dependence in the time series. Limitations of the biological data (relatively short and non-stationary time series, characterized by few discrete recruitment events each year) and the non-linear relationship expected with the physical forcing precluded use of correlative analyses to examine relationships with physical data.

1703 5.6 A 3-Box Model

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1705 This is a summary of the development of the evolution equations implemented in the
1706 3-box model that is sketched in Figure 6.

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1710 **Box 0: Columbia River Larval Crab Source Layer**

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1712 Box 0 is the larval source reservoir at the CR mouth. For the calculations in this paper,
1713 it has a fixed volume and a time-dependent larval inventory, depending on seawater
1714 entrainment through frontal and basal mixing processes (below) during the spread of a
1715 CR plume (Figure 6, panel 1, Supplementary Table 2). It is straightforward to extend
1716 this setup to explore effects of a continuous supply of new larvae. We do not consider
1717 this situation here.

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1722 The storage reservoir is prescribed independently of the instantaneous plume
1723 footprint, with fixed area and volume (see Supplementary Table 2):

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$$A_{0,\text{store}} = \frac{1}{2}\pi R_{0,\text{store}}^2 \quad \text{and} \quad V_0 = A_{0,\text{store}} d_{\text{mix,max}}. \quad (8)$$

1728

1729

1730 We take $R_{0,\text{store}}$ to scale as the local Rossby radius, $R_{0,\text{store}} = \alpha_R L_R$. The Box 0
1731 storage area is also taken to be semi-circular, consistent with a source region extending
1732 seaward from the CR mouth. The initial condition for the normalized concentration
1733 $C_0(0) = 1$.

1736

1737

1738 **Basal entrainment and mixing**

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1740 Depending on the strength of the stratification, the occurrence and extent of basal
1741 mixing is governed by drag imparted by the spreading plume on the underlying layer
1742 of seawater. The drag force depends on the instantaneous surface area of the CR
1743 plume base and on the magnitude of velocity gradients at the plume-seawater density
1744 interface. A conventional metric is the shear velocity $u_* = \sqrt{C_d} |V_{CR} + V_{\text{wind}}|$, which
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depends on the total budget of kinetic energy delivered as a result of motions related to plume spreading, tidal ebbs and drag by surface wind stresses. The speed of the outflow V_{CR} will vary in time, depending on tidal effects and the rate at which water is delivered by snow melt and intense atmospheric rivers.

Following [45, 47, 70–73] an instantaneous basal entrainment and mixing efficiency can be written in terms of a local bulk Richardson number:

$$Ri_{\text{bulk}} = \frac{g'_{CR} h_t}{V_t^2}, \quad f_{\text{Ri}} = \max \left(0, 1 - \frac{Ri_{\text{bulk}}}{Ri_{\text{crit}}} \right) \quad (9)$$

where we take Ri_{crit} to be in the range 0.05-0.08. Assuming maximum intrusion speeds near the source of a few m/s and plume thicknesses of order 10 m these critical values are reasonable for both larva-free flows and in flows where particle inertial effects related to ~ 6 mm crab larvae are included (i.e., Stokes numbers are plausibly order 0.01-0.1 for slip velocities of order 0.01 m/s and larvae drag coefficients of around 1-2) [72]. This picture of purely mechanical entrainment is conservative, and most justified for strong spring outflows where shearing rates are sufficiently high that accumulation effects of larvae swimming upward into plume fronts during spreading can be neglected [27, 40, 59].

