

Annual Review of Marine Science

Upwelling Bays: How Coastal Upwelling Controls Circulation, Habitat, and Productivity in Bays

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Annu. Rev. Mar. Sci. 2020. 12:415–47

First published as a Review in Advance on September 17, 2019

The *Annual Review of Marine Science* is online at marine.annualreviews.org

<https://doi.org/10.1146/annurev-marine-010419-011020>

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Keywords

upwelling shadow, upwelling trap, headland, wind forcing, stratification, phytoplankton bloom, ocean acidification, hypoxia, larval dispersion

Abstract

Bays in coastal upwelling regions are physically driven and biochemically fueled by their interaction with open coastal waters. Wind-driven flow over the shelf imposes a circulation in the bay, which is also influenced by local wind stress and thermal bay–ocean density differences. Three types of bays are recognized based on the degree of exposure to coastal currents and winds (wide-open bays, square bays, and elongated bays), and the characteristic circulation and stratification patterns of each type are described. Retention of upwelled waters in bays allows for dense phytoplankton blooms that support productive bay ecosystems. Retention is also important for the accumulation of larvae, which accounts for high recruitment in bays. In addition, bays are coupled to the shelf ecosystem through export of plankton-rich waters during relaxation events. Ocean acidification and deoxygenation are a concern in bays because local extrema can develop beneath strong stratification.

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INTRODUCTION

Bays are connected to the coastal ocean, and in upwelling regions they exhibit characteristic patterns and processes driven primarily by this interaction with the ocean. The term upwelling bay refers to these bays, which are driven physically and fueled chemically and biologically by the coastal upwelling in the contiguous ocean. Thus, upwelling bays contrast with bays dominated by freshwater inflow (i.e., estuaries), although they are similarly sheltered and often stratified. Upwelling bays provide high levels of productivity that are comparable to those of estuaries, although the processes and habitats can be quite different. Furthermore, bays offer refuge from the ocean, which is valued by both humans and marine biota. The fundamental role of circulation in defining spatial patterns and connectivity among habitats is the foundation of this review, but the motivation for it is ecological. It provides a synthesis of the physical forcing and physical responses that set up patterns in water properties, stratification, and retention, which in turn explain patterns in pelagic and benthic habitats and connectivity between communities and habitats.

COASTAL UPWELLING

Cold, nutrient-rich water upwells from depth along the midlatitude west coasts of the world's major continents, forming a foundation for the large marine ecosystems in the four main eastern boundary upwelling systems: the Benguela (Hutchings et al. 2009), Humboldt (Montecino & Lange 2009), California (Checkley & Barth 2009), and Canary (Aristegui et al. 2009) Current Systems (**Figure 1**). At the heart of these regional upwelling systems is wind forcing along the coast, with alongshore winds driving surface waters offshore and creating a horizontal flux divergence that requires an upward vertical flux to converge on the surface. This upward flux of waters from the dark depths into the light-filled near-surface zone results in a persistent supply of nutrients that fuels photosynthesis and accounts for high levels of productivity. However, wind-driven coastal upwelling is not confined to eastern boundary upwelling systems and is observed in many other locations, sometimes as brief anomalous events [e.g., off the coast of North Carolina (Rennie et al. 1999)] but often as reliable seasonal phenomena [e.g., Somalia, Yemen, Oman, southwest India, and southern Australia (Kämpf & Chapman 2016)]. While this review is based on examples from well-studied bays in eastern boundary upwelling systems (**Table 1**), the principles and patterns are expected to be common to all bays in regions where upwelling occurs.

This article is focused on places where alongshore winds drive offshore Ekman transport, yielding marked upwelling along the coast. The upwelling response has three components that are readily observed (Crepon & Richez 1982, Brink 1983, Hermann et al. 1989): (*a*) alongshore surface wind stress that drives offshore Ekman transport, with a lowering of sea level along the coast and a raising of isotherms; (*b*) a cross-shore pressure gradient due to sloping sea level that drives a fast alongshore barotropic flow (i.e., a shelf jet); and (*c*) changes in the cross-shore pressure gradient with depth due to sloping isotherms (baroclinic forcing), which result in weaker alongshore flow at depth. This two-dimensional textbook view of wind-driven upwelling is simplistic, but it captures the essence of the physical phenomenon and allows the identification of key chemical and biological components. The chemical properties of upwelled water vary depending on the region and the depth of source waters, but in general these waters are enriched by decomposition, so in addition to high nutrient levels, they exhibit high CO₂ concentrations, low pH, a low aragonite saturation state, and low levels of dissolved oxygen (Chavez et al. 2018). High nutrient availability fuels high rates of photosynthesis in the euphotic zone, which in turn support high levels of biological productivity in the form of dense nearshore kelp forests and dense offshore phytoplankton blooms. These habitats support primary and secondary consumers as well as an abundance of marine life at higher trophic levels, including fish, sharks, birds, and mammals (Croll et al. 2005).

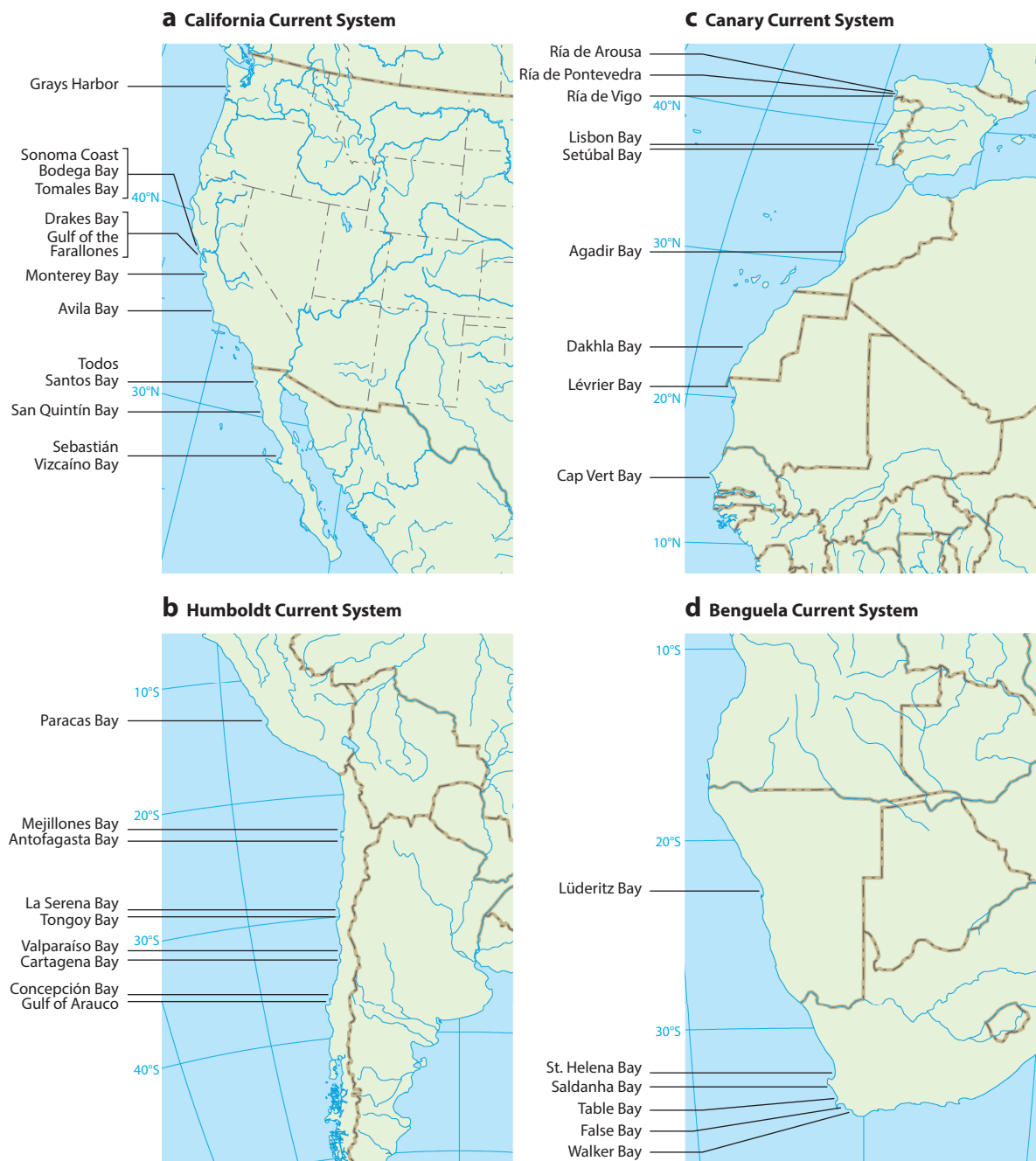


Figure 1

The locations of bays in eastern boundary upwelling systems (precise latitudes and sizes are given in **Table 1**). National borders (*brown*) and major rivers (*blue*) are also shown.

Table 1 Examples of upwelling bays in eastern boundary upwelling systems (see Figure 1)

Bay	L:W ^a	Orientation ^b	Size ^c	Type ^d	Latitude	Selected reference ^e
California Current System (Checkley & Barth 2009)						
Grays Harbor	2:1	Enclosed	20	Cm.	46.9°N	Hickey & Banas 2003
Sonoma Coast	1:5	Shadow and trap	100	WB	38.5°N	Halle & Largier 2011
Bodega Bay	1:3	Shadow and trap	10	Sm.	38.3°N	Roughan et al. 2005
Tomas Bay	10:1	Enclosed	20	Cm.	38.2°N	Largier et al. 1997
Drakes Bay (Farallones)	1:2	Shadow	20	WB	38.0°N	—
Gulf of the Farallones	1:4	Shadow	100	WBS	37.8°N	Steger et al. 2000
Monterey Bay	3:4	Shadow	30	SB	36.8°N	Graham & Largier 1997
Avila Bay	1:2	Shadow	20	Sm.	35.1°N	Walter et al. 2017
Todos Santos Bay	3:2	Trap	20	SB	31.8°N	Argote-Espinoza et al. 1991
San Quintín Bay (inner)	8:1	Enclosed	15	Cm.	30.5°N	Canu et al. 2016
San Quintín Bay (outer)	1:2	Shadow	25	WB	30.3°N	—
Sebastián Vizcaíno Bay	3:2	Trap	150	SB	28.3°N	Martínez-Fuentes et al. 2016
Humboldt Current System (Montecino & Lange 2009)						
Paracas Bay	1:3	Shadow	60	WB	13.7°S	Kahru et al. 2004
Mejillones Bay	1:2	Shadow	30	SB	23.0°S	Marin et al. 2001
Antofagasta Bay	3:2	Trap	30	SB	23.6°S	Castilla et al. 2002
La Serena Bay	1:4	Shadow and trap	100	WBS	30.0°S	Tapia et al. 2014
Tongoy Bay (La Serena)	3:4	Shadow	10	SB	30.3°S	Lagos et al. 2016
Valparaíso Bay	1:4	Shadow	25	WB	33.0°S	Aiken et al. 2008
Cartagena Bay	1:2	Shadow and trap	6	Sm.	33.5°S	Bonicelli et al. 2014
Concepción Bay	2:1	Shadow	20	EB	36.6°S	Valle-Levinson et al. 2004
Gulf of Arauco	1:1	Shadow	40	SB	37.1°S	Valle-Levinson et al. 2003
Canary Current System (Aristegui et al. 2009)						
Ría de Arousa	4:1	Shadow	30	EB	42.5°N	Álvarez-Salgado et al. 1996
Ría de Pontevedra	4:1	Shadow and trap	25	EB	42.4°N	Aguir 2016
Ría de Vigo	4:1	Shadow and trap	25	EB	42.2°N	Barton et al. 2015
Lisbon Bay	1:1	Shadow	40	WBS	38.6°N	Oliveira et al. 2009
Setúbal Bay	3:5	Shadow	50	WBS	38.3°N	Oliveira et al. 2009
Agadir Bay (Cape Ghir)	2:5	Shadow	50	WB	30.6°N	Van Camp et al. 1991
Dakhla Bay (Río de Oro)	4:1	Shadow	40	EB	23.8°N	El Asri et al. 2019
Lévrier Bay (Nouadhibou)	1:4	Shadow	100	WB	20.9°N	Mohammed et al. 2014
Cap Vert Bay	1:4	Shadow	50	WB	14.7°N	Roy 1998
Benguela Current System (Hutchings et al. 2009)						
Lüderitz Bay	1:2	Shadow	10	Sm.	26.6°S	Molloy & Bolton 1995
St. Helena Bay	1:2	Shadow	50	WBS	32.6°S	Pitcher et al. 1996
Saldanha Bay	1:1	Enclosed	12	Cm.	33.0°S	Monteiro & Largier 1999
Table Bay	1:1	Shadow	12	SB	33.9°S	Brown & Hutchings 1987
False Bay	1:1	Trap	30	SB	34.2°S	Grundlingh & Largier 1991
Walker Bay	1:2	Shadow	20	WB	34.4°S	Jury 1988

This table is not a comprehensive list, nor is it balanced in geographic representation; it is based on my experience in addition to published literature, and it is notably missing many bays outside of eastern boundary upwelling systems that are at times also influenced by wind-driven or current-driven upwelling over the shelf.

