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Frontal eddies provide an oceanographic triad for favorable larval fish habitat

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Abstract

Frontal eddies form on the shoreward edge of boundary currents, on average at weekly intervals and can last up to several weeks. This duration allows zooplankton production and completion of the larval stage of fish but may be too ephemeral for longer food chains with planktonic predators to establish. Therefore, frontal eddies may provide a suitable offshore nursery habitat, by entraining and retaining inner-shelf water, preconditioned with coastal plankton and ichthyoplankton, into an upwelling favorable cyclonic eddy. Here, we briefly describe the behavior of frontal eddies formed by western boundary currents in the context of the fundamental ocean triad, which incorporates three processes for the successful reproduction of fish: nutrient enrichment, food concentration, and retention of larvae. We adapt this hypothesis for frontal eddies adjacent to the substantial fisheries production of continental shelves, creating conditions for enhanced recruitment potential of larval cohorts at a finer scale than previously considered. We review the evidence and investigations of frontal eddies in their capacity to entrain coastal water, sustain the plankton community through eddy uplift and retain distinctive coastal communities of larval fish offshore until larval development is complete. The process of frontal eddy formation is complex and such habitats are irregular yet ubiquitous, which present challenges and opportunities for their study. With the advance of ocean observing systems and integration of physical and biological sampling, frontal eddies provide a novel focus for understanding fisheries production and connectivity of coastal ecosystems.

Larval fish survival during their early life history involves a balance of environmental risk and opportunity, which has been a source of enduring interest for natural historians and fisheries scientists for over 100 years (Dannevig 1907; Houde 2008; Hare 2014). Understanding this balance is important, as it may reveal quantitative environmental signals that could enable fisheries forecasts and facilitate the rebuilding of depleted stocks. Current strength and coastal winds are frequent correlates of fish recruitment (Schilling et al. 2020, 2022). Sometimes, the timing and location of spawning seems perplexing (Bakun and Broad 2003; Reglero et al. 2018), but these can often be rationalized in a dynamic oceanographic context. For example, the "optimal environmental window" (Cury and Roy 1989) describes a dome-shaped relationship between reproductive success and wind intensity. Winds that are too low limit vertical mixing of nutrients, yet too high can cause turbulence and dilute fine scale patches of larval prey (Bakun 1996, 2010). This mechanism was an important step to another conceptual model of fish reproduction involving three oceanographic steps, which Bakun (1996) described as

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the "fundamental triad" (an analogy to the essential elements of a musical chord). His three-stage hypothesis of favorable reproductive habitat requires: (i) enrichment with nutrients such as by upwelling and vertical mixing, (ii) concentration of food by convergence and through frontal formation, and (iii) retention to ensure that the larvae are geographically maintained and facilitating drift toward appropriate habitat. This hypothesis describes the important factors for favorable fish reproduction that may include major currents, coastal winds, and buoyant plumes of terrestrial runoff (Bakun 1996). Subsequent studies have shown a triad of events is evident in the reproduction of several pelagic fish stocks in the Mediterranean (Agostini and Bakun 2002), the Benguela system (Hardman-Mountford et al. 2003; Lett et al. 2006), Humboldt or Peru Current (Lett et al. 2007), and eastern and western Australia (Condie et al. 2011). This conceptual model was also incorporated into a model of fish recruitment in rivers (Hoagstrom and Turner 2015; Humphries et al. 2020), and demonstrated the additional aspects to the basic triad such as temperature and the role of predators. We explore this more nuanced view of the fundamental triad in this synthesis of frontal eddies in the coastal ocean.

Bakun (2006) further developed this fundamental triad in the context of ocean eddies that provide key structures for nursery habitat of pelagic fish. Larger ocean eddies (i.e., 50–100 km) are evident in sea level anomalies as a surface depression (with cyclonic geostrophic circulation) or a surface elevation (producing anticyclonic circulation). Cyclonic (anticyclonic) circulation is usually characterized by surface divergence (convergence), leading to upwelling (downwelling) through eddy pumping (McGillicuddy 2016). The closed circulation of eddies may concentrate larvae into patches in the upper mixed layer (Abernathey and Haller 2018), and when fully coherent may act to retain larval fish near the spawning area to enable population persistence (Sinclair 1988). In support of this process, Condie and Condie (2016) showed that ocean eddies have the capacity to retain plankton for up to 2 months. Others have shown eddies contain coastal larval fish assemblages (Shulzitski et al. 2018; Garcia et al. 2022) and can contribute to the connectivity of coastal populations (Hare et al. 2002; Sponaugle et al. 2005; Booth et al. 2007; Mullaney et al. 2011).

Eddies that interact with the continental shelf may be particularly important for fish production, where continental shelves yield 90% of global fisheries landings (Pauly et al. 2002) due to the proximity to ports and markets, and the interaction of wind, ocean, tide, and topography. In the mid latitudes, sporadic upwelling-favorable wind stress and western boundary currents (WBCs) sweep along the shelf edge creating conditions favorable for productive ecosystems (Lucas et al. 2011; Rossi et al. 2014; McGillicuddy 2016). The distinctive frontal edge of a warm WBC can undertake dynamic instabilities which may sometimes form into frontal eddies from an encircling filament (Fig. 1). Frontal eddies are mostly studied along the inshore edge of WBCs, as they are relatively frequent due to the favorable conditions for instabilities (density gradients, shear, winds, topography, and coastal boundary) and their easy identification in satellite sea surface temperature (SST) imagery along the warm WBC water originating from the tropics. Hence, the encircling filament has a warm signature, contrasting with the cold coastal or upwelled water encircled and trapped within the eddy.

Where cyclonic eddies are constrained between the coast and the current jet, they impinge on continental shelves and entrain the shelf water (Everett et al. 2015), preconditioned with zooplankton and fish larvae (Okazaki et al. 2002, 2003; Shulzitski et al. 2018). The inner shelf water of most temperate coasts is characterized by a coastal fringe of water with higher concentration of chlorophyll *a* (Chl *a*) (Lucas et al. 2011; Everett et al. 2014) and a higher biomass of small zooplankton (Marcolin et al. 2013; Vandromme et al. 2014), generated by the interaction of coastal runoff, coastal winds and upwelling (Fig. 1). Entrainment of productive waters at the shelf-break is also likely (Le Fevre 1987), although less understood. These preconditioned shelf waters can be advected by frontal eddies offshore and be nurtured and retained within the eddy some distance away from the coast in waters that are more oligotrophic. As such, frontal eddies are a prime candidate for creating the conditions required for an ocean triad (Schmid et al. 2020).

In this review, we provide a planktonic perspective of the formation and characteristics of WBC frontal eddies with respect to the Bakun (2006) ocean triad of successful larval habitat. We propose a modified process for the completion of the larval phase within the comparatively ephemeral frontal eddies as they interact with the shelf (Kasai et al. 2002; Everett et al. 2015). We review the evidence of how WBC frontal eddies form a triad of steps to (i) *entrain* inner shelf water which is preconditioned with plankton and ichthyoplankton (Fig. 1a); (ii) *sustain* these assemblages in an upwelling favorable eddy (Fig. 1b); and (iii) *retain* the larvae near the coast and reduce dispersion (Fig. 1c; Table 1). We illustrate how these three steps form a conceptual model for successful ichthyoplankton production in three relatively well studied WBC systems—the East Australian Current (EAC); the Kuroshio Current (KC) and the Florida Current (FC)–Gulf Stream (GS) system. Together, we find that these three systems with different research histories (e.g., coral reefs or anchovy fisheries), reveal different aspects of the triad, and also reveal additional components to this model. We conclude with how we can assess the frontal eddy triad and consider possible approaches to test the effect on fine-scale planktonic ecosystems and broad-scale fisheries recruitment.