By considering the instantaneous power delivered to do the work of mechanical mixing, which scales as ρu_*^3 , the stabilizing power that modulates the speed of mixing across a stabilizing interface as the plume spreads, $g\Delta\rho h_t V_{\text{mix}}$, and neglecting particle inertial or drag effects of the larvae, we obtain a scale for the evolution of a mixing layer containing crab larvae $V_{\text{mix}} \sim d(h_{\text{mix}})/dt$ [72]. With Ri_{crit} and the mixing efficiency Λ_b specified on the basis of theoretical, experimental and numerical studies [46, 47].

$$V_{\text{mix,base}} = f_{\text{Ri}} \cdot \chi_{\text{mix}} \frac{\Lambda_b u_*^3}{g'_{CR} h_t}. \quad (10)$$

Here χ_{mix} is the order-one tuning coefficient listed in Supplementary Table 2. Mixing is suppressed as Ri_{bulk} increases to Ri_{crit} and vanishes for $Ri_{\text{bulk}} \geq Ri_{\text{crit}}$. As the mixed layer grows, the model separately updates the density and reduced gravity of Box 1 from the fraction of seawater incorporated into the plume. This evolving g'_1 is carried forward into the JDF transport calculation; the CR entrainment closures themselves use the prescribed source value g'_{CR} .

Plume spread, frontal entrainment and mixing: A kinematic parameterization

As the CR plume spreads, the leading edge sweeps outward, continuously penetrating denser seawater while creating new frontal interfacial area. Thus, in addition to mixing driven by shear at the base of the plume, the model includes a second entrainment mechanism associated with frontal collapse to produce complex overturning over the scale of the plume depth h_{front} [74–76]. Beyond the largest-scale motions, the kinematics of natural flow fronts are complex, involving transient turbulent instabilities that manifest as relatively small-scale lobe-and-cleft structures.

To capture the maximum larval pickup by the largest energy-carrying scales at the plume front we first let $R(t)$ denote the radius of a plume spreading as an approximately semi-circular disk with local front thickness $h_{\text{front}}(t)$. The instantaneous frontal propagation speed is taken to scale as the “free-fall” or collapse speed $dR_{\text{mix}}/dt = \sqrt{g'_{\text{CR}} h_{\text{front}}}$, where g'_{CR} is the prescribed source reduced gravity and h_{front} evolves as the semi-circular plume spreads. We note that this scaling is justified over the evolution of buoyancy-controlled spreading because the plumes generally reach the Rossby radius before a transition to self-similar spreading occurs [77]. Assuming the frontal collapse-governed spread also drives the largest energy-carrying entraining

motions at the flow front, the corresponding frontal entrainment velocity is:

$$V_{\text{mix,front}} = f_{\text{Ri,front}} \alpha_{\text{front}} \frac{dR_{\text{mix}}}{dt}. \quad (11)$$

Here α_{front} is an entrainment coefficient for frontal mixing and $f_{\text{Ri,front}}$ is a suppression factor that limits mixing when stratification is too strong for overturning motions to produce plume-seawater interfacial breaking waves. We implement the same Richardson-number control as for basal mixing.

To combine the basal and frontal contributions to overall mixing, the model associates each with a characteristic entraining surface area that evolves in time. The basal mixing acts over the basal area

$$A_{\text{base}} = \frac{1}{2} \pi R_{\text{mix}}^2, \quad (12)$$

while frontal mixing acts over an approximate vertical frontal area

$$A_{\text{front}} = \pi R_{\text{mix}} h_{\text{front}}. \quad (13)$$

The effective mixing velocity used in the model is then an area-weighted combination:

$$V_{\text{mix}} = \frac{V_{\text{mix,base}} A_{\text{base}} + V_{\text{mix,front}} A_{\text{front}}}{A_{\text{base}} + A_{\text{front}}}. \quad (14)$$

This construction ensures that frontal mixing matters most when the frontal surface area is dynamically important in its contribution to total mixing layer growth, while basal mixing dominates when the plume behaves more like a broad shallow lens. The effective mixing velocity V_{mix} is then used to evolve the overall mixed-layer thickness

1887 according to (see Supplementary Table 2):

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1894 **Evolution equation for Box 0, the larval source**

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1896 The entraining exchange area is tied to the instantaneous plume footprint $A_{\text{ent}}(t) =$

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1898 $\frac{1}{2}\pi R_{\text{mix}}(t)^2$ (Figure 6, panel 1). The volumetric flow from Box 0 into Box 1 is, then,

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1904 Here $\Gamma_b = \min[\max(d_{\text{mix}}/h_t, 0), 1]$ tracks the fraction of the instantaneous plume

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1906 thickness penetrated by the growing mixed layer. It therefore distinguishes the

1907

1908 instantaneous vigor of mixing, represented by V_{mix} , from the accumulated vertical

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1910 penetration required for that mixing to entrain larvae from Box 0. Consistent with

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1912 the picture of highly turbulent spring CR plumes ($Ri \ll Ri_{\text{crit}}$), we neglect potential

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1914 complicating effects of larval detrainment over the relatively short duration of larval

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1921 **Box 1: Radially-Spreading Turbulent CR Gravity Current**

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1924 Box 1 receives larvae from Box 0 through frontal and basal entrainment and loses it

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1926 by advective export toward JDF (Figure 6, panel 1).

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$$\frac{d}{dt}d_{\text{mix}} = V_{\text{mix}}. \quad (15)$$

$$Q_{01}(t) = \Gamma_b(t) V_{\text{mix}}(t) A_{\text{ent}}(t). \quad (16)$$

$$\frac{dC_0}{dt} = -\frac{Q_{01}}{V_0}C_0. \quad (17)$$

Entrainment cross-section and evolving control volume	1933
	1934
The evolving exchange area linking Box 0 to Box 1 is the instantaneous plume footprint,	1935
	1936
	1937
$A_{\text{in}} = A_{\text{ent}} = \frac{1}{2}\pi R_{\text{mix}}(t)^2$	1938
	1939
and the instantaneous effective control volume $V_{\text{eff}} = A_{\text{in}} h_{\text{front}}(t)$. As the plume spreads, seawater and larvae enter Box 1 over the characteristic filling time scale	1940
	1941
	1942
	1943
	1944
$\tau_{01} = \frac{V_{\text{eff}}}{Q_{01}}.$	1945
	1946
	1947
	1948
The larval concentration and plume density therefore evolve on the geometry of the spreading plume through the Box-1 filling time scale τ_{01} .	1949
	1950
	1951
The time-dependent input to Box 1 is set by the full Columbia River outflow calculation through $Q_{01}(t)$. Thus, variations in river discharge, tides, plume geometry, and the evolving mixing state are carried into the Box-1 filling time scale	1952
	1953
	1954
	1955
	1956
	1957
$\tau_{01}(t) = \frac{V_{\text{eff}}(t)}{Q_{01}(t)}.$	1958
	1959
	1960
	1961
Loss from Box 1 is represented relative to this same instantaneous filling time scale through the dimensionless control parameter	1962
	1963
	1964
	1965
	1966
$\Pi_{CR} = \frac{\tau_{01}}{\tau_{1,\text{out}}}.$	1967
	1968
	1969
	1970
Accordingly,	1971
$\tau_{1,\text{out}}(t) = \frac{\tau_{01}(t)}{\Pi_{CR}}.$	1972
	1973
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	1978

1979 The Box-1 evolution equation is therefore

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1986 In an individual calculation, Π_{CR} is prescribed and remains fixed, whereas $\tau_{01}(t)$

1987 varies with the calculated CR outflow. Consequently the absolute export time scale

1988 varies in step with the time-dependent input, while their ratio remains Π_{CR} . This

1989 construction preserves the full time dependence of the CR pickup signal while allowing

1990 the relative importance of export to be varied with a single dimensionless parameter.

1991

1992 If $\Pi_{CR} \ll 1$, filling is fast compared with export and the time dependence of larval

1993 pickup is preserved; if $\Pi_{CR} \gg 1$, export is fast relative to filling and the signal is

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2000 **Box 2: Juan de Fuca Strait to Victoria Sill**

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$$\frac{dC_1}{dt} = \frac{1}{\tau_{01}(t)} [C_0 - \Pi_{CR} C_1]. \quad (23)$$

Box 2 receives larvae first carried northward from Box 1 in what is essentially a pipe flow driven by the combined effects of wind stresses and buoyancy forces. During downwelling wind conditions, motions related to onshore Ekman transport along the west coast of Washington inhibit entrainment and we neglect dilution related to such effects.