^aApproximate ratio of length (cross-shore distance) to width (alongshore distance).

^bOrientation of the bay to the prevailing winds and currents, specifically indicating whether the bay is downwind of a headland (upwelling shadow) or upwind of a headland (upwelling trap).

^cApproximate maximum dimension in kilometers, irrespective of whether that dimension is length or width.

^dType of bay within the typology described in the main text: WB, wide-open bay; SB, square bay; EB, elongated bay; WBS, wide-open bay with a marked step at one end; Sm., small bay; Cm. semiencloded bay with a constricted mouth.

^eA published paper that provides further information on the bay. A dash indicates that there is no suitable paper for that bay.

UPWELLING INDICES

Upwelling has many faces, and so it should have many indices. The index should track the phenomenon of interest (e.g., winds that drive upwelling, water temperature, nutrient availability, or transport probability) at the scale of interest. And to assess the influence of upwelling on a phenomenon not inherent to upwelling, the index should have demonstrated skill; that is, the index is an independent variable that can explain a significant amount of variance in the dependent variable—the phenomenon of interest. Thus, while the Bakun index (Bakun 1973) may index the regional flux of deep water into the euphotic zone, it will not necessarily be effective in indexing localized upwelling in a bay, and it may be unrelated to daily variations in temperature or nutrient delivery in the bay. While local data can be used directly as an index, it is also possible to develop indices from regional data, as García-Reyes et al. (2014) and Jacox et al. (2018) did for nutrients. For indexing upper-trophic-level populations or productivity at the ecosystem scale, multidimensional indices have shown skill (Sydeman et al. 2014), going well beyond the physics of upwelling.

Along the shoreline, high levels of biomass are also observed in subtidal and intertidal benthic communities.

Upwelling has many facets, and different people use the term to refer to different aspects of these complex systems. Some use it to refer to the winds that blow alongshore (with the coast on the left in the Northern Hemisphere and on the right in the Southern Hemisphere), while others use it to refer to the presence of cold surface waters, the strong alongshore currents, or the upward-sloping isotherms. Beyond the physical aspects, upwelling is also used to refer to high nutrient concentrations, dense diatom blooms, water properties such as low pH and low oxygen, or distinct ecological communities and ecosystems. Strictly speaking, upwelling refers to the upward flux of deep waters, which is a process rather than a consequence, but the word has taken on many useful meanings because this wind-driven phenomenon has so many important consequences (see the sidebar titled Upwelling Indices).

EFFECTS OF TOPOGRAPHY ON WINDS AND CURRENTS

Anyone who has looked at a satellite image of sea surface temperature realizes that the textbook two-dimensional view of upwelling does not capture its full complexity (**Figure 2**). There are zones where colder surface water reflects enhanced upwelling or rapid offshore transport of newly upwelled water away from upwelling centers (Kämpf & Chapman 2016). And zones of warmer surface water are found offshore as well as in locations where upwelling is weaker or locally absent, allowing for warming of surface water due to the persistently positive surface heat flux in upwelling regions (Lentz 1987). While the two-dimensional model may be a valid reduction of the physical system, it neglects many features that are critical in the ecological responses to upwelling. Important patterns observed in pelagic habitats, plankton blooms, and larval dispersal require a three-dimensional view (or at least a two-dimensional plan view in addition to the two-dimensional section view). Three-dimensional patterns result from the spatial structure of winds as well as from the interaction of currents with topographic features (both shelf bathymetry and coastline form). While upwelling also varies latitudinally and regionally in association with large-scale wind patterns and shelf topography [e.g., at Hecate Bank (Castelao & Barth 2005) and the Aveiro shelf (Oliveira et al. 2019); see also Figueroa & Moffat 2000, Pringle 2002], the focus here is on the effect of coastal topography in the form of bays and headlands.

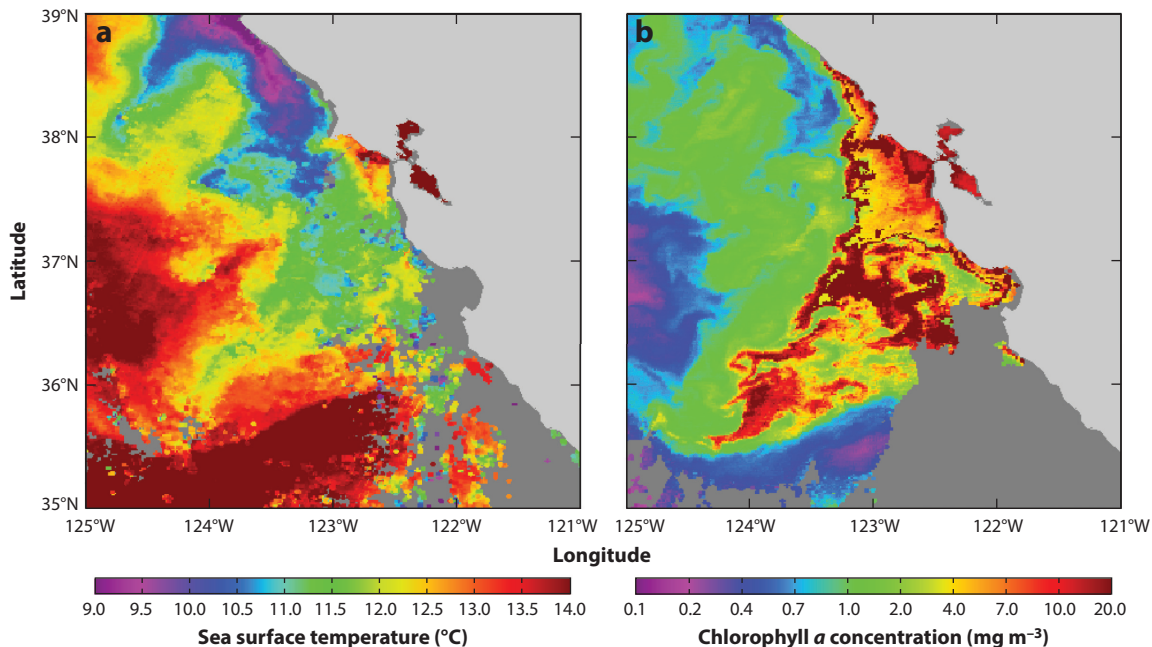


Figure 2

(a) Sea surface temperatures and (b) surface chlorophyll *a* concentrations for coastal waters in and adjacent to three bays in northern California on May 9, 2017: the Gulf of the Farallones (37.5–38°N), the Sonoma Coast (38–39°N), and the partially obscured Monterey Bay (36.5–37°N). The dark gray areas show where cloud cover has obscured the sea surface, and the light gray areas represent land. The upwelling center at Point Arena (39°N) is evident from 9°C water at the surface, which warms marginally as it streams south in a bifurcated upwelling plume, with one branch directed offshore and a second branch following the coast. These waters also exhibit very low chlorophyll concentrations ($<1 \text{ mg m}^{-3}$). In Drakes Bay, immediately south of Point Reyes (38°N), the surface waters are warm ($>12^\circ\text{C}$) and the chlorophyll levels are high ($>10 \text{ mg m}^{-3}$). High-chlorophyll waters extend throughout the greater Gulf of the Farallones region, which extends from Bodega Bay to Monterey Bay, and also offshore in a plume of aged upwelled water that separated from the coast at Point Reyes (surface temperatures of 11–12°C). Data are from satellite sensors [NOAA Advanced Very High Resolution Radiometer (AVHRR) for temperature, and NASA Aqua Moderate Resolution Imaging Spectroradiometer (MODIS) for chlorophyll]; images were produced by NOAA CoastWatch.

Coastal topography influences upwelling by modifying airflow (alongshore wind; **Figure 3**) or water flow (shelf jets; **Figure 4**). Thus, the height and acuity of coastal headlands are primary considerations. Headlands that extend above the marine atmospheric boundary layer can completely block and deflect the upwelling winds, producing either a wind shadow where the airflow separates from the coast (e.g., in Monterey Bay and Table Bay; **Figure 3**) or accelerated winds around the headland due to hydraulic control of the attached airflow [e.g., at Point Arena (Winant et al. 1988) and Punta Lengua de Vaca (Garreaud et al. 2011)]. By contrast, upwelling winds may pass over low-lying headlands, precluding a wind shadow and at times enhancing localized upwelling along the coast downwind of the headland, where the wind is offshore [e.g., in Bodega Bay (Roughan et al. 2005)] and sometimes locally accelerated [e.g., in Table Bay (Jury 1980)]. Even with a homogeneous wind field, unperturbed by headlands, bays result in changes in the local orientation of the wind to the shoreline. This has been explored through semirealistic models (e.g., Penven et al. 2000 for St. Helena Bay) and idealized models (e.g., Crepon & Richez 1982, Crepon et al. 1984, Oey 1996) that highlight the role of the baroclinic Kelvin wave response (important for poleward flow at depth and during relaxation) and the development of cyclonic circulation in the lee of the headland.

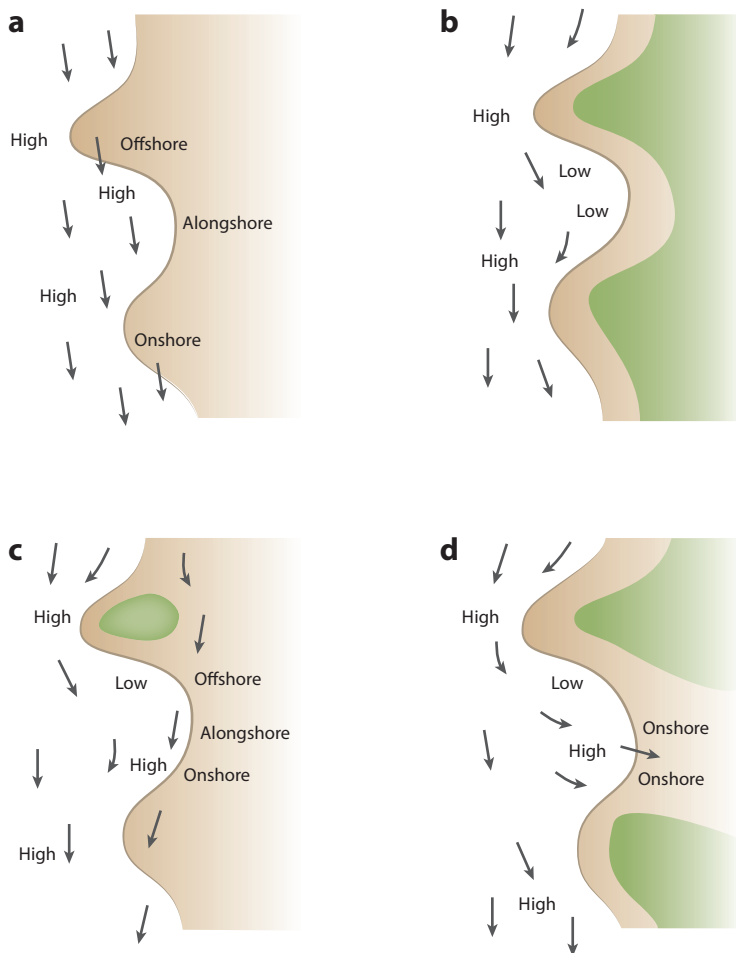


Figure 3

Typical wind patterns in upwelling bays (drawn for the Northern Hemisphere). Wind vectors are represented by arrows, and the annotations refer to wind velocity; shorelines are shown in brown, and topography that is higher than the thickness of the marine atmospheric boundary layer is shown in green. (a) Low-lying lands do not block the wind and the bay is fully exposed to surface wind stress, as observed in St. Helena Bay when the marine layer is thick (Jury 1985), including alongshore winds that can drive Ekman upwelling midbay, offshore winds that can drive localized upwelling along the upwind shore of the bay, and onshore winds that can drive localized downwelling or trapping along the downwind shore of the bay. (b) Elevated land blocks the marine atmospheric boundary layer and shelters most of the bay, as observed in Monterey Bay (Paduan & Rosenfeld 1996). (c) An elevated headland on the upwind side of the bay creates a localized wind shadow and allows winds to pass inland of the headland, as observed in Table Bay (Jury 1988) and Mejillones Bay, resulting in alongshore winds midbay and onshore winds along the downwind shore. (d) Between two blocking headlands, a valley extends inland from the bay, allowing onshore winds, specifically diurnally enhanced sea-breeze winds, as observed in Todos Santos Bay (Ladah et al. 2005).

In blocking and deflecting the shelf jet, the acuity of the headland is important (**Figure 4**). For smooth topographic variability (i.e., slowly varying or muted headlands), the jet will remain attached and speed up, enhancing onshore flow in the bottom Ekman layer, which together enhance upwelling at the headland and allow offshore flow near the surface due to centrifugal forcing and

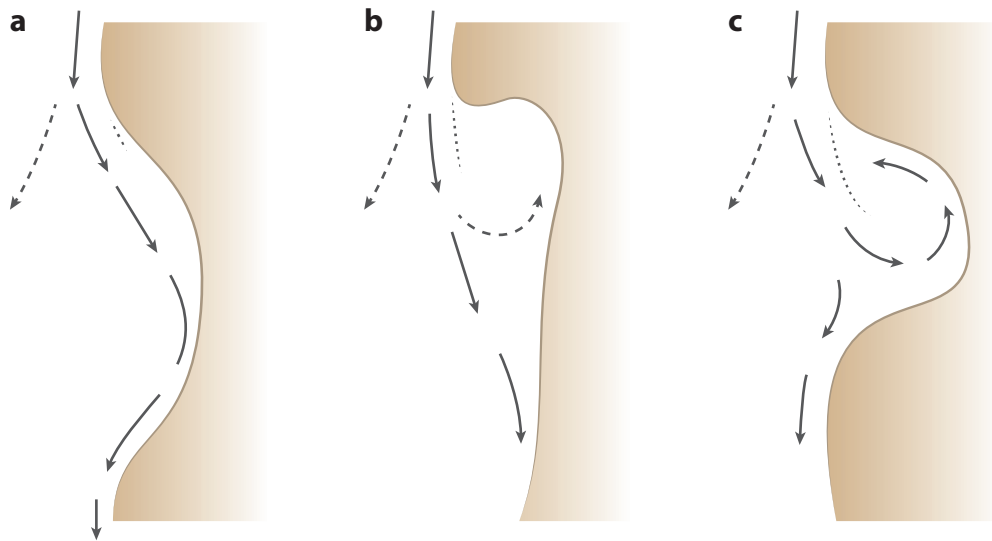


Figure 4

Typical water flow patterns in upwelling bays due to the interaction of the shelf jet with topography (drawn for the Northern Hemisphere). Current vectors are represented by arrows, and the shorelines are shown in brown. (a) A wide-open bay with shelf-jet throughflow, yielding anticyclonic circulation in the bay that may be accompanied by a mesoscale anticyclonic eddy offshore (e.g., Largier et al. 1993); this pattern is typical of the Sonoma Coast and also represents the subsurface flow of water through Antofagasta Bay. The jet may partially separate adjacent to the upstream headland (*dotted line*), and onshore advection may be observed midbay. The dashed arrow indicates an offshore branch that forms if the jet bifurcates (e.g., Halle & Largier 2011). (b) A wide-open bay defined by a step in the coastline with separation of the shelf jet, which is typical of the Gulf of the Farallones and St. Helena Bay. Water level is elevated in the upwelling shadow, and surface water is warmer and stratified. Shear and a thermal front are observed at the separation point (*dotted line*). The circulation in the bay tends to be weakly cyclonic, and onshore advection may be observed midbay (*dashed arrow*) (e.g., Pitcher et al. 2010). The dashed arrow offshore indicates an offshore branch that forms when the jet bifurcates (e.g., Shannon 1985, Kaplan et al. 2005). (c) A square bay with a headland eddy due to separation of the shelf jet, yielding strong cyclonic circulation in the bay and onshore advection midbay; this pattern is typical of Monterey Bay (Paduan & Rosenfeld 1996). The surface water in the bay is much warmer and strongly stratified, yielding a strong thermal buoyancy front along the separation line (*dotted line*) (e.g., Lagos et al. 2002, Woodson et al. 2009). The dashed arrow indicates an offshore branch that forms when the jet bifurcates (e.g., Rosenfeld et al. 1994).

upwelling to persist when the wind weakens (e.g., Point Arena, California). Although current-driven upwelling receives little attention in wind-driven upwelling regions, it is well recognized in low-wind regions where upwelling occurs at headlands and inward steps in the coastline [e.g., Smoky Cape, Australia (Roughan & Middleton 2002); Cabo Catoche, Yucatán (Reyes-Mendoza et al. 2016); and Durban Bight, South Africa (Lutjeharms et al. 2000)]. Alternatively, for sharp topography, the jet can separate at the apex of the headland and flow offshore [e.g., at Cape Blanco (Barth et al. 2000) and Point Reyes (Kaplan et al. 2005)], with a cyclonic circulation inshore. The formation of cyclonic headland eddies depends on the flow speed, headland size, and lateral eddy flux, as outlined by the island wake parameter (Wolanski et al. 1984, Barton 2001). In both cases, regardless of whether the jet separates or remains attached to a convex shoreline, one expects enhanced upwelling at the headland—an upwelling center. This upwelling is due to one or more of the following contributions: centrifugal forcing on convex surface-intensified flow, bottom Ekman transport due to accelerated flow, surface Ekman transport due to accelerated wind (sometimes the shear line or curl is a bit offshore; e.g., Enriquez & Friehe 1995), viscous production of vorticity that forms a small bottom-attached eddy or feeds a mesoscale cold-core eddy (Oey 1996), and divergence due to lateral entrainment into detached surface-intensified flow.

Many headlands fall between these two end members; the upwelling jet may separate temporarily and then reattach to the shore boundary, the jet may separate at some times and remain attached at other times, or both separated and coastal jets may be observed simultaneously. Bifurcation of the upwelling jet was first noted by Shannon (1985), who noted the tendency for a barotropic flow at Cape Columbine to follow the shelf edge as the shelf broadens downstream of the headland. But this bifurcation happens even without a widening of the shelf, simply due to the inertia of the jet at a sudden change in shoreline direction [e.g., at Point Año Nuevo (Rosenfeld et al. 1994)]. High-frequency radar observations of surface currents at Point Arena show that the flow can alternate between attached and separated configurations, sometimes curving cyclonically to follow the coast and isobaths, sometimes going straight and crossing isobaths (Halle & Largier 2011), and sometimes separating partially before turning back onshore and reattaching. It is expected that switching between attached and separated jets depends on fluctuations in the strength and orientation of the flow upstream of the headland due to changes in wind forcing and the strength or proximity of a mesoscale eddy upstream of the headland [e.g., the Mendocino Eddy (C.M. Halle & J.L. Largier, unpublished manuscript)]. This switching may also be controlled by alongshore gradients in surface wind stress that account for gradients in sea level: If a wind shadow exists, there will be an upstream slope in sea level that enhances the reverse pressure gradient due to the Bernoulli effect and enhances the tendency for flow separation, whereas if upwelling winds are strong downstream of the headland, the reverse pressure gradient will be weakened and separation less likely.

Given that bays are defined by headlands, this diversity in the form and influence of headlands yields a diversity of phenomena. Bays may be demarcated by both upstream and downstream headlands (e.g., Monterey Bay and False Bay) or just one or the other (a step in the coastline, e.g., Lisbon Bay and Sebastián Vizcaíno Bay). Upwelling bays exhibit marked spatial patterns in flow, stratification, and water properties that are attributable to the downstream effects of an upstream headland, the upstream effects of a downstream headland, or both. The upstream headland may produce flow separation, recirculation, and onshore flow (**Figure 4**) as well as a wind shadow and surface warming (**Figure 3**). The downstream headland may result in onshore winds and flow convergence. In elongated or narrow bays, the direct influence of these shelf winds and currents may be absent at locations farther from the mouth of the bay, so that thermal gradients and local winds may be more important. Characteristic patterns emerge from these flow dynamics.

SPACE-TIME PATTERNS IN CIRCULATION AND STRATIFICATION

The combined influences of the shelf jet, local wind stress, and thermal gradients drive circulation in bays, resulting in common patterns that have been observed in upwelling bays worldwide. While the descriptions of the patterns here are anchored in the primary literature, the commonality of these patterns across bays is supported by unpublished data, secondary literature, and personal observations. There is thus a bias toward my experience, while other good examples may be omitted. Nevertheless, other upwelling bays should slot easily into the patterns and categories described here—indeed, that will be a measure of the success of this review.

Winds exhibit distinct patterns in upwelling bays, which are well known by people who live in these regions. These wind patterns affect human activities both directly (e.g., sunbathing, wind-surfing, and small-boat navigation) and indirectly (through their influence on bay ecosystems). Local wind stress is an important determinant of the circulation, stratification, and water properties in a bay. The spatial pattern of surface wind stress can affect the oceanography of the bay through vertical mixing, surface warming, localized upwelling where the winds are cross-shore, large-scale Ekman upwelling where the winds are alongshore, and enhancement (e.g., Ría de Vigo)

or suppression (e.g., Tomales Bay) of buoyancy-driven vertical circulation due to density differences between the bay and the ocean.

In some bays, an upwind headland casts a wind shadow over part of the bay (**Figure 3**), as in the northern portion of Monterey Bay (Paduan & Rosenfeld 1996), the southern portions of Table Bay and St. Helena Bay during shallow marine layers (Jury 1985, 1988), and the southern portion of La Serena Bay [i.e., Tongoy Bay (Garreaud et al. 2011)]. This is true for bays that are downwind of headlands, commonly referred to as upwelling shadows (Graham & Largier 1997, Kämpf & Chapman 2016). However, other upwelling-shadow bays do not experience a wind shadow, because the headland is too low to block or stall airflow in the atmospheric boundary layer, and offshore winds are observed along the upwind shore of the bay (i.e., the downwind shore of the headland), while alongshore winds blow along the landward edge of the bay, as in St. Helena Bay (Shannon 1985, Jury 1985), Drakes Bay (J.L. Largier, unpublished information), Table Bay (Jury 1985, 1988), and Bodega Bay (Roughan et al. 2005). Localized, small-scale upwelling and upwind flow at depth occur near the upwind shore in some bays [e.g., Bodega Bay (Roughan et al. 2005) and Avila Bay (Walter et al. 2017)] and specifically where wind crests the headland through valleys, forming fast downwind jets [e.g., Ría de Vigo (Gilcoto et al. 2017), Tongoy Bay (Garreaud et al. 2011), and the Gulf of Arauco (Valle-Levinson et al. 2003, F.J. Tapia, unpublished information)].

Many variations on this theme have been observed, including reattachment of the wind downstream, resulting in localized onshore winds that can suppress upwelling [e.g., in La Serena Bay (Tapia et al. 2014) and St. Helena Bay (Jury 1985, Pitcher & Weeks 2006, Pitcher et al. 2014)] prior to the airflow realigning with the coast. And where winds blow parallel to the landward edge of the bay, Ekman upwelling may be seen downwind of the headland (e.g., St. Helena Bay, Table Bay, and Drakes Bay). Temporal variability can be marked, with wind shadows occurring on some days and not on others in response to changes in the thickness of the marine atmospheric boundary layer relative to the altitude of the headland. The effect of Table Mountain on Table Bay is a good example, with shallow southeasters being blocked by the mountain, resulting in calm hot weather in downtown Cape Town, and deep southeasters cresting the mountain as a dense, supercritical flow visible as a smooth sheet of clouds over the mountain (referred to locally as “the tablecloth”), strong gusty winds in the city (i.e., turbulence in the hydraulic jump), and intense speeds and turbulence resulting in very high wind stress on the surface of Table Bay. Occasionally, the marine atmospheric boundary layer is thick enough that it flows subcritically over the mountain and imposes normal strong wind stress on Table Bay. This Table Mountain example also illustrates what happens when a valley is found inland of a blocking headland, with the Cape Flats jet exhibiting extreme wind speeds during shallow-southeast conditions as winds are funneled over the low-lying land between Table Mountain and the Cape Fold Belt mountains found farther inland: This jet blows offshore across the southeast shore and then alongshore over the east shore of Table Bay, resulting in strong upwelling and some of the coldest surface waters observed in this region. Comparable wind patterns occur where dense airflow crests headlands upwind of other upwelling bays [e.g., St. Helena Bay (Jury 1985, Lamberth & Nelson 1987) as well as Ría de Vigo (Gilcoto et al. 2017) and the Gulf of Arauco; **Figure 3**].

In contrast to bays that are downwind of a prominent headland (upwelling shadows), other bays are characterized by their location upwind of a prominent headland. In this case, winds blow into the bay, often trapping waters in the bay. These bays have been previously referred to as upwelling traps [e.g., Antofagasta Bay (Castilla et al. 2002, Largier 2002, Piñones et al. 2007); other examples of upwelling-trap bays oriented into the prevailing wind are False Bay, Todos Santos Bay, and Sebastián Vizcaíno Bay (see **Table 1**)]. This concept has not previously been fully described and goes beyond just the wind pattern; the three key elements are onshore wind, a trapped warm surface layer, and throughflow of cold upwelled water below a strong thermocline. In upwelling

traps, the prevailing alongshore wind blows into the mouth of the bay, onshore and over the downwind headland [e.g., at Muizenberg Beach in False Bay (Jury 1988) and La Rinconada Beach in Antofagasta Bay (Piñones et al. 2007)] or in the form of a sea breeze up a valley [e.g., in the Estero region of Todos Santos Bay (Ladah et al. 2005) and near the Salinas River Valley in Monterey Bay (Woodson et al. 2008)].

In the absence of stratification, an onshore wind may drive localized downwelling (Fewings et al. 2008, Kämpf 2017), but in bays where lateral trapping prevents flushing by alongshore flow, surface waters can warm enough to prevent overturn. This stable thermally stratified layer is then trapped against the shore by the onshore wind stress. Where onshore winds exhibit a marked diurnal cycle, it is in phase with surface heating that builds thermal stability in sync with afternoon strengthening of wind stress (Kaplan et al. 2003, Narvaez et al. 2006). While the feature may relax partially overnight, observed as a poleward propagation of the buoyant layer in Antofagasta Bay, it does not escape the bay quickly enough and is pushed back into the corner the next morning as the sea breeze resumes. Indeed, these features persist for many days and may even persist through relaxation events—e.g., the temperature record at the La Rinconada site in Antofagasta Bay exhibits a 12-day decorrelation time (Piñones et al. 2007), which clearly exceeds the timescale of synoptic variability. In addition to wind, these bays are fully exposed to the alongshore shelf jet and often immediately downstream of an upwelling center (e.g., Punta Coloso and El Cobre for Antofagasta Bay, and Punta Baja for Sebastián Vizcaíno Bay). In upwelling traps, this cold water follows a path through the bay, beneath the trapped warm surface layer, resulting in a very strong and sharp thermocline (Castilla et al. 2002) as water is readily removed from below the thermocline by the cold-water throughflow and removed from above the thermocline by wind-driven circulation in the surface layer. This stratification reduces viscous drag on the sub-thermocline throughflow. It is also important in supporting internal wave activity (Woodson 2018), as observed in Antofagasta Bay (Castilla et al. 2002) and Todos Santos Bay (Filonov et al. 2014) (**Figure 5**).

In addition to the effect of local wind stress, characteristic patterns in bays are set up by the influence of the shelf jet on bay circulation (**Figure 4**). Depending on the bathymetry, vorticity, and local pressure gradients, the alongshore shelf jet may separate from the shore and flow past the bay or remain attached and flow through the bay. The shelf jet may separate fully and flow offshore, in which case weak cyclonic circulation develops inshore [e.g., the Gulf of the Farallones (Kaplan et al. 2005), Cape Blanco (Barth et al. 2000), and Cape Columbine (Shannon 1985)], or the jet may curve shoreward after separation and form a strong headland eddy [e.g., Monterey Bay (Graham & Largier 1997, Paduan et al. 2018)]. Flow separation is more common in upwelling-shadow bays with prominent upwind headlands, while an attached shelf jet is more typical of an upwelling-trap bay (e.g., Antofagasta Bay). However, elements of an upwelling shadow and upwelling trap may be seen in the same bay (e.g., Ría de Vigo and Ría de Pontevedra) where the upwelling jet splits, with some flow past the bay and some through the outer bay (Barton et al. 2015, Aguiar 2016, Piedracoba et al. 2016). In upwelling-trap bays (e.g., False Bay, Todos Santos Bay, and Antofagasta Bay), partial separation of the shelf jet may occur at the upwind headland, but the flow continues along an anticyclonic sub-thermocline path through the bay. In an upwelling-shadow bay (e.g., Monterey Bay), the separated jet converges on the shore midbay, feeding into a cyclonic headland eddy, but some part of the onshore flow may curve anticyclonically and flow into the downwind corner and then out of the bay (Paduan & Rosenfeld 1996, Paduan et al. 2018) (**Figure 6**), as in an upwelling-trap bay. Whatever the nature of the shelf-driven bay circulation, it is confined to the outer bay, typically no more than one bay width into an elongated bay [e.g., Ría de Vigo (Barton et al. 2015, Piedracoba et al. 2016)]. This circulation fills the outer bay with cold, nutrient-rich water.

The third key forcing of upwelling bays is due to the difference in density between cold upwelled waters over the shelf and warmer waters in the bay, which is visible in both plan-view

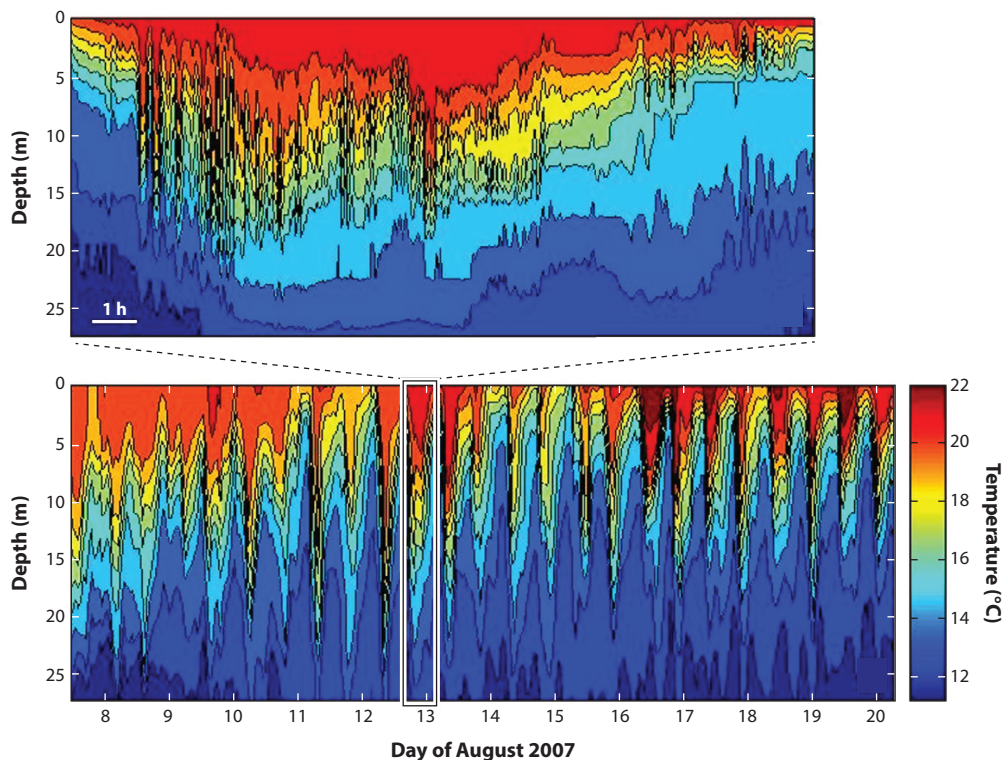


Figure 5

High-frequency profiles of temperature observed near San Miguel in Todos Santos Bay (31.89°N) in August 2007, where southward-flowing cold water subducts beneath the warm surface waters in the bay. Fluctuations in stratification are dominated by internal tides, with associated pulses of high-frequency internal wave energy that is important in onshore transport of nutrients and plankton (Ladah et al. 2005, 2012). Figure adapted from Filonov et al. (2014) with permission from Elsevier.

patterns of sea surface temperature (**Figures 2, 6, and 7**) and section-view patterns of cold water at depth (Largier et al. 1997, Monteiro & Largier 1999, Barton et al. 2015). While this buoyancy forcing may be enhanced by land runoff to the bay, the focus here is on thermal buoyancy, as this is typically dominant during the upwelling season [which is also the dry season in the Mediterranean climates that characterize coastal upwelling regions, specifically at middle and low latitudes (Largier 2010)]. In the absence of other forcing, one expects surface water in the bay to warm up, whereas shelf waters are kept cool by upwelling. As the bay warms, a steady thermal exchange flow may develop, but this is seldom seen, as the setup time is longer than the timescale of synoptic variability in upwelling winds. What is commonly observed are nonsteady intrusions of cold, dense waters into a bay following an upwelling event over the shelf, as in Saldanha Bay (Monteiro & Largier 1999), Ría de Vigo (Piedracoba et al. 2005, Barton et al. 2015, Gilcoto et al. 2017), and Tomales Bay (Largier et al. 1996), as well as the draining of cold, dense water from the bay following the warming of shelf waters during relaxation events, as in Ría de Vigo (Barton et al. 2015, 2016). While typically weak, this vertical exchange flow can be enhanced by winds when the surface stress is in the same direction as the buoyant outflow [e.g., as in Ría de Vigo (Gilcoto et al. 2017)], but it can also be stalled by winds that blow in the opposite direction [e.g., as in Tomales Bay (J.L. Largier, unpublished information)] or by strong vertical mixing due to winds or tides. In an elongated bay, one would expect shelf-driven circulation in the outer bay and thermal

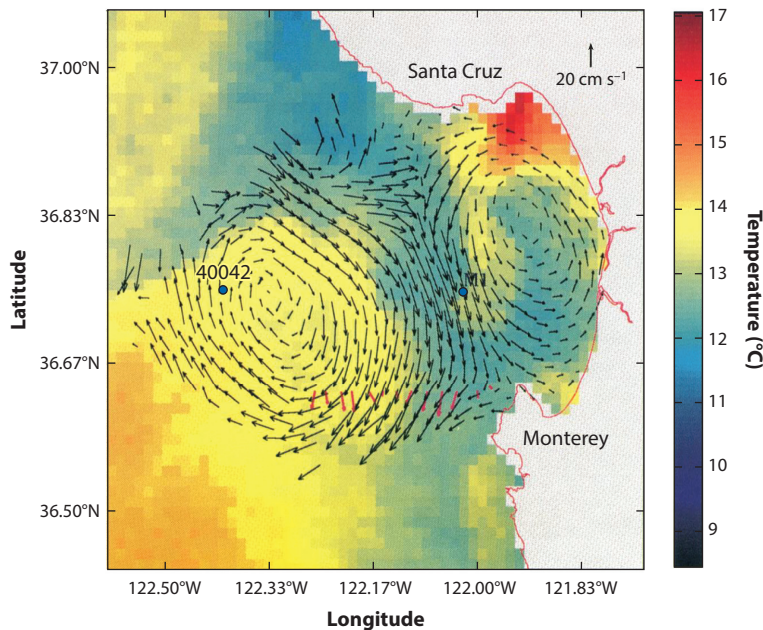


Figure 6

The characteristic circulation pattern observed in Monterey Bay, showing surface temperatures and surface currents on August 6, 1994. Black arrows represent velocities measured with high-frequency coastal ocean dynamics applications radar (CODAR), and magenta arrows represent near-surface currents measured with vessel-mounted acoustic Doppler current profilers (ADCPs). Moored buoys provide data on wind and sea temperature at the black dots labeled “40042” and “M1.” Blue areas indicate cold water from the upwelling center at Point Año Nuevo (37.1°N) streaming south and curving into the bay, entrained by a cyclonic eddy in the bay (with a second branch directed offshore). Red and yellow areas indicate warm surface waters retained in the upwelling shadow in northern Monterey Bay. Figure adapted from Paduan & Rosenfeld (1996) with permission; copyright 1996 American Geophysical Union.

exchange flows midbay, where the longitudinal thermal gradient is strongest and tides and winds are typically weak (Largier 2010). This bay–ocean buoyancy forcing is one element of remote wind forcing (*sensu* Wong & Valle-Levinson 2002), and the other is subtidal fluctuations in bay–ocean water levels. These elements are referred to as remote wind forcing because they are due primarily to wind-driven fluctuations in the density and water level over the shelf—i.e., they are not locally imposed by winds in the bay. The direct effect of wind stress on the surface of the bay (local wind forcing) is often highly correlated with this remote wind forcing, which can lead to difficulty in interpreting the dynamics from correlated observations (e.g., Gilcoto et al. 2017).