Frontal eddy characteristics

Although there is no unambiguous definition of a frontal eddies, they are typically coherent, rotating eddies that form

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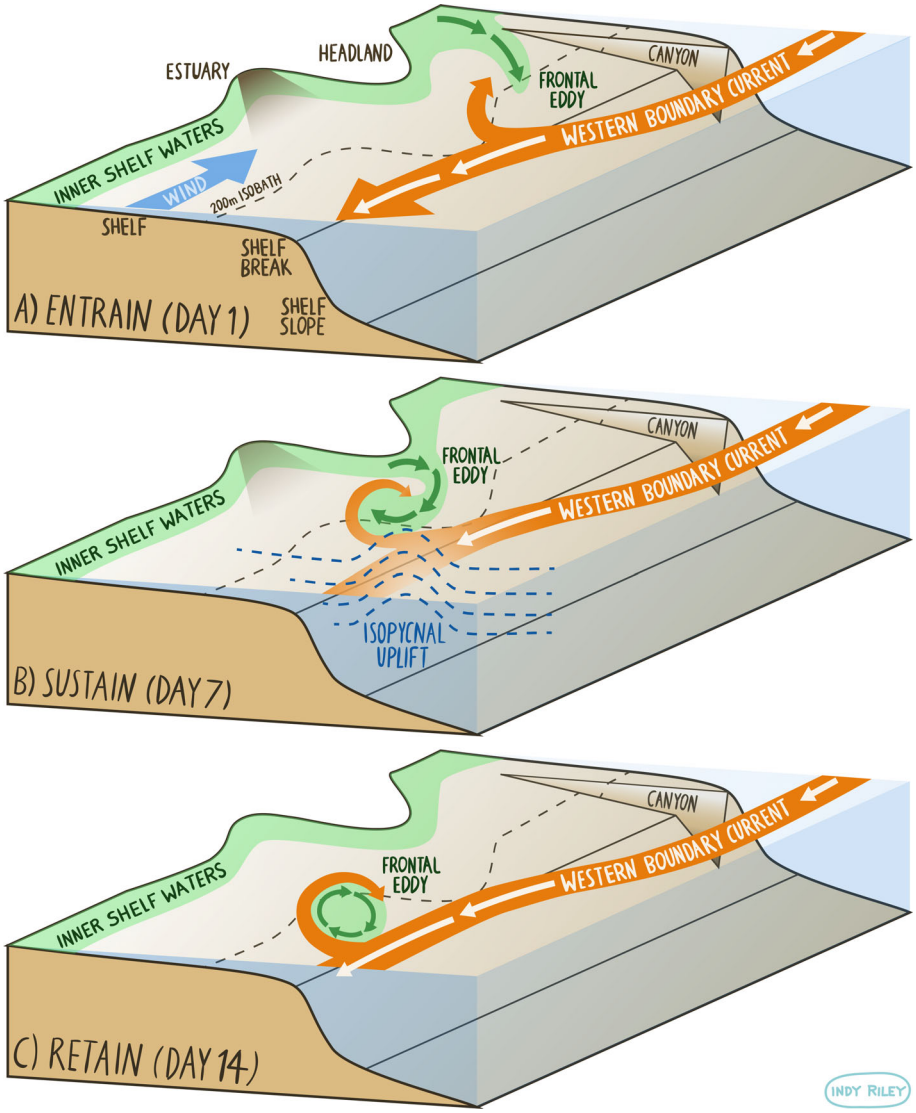

Fig. 1. Adaptation of the Bakun (1996, 2010, 2013) conceptual model for a frontal eddy triad (showing rotation for the southern hemisphere), which links coastal spawning areas and preconditioned waters of the inner shelf with the frontal instability of a WBC. These fine-scale features may form offshore nursery grounds for the duration of the larval period before active swimming. (**a**) The frontal eddy is formed by a meander or billow of the front which entrains water from over coral reefs, or inner shelf water from areas several times greater that the eddy itself; (**b**) the forced eddy during spin-up causes an uplift of isotherms in the center of the eddy, sustaining the production of plankton; (**c**) the frontal eddy may be blocked by other eddies, or may stall, or may roll along the edge of the WBC, at a slower speed than the current itself which retains the larvae within the eddy and reduces their advection. Also shown are other processes that can influence eddy formation, such as opposing winds, estuarine plumes, headlands or submarine canyons (*see* Table 1).

along the frontal edge of an unstable flow, such as the cyclonic structures on the in-shore flank of strong WBCs. They have typical horizontal length scales of 10–60 km, typically in the submesoscale, which is small enough that their dynamics cannot be explained by the geostrophic balance (the approximate balance between the Coriolis force and horizontal pressure gradients) that adequately describes larger mesoscale eddies. Submesoscale flow has high Rossby number ($\mathrm{Ro} = \zeta/f \sim O[1]$), so the magnitude of the total vorticity is much greater if the sense of rotation of the eddy is the same as the planetary vorticity. This is the case for a cyclonic eddy. Submesoscale flow also has high Richardson number ($\mathrm{Ri} = N/U_z$) meaning that vertical gradients in density (buoyancy frequency, N) are as important as vertical gradients of the horizontal velocity (U_z).

At the submesoscale, all terms in the equations of motion are potentially important. In particular, most frontal eddies are highly nonlinear. This nonlinear behavior contributes to the capacity of frontal eddies to entrain and retain fluid (purely linear features are incapable of eddy trapping; McGillicuddy 2016), inducing motions that can transport nutrients vertically into the eddy core and periphery through

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Table 1. Summary of quantifiable oceanographic and planktonic processes and metrics for the three steps leading to success of a larval cohort, through frontal eddy formation by a WBC (Fig. 1). Adapted from Bakun (1996, 2006).

	Oceanographic	Planktonic
Inner shelf preconditioning, and eddy formation	Topography, headland, canyon (Kourafalou and Kang 2012) River outflow, estuary, low salinity (Lee 1975) Opposing winds to WBC (Androulidakis et al. 2014; Mantovanelli et al. 2017) Tidal bore, internal waves (Leichter et al. 2014)	Coastal production from inner shelf upwelling, estuarine run-off and formation of the "green ribbon" (Lucas et al. 2011; Everett et al. 2014) Coastal spawning (Okazaki et al. 2002; Sponaugle et al. 2005; Neira and Keane 2008)
Entrain	Water mass conservation (Schaeffer et al. 2017) Particle tracking of eddy particles to the shelf EAC (Everett et al. 2015; Roughan et al. 2017); KC (Kimura et al. 1997, 2000); LC–FC–GS (Limouzy-Paris et al. 1997; Sponaugle et al. 2005, 2012; Vaz et al. 2016; Kourafalou et al. 2018)	The plankton assemblage as an indicator of coastal entrainment EAC (Everett et al. 2012; Matis et al. 2014; Garcia et al. 2022); KC (Kasai et al. 2002; Okazaki et al. 2002, 2003); LC–FC–GS (Limouzy-Paris et al. 1997; Sponaugle et al. 2005; Govoni et al. 2010)
Sustain	Isotherm uplift during spin-up and spin-down dynamics (Bakun 2010, 2013; McGillicuddy 2016); EAC (Macdonald et al. 2016; Roughan et al. 2017; Schaeffer et al. 2017); LC–FC (Lee et al. 1991)	Plankton production, nutrients, and Chl *a* concentration; EAC (Everett et al. 2011; Mullaney and Suthers 2013); KC and production of nauplii; (Kimura et al. 1997, 2000; Nakata et al. 2000; Govoni et al. 2013); LC–FC, improved larval fish growth (Shulzitski et al. 2015, 2016; Schmid et al. 2020) A loophole of reduced larval mortality (Bakun 2013)
Retain	Eddy behavior, vortex stretching, increasing vorticity; eddy blockage (Le Henaff et al. 2014); eddy lean or posture (Roughan et al. 2017) Ratio of mean flow to eddy advection; EAC, particle tracking and retention of particles within the eddy over time; residence time within eddy (Everett et al. 2015; Macdonald et al. 2016); eddy translocation along coast (Schaeffer et al. 2017); LC–FC, (Lee et al. 1991, 1992; Kourafalou and Kang 2012; Vaz et al. 2016; Limer et al. 2020)	A broad, overlapping size frequency distribution from protracted entrainment, larval survival and retention within the eddy EAC, (Mullaney and Suthers 2013); LC–FC, completion of the early life history phase and connectivity with adult habitats (Limouzy-Paris et al. 1997; Sponaugle et al. 2005, 2012; Shulzitski et al. 2018; Schmid et al. 2020)

frontal dynamics, as well as increasing their lifetime beyond what might be expected from linear forcing alone.