Depending on the strength of southerly winds at the mouth of JDF and the extent of entrainment into outflows from the strait (particularly during strong tidal ebbs), entrained larvae are carried eastward in the current, driven by effects of onshore Ekman transport, buoyancy forces and by tidal floods that vary in strength (Figure 6, panels 2 and 3). Whereas the effect of strong winds at the CR mouth is unclear in terms of its contribution to the amplitude of the pickup signal, the extent of the larval pickup signal retained in the Salish Sea is almost certainly reduced by strong winds that carry larvae northward beyond the mouth of JDF (Figure 5).

The model retains the signed tidal velocities explicitly. The buoyancy-driven velocity of the Box-1 water entering JDF is

$$V_{\text{gr,in}}(t) = \sqrt{2g'_1(t) f_{g'} h_{\text{in}}(t)}, \quad (24)$$

where $g'_1(t)$ is the evolving reduced gravity of Box 1 and $f_{g'}$ is the JDF reduced-gravity scaling. The onshore Ekman velocity scale is

$$V_{\text{Ek}} = \frac{\tau_w}{\rho_{\text{CR}} f_{\text{JDF}} h_E}, \quad h_E = \sqrt{\frac{2K_e}{f_{\text{JDF}}}}. \quad (25)$$

At the mouth and western JDF, we define the net eastward transport velocity, expressed on the Box-2 inflow thickness, as

$$\bar{V}_{12}(t) = V_{\text{Ek}} + V_{\text{gr,in}}(t) + u_{\text{tide,PA}}(t) - \frac{h_{\text{in}}(t)}{h_{\text{out}}(t)} V_{\text{alongshore}}. \quad (26)$$

The tidal velocity $u_{\text{tide,PA}}(t)$ enters with its calculated sign. When $\bar{V}_{12} > 0$, the corresponding characteristic delivery time scale from the mouth of JDF toward Victoria Sill is

$$\tau_{12} = \frac{h_{\text{in}}}{\bar{V}_{12}}. \quad (27)$$

At the eastern end of JDF, the corresponding buoyancy-driven velocity is

$$V_{\text{gr,out}}(t) = \sqrt{2g'_2(t) h_{\text{out}}(t)}, \quad (28)$$

and the transport velocity carrying larvae past Victoria Sill is

$$\bar{V}_{2,\text{out}}(t) = V_{\text{Ek}} + V_{\text{gr,out}}(t) + u_{\text{tide,PT}}(t). \quad (29)$$

2071 Again, the tidal velocity enters with its calculated sign. When $\bar{V}_{2,\text{out}} > 0$, the
 2072 characteristic time scale is

$$2074 \quad \tau_{2,\text{out}} = \frac{h_{\text{out}}}{\bar{V}_{2,\text{out}}}. \quad (30)$$

2076 The evolution equation for the larval concentration delivered through JDF is then

$$2079 \quad \frac{dC_2}{dt} = \frac{1}{\tau_{12}}C_1 - \frac{1}{\tau_{2,\text{out}}}C_2 = \frac{1}{\tau_{12}}(C_1 - \Pi_{JDF}C_2), \quad (31)$$

2082 where

$$2084 \quad \Pi_{JDF} = \frac{\tau_{12}}{\tau_{2,\text{out}}}. \quad (32)$$

2087 Thus, strong northward transport past the mouth of JDF increases τ_{12} and Π_{JDF} ,
 2088 progressively weakening the delivered pickup signal. The approximate factor-of-two
 2089 decrease in plume thickness across Victoria Sill enters through the distinct values of
 2090 h_{in} and h_{out} (Supplementary Table 3).

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and test in this manuscript. H. J. G. and A. M. J. developed the conceptual and	2154
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carried out the calculations. H. J. G. and A. M. J. wrote the manuscript.	2156
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