Surface warming and bay–ocean thermal gradients are important in accounting for stratification and surface fronts in bays. Marked fronts develop where warm surface waters in the bay meet the alongshore flow of cold waters over the shelf, forming an arrested buoyancy front [e.g., Monterey Bay (Graham & Largier 1997, Woodson et al. 2009, Ryan et al. 2014) and Antofagasta Bay (Lagos et al. 2002)]. Lagos et al. (2002) showed the persistence of the front between warm surface waters in Antofagasta Bay and the cold upwelled waters streaming past and through the bay. Thermal stratification in upwelling bays appears to be strengthened by the presence of very cold subsurface water—colder than that observed at similar depths over the adjacent open shelf [e.g., Drakes Bay (J.L. Largier, unpublished data)]. Whether due to topographic effects [such as canyon-induced upwelling in the Gulf of Arauco (Sobarzo et al. 2016)], the tendency for enhanced

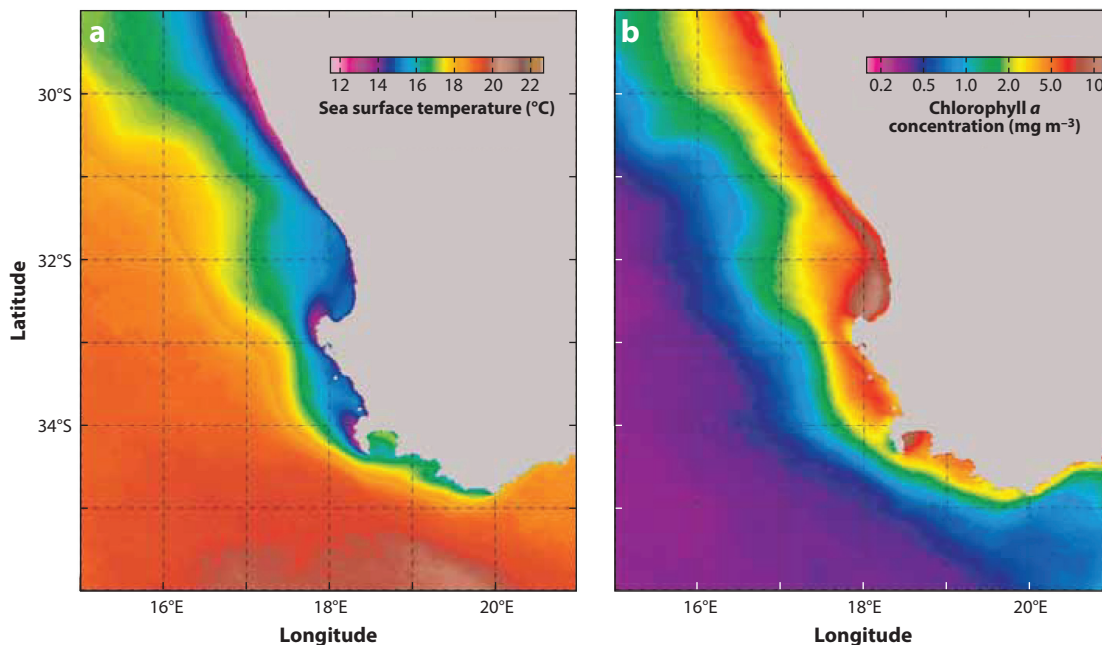


Figure 7

(a) Sea surface temperatures and (b) surface chlorophyll *a* concentrations for coastal waters in the southern Benguela Current, showing local minima in temperature at upwelling centers and local maxima in temperature in four bays: Walker Bay (34.4°S, 19.2°E), False Bay (34.2°S), Table Bay (33.9°S), and St. Helena Bay (32.6°S). Associated maxima in surface chlorophyll in the bays extend northward from the bays that are upwelling shadows. Satellite data are averaged from July 1998 to June 2003. Figure adapted from Weeks et al. (2006) (in which seasonal and synoptic variability are also shown) with permission.

upwelling at headlands, or the feedback by which vertical mixing is reduced by stratification, the presence of very cold bottom waters in bays enhances thermal stratification and associated effects. Intense (strong and thin) thermoclines are observed in both upwelling shadows [e.g., Monterey Bay (Woodson et al. 2009)] and upwelling traps [e.g., Antofagasta Bay (Castilla et al. 2002)], often supporting thin-layer subsurface chlorophyll maxima (Castilla et al. 2002, Ryan et al. 2010, Durham & Stocker 2012, Lucas et al. 2014) or very high concentrations of phytoplankton trapped in the shallow, light-filled surface layer [e.g., St. Helena Bay (Lucas et al. 2014) and the Gulf of the Farallones (Vander Woude et al. 2006)]. Furthermore, energetic internal waves are observed on this marked stratification and may be important in transporting plankton shoreward [e.g., as in Antofagasta Bay (R. Guíñez, unpublished information) and Todos Santos Bay (Ladah et al. 2005)].

An additional factor is the pulsed nature of forcing, yielding patterns of temporal variability in winds, currents, water levels, and water density. In contrast to estuaries, where time-dependent forcing is due primarily to tides and freshwater inflow, in upwelling bays temporal variability is associated primarily with synoptic fluctuations in winds, which in turn result in fluctuations in the above three dynamics: wind forcing on the bay, the strength and orientation of the shelf jet, and bay–ocean density and water-level gradients. As noted above, this variability has been addressed elsewhere by differentiating between local winds that influence the bay directly and remote winds that influence the flow, water level, and density of waters over the shelf. Remote wind forcing is important in exchange between Chesapeake Bay and the ocean (Rennie et al. 1999, Wong & Valle-Levinson 2002), owing to changes in ocean water level, as well as in Ría de Vigo and Ría de Pontevedra (Gilcoto et al. 2007) and Saldanha Bay (Monteiro & Largier 1999), owing to changes

in ocean density. However, in upwelling bays, forcing by the alongshore flow is often more important. Wind fluctuations are notably important where separation features develop during upwelling winds, because these features relax as winds weaken, often leading to flushing of the bay. Elevated water level and low water density in the bay result in a poleward propagation of water out of the bay in the form of a coastal buoyancy current pulse. This has been observed at the upwind ends of the Gulf of the Farallones (Wing et al. 1995), St. Helena Bay (Nelson & Hutchings 1987), the Santa Barbara Channel (Washburn et al. 2011, Suanda et al. 2016), the Gulf of Cádiz (Relvas & Barton 2002), and Monterey Bay (Woodson et al. 2009). In smaller bays, like Bodega Bay (Morgan et al. 2012) and Cartagena Bay (Bonicelli et al. 2014), observations of larval concentrations, water properties, and GPS-tracked drifters show complete replacement of bay waters during relaxation flows. In bays upwind of a freshwater source [e.g., Ría de Vigo, which is upwind of the Minho and Douro Rivers (Barton et al. 2016); Grays Harbor, which is upwind of the Columbia River (Hickey & Banas 2003); and the Gulf of Arauco, which is upwind of the Itata and Biobio Rivers (Sobarzo et al. 2007)], not only do the shelf waters warm, but salinity is also lowered as flow reversals transport river plume waters past the mouth of the bay, resulting in enhanced bay–ocean density gradients that can drive an inverse vertical circulation that can flush the bay in days (Barton et al. 2015), including semiencloded bays (e.g., Hickey & Banas 2003).

TYPES OF BAYS

In upwelling regions, the interactions of winds and currents with the topographic structure and surface heating produce characteristic physical structures as described above, and these interactions lead to specific ecological consequences. Bays can be divided into different types based on the three primary drivers of circulation in upwelling bays (local wind stress, the influence of shelf jets, and bay–ocean differences in buoyancy and water level), with the type determined primarily by the degree of exposure to the strong winds and currents found over upwelling shelves. Bays of the same type are expected to be very similar in oceanographic form and function even though they are located in different regions. One can identify three major types of upwelling bay within a continuum: (*a*) wide-open bays (width much greater than length), which are highly exposed to shelf forcing (e.g., the Sonoma Coast); (*b*) square bays (width approximately the same as length, although they are not necessarily square in shape), where shelf forcing is important but not dominant (e.g., Monterey Bay); and (*c*) elongated bays (width much less than length), exhibiting longitudinal zones with shelf forcing restricted to the outer bay (e.g., Ría de Vigo).

Further subcategories of these major types can be identified based on size [small bays, with sizes less than the Rossby radius—e.g., Bodega Bay (Roughan et al. 2005)], depth [shallow bays, with depths shallow enough to slow Ekman transport, buoyancy-driven shear flow, and vertical circulation—e.g., San Quintín Bay (Canu et al. 2016)], mouth constriction [semiencloded bays, with mouths narrower than the bay landward of the mouth, so that tidal pumping is important—e.g., Tomales Bay (Largier et al. 1997)], and asymmetry [step bays, with a headland only at one end of the bay, so that the coastline form is best described as a step—e.g., St. Helena Bay (Penven et al. 2000)]. Although the term bay is used loosely across the literature, it can be distinguished by the dominant drivers of circulation: Here I consider bays (forcing by winds, shelf currents, and surface heating) to be distinct from estuaries (forcing by tides, river through-flow, and freshwater buoyancy), coves (forcing by wave-driven flow), tidal bays (forcing by tides), and lagoons (forcing by tides and waves). Thus, in this review of upwelling bays, the effects of waves, river inflows, and tides on bay-scale circulation and stratification patterns are treated as secondary.

While the degree of exposure is the basis for differentiating between wide-open, square, and elongated bays, additional dynamical insight is gained from analysis of the three forcing terms:

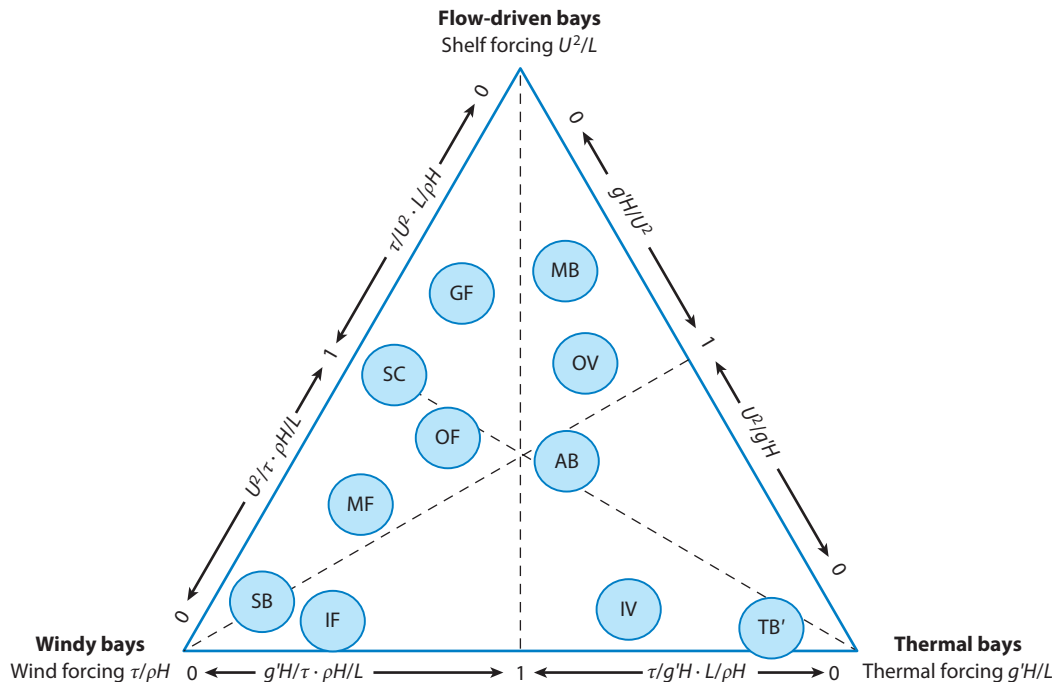


Figure 8

Differences between bays based on the relative strengths of three types of forcing: wind forcing, thermal forcing, and shelf forcing. The top apex represents bays dominated by the influence of shelf flows, the bottom left apex represents bays dominated by the influence of wind forcing, and the bottom right apex represents bays dominated by the influence of thermal forcing. Specific bays are classified according to typical forcing: Antofagasta Bay (AB), inner False Bay (IF), middle False Bay (MF), outer False Bay (OF), the Gulf of the Farallones (GF), outer Monterey Bay (MB), inner Ría de Vigo (IV), outer Ría de Vigo (OV), Saldanha Bay (SB), the Sonoma Coast (SC), and Tomales Bay in the days after an upwelling event (TB').

shelf forcing (the inertia and vorticity of circulation over the shelf), wind forcing (local surface wind stress), and thermal forcing (pressure gradients due to ocean–bay differences in density and water level). The importance of these terms is scaled by U^2/L , $\tau/\rho H$, and $g'H/L$, respectively, where U is the velocity scale of the shelf jet, L is the length scale of the bay, H is the depth scale of the bay, τ is the surface wind stress, ρ is water density, $g' = g \Delta \rho / \rho$ is reduced gravity, g is gravity, and $\Delta \rho$ is the scale of the bay–ocean density difference. Bays can be categorized in a three-apex schematic (**Figure 8**), with end members conceived of as (a) thermal bays, in which the bay circulation is driven entirely by buoyancy; (b) windy bays, in which the bay circulation is driven entirely by local wind stress, similar to a wind-driven lake; or (c) flow-driven bays, in which the bay circulation is driven entirely by shelf flow. The edges of the triangle can be conceived of as (a) a wind shadow, with no wind forcing, where the relative importance of thermal effects to shelf-jet effects is given by $g'H/U^2$; (b) active shelf upwelling, with no thermal forcing, where the relative importance of wind relative to inertia is given by $(\tau/U^2)(L/\rho H)$; and (c) a wind-forced thermal bay, with no shelf-flow forcing, where the importance of wind relative to thermal effects is given by $(\tau/g'H)(L/\rho H)$. While it is desirable to categorize bays according to the dominant forcing, in reality most upwelling bays exhibit time-dependent shifts in the relative importance of terms associated with synoptic and seasonal variability, and in elongated bays there are differences between inner and outer zones. Thus, I suggest a simpler scheme that categorizes bays in terms

of their shape (openness) and exposure to the strong winds and currents found over upwelling shelves.

Wide-open bays (width:length > 2:1) are often called embayments or gulfs, but equally often they are not distinct and have not been given a geographic name—e.g., the region between Point Arena and Point Reyes, which is referred to as the Sonoma Coast (Largier et al. 1993, 2006; Wing et al. 1995; Halle & Largier 2011). Here, winds blow strongly and the inertia of the alongshore shelf jet typically dominates the bay, often flowing through the bay without fully separating from the coast (**Figure 3a**). In wide-open bays, the orientation of the shelf edge can often become important because the barotropic alongshore jet will track the topography, resulting in separation from the shoreline and the development of a cyclonic eddy inshore of the jet [e.g., downstream of Cape Columbine offshore of St. Helena Bay (Shannon 1985, Penven et al. 2000) and off northern Portugal in the vicinity of Aveiro (Oliveira et al. 2019)]. Alongshore winds can also separate from the shoreline, resulting in a band of wind stress curl offshore (e.g., Jury 1985, 1988; Enriquez & Friehe 1995) and an associated upward slope in the water level toward the coast that weakens or reverses alongshore flow close to the coast (i.e., a cyclonic circulation feature and retention of waters over the inner shelf). This is typical of step bays, such as the Gulf of the Farallones, La Serena Bay, and St. Helena Bay, all of which are wide-open bays but defined by a marked upwind boundary where the coastline exhibits a step and winds tend to separate from the coast. In these large step bays, there is often a distinct smaller bay with a specific name (Drakes Bay, Tongoy Bay, and Agterbaai, respectively), because here the winds are weak and the waters warm in an upwelling shadow. Downwind of this sheltered bay, wind stress tends to be onshore (e.g., Jury 1985), resulting in shoreward transport of near-surface plankton and surface flotsam (Halle & Largier 2011, Pitcher et al. 2014). Although not linked to specific bays, Point Conception (California) and Cape Sagres (Portugal) are major step breaks in shoreline orientation and exhibit comparable features, including an offshore band of wind curl, a tendency for poleward flow nearshore, and an upwelling-sheltered region (i.e., the Santa Barbara Channel in California and the Algarve in Portugal).

Square bays (width:length \sim 1:1) have received attention either as an upwelling shadow (where the jet separates and forms an eddy, with a partial wind shadow—e.g., Monterey Bay) or as an upwelling trap (where the jet flows into and sometimes through the bay beneath a warm layer, which is trapped in the bay by onshore winds—e.g., Antofagasta Bay) (see **Table 1** and the section titled Space-Time Patterns in Circulation and Stratification). These bays are demarcated by two headlands, and because they are narrower than wide-open bays, the shelter of the upstream headland stretches across much of the bay. Wind-driven coastal upwelling is disrupted in these bays due to headland shelter from the regional wind, the orientation of the wind (often onshore in the bay), or the scale of the bay. Winds are onshore in upwelling traps and also tend to be onshore in upwelling-shadow bays downwind of the wind shadow [e.g., St. Helena Bay (Jury 1985; **Figure 7**)—markedly so where a low-lying valley extends landward from the bay (**Figure 3d**). In Monterey Bay, diurnal sea breezes blow strongly up the Salinas Valley, and the same happens with sea breezes in the Gulf of the Farallones that blow strongly through the Golden Gate. Comparable onshore sea breezes are also observed in upwelling traps such as Antofagasta Bay and Todos Santos Bay.

When bay width (alongshore dimension) is similar to length (cross-shore dimension), a marked and reliable separation-driven headland eddy typically forms (Paduan et al. 2018) and tends to fill much of the bay, continuously importing shelf waters into the bay (**Figure 6**). The presence of the downwind headland is important in constraining the size of the headland eddy (see Penven et al. 2000) and in producing an upwind pressure gradient that can enhance the recirculation eddy in the bay or at least drive an upwind return flow at depth (e.g., Roughan et al. 2005). In Monterey Bay,

the eddy transit time is days—long enough for surface waters to warm up in the absence of local upwelling and strong wind-driven mixing. Surface temperature increases several degrees, and the retention time for water in the eddy has been estimated at eight days (Graham & Largier 1997). St. Helena Bay has a similar eddy timescale (Penven et al. 2000). A significant thermal structure develops, which leads to two-layer stratification and circulation adjacent to the upwind headland. Where warm surface water meets cold upwelled water at the mouth of the bay, a marked thermal front develops (see the section titled Space-Time Patterns in Circulation and Stratification). Similarly, a warm surface layer develops in upwelling-trap bays, with a strong and shallow thermocline and a marked front again forming where inflowing cold upwelled water plunges beneath the warm layer in the bay (Lagos et al. 2002). Although the mechanism is different to upwelling-shadow bays, the retention time for this surface layer in Antofagasta Bay is also several days (Piñones et al. 2007).

Elongated bays (width:length < 1:2) are longer than they are wide and thus extend landward beyond the direct influence of shelf circulation, so that there are distinct longitudinal zones in the bay. For example in the 12-km-wide Ría de Vigo, shelf-driven circulation dominates the outer ~12 km of the bay (Barton et al. 2015, Piedracoba et al. 2016), while buoyancy gradients and local wind forcing dominate the midbay (Barton et al. 2015, Gilcoto et al. 2017). Local wind forcing may play an important role in either countering or reinforcing the buoyancy-driven vertical circulation: In Ría de Vigo, winds blow out of the bay during coastal upwelling events, which accelerates the response of the bay to buoyancy forcing (Gilcoto et al. 2017), whereas in Tomales Bay, winds blow into the bay during coastal upwelling events, stalling the buoyancy circulation by opposing it and by vertical mixing [resulting in very long residence times in the bay (Largier et al. 1997)]. As all three primary drivers weaken in the inner bay, other types of forcing can become important—specifically, a dense bottom layer can intrude slowly into elongated bays, taking a few days to do so in Ría de Vigo (Barton et al. 2017), in bays in Oregon (Hickey & Banas 2003), and in Tomales Bay (Harcourt-Baldwin 2003). Similar density-driven intrusions are also observed in Saldanha Bay (Monteiro & Largier 1999) and Concepción Bay (Arcos & Wilson 1984).

In addition to forcing terms characteristic of upwelling bays, tides and river inflow can be important in elongated bays. Tidal currents may be strong because elongated bays often exhibit lateral constrictions, which introduce tidal pumping (Chadwick & Largier 1999). In these cases, which are a hybrid of tidal bay and upwelling bay, the shelf-driven exchange is replaced with tide-driven exchange, which similarly fills the outer bay with cold upwelled waters [e.g., Tomales Bay (Largier et al. 1997) and San Quintín Bay (Canu et al. 2016)]. River inflow, even if seasonally weak (as in Mediterranean-climate zones), can play a role in the innermost zones of the bay, where the bay is thermally saturated and winds are weak (Largier et al. 1996, Largier 2010).

PLANKTON AND PELAGIC PRODUCTIVITY

The primary ecological consequence of bays in upwelling regions is their high productivity (Figures 2 and 7), since nutrient-rich upwelled waters can be retained long enough to allow dense phytoplankton blooms to develop, which in turn support abundant food webs. In the absence of bays, blooms typically develop offshore (Hutchings et al. 2006, Largier et al. 2006, Kämpf & Chapman 2016). Not only are high-nutrient upwelled waters retained in the bay, but they are also retained near the surface by thermal stratification, so that phytoplankton are exposed to elevated light levels. High surface chlorophyll has been observed in upwelling shadows in Monterey Bay (Ryan et al. 2005), the Gulf of the Farallones (Vander Woude et al. 2006), Lisbon Bay (Oliveira et al. 2009), and St. Helena Bay (Pitcher et al. 1996, 2010; Weeks et al. 2006) (see Figure 9), and typically these surface blooms are dominated by diatoms, supporting large-celled food webs (Hutchings et al. 2006). While these dense surface blooms are local sinks for atmospheric carbon

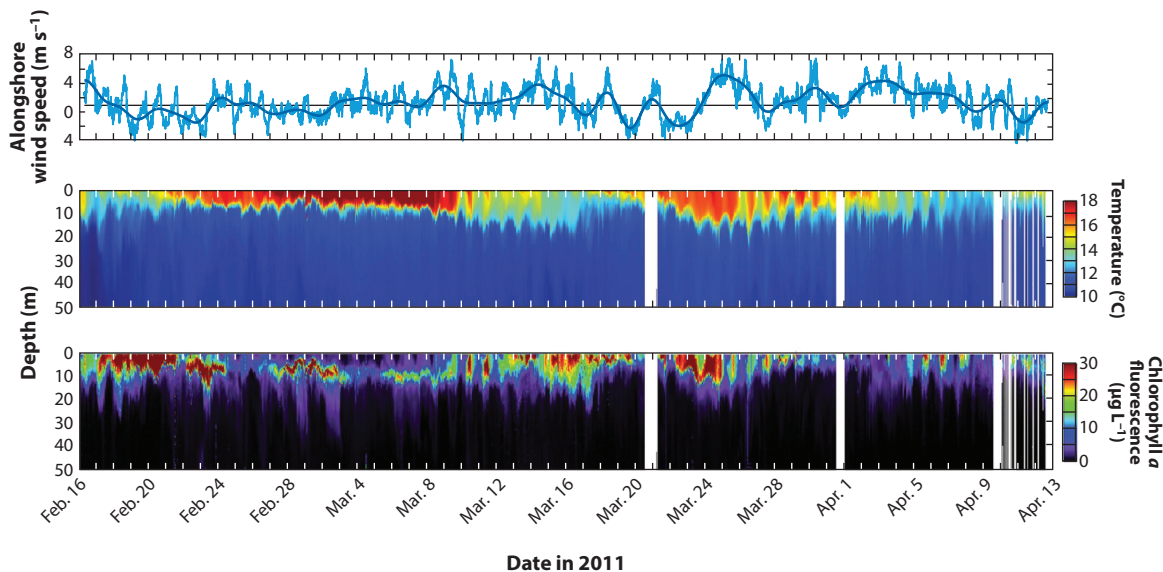


Figure 9

High-frequency time series of profiles of temperature and chlorophyll *a* fluorescence in St. Helena Bay from February to April 2011. The 62-m-deep site is in the middle of this wide-open bay, approximately 50 km north of the headland at Cape Columbine (32.8°S). In the top panel, the bold black line is 33-h, low-passed alongshore wind speed (positive values are upwelling favorable). Cooler surface waters and weaker stratification during upwelling events are replaced by warmer surface waters and very strong stratification during relaxation events. Warm surface water is more persistent in the bay closer to the cape. During upwelling, the chlorophyll concentration is highest in the surface mixed layer (e.g., February 18–22), whereas a subsurface chlorophyll maximum is observed during relaxation events (e.g., March 1–9), when nutrients above the thermocline are depleted. While the influence of internal tides is evident in these high-frequency data, variability is dominated by diurnal fluctuations in stratification and chlorophyll levels that correlate with sea-breeze forcing in the bay. Figure adapted from Lucas et al. (2014) with permission from Elsevier.

dioxide (very low surface $p\text{CO}_2$ and trapping of cold, high $p\text{CO}_2$ below the surface), the areas of upwelling bays are assumed to be too small to be significant in regional carbon fluxes (let alone global fluxes). However, the low surface $p\text{CO}_2$ is important in mitigating the effects of ocean acidification locally in bays, in contrast to high exposure at headlands, where upwelling centers occur and carbonate undersaturated water can break the surface (Feely et al. 2008).

Phytoplankton provide the base of the pelagic food web (Kudela et al. 2008a), supporting high levels of zooplankton (Peterson et al. 1988, Graham et al. 1992), fish (Hutchings et al. 2006), and upper-trophic-level consumers such as birds, sharks, and mammals in bays. For example, krill aggregations occur in the vicinity of the thermal front in northern Monterey Bay, which in turn support feeding whales (Croll et al. 2005). Thus, bays partially resolve the paradox of productivity in upwelling regions (Largier et al. 2006): The strong winds that supply nutrients to the euphotic zone also lead to a reduction in light exposure through deep mixing of phytoplankton, as well as increased plankton loss through offshore transport. Stratification in bays maintains high light levels for phytoplankton, and the bay circulation retains both phytoplankton and zooplankton in coastal habitats. Thus, bays are reliable high-productivity areas, where conditions conducive for phytoplankton blooms occur in sync with the wind-driven supply of nutrients to the euphotic zone.

Phytoplankton productivity in bays can also be exported to adjacent shelf waters during relaxation events, where it can initiate a spatially extensive bloom. When upwelling relaxes, part of the in-bay bloom is advected out of the bay and spreads in a coast-attached, stratified poleward

flow, greatly increasing the total biomass of the bloom. This occurs regularly when the Drakes Bay bloom in the Gulf of the Farallones spreads northward to Bodega Bay and beyond (Send et al. 1987, Kaplan & Largier 2006, Vander Woude et al. 2006, Kudela et al. 2008a). Blooms that originate in Monterey Bay also spread northward during relaxation, so that the greater Gulf of the Farallones region, which extends 200 km from north of Bodega Bay to south of Monterey Bay and encompasses multiple bays, is characterized by persistently high surface chlorophyll (García-Reyes & Largier 2012). This region is well recognized as a highly productive marine ecosystem with abundant sharks, birds, and mammals, hosting 3 federally proclaimed marine protected areas (the Cordell Bank, Greater Farallones, and Monterey Bay National Marine Sanctuaries) and 12 state-proclaimed marine protected areas. Álvarez-Salgado et al. (2000) also addressed outwelling from the Rías Baixas (Spain), and poleward advection of high-chlorophyll water past Point Conception (California) has been observed by Washburn et al. (2011) and Nidzieko & Largier (2013). Regional bay-anchored productivity appears to also characterize the vicinity of La Serena and Tongoy Bays (Chile), Lisbon and Setubal Bays (Portugal), the Gulf of Arauco and Concepción Bay (Chile), Mejillones and Antofagasta Bays (Chile), and the southern Benguela Current from False Bay to St. Helena Bay (South Africa).

Persistent high surface chlorophyll levels due to phytoplankton blooms are also observed in constricted elongated bays without recirculating eddies, such as Tomales Bay, where the outer bay is filled with cold, high-nutrient coastal waters and a midbay chlorophyll maximum is observed (Kimbrow et al. 2009); a similar feature occurs in the shallow Drakes Estero (Buck et al. 2014). This chlorophyll maximum accounts for the high growth rate of native oysters in midbay. However, during relaxation events, the outer bay may fill with high-chlorophyll coastal waters imported from the shelf, which is more typical in Grays Harbor, where open-coast blooms are more common (Hickey & Banas 2003). A different situation occurs in deeper, nonconstricted elongated bays with shorter residence times, such as Ría de Vigo, where phytoplankton blooms are not steady but rather pulse in sync with synoptic variability over the shelf. The depth of the bay allows vertical exchange flows, with a dense subsurface inflow of upwelled water during coastal upwelling events that fuels midbay blooms when the cold, high-nutrient water enters the euphotic zone. Alternatively, a surface inflow of buoyant coastal waters occurs during relaxation (Barton et al. 2015, 2016; Gilcoto et al. 2017), which imports active blooms from the coastal ocean. The highest concentrations of phytoplankton occur during buoyant inflows from the shelf, which is also when harmful algal blooms are most likely to occur in Ría de Vigo (Figueiras et al. 1996, Crespo et al. 2006).

In upwelling bays where the surface layer persists long enough that nutrients can be fully depleted, surface chlorophyll is low at times. However, a strong subsurface chlorophyll maximum develops on the shallow thermocline, which is typically well inside the euphotic zone [e.g., Antofagasta Bay (Castilla et al. 2002)]. These thin-layer phytoplankton blooms have been studied in northeast Monterey Bay (Ryan et al. 2010) and St. Helena Bay (Lucas et al. 2014) (**Figure 9**). The blooms become horizontally extensive as they are spread out by the shear between the two layers that characterize stratified upwelling bays.

In upwelling bays, a surface band of high chlorophyll may be observed along the thermal front between the low-chlorophyll, warm, aged upwelled waters within the bay and the low-chlorophyll, cold, newly upwelled waters near the mouth, specifically on the stratified side of the front, where a nonzero nutrient flux is combined with vertical stability that ensures good light for phytoplankton. This front-associated phytoplankton biomass is important because it co-occurs with frontal aggregations of zooplankton and meroplankton consumers (Franks 1992, Ryan et al. 2014, Weidberg et al. 2014). In general, high levels of zooplankton are present in upwelling bays (Graham et al. 1992), and aggregations of zooplankton on fronts are important for foraging fish and whales as well as for birds.

Phytoplankton distributions are also important for shoreline benthic consumers. Surface blooms are readily delivered to shore through onshore winds (e.g., Narvaez et al. 2006) and wave-driven nearshore circulation (McPhee-Shaw et al. 2011), which is expected to be strongest on dissipative shores (Morgan et al. 2015). Alternatively, subsurface phytoplankton are delivered to shoreline habitats through internal waves on shallow thermoclines, which can swash thermocline water up to the surface (e.g., Lucas et al. 2011)—a process similar to the delivery of mussel larvae to shoreline habitats (Ladah et al. 2005) and addressed more broadly by Woodson (2018). This process is important in stratified upwelling bays such as Antofagasta Bay, where dense beds of filter-feeding *Pyura* along the shoreline were apparently supported by subsurface phytoplankton found offshore (Castilla et al. 2002, 2004), and is also evident in St. Helena Bay (**Figure 9**).

Phytoplankton patterns in upwelling bays are also expressed in the abundance of specific taxa (Pitcher & Nelson 2006). Much attention has been given to harmful algal bloom species that favor the sheltered and stratified bay waters (Pitcher et al. 2010), consistent with the importance of dinoflagellates as harmful algal bloom species (in addition to *Pseudo-nitzschia*, which also favors warmer stratified waters). This is a persistent local issue, e.g., in northeast Monterey Bay (Ryan et al. 2009), St. Helena Bay (Pitcher & Weeks 2006), and historically in Drakes Bay (Lewitus et al. 2012). These bay blooms also act as an inoculum for more widespread harmful algal blooms outside of bays, which may occur during relaxation events (Ryan et al. 2009), such as the *Gonyaulax* bloom in the Sonoma Coast embayment in August 2011 that originated in Drakes Bay (Rogers-Bennett et al. 2012). Similarly, a coast-wide *Pseudo-nitzschia* bloom that developed along the US west coast during quiescent marine-heat-wave conditions in the summer of 2015 (McCabe et al. 2016) likely spread out from preexisting localized blooms in bays.

BENTHIC HABITAT PATTERNS

Subtidal benthic invertebrate communities depend on bay circulation, stratification, and near-surface productivity to deliver larval recruits, to deliver particulate food, and to maintain suitable water properties. In upwelling bays, there is an elevated likelihood of local recruitment associated with retention in the bay (see the section titled Dispersal of Meroplankton) as well as the potential for recruitment of larvae spawned at distant locations owing to the exchange of bay and shelf waters. For food subsidies, a bay effect is also expected due to the recurrent pattern of surface productivity outlined in the preceding section (Plankton and Pelagic Productivity), but there are few studies that link patterns of growth to patterns of allochthonous fluxes in bays.

Most recent attention has been given to changing water properties associated with ocean acidification and deoxygenation, which are primary threats to benthic communities under a changing climate. As pH, aragonite saturation state, and dissolved oxygen levels trend downward, new minima are expected in subsurface waters, specifically below the euphotic zone and near the bottom in bays. Recent work in St. Helena Bay (Pitcher et al. 2014), Monterey Bay (Booth et al. 2012), Mejillones Bay (Fajardo et al. 2018), Tongoy Bay (Lagos et al. 2016), Cartagena Bay (J. Bonicelli, unpublished data), the Gulf of Arauco (F.J. Tapia, unpublished data), and the Gulf of the Farallones (K.M. Hewett & J.L. Largier, manuscript in review) makes it clear that these chemical conditions are highly variable, reflecting seasonal, synoptic, and/or diurnal fluctuations. These conditions are also spatially patchy, with a mosaic of minima that can be expected to relate to patterns of circulation, stratification, near-surface productivity, and light penetration as well as to patterns in the organic content and state of sediments. High-frequency variability is associated with internal tides and waves [e.g., St. Helena Bay (Lucas et al. 2014)] and with the internal-tide pulsing of deep water out of canyons [e.g., Monterey Bay (Walter et al. 2014)]. Synoptic-scale canyon upwelling and the intrusion of cold, low-oxygen waters into the Gulf of Arauco have also been observed (Sobarzo et al. 2016).

The biggest concern, however, is where stratification persistently separates high levels of photosynthesis above the thermocline from high levels of decomposition and respiration below the thermocline, which occurs when the thermocline is deeper than the euphotic zone (e.g., during dense surface blooms). In this scenario, bays may be subject to abiotic forcing similar to that in dead-zone phenomena beneath river plumes (Diaz & Rosenberg 2008), with hypoxia occurring as multiday events during times of high stratification that are persistent enough to result in algal die-off in the surface layer. Preliminary data off Bodega Head show that local sub-thermocline hypoxia is correlated with high-chlorophyll surface plumes during relaxation events (K.M. Hewett & J.L. Largier, manuscript in review). The influence of additional nutrients, organic loading, turbidity, and buoyancy associated with land runoff may be important at the scale of bays—e.g., the contribution of wastewater loading to Santa Monica Bay (Howard et al. 2014). Small-scale variability (events and patches) is also expected to be the critical issue as pH and aragonite saturation state decrease with ocean acidification. Coherent structures in circulation, stratification, and near-surface productivity suggest that specific habitat zones should be identifiable in bays (e.g., Fajardo et al. 2018) and over the shelf (Grantham et al. 2004).

Sub-thermocline hypoxia and acidification are also a concern for aquaculture in upwelling bays, where shallow strong stratification can allow this water to move into nearshore regions that are typically unstratified and ventilated. For example, hypoxia has been a concern for scallop farming in Tongoy Bay (Lagos et al. 2016) and oyster farming in the Gulf of Arauco (F.J. Tapia, unpublished information), while low-aragonite-state intrusions are a significant concern for oyster farmers in Tomales Bay, Humboldt Bay, and Netarts Bay (Barton et al. 2012). The absence of reports of low-oxygen, low-pH, or low-aragonite-state intrusions affecting mussel farming in Ría de Vigo (Figueiras et al. 2002) and other bays in northwest Spain is likely due to the short residence times of these bays, a result of regular flushing by density-driven vertical exchange flows.

In shallow benthic habitats, the growth of algae also exhibits a pattern that is associated with the oceanography of upwelling bays. Broitman & Kinlan (2006) explored the idea that fixed macrophytes such as kelp do best in cold and clear upwelled water that flows rapidly past headlands, while planktonic photosynthesizers do better in retentive and stratified bays. Phytoplankton are quickly washed away from headlands, whereas kelp can hold on. However, kelp cannot establish itself at depth in turbid bay environments, whereas phytoplankton can remain near the surface in stratified water and continue to grow. The same principle is expected to hold at smaller scales in upwelling bays—i.e., phytoplankton win in the warm, stratified inner bay, while kelp win in the clear, high-nutrient waters in the outer bay—and thus different communities are expected to occur in the different regions of the bay. This appears to be the case in Tomales Bay, Ría de Vigo, and False Bay, but the observed patterns may be confounded by parallel patterns in substrate (i.e., rocky shore versus sand or mud substrate) and need further analysis.

DISPERSAL OF MEROPLANKTON

The same tendency for retention in bays that promotes phytoplankton and zooplankton population blooms makes upwelling bays important sites for recruitment of planktonic propagules (e.g., Largier 2004). Retention timescales exceed synoptic variability timescales and are a significant fraction of typical planktonic larval durations, which are weeks to months (Shanks et al. 2003). Furthermore, for highly fecund populations, the probability of survival to recruitment is so low that even a very small probability of retention may be demographically important (e.g., in a bay with a 5-day e -folding retention time, 1% of larvae will remain in the bay after 23 days). Furthermore, retention may be greatly enhanced by the interaction of meroplankton with vertical shear (Yanicelli et al. 2006; S.G. Morgan, C.D. Dibble, M.G. Susner, G. Thomas, T.G. Wolcott,

et al., manuscript in review) and fronts (Shanks et al. 2000, Weidberg et al. 2014). Thus, bay populations may be able to maintain themselves through self-recruitment, which is essential for long-term persistence (Hastings & Botsford 2006, White et al. 2010), and bays therefore may act as anchors for widespread metapopulations that at times may be washed out from more exposed habitats along the coast (Largier 2003, White et al. 2010). The productive and sheltered nature of bay habitats can also enhance post-settlement survival, ensuring greater reproductive output and strengthening the resilience of the bay-based population.

At the same time, larvae spawned at distant locations may collect in bays and also recruit at higher levels than on the open coast. Once larvae are entrained into upwelling bays, several mechanisms allow for their accumulation in the bay, so that specific taxa may exhibit much higher planktonic concentrations in bays than elsewhere. First, buoyant or vertical swimming larvae may accumulate at fronts (Franks 1992, Shanks et al. 2000, Weidberg et al. 2014), which are common in bays [e.g., Antofagasta Bay (Lagos et al. 2002) and Monterey Bay (Woodson et al. 2009)]. Second, the tendency for late-stage larvae to remain below the surface (Morgan et al. 2009) serves to concentrate them in localized upwelling in bays where offshore winds drive sheared flow [e.g., Bodega Bay (Roughan et al. 2005)], so that if larvae remain at depth, they will be concentrated in this vertical circulation (S.G. Morgan, C.D. Dibble, M.G. Susner, G. Thomas, T.G. Wolcott, et al., manuscript in review). Finally, several mechanisms promote the delivery of meroplankton to the shore in bay environments, including onshore flows within upwelling shadows (e.g., Monterey Bay and St. Helena Bay) and onshore winds in upwelling traps (e.g., Antofagasta Bay and False Bay) and upwelling shadows (e.g., the Gulf of the Farallones and La Serena Bay). Also, internal tides and internal waves [e.g., St. Helena Bay (Pfaff et al. 2015)] plus sea-breeze-driven internal seiches [e.g., Cartagena Bay (Narvaez et al. 2006) and Monterey Bay (Woodson et al. 2008)] are important in delivering larvae to adult habitat on the shore. Notably, in Todos Santos Bay wind-driven diurnal pulses in recruitment are observed along the downwind shore of the bay, while semidiurnal internal-tide pulses in recruitment are observed along the shore of the bay not exposed to winds (Ladah et al. 2005).

In general, bays are important for breeding and feeding of fish and invertebrates (Largier 2004, Kämpf & Chapman 2016), but the bay effect may extend well beyond the bay itself owing to poleward, coast-trapped, stratified flows during relaxation events. High concentrations of larvae and juveniles accumulated in the bay during upwelling [e.g., Bodega Bay (Morgan et al. 2011) and Drakes Bay (Wing et al. 1998)] may be exported alongshore to the north during relaxation, as illustrated by surface currents and drifters (Kaplan et al. 2005; S.G. Morgan, C.D. Dibble, M.G. Susner, G. Thomas, T.G. Wolcott, et al., manuscript in review). Similarly, drifters deployed in St. Helena Bay moved south while remaining close to shore (Nelson & Hutchings 1987, Largier & Boyd 2001), illustrating opportunities for settlement poleward of bays. However, this transport is less likely in upwelling traps such as Antofagasta Bay, as the bay is not fully flushed during relaxation events [12-day timescale at the La Rinconada site (Piñones et al. 2007)] and the layer of warm water is often too small to propagate as a coherent coastal buoyancy current. This absence of alongshore larval transport is consistent with the highly localized distribution of *Pyura* in the bay (Castilla et al. 2004).

Opportunities for the introduction of alien species—specifically, species that like warmer waters—are found in the benign and productive habitats in upwelling bays. And their populations may grow in the bay due to larval retention, just like the native species. The high occurrence of invasive species has been documented in Tomales Bay (Ruiz et al. 2013), but studies to date are inadequate to separate these oceanographic determinants from human activity and other factors.

HUMAN INTERACTIONS

In upwelling regions, bays offer shelter from the wind and access to warmer waters in addition to harbor sites and productive fisheries. Cities have developed alongside upwelling bays, including major cities such as San Francisco (the Gulf of the Farallones), Lisbon (Lisbon Bay), Cape Town (Table Bay and False Bay), Valparaíso (Valparaíso Bay), Concepción (the Gulf of Arauco and Concepción Bay), and Vigo (Ría de Vigo). Beyond maritime activities and recreational activities, this development has resulted in the intentional and unintentional discharge of pollutants to bays. Pollutant loading and the retentive nature of bays results in some bays exhibiting notable water quality degradation, including pathogen pollution, organic pollution, and toxic pollution. Furthermore, due to the high levels of biological productivity, many of these pollutants are rapidly ingested in bay food webs. Some attention has been given to the input of agricultural nutrients and their role in triggering the dominance of specific toxic algae (Kudela et al. 2008b, Ryan et al. 2009), the importance of wastewater discharges (Coulliette et al. 2007, Howard et al. 2014), and the fate of estuarine and stormwater plumes (e.g., Fischer et al. 2014). More recently, there has been interest in identifying which pollutant discharges may affect fishery-oriented marine protected areas and in gaining a better understanding of why certain recreational beaches are more exposed to fecal bacteria, how wildlife are exposed to land-based diseases, and how plastic debris is transported and taken up in coastal food webs. New data and analyses are needed to assess these concerns.

CONCLUSION

Bays offer the most productive nearshore waters in upwelling regions, largely because they can retain high-nutrient upwelled water near the surface and within a confined region long enough for major phytoplankton blooms to develop. Elsewhere along upwelling coasts, nearshore waters are cold and phytoplankton concentrations are low, with blooms developing only once these waters have been transported far from the shore and beyond the habitat of important coastal consumers and ecological communities. Bays also provide warm surface waters that are replete in dissolved oxygen and mostly spared from low pH and the direct effects of ocean acidification, owing to the influence of photosynthesis. However, in sub-thermocline waters below the euphotic zone, severe hypoxic and ocean acidification effects are expected due to locally enhanced upwelling near headlands or canyons, strong stratification, and a downward flux of organic material from surface blooms.

The circulation in upwelling bays is driven by the influence of shelf circulation, local wind stress, and bay–ocean buoyancy/sea-level gradients, as well as wind-correlated fluctuations in each of these terms. Comparison of observations from many bays worldwide reveals common patterns in circulation and stratification that are critical to the nature and level of pelagic and benthic productivity in upwelling bays.

The retentive circulation and stratification in bays also offer important recruitment opportunities for benthic populations with planktonic early life stages. In many upwelling bays, there is a finite probability that meroplankton will be retained in the bay for the entire planktonic larval duration, and increased recruitment probability can result from behavior in concert with predictable hydrographic features. This potential for strong local recruitment is matched by flow patterns that can entrain and accumulate remotely spawned larvae, ensuring connectivity across a metapopulation. Together, all of this suggests that bays may anchor the upstream boundaries of populations in upwelling regions and offer opportunities for new introductions of alien populations.

Finally, bays have ecological importance beyond their boundaries, as both holoplankton and meroplankton biomass may be accumulated during upwelling events and then exported to

adjacent shelf regions during subsequent relaxation events. The plankton that accumulate in a bay are typically transported in a shore-attached, stratified, poleward flow that supports renewed blooming of phytoplankton as well as delivery of meroplankton to nearshore waters and shore habitats along the coast adjacent to the bay.

Recent analyses that combine observations of plankton with observations of productivity and transport offer exciting new advances in more fully identifying, understanding, and quantifying the critical roles that bays play in coastal upwelling ecosystems. Furthermore, these insights go beyond bays in upwelling regions and point to the general role of bays as nexuses for the coastal ocean.

SUMMARY POINTS

1. The cape-and-bay pattern is a fundamental scale of alongshore variability in coastal upwelling that is critical for regional ecosystem productivity.
2. Upwelling bays exhibit common patterns in circulation, stratification, and ecological responses that fit well with upwelling-shadow and upwelling-trap paradigms.
3. Upwelling bays are physically forced by three dominant terms: the inertia of shelf currents, surface stress due to local winds, and bay–ocean thermal/sea-level gradients.
4. Upwelling bays can be classed by their exposure to shelf forcing as wide-open bays, square bays, or elongated bays.
5. Fueled by upwelled nutrients, bays are hot spots for phytoplankton production that supports local consumers and is also exported to open coastal waters during relaxation.
6. Sub-thermocline water in bays is susceptible to regional extremes in oxygen, pH, and aragonite saturation levels due to strong stratification, high productivity near the surface, and the retention of waters in the bay.
7. Upwelling bays can retain and accumulate planktonic larvae from both local and remote sources, which can recruit in the bay as well as drive recruitment events when water is transported poleward out of the bay during relaxation.
8. Bays are susceptible to environmental risks associated with harmful algal blooms, invasive species, and pollution.

FUTURE ISSUES

1. An improved understanding of the dynamics controlling the separation of the upwelling jet at a headland is needed to resolve bifurcation and switching between separated, attached, and reattached flow structures.
2. Improved articulation of the dynamics controlling the spatial intensification of upwelling and the persistence of these upwelling centers at headlands will allow assessment of the generality of observations that the coldest/deepest waters are found in the sub-thermocline layer in the lee of the headland.
3. Observations and studies of local wind stress will inform spatial patterns of onshore delivery of plankton and allow the identification of locations where thermal exchange flows may be disrupted or enhanced by wind-driven strain or mixing.

4. Despite the recognition of spatial patterns in pelagic habitat that characterize upwelling bays, little attention has been given to how this explains patterns in both deep benthic and shallow subtidal communities.
5. Recent attention to the loading and exchange time of sub-thermocline layers is critical to explaining small-scale patches and events that represent extrema in the deoxygenation and acidification of coastal waters.
6. A fuller understanding of the influence of bays on the regional ecosystem is needed, including the effects of exported bay productivity and propagules, the potential for accumulation of remote larvae, and the initiation of harmful algal blooms.
7. As attention is given to the intensification or weakening of coastal upwelling under climate change, are bay–ocean interactions and associated ecosystem benefits resilient given that the juxtaposition of open and sheltered waters may allow the fundamental role of bays to continue irrespective of upwelling strength?
8. Beyond this focus on bays in upwelling regions, a broader assessment of the ecological importance of bays is needed through comparative study (i.e., going beyond bays driven by fresh water or upwelling), including the development of general paradigms for the role of bays.

DISCLOSURE STATEMENT

The author is not aware of any affiliations, memberships, funding, or financial holdings that might be perceived as affecting the objectivity of this review.

ACKNOWLEDGMENTS

This review has benefited from many collaborations and countless conversations, which have provided a foundation for the development of the ideas and the synthesis presented here. I am grateful for the ready exchange of ideas in our community and the collegiality that I have experienced over three decades and four continents.

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