Frontal eddies may have different dynamics over their life-cycle. Typically, frontal eddies are small, *O*(10–60 km or more) in diameter and are often short-lived (up to several weeks; Schaeffer et al. 2017). Frontal eddies begin with length-scales on the order of the internal Rossby radius of deformation, often between 10 and 20 km at the latitude of most upstream WBCs. Many frontal eddies can be torn apart quickly by strong lateral shear of the main current or squeezed out between the current and shoaling nearshore bathymetry. Tangential forcing from the boundary current (i.e., ageostrophic circulation) can allow them to survive and grow (Gula et al. 2016), with turbulent frictional effects causing smaller anticyclonic turbulence and mixing around the edge (Bakun 2013). In general, during the forced eddy spin-up phase there is uplift at the center of a cyclonic eddy (Bakun 2010), evidenced by doming of the isotherms by several meters per day. Once the eddy is no longer forced and is freely spinning during a phase of relaxation or spin-down, a cyclonic eddy is characterized by downwelling at the center and upwelling around the eddy edge (Bakun 2010; Schmid et al. 2020). Therefore, being squeezed sometimes between the shelf and the boundary current, frontal eddies can oscillate between being these two states during their lifetime (Everett et al. 2015), further nurturing the planktonic ecosystem.

Long-lived frontal eddies can grow in size reach length scales on the order of 100 km, with a surface depression large enough to be measured by altimetry (Mullaney and Suthers 2013; Roughan et al. 2017). They were first referred to as "spin-off" eddies (Lee 1975) as they grew out from a wave-like meander along the front of the main flow (in their case the GS). These cyclonic eddies often spin off the edge of the main flow to form a separate dynamical structure (Fig. 1). Other authors also used the term "billow" or "shingle" to describe the wave-like pattern of the undulating flow in temperature observations along the meanders of the main jet (Lee et al. 1991; Everett et al. 2011; Macdonald et al. 2016).

The flow of WBCs along continental shelves constrains frontal eddies between the edge of the main flow and the

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coast (Lee et al. 1991; Bakun 2006). This has many implications for the eddy life cycle and duration, with many sources of forcing and instability which can feed the structure. Instabilities are spurred by the bathymetry and coastline (Lee 1975; Kourafalou et al. 2018); or by enhanced horizontal shear gradients and horizontal density gradients due to river outflow and coastal upwelling (Lee 1975; Roughan et al. 2017) or by frequent counter-current flow driven by alongshore wind stress opposed to the WBC direction (Androulidakis et al. 2014; Le Henaff et al. 2014; Schaeffer et al. 2017).

Formation and growth by entrainment

Frontal eddy formation is still not fully understood. In addition to intrinsic instability of the WBC, studies have linked eddy formation to topography, for example, in the GS system (Gula et al. 2016) or to local wind stress, where the perturbation of the shear flow by the wind can lead to formation of a frontal instability (Mantovanelli et al. 2017). Such unstable barotropic modes of a WBC can occur due to small perturbations in the region of high horizontal shear (Lee and Mayer 1977). These modes, or meanders, are traveling waves, their crests defined as the shoreward displacement of the jet (Bane and Brooks 1979). Meander wavelengths are of the order of tens to hundreds of kilometers, with periods of several days to weeks. These meanders travel, intensify, and sometimes generate a counter-flow filament of warm WBC water from their crest. The filament of vorticity folds-up back onto the main flow, forming a closed elongated circulation of a frontal eddy (Fig. 1).

WBCs are sites of large horizontal and vertical velocity shear, as well as strong horizontal and vertical buoyancy gradients. As such, frontal eddies are thought to form primarily due to shear driven instability processes (Ivanov and Ginzburg 2002), although thermally driven processes such as conditional symmetric instability may also play a role. The fact that frontal eddies form in these high gradient regions enhances their impact on the resulting ecosystem, as they mix and stir tracers (such as nutrients or larval fish; Garcia et al. 2022) both horizontally across the shelf and WBC front, and vertically, as will be discussed in the following section.

Gula et al. (2016) ran a high resolution (750 m in the horizontal) numerical model of the GS region to study the formation mechanism of the frontal eddies. They show the formation of these features is strongly tied to topographic interaction of the boundary current with the continental slope. The bottom drag of the current against the sloping bathymetry generates a high cyclonic vorticity regime that is inherently unstable. However, when the WBC is constrained to the shelf, strain is also high, which stabilizes the flow. As the GS moves downstream and separates from the narrow continental shelf $\sim 27°$N, the strain relaxes and the vorticity filament rolls up into a vortex street (Gula et al. 2016). As these eddies move toward higher latitudes, they can extract kinetic energy from the mean flow (barotropic energy conversion), growing in size and deepening vertically. Hence, in the FC–GS, the interaction of the WBC with bathymetry is key for the formation of frontal eddies (Kourafalou and Kang 2012). However, the dynamics that lead to the genesis of frontal eddies in other WBC systems is still an open question and given the diversity of oceanographic conditions in those systems, other mechanisms, such as local wind forcing may contribute (Mantovanelli et al. 2017).

Physical characteristics and upwelling to sustain plankton

Cyclonic structures are typically characterized by a surface divergence associated with upwelling, in the center for geostrophic eddies. Moreover, submesoscale processes are characterized by relatively high vertical velocities (order of 10s m d^{-1}; Mahadevan 2016), which enhanced the upwelling process (Taylor and Ferrari 2011). Within a frontal eddy, the upwelling area is not necessarily in the center, due to its nonlinearity and fast advection (Schaeffer et al. 2017), but the enhanced vertical flux injects deep nutrients to the surface, available to sustain the enrichment of phytoplankton (Levy et al. 2018).

Few observations of the vertical structure of frontal eddies exist due to their ephemeral nature and challenge to observe in situ. However, a rigorous observational study of one such frontal eddy showed that although it formed on the shelf in less than 200 m of water, as it was drawn off the shelf, the eddy stretched vertically to more than 800 m depth (Roughan et al. 2017). The eddy was located approximately 200 km north east of Sydney on the continental side of the EAC (latitude $\sim 32.5°$S). In addition, as the eddy was located adjacent to the continental slope, it tilted onto the shelf, similar to that observed when a cyclonic eddy interacts with the shelf (Oke and Griffin 2011), driving an asymmetric uplift.

Eddy behavior and translocation to retain plankton

A frontal eddy can grow and propagate poleward along the main flow of the WBC with similar phase speed as the meanders, between 8 and 60 km d^{-1} (James et al. 1999; Gula et al. 2016; Schaeffer et al. 2017), hence much slower than the WBC jet which can travel up to 200 km d^{-1}. The size, evolution, and propagation speed of the frontal eddies are dependent on transient conditions. These include the position of the WBC over topographic features, wind stress, and intrinsic instabilities of the meandering WBC jet. Several studies (Kang and Curchitser 2015; Gula et al. 2016) show regions of eddy growth, where the mean flow feeds the eddy, and eddy decay, where the eddy loses energy and feeds mean flow. In the GS, this eddy growth region is prominently linked to the Charleston Bump, at around 31°N, which destabilizes the jet and is the peak of barotropic energy flux. Other studies have observed a stalled (in advection) and growing eddy in response to upstream winds which oppose the main poleward propagation, and provides more energy through enhanced strain (Archer et al. 2017; Schaeffer et al. 2017). Not all frontal

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eddies that form will continue to grow, and the factors controlling their decay require further investigation (Schmid et al. 2020).

Evidence of the triad in WBC frontal eddies

East Australian Current

The EAC flows from north to south along eastern Australia, closing the circulation of the South Pacific gyre. Frontal eddies intensify where the current is most coherent and jet-like, south of three major topographic features—North Cape-Fraser Island (26°S), Cape Byron (29°S), and Smoky Cape (31°S). Strong shear between the current and the inner-shelf water generates billows at the shelf edge which occasionally build into a frontal eddy. Schaeffer et al. (2017) made a 14-month census of frontal eddy formation from a high-frequency (HF) radar at Coffs Harbour (30°S), resolving features with high resolution ($\sim$ 1.5 km) out to $>$ 100 km offshore. The unusually narrow continental shelf ($<$ 30 km wide) enabled a view of the inner shelf and the edge of the EAC (Fig. 2). The frequency of frontal eddies was irregular but on average the eddies formed weekly and could be tracked for up to a month (Schaeffer et al. 2017).

The inner shelf water is preconditioned with elevated nutrients (Roughan and Middleton 2002) and phytoplankton (Armbrecht et al. 2014, 2015; Everett et al. 2014) due to the persistent upwelling south of prominent headlands and episodic favorable coastal winds (Schaeffer et al. 2013). The inner shelf water is also characterized by a higher concentration of larval fish (Mullaney et al. 2011) and a greater species diversity including those of fisheries importance (Schilling et al. 2022). Entrainment of these coastal assemblages into the eddy is evident from the cooler SST and higher Chl *a* compared to the shelf waters and offshore (Everett et al. 2011, 2014). The capacity to entrain inner shelf water was demonstrated by a numerical simulation of a cyclonic eddy (Everett et al. 2015; Macdonald et al. 2016), showing that water in the 100 km diameter eddy was drawn from the inner shelf and from over 4° of latitude (Fig. 3). The degree of entrainment and daily growth of the eddy depended on the degree of interaction with the shelf bathymetry (as represented by the distance offshore). For example, the estimated entrainment varied from 0.2 to 0.6 Sv when $<$ 10 km from the shelf (Everett et al. 2015).

Once formed, frontal eddies are upwelling favorable, bringing nutrients into the euphotic zone and sustaining the planktonic ecosystem (Everett et al. 2011). Primary production could be sustained as the 19°C and 21°C isotherms are uplifted by 35 and 55 m over 10 h and 1 d, respectively (Schaeffer et al. 2017). In a detailed study of a small (35 km diameter) frontal eddy, Roughan et al. (2017) reported the 17°C isotherm was raised from 210 to 125 m in 25 km (3.5 m per km) and that it was disproportionately more productive than an older larger cyclonic eddy in the vicinity. The upper mixed layer of the frontal eddy transported offshore a high proportion of fish larvae of coastal origin and of fisheries importance, relative to those of oceanic origin (larval myctophids, or lantern fish; Garcia et al. 2022). This entrainment into the frontal eddy was measured using a newly developed larval entrainment index—the ratio of coastally spawned fish larvae to myctophid larvae—as a tracer of coastal entrainment with respect to water density and depth.

An earlier study of a frontal eddy in this region observed a greater biomass of zooplankton (salps and juvenile krill) and larval sardine, mackerel and scad when compared with the surrounding shelf waters (Mullaney and Suthers 2013). The fish larvae within the frontal eddy were twice the length of those found outside, implying that they were retained in the eddy and that their chances of survival were improved. This eddy continued to entrain shelf water and grew over its 14-d life with the surface area doubling, and only shifted south by 100 km, which was substantially less than flow in the EAC. In other words, the entrained larvae were geographically retained and not dispersed too far from the coastal zone.

From their 14 month census, Schaeffer et al. (2017) observed that the advection of eddies was significantly slower than the mean EAC flow, as eddies would either stall at certain locations, or slowly roll along the frontal edge. However, sometimes they would be transported up to 500 km south or even out into the Tasman Sea (Roughan et al. 2017) where the fate of larvae dispersed far from the spawning area is not known. However, temperate reef fish larvae have good swimming capacity (Downie et al. 2021) and there are larger circulation features in the area that are able to transport larvae back to the coast (Cetina-Heredia et al. 2019; Malan et al. 2020). In summary, these studies detail the potential for the frontal eddy triad to entrain shelf water and to sustain and retain ichthyoplankton (Table 1).

Kuroshio Current

The elements of a frontal eddy triad were described off eastern Japan in a series of voyages and papers over more than a decade, concerning the interaction between the major anchovy spawning area in the Enshu-nada Sea and the KC (Kimura et al. 1997; Kasai et al. 2002; Fig. 4). Downstream of where the Kuroshio interacts with the coastline (west of Cape Shionomisaki) the frontal edge forms wave-like meanders every 1–3 weeks, with wavelengths from 100 to 400 km (Kimura et al. 1997). These are significantly larger, but occur slightly less frequently (36 yr^{-1}) compared to the EAC ($>$ 40 yr^{-1}; Schaeffer et al. 2017).

Okazaki et al. (2002) describe these frontal eddies as "an oasis in the desert" compared to the warm oligotrophic waters of the KC. Entrainment of the characteristically low-salinity coastal waters, containing larval anchovy (*Engraulis japonicus*), was traced across the shelf toward the Kuroshio Front (Okazaki et al. 2003) by the tracks of Lagrangian drifters (Kasai et al. 2002). Around the Kuroshio Front, production of

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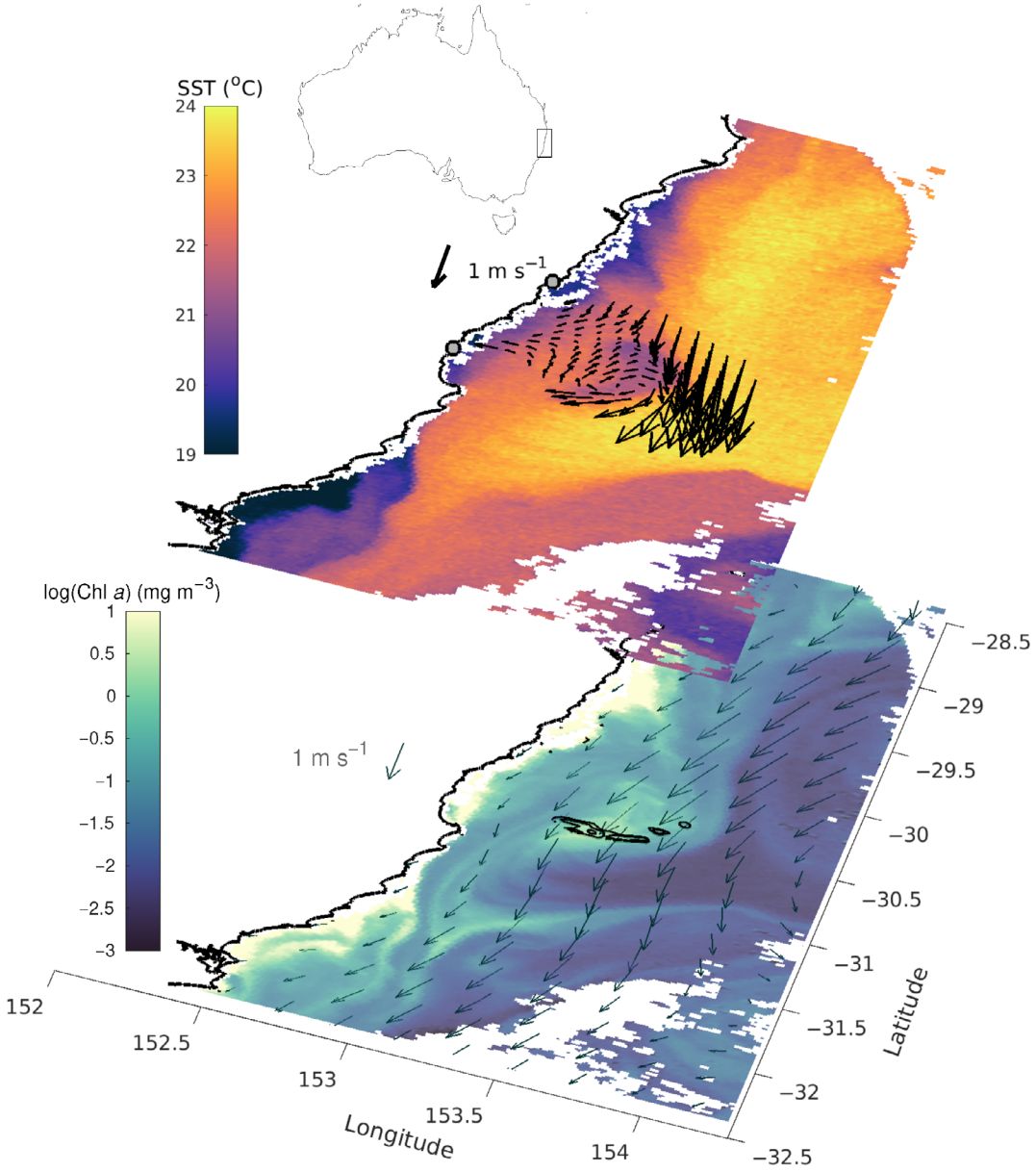

Fig. 2. A short-range HF radar system (WeRa, stations shown by gray dots) deployed ~ 30°S off the town of Coffs Harbour showing a frontal eddy. Frontal eddies propagate along the inside edge of the EAC (velocity vectors from radar in top panel) but are not resolved by satellite altimetry (gray geostrophic velocity vectors in bottom panel). Note the impact on the uplift of cold water (SST, top panel) and phytoplankton blooms (surface Chl *a* in bottom panel) corresponding to surface divergence (contours of 0.2–0.5|*f*| in bottom panel). Figure is modified from Schaeffer et al. (2017).

phytoplankton was initially nutrient limited but once entrained into a frontal eddy the phytoplankton biomass increased from < 1 to > 2 mg m^{-3} in less than a week (Kimura et al. 1997, 2000). In response, the abundance of copepod nauplii doubled within 2 d (Nakata et al. 2000; Okazaki et al. 2002) and the associated anchovy larval growth rates improved in relation to the concentration of food (nauplii; Okazaki et al. 2003). A number of these studies assert that production in the frontal region remains low and it is only entrainment into an eddy that leads to new production (Kimura et al. 1997; Kasai et al. 2002).

The final stage of the frontal eddy triad (retain) was evident as the frontal eddy protected the larvae from dispersal (Okazaki et al. 2002), and the eddies tended to return to the coast on average every 10 d, approximately 18 times per summer (Kimura et al. 2000). Kasai et al. (2002) conclude that "The entrainment process, which was probably caused by offshore movement of the Kuroshio, holds the key to successive

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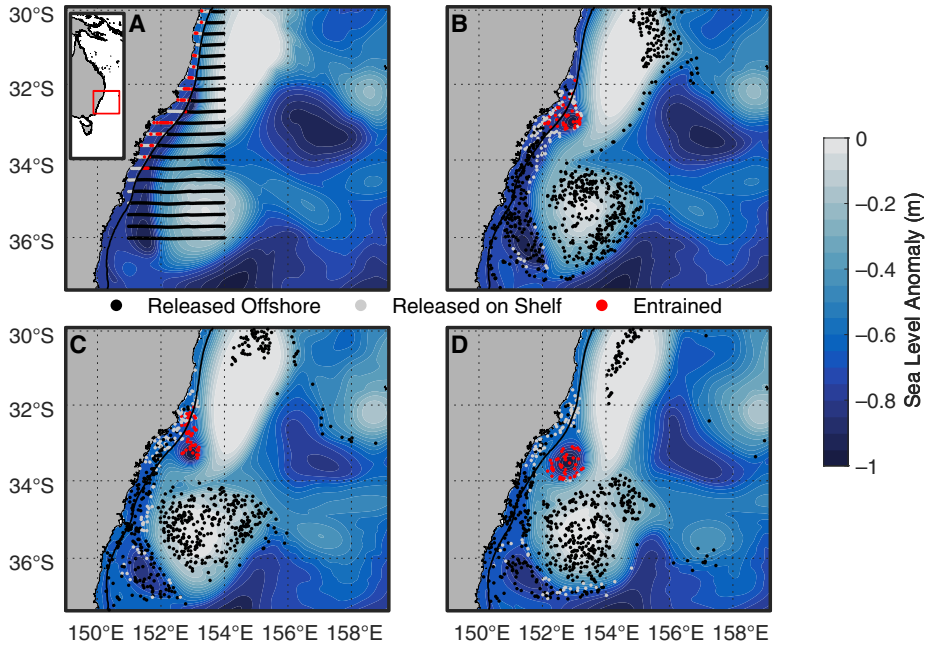

Fig. 3. Entrainment by a frontal eddy interacting with the shelf, is evident in a high-resolution simulation of an event northeast of Sydney, Australia commencing in late September 2009. Panels show the distribution of seeded particles at 50 m depth on (**a**) 29 September, (**b**) 2 October, (**c**) 5 October, and (**d**) 9 October. The particles released on the shelf are gray, and those entrained into the frontal eddy were colored red and backtracked to their origin on the shelf, demonstrating entrainment of shelf waters from over 4° of latitude, as well as retention of particles within the eddy, compared to the advection of particles outside the eddies. The color scale shows the sea-level anomaly. Figure modified from Everett et al. (2015).

survival and recruitment of fish larvae in the Kuroshio system" (p. 185), although evidence for the relationship between frontal eddy triad and recruitment is still lacking. To the southwest off northeastern Taiwan, around 45% of the fish catch of various mackerels (*Trachurus* sp., *Scomber* spp) is described by the fluctuating path of the Kuroshio, in driving upwelling and phytoplankton production during the main spawning period in mid to late winter (Oey et al. 2018). They suggested that plankton production is the probable driver of recruitment and fish catch, although the relative frequency of frontal eddy formation during offshore vs. onshore shifts by the Kuroshio is unknown.

The Loop Current, FC, and GS system

The Loop Current (LC) sweeps anticyclonically around the Gulf of Mexico exiting southward into the Straits of Florida to become the FC and GS (Kourafalou and Kang 2012), thus comprising the north Atlantic WBC system (Le Henaff et al. 2014). Frontal eddies 80–120 km diameter and > 1000 m depth form over the shelf in the eastern Gulf, associated with the Mississippi fan and the source water (Le Henaff et al. 2014). Frontal eddy formation is also associated with the LC shedding a large anticyclonic eddy and facilitated by winds and upwelling in the eastern Gulf of Mexico (Androulidakis et al. 2014). These eddies, though formed away from coral reefs may interact with the southwestern tip of the Florida Shelf, around the remote and pristine coral reefs of the Dry Tortugas and Pulley Ridge (Kourafalou and Kang 2012; Vaz et al. 2016).

In the Straits of Florida, frontal eddies have been studied for decades. Lee (1975) was the first to record a number of cyclonic current reversals offshore of southeast Florida, which he termed "spin-off eddies." They were described as small diameter eddies that propagate northward at speeds of 20–50 cm s^{-1}, observed off Miami and Boca Raton (Fig. 5). They occurred on average once a week and penetrated vertically to approximately 200 m (Lee and Mayer 1977). Because they form out of the strong FC jet as it flows poleward along the continental shelf, frontal eddies are elongated in the along-shelf direction (ratio ~ 2 : 1) and are advected downstream by the jet itself (Archer et al. 2015; Fig. 5). The frontal eddies are present throughout the year and over a range of topographies along the channel, which indicates that no single forcing mechanism dominates. Instead, there is a complex interplay of factors, including wind, coastal geometry, and the location and orientation of the WBC jet to the local bathymetry (Gula et al. 2016). As these eddies move poleward with the WBC jet, they may pause in their transit through the Straits, stalled by southward winds, or by topographic interaction. Nomenclature for these events has varied depending on location and study: spin-off eddy (Lee 1975), shingle (Lee et al. 1991), frontal eddy (Fiechter and Mooers 2003), and submesoscale vortex (Shay et al. 2002).

Other studies have investigated the critical role of frontal eddies on the transport of nutrients and larvae from the FC to the fringing reefs of the Florida Keys (Lee et al. 1991; Hitchcock

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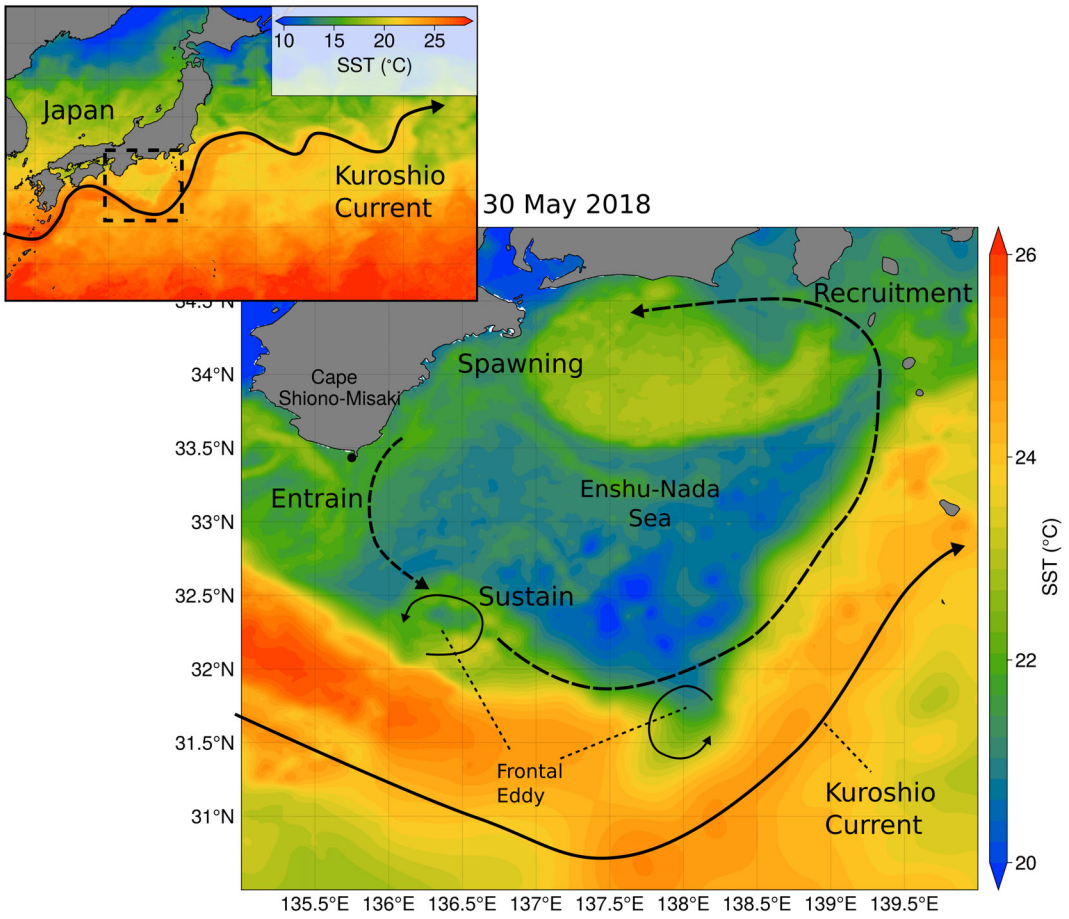

Fig. 4. Synthesis of frontal eddy triad process in the KC and Enshu-nada Sea System, illustrated with the Group for High-Resolution Sea Surface Temperature (GHRSST) L4 Global Foundation Temperature dataset (JPL MUR MEaSUREs Project 2015) image of 30 May 2018. The connectivity of coastal spawning by frontal eddies is based on the work of Kimura et al. (1997), Kasai et al. (2002), and Okazaki et al. (2002). Undulation of the front is generated at Cape Shionomisaki which promotes the entrainment of larval anchovy and contributes to additional primary production to the coastal ecosystem (JPL MUR MEaSUREs Project 2015).

et al. 2005; Richardson et al. 2009). When the FC meanders onto and off the reef tract, it drives upwelling and open ocean water onto the reefs through bottom stress and increased internal wave activity (Leichter et al. 2014). This provides a pathway for deep nutrient-rich water onto the reef, impacting the overall productivity and reef community (Sponaugle et al. 2005; Leichter et al. 2014). Therefore, the presence of frontal eddies leads to entrainment of coastal water and retention of coral reef meroplanktonic larvae of fish and invertebrates (e.g., in the north east Gulf of Mexico, Limer et al. 2020; in the Florida Straits, Lee et al. 1991; Shulzitski et al. 2018). In summary, the meanders of the current and associated frontal eddies form a complex eddy system (Kourafalou et al. 2018).

There have been no direct descriptions of the larval entrainment process by frontal eddy formation, as the currents are dynamic and entrainment from shelf waters occurs throughout the region. However, inferences of entrainment can be gleaned from analysis of larvae sampled from a frontal eddy. For example, Sponaugle et al. (2005) report of a frontal eddy within the remnants of a larger cyclonic eddy off the Florida Keys. Using light-traps near a reef to sample larval fish for 6 weeks, they observed a pulse of presettlement larval fish associated with the passage of the frontal eddy. The ages of the larvae (estimated from daily growth rings of the ear-bone or otoliths) ranged from 2 weeks to 2 months, suggesting that the eddy continued to entrain shelf waters and retain the larvae along the length of the Florida Keys. The range of ages is an important criterion of larval retention (Table 1), which few other studies of frontal eddies have so clearly demonstrated. The larvae were retained inside the eddy, and the advection of the eddy was relatively slow and substantially less than the main current. The larval retention is evident in the slower transit of eddies in the lower (western) keys, which directly enhances the settlement of reef fish here compared to the upper (eastern) keys (Sponaugle et al. 2012).

The planktonic ecosystem of nutrients, phytoplankton, and zooplankton is also enhanced within cyclonic eddies entering the Straits of Florida (Hitchcock et al. 2005).

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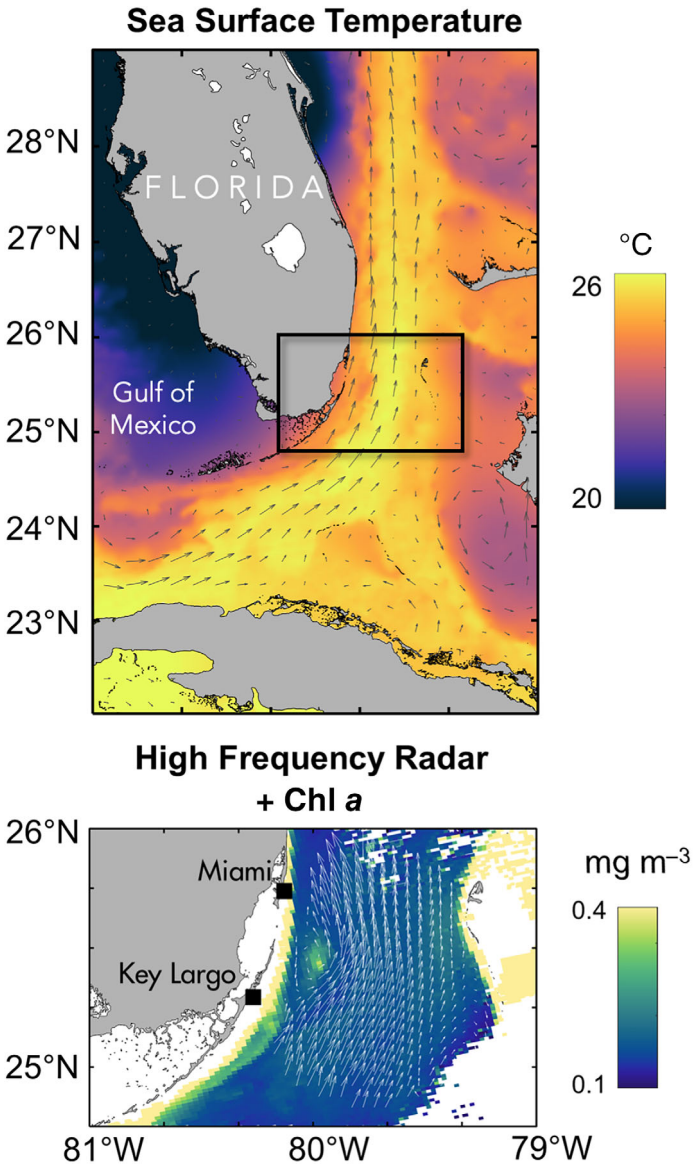

Fig. 5. Frontal eddies along the inshore edge of the FC, associated with cold water upwelled from depth. (Top) SST from the GHRSST and superimposed geostrophic currents from the DUACS product (previously AVISO) for 20 January 2005. This map shows more than seven frontal eddies as cold spots in SST, within the Florida Straits and extending as far north as 29°N. The black box denotes the region shown in the lower panel. (Bottom) Chlorophyll from MODIS AQUA, and superimposed surface currents from HF radars (HF radar data from Archer et al. 2018). This map shows a frontal eddy enriched with high Chl *a* content in its core, due to upwelling of cold nutrient-rich subsurface water and entrainment of coastal water.

Shulzitski et al. (2015) showed in various eddies over three voyages, significantly higher growth rates of four species of larval fish compared to those sampled outside the eddy in the Straits of Florida. As expected for an uplifting eddy, they found the eddy habitat tended to be cooler and more saline and more productive in terms of fluorescence (i.e., phytoplankton biomass; Shulzitski et al. 2018). Most remarkably, they found the higher growth rates of larvae inside the eddy were similar to the pattern of daily growth rates back-calculated from otoliths of surviving fish that had completed the larval phase and settled as juveniles onto reef habitat (Shulzitski et al. 2016). In contrast, fish larvae from the FC did not grow as well, and the slower pattern of larval growth was not evident in the otoliths of surviving reef fish.

Recently, a towed imaging camera system revealed significantly higher abundance of ichthyoplankton (up to 5.6 ind. m^{-3}) and copepods (up to 60 ind. m^{-3}) in a cyclonic eddy off the western Florida Keys compared to the FC (Schmid et al. 2020). They specifically interpreted their findings of this decaying eddy in terms of an ocean triad of entrainment, plankton production (sustain) and concentration (retain). Consistent with that expected during spin-down and the relaxation phase (Bakun 2010, 2013), they observed upwelling around the edge of the eddy where the mixed layer depth was the shallowest and was the deepest at the eddy center. Despite this eddy being close to eddy dissipation, the fine-scale imaging system revealed larval retention and a spatial overlap around the eddy edge between larval fish and their preferred small cyclopoid prey *Oithona* (Schmid et al. 2020). Similarly, larval sailfish were also observed only around the eddy edge in this same region (Richardson et al. 2009). Further research is needed on these fine-scale processes of frontal eddies, especially during the relatively unstudied phase of unforced eddies and spin-down (Schmid et al. 2020).

Frontal eddies formed in the Straits of Florida continue into the GS, and further eddies are produced around a topographic feature known as the Charleston Bump. Govoni et al. (2013) found an abundance of commercially important, shelf-spawned species at the front between shelf water and the GS. They also suggest that the eddies and fronts of this region have a residence time of ~4 weeks providing an offshore nursery area (Govoni et al. 2010), which may be subsequently transported north and westwards back to the coast (Hare and Cowen 1996; Hare et al. 2002).

Conclusions and caveats

Frontal eddies are difficult to study as they are transient and fast-moving compared to mesoscale eddies and were previously too small for routine observation and sampling. There can be considerable challenges in the detection of frontal eddies, as they can be flooded with warmer water of the WBC (Roughan et al. 2017), or during the summer months when there is little temperature gradient between the inner shelf water and the WBC (Leichter et al. 2014). In the past, focused studies of small frontal eddies < 60 km diameter have been opportunistic (Everett et al. 2011; Mullaney and Suthers 2013), whereas the directed studies of the larger (mesoscale) cyclonic eddies in the Kuroshio (Kimura et al. 1997) and Straits of Florida were strategically planned (Shulzitski et al. 2015) or facilitated by long-term remote-sensed observations (Schaeffer

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et al. 2017). Our three examples show that frontal eddies form irregularly (but often) where boundary currents interact with the continental shelf, causing velocity shear with the more static inner shelf water. We propose that frontal eddies along the inshore edge of WBCs present a triad of oceanographic conditions and a larval fish nursery ground and may disproportionately contribute to coastal fisheries because they are small, common, and of sufficient duration for larval fish development (Govoni et al. 2010). In all three WBCs, entrainment of coastal larvae away from the shelf was established and various aspects of enhanced planktonic production was evident in the eddy. The inner shelf water was already primed (preconditioned) with phytoplankton and small zooplankton. The enhanced larval growth rates found in the eddy, which were further observed in the recruited individuals on reefs of the Florida Keys, is a particularly important aspect of the frontal eddy triad. Finally, all studies noted that eddies have the capacity to retain their larvae, as well as reduce the advection downstream away from adult habitats. Sometimes, the entrainment of fish larvae offshore is considered a loss for recruitment, whereas the frontal eddy triad suggests the opposite: a ubiquitous and ephemeral offshore nursery area.

Support for the fundamental triad of frontal eddies emerges from a synthesis of the three contrasting WBCs. The EAC is a comparatively weak WBC, but interacts with a narrow continental shelf (15–40 km), which shortens the spatial scales for shelf interaction and the logistics for observation (Schaeffer et al. 2017). In contrast, the KC has a 200 km wide shelf and has a well-documented frontal eddy triad for larval anchovy (Kasai et al. 2002), but the smaller eddies are unexplored. Eddies of the FC–GS have the longest record of observation with particular focus on the biophysics of eddy formation and ecology of coral reef fish larvae and zooplankton (Lee et al. 1991; Sponaugle et al. 2005, 2012) and the GS interacting with the Charleston Bump (Govoni et al. 2010, 2013). All three boundary currents have comparable locations for shelf interaction, eddy formation, and inner shelf entrainment—Smoky Cape, Cape Shionomisaki, and Cape Canaveral which provide geographic reference points for an intercurrent comparison of eddy triad formation. For example, the LC has a particular role in the formation of frontal eddies in the eastern Gulf of Mexico (Kourafalou and Kang 2012), similar to the separation and retroflection zone of the EAC (Suthers et al. 2011). Furthermore, a recent analysis aligned the EAC and FC in a jet-following coordinate frame and found the two currents are remarkably similar (Archer et al. 2018); a similar analysis of frontal eddy formation among WBC would be remarkably useful.

A roadmap for further study

Fine-scale features of frontal eddies

Over their relatively short life, frontal eddies may reinteract with the shelf and reengage with other eddies (Kourafalou and Kang 2012) and with the boundary current (Everett et al. 2015). The consequences of such perturbations to the planktonic food web during forced (spin-up) and relaxation phases (spin-down) would likely create a mosaic of food webs at different stages of ecological succession. A worthy goal would be to examine the fine scale conditions for ichthyoplankton within the eddy triad and around the edges using imaging systems such as In Situ Ichthyoplankton Imaging System (ISIIS; Cowen and Guigand 2008) and Zooglider (Ohman et al. 2019). The importance of fine-scale features such as upwelling around the eddy edge (Bakun 2006) and wrap-around filaments (Govoni et al. 2013) is still relatively unknown. For example, in the Straits of Florida, a large pelagic fish (sailfish, *Istiophorus platypterus*) spawned around the eddy frontal edge (rather than larvae entrained from shelf water) and where the first-feeding copepod prey were most abundant compared to the interior of the eddy (Richardson et al. 2009). Novel towed and underway platforms (Roughan et al. 2017) or the ISIIS (Cowen and Guigand 2008) could specifically examine these processes, especially later in the eddy life during the enigmatic conditions of eddy spin-down and dissipation (Schmid et al. 2020). Although the prospects for larval growth in frontal eddies are regarded as good, the fine-scale conditions for larval mortality remain a critical unknown factor, which we explore below.

Ecological succession and predator "loopholes"?

The sporadic and ephemeral nature of frontal eddies may be insufficient for predator populations to establish and planktivorous fish (including schools of spawning adults) may not locate an offshore eddy. This same speculation was articulated over 40 years ago (Lee et al. 1981, p. 136), and remains a critical question for the frontal eddy triad hypothesis. Visual predators such as birds and other large marine fauna may target fronts and large eddies (Bertrand et al. 2014; Scales et al. 2014), and while these are not planktivorous, they may target shoals of forage fish, which would be predators of ichthyoplankton. However, frontal eddies are small and often hard to detect by humans or other predators (Leichter et al. 2014). From a zooplankton perspective, more eutrophic systems like cyclonic eddies are characterized by shorter food chains and more herbivory than oligotrophic systems (Armengol et al. 2019). Furthermore, younger planktonic ecosystems found around tidal fronts (< 14 d) have largely herbivorous communities, compared to the longer food chains found in longer duration shelf-break fronts which include more predatory zooplankton and larger megafauna (Le Fevre 1987). Ultimately, however, the composition of the entrained source water will affect development of the predator field along with water temperature and season.

The fundamental ocean triad does not mention the effects of predation but elsewhere Bakun (2010) suggested that some situations could present species with an ecological "loophole" of lower predation rates. Bakun (2010) cited situations where larval tuna occur in poor nutritional waters, which have even

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poorer predator fields. Bakun (2013) also suggested a related process how entrainment of a spawning event at the eddy edge can swamp their predator field (until the tuna larvae themselves become cannibalistic in a density-dependent process). A similar situation was described for sporadic downwelling events providing larval fish with a loophole of optimal food and predator conditions (a safe-site, sensu Frank and Leggett 1982). The intensity of predation pressure on ichthyoplankton is difficult to assess as the process is spatially and temporally dynamic, from the daily vertical migration of omnivorous krill and copepods to the sporadic occurrence of fish schools. The survival of larval fish is a balance between finding prey for rapid growth and yet avoiding being eaten. A quantitative way forward to assess this balance in a frontal eddy triad is from the larval cohort's biomass specific growth to mortality ratio (Houde 1997; Hinchliffe et al. 2021, 2023; Suthers et al. 2022), sometimes referred to as the recruitment potential (Secor and Houde 1995). The relative preponderance of larger fish larvae would be an important characteristic of the frontal eddy triad, which suggests aspects of faster growth, lower predation and larval retention (Mullaney and Suthers 2013).

Does the frontal eddy triad improve recruitment?

This is the critical and most difficult question. Ultimately, juvenile fish need to return back to the coast via ocean transport (Hare et al. 2002; Malan et al. 2020) and by directional swimming back to the coast (Downie et al. 2021). Only one study provides the evidence that the otolith growth history of a larval life within a productive eddy, results in successful recruitment (Shulzitski et al. 2016). There could be other signatures of a frontal eddy within the body tissues of newly settled fish, such as fatty acid profiles from eddy-specific phytoplankton (Fraser et al. 1989), or stable isotope composition (Syahailatua et al. 2011). The recruitment potential (i.e., larval mortality/growth [M/G] ratio) of frontal eddies at various times of year would be a useful investigation, relative to larvae in the inner shelf source water or in the adjacent boundary current (Hinchliffe et al. 2023). A most intriguing test would be restocking of a frontal eddy with fertilized eggs of valuable or overfished species which were reared in a hatchery (and genetically identifiable), realizing a century-old dream (Dannevig 1907).

Testing the frontal eddy triad model

We suggest several tests of the frontal eddy triad and how to operationalize our conceptual model as a quantitative tool for fisheries forecasts. First, we need to assess if the recruitment potential (M/G ratio) of larval fish in a frontal eddy improves survival compared to the source waters of the inner shelf (or coral reef). Second, determine the significance of fine-scale patchiness within frontal eddies such as wrap-around filaments and upwelling along the edge (Bakun 2006; Richardson et al. 2009). In particular, we need to identify species of phytoplankton and zooplankton that characterize frontal eddies or their filaments (Okazaki et al. 2002; Schmid et al. 2020). Ideally, these characteristic plankton would have trophic signatures that are passed on to ichthyoplankton. Last, we suggest spatial models of the seasonal and interannual distribution of frontal eddies from remote sensing products (SST anomaly, ocean color, HF radar) and weight them by seasonal spawning activity of key species. The match of eddy activity with spawning activity is important—for example, Sponaugle et al. (2005) found no larval pulse associated with the passage of a frontal eddy in late summer. The significance of frontal eddies for fisheries could only be tested where there is long-term observing of larval fish and fisheries (McClatchie et al. 2014), together with an analysis to detect small eddies from remote sensing (Everett et al. 2012) or HF radar (Kim 2010). Another useful project is to calculate the frequency and volume of entrainment, as a function of larval survival relative to the condition of no frontal eddy formation.

Frontal eddy triads in other current systems

It is likely that submesoscale eddies of eastern boundary currents (Benguela Current, Shannon et al. 1984; California Current, Kim 2010; Nagai et al. 2015) may also provide a similar habitat, adjacent to the coastline. In a simulation of cold-core eddies of the California Current, (Logerwell and Smith 2001) concluded that modeled cold-core eddy habitat had a 10-fold greater production index than in all other regions. Other coasts have observed the ability of anticyclonic eddies to entrain coastal water, such as by the poleward Norwegian Coastal Current (Fossheim et al. 2005), who also noted that the effect on larval capelin growth and survival was unknown. Anticyclonic eddies of the poleward Leeuwin Current off western Australia have greater Chl *a* concentrations than cyclonic eddies and entrain larval fish of coastal origin which are larger than those found on the adjacent shelf (Holliday et al. 2011), which implies an oceanographic triad.

Other current systems may also harbor the conditions necessary for the oceanographic triad. For example, the WBCs of the southwest Indian Ocean, the southward flowing Agulhas Current and the northwards flowing Somali Current, are known for vigorous eddy fields that strongly interact with the east-African continental shelf (Lamont et al. 2016; Malan et al. 2018). Highly productive frontal eddies with characteristic warm water shingles have been observed (Krug et al. 2017) and simulated (Tedesco et al. 2019) in the Agulhas system. Noyon et al. (2019) describe the ontogeny of a small frontal eddy off the southern shelf of Madagascar, which entrained shelf water and retained it over 4 months while it drifted across to the South African coast. Although, to our knowledge, there is no direct evidence for a triad in this region, the necessary oceanographic conditions for a frontal eddy triad are evident and further research should focus on linking the physical oceanography and ecology of the coastal region, sometimes known as the Natal nursery area (Hutchings et al. 2002). In

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addition, the eddies associated with the eastwards flowing Antarctic Circumpolar Current may also play a role in the provision of nutrients into the euphotic layer, particularly iron, in the high-nutrient low-chlorophyll Southern Ocean (Chapman et al. 2020) although the evidence to confirm this hypothesis is lacking due the lack of in situ observations. With the advance of ocean observing systems worldwide, and changing boundary currents, the frontal eddy triad of favorable larval fish habitat may emerge as a new focus for fisheries oceanography.

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Conflict of Interest

The authors have no conflict of interest to declare.

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