The Consequences of Eddies on Biological Productivity:

Western versus Eastern Boundary Currents

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Dynamics of Marine Ecosystems

12/7/15

An eddy is a result of the turbulent transfer of momentum of a fluid through time and space, which in the ocean can have physical, biological, as well as chemical consequences. To catalogue the effect of eddies in oceans around the world, this paper will summarize studies on biological productivity in eddies in and around the Gulf Stream, Kuroshio Current, East Australian Current, California Current, and Peru Current. In high energy ocean regions such as the Gulf Stream, Kuroshio current, other western boundary or eastern boundary currents, eddies are commonplace when meanders break off from the dominant current (Chen et al., 2014). In the northern hemisphere, an eddy breaking off a western boundary current and propagating towards the west-northwest is an anticyclonic eddy (warm core ring) and an eddy propagating towards the west-southwest is a cyclonic eddy (cold core ring). In the formation of a cyclonic eddy, the thermocline arranges itself in a bell-like shape pointing towards the surface, and the sea surface itself depresses downwards in response (Kumar et. al, 2007). The rising of the thermocline induces colder waters to upwell, which can also shift the nutricline upwards towards the surface (Kumar et. al, 2007). Anticyclonic eddies would have the opposite arrangement. Exceptions to this rule exist but are few and characterized by exceptionally unique dynamics beyond the scope of this paper.

Warm core or cold core rings are distinguished by their relative temperature departure compared to their surroundings, which occurs as a result of the shifting of temperature gradients. Temperature is not the only variable changed by eddy transport, however, as salinity, nutrients, oxygen concentration, and biomass may be advected towards regions differing from the water mass of the eddy itself (Gruber et al., 2011). The characteristics of an eddy will often differ widely from the waters it is surrounded by, and for this reason primary productivity within the eddy will often vary wildly from the water surrounding the eddy (Gruber et al., 2011). The characteristics of an eddy's origin point, such as bathymetry, temperature, salinity, nutrient concentrations, and current velocities will determine not only how an eddy propagates through space, but its physical, biological, and chemical properties(Stramma, et. al, 2013). The Gulf Stream, Kuroshio, and East Australian Currents currents have been used as an example by many authors to demonstrate an increase in primary productivity in cold core eddies (Suthers, et al., 2011) . Global distribution of productivity in the ocean can be explained by understanding the strength of vertical exchange, which these cold core eddies fundamentally affect. (Gruber, 2011) Warm core rings in these regions on the other hand have been found to diminish primary productivity locally, bringing tropical species to the continental shelf where colder slope water is found (The Ring Group, 1981).

Eastern boundary currents, on the other hand, are typically more productive near the shore than western boundary currents (Gruber et al., 2011). As a result, upwelling strength is the dominant factor in determining local primary productivity and the presence of eddies only serves as a 'leak' for nutrients, moving them offshore (Gruber et. al, 2011). Increased eddies result in an in primary production offshore and a decrease in primary production towards the shore for eastern boundary currents (Stramma et. al, 2013) (Gruber et. al, 2011).

The Western Boundary Currents

The Gulf Stream, a western boundary current, produces eddies from meanders in the mean flow. Cold core, or cyclonic eddies are eddies that propagate southwest from the Gulf Stream. These rings drift into the Sargasso Sea and are temperature minima as well as salinity and oxygen maxima. As a result, a physical, biological, and chemical gradient is induced between the eddy and the surrounding water. At the center of the cold eddy is the area of highest productivity and highest biomass (The Ring Group, 1981). A cold core eddy's effect on biological productivity changes as the ring ages, and its temperature gradient becomes less due to surface heating. As an eddy ages the waters become remarkably less productive and species respond dramatically. N. megalops, a type of fish, decreases its respiration rate by 5 to 20% in rings older than six months. (The Ring Group, 1981). Growth rates in the once cold eddy are reduced in comparison to populations still living in Slope Water. Other fish move to deeper waters to recreate the cold environment that once was at the center of the eddy.

Eventually, a cold core ring is reunited with the Gulf Stream. Populations within the eddy can be reunited with Slope Water, and intermingle with the populations they originated from. This has important implications if the stressed marine population within the ring underwent large scale genetic selection, or if returning individuals become sterile from the experienced stress (The Ring Group, 1981). This can affect how the species moves forward, especially if species who become trapped in an eddy effectively have their genes removed. In the assessment of whether this is a negative or a positive effect requires additional information, however. The net addition of organic material to the northern Sargasso Sea is 5 x 10^{11} grams of carbon each year (The Ring Group, 1981). The loss of organic matter through the thermocline was ten times as large. However, at any time around 10% of the Sargasso Sea is occupied by eddies where the primary productivity is 50% greater than the surrounding waters (The Ring Group, 1981). Ultimately, primary productivity would decline by 5% if no rings existed (Chen, 2014).

Warm core rings, or anticyclonic eddies have very different properties and movement. Warm core rings transport warm Sargasso Sea water onto the continental shelf (Chen, 2014). Sargasso sea water has low biomass levels but a large amount of species of equal abundance. Slope water has a very high biomass with relatively few species (Chen, 2014). When a warm core ring introduces tropical biota to the cold shelf water, species can become stressed. Multiple instances of tropical turtles and fish appearing on the continental shelf within a warm core eddy have been reported in the last century (Chen, 2014). The most notable effect of warm core rings in colder areas is not the unproductive downwelling at the center of the eddy however, but the upwelling that has been reported at the periphery, or boundary of the eddy (Hitchcock et al., 1985). Observational and modelling studies have confirmed a local maximum of upwelling on the boundary of warm core rings, but the overall effect of warm core rings is not productive (Hitchcock et al., 1985).

The Kuroshio current is the western boundary current of the Pacific Ocean and shares similarities with the Gulf Stream. Both generate numerous mesoscale eddies throughout the course of a year, both warm (anticyclonic) and cold (cyclonic), which have been found to last up to a year (Chen et al., 2013). Cold core eddies originate north of the mean flow of the Kuroshio Current and propagate southwest, eventually to be reabsorbed by the mean flow. Cold core eddies have been found to enhance productivity through localized upwelling as well as transport fish larvae to locations more suitable for their development (Waku et al., 1998). According to Chen et al., 2013, 40 gC $m^{-2}yr^{-1}$ of carbon production can be attributed to eddy activity in the region, a third of the total primary production and on par with the Gulf Stream. The Kuroshio

Current along the coast of southern Japan has a bimodal characteristic which influences eddy activity: a straight and a meandering mode [**Figure 1]** (Kasai, 2002).

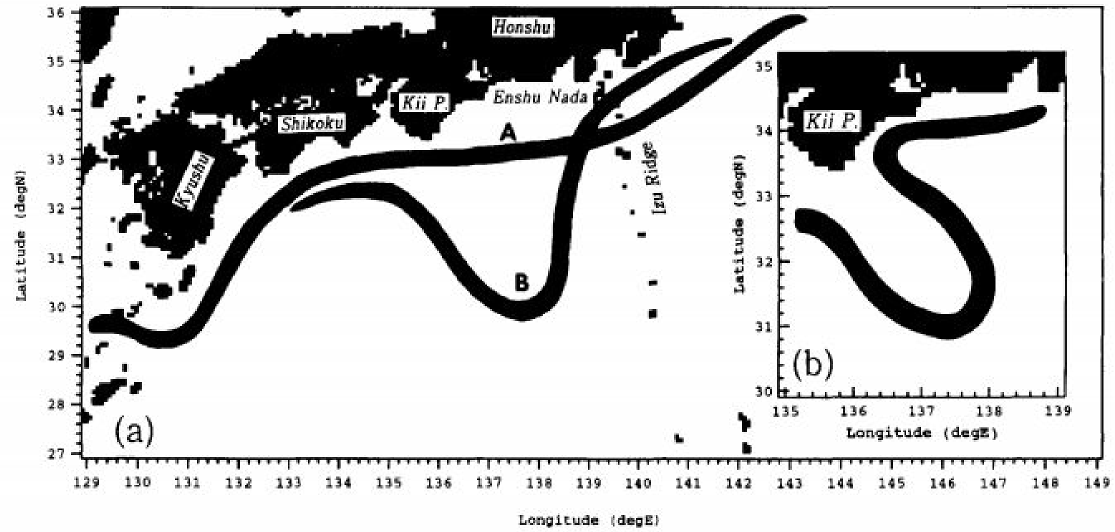

Fig. 1. (a) The typical path of the Kuroshio non-large meander (A) and the large meander (B) in the ocean south of Japan (Kawabe, 1980). (b) The "S"-shaped pattern of the Kuroshio path (Nitani, 1977).

Figure 1 from Sakaida's 1998 paper 'The behavior and the role of the anti-cyclonic eddy in the Kuroshio large meander development.' This demonstrates the bimodal meandering of the Kuroshio south of Enshu Nada, which influences eddy activity.

Determining on the mode, eddy activity will vary from high to low activity. Kasai (2002) went to Enshu-nada off the southern coast of Japan to study the effect of cold core eddies on anchovy larval transport during the meandering mode. The particular eddy studied was only 100m deep, typical of the shallow cold core structure in this region. The eddy studied was directly linked with nutrient poor water being entrained into the eddy and being boosted with nutrients and productivity (Kimura, 1997). Before entrainment into the eddy, fish larvae would have ran out of food, but were spared by upwelling within the eddy (Kasai, 2002). Additionally, the Kuroshio Current often acted as a barrier to recruitment onshore, had fish larvae ventured south of the mean flow (Kasai, 2002). Eddies allow larvae a chance to bypass the Kuroshio Current. Chlorophyll concentrations increased from 1.3 µg per liter in frontal waters to 2.4 µg per liter in the eddy (Kasai, 2002). The eddy provided a sanctuary for fish larvae to grow and then head back to the coast as the eddy reached the end of its life, as seen in **Figure 2**(Kasai, 2002). In response to these findings, Chen (2013) determined that Gulf Stream and Kuroshio Current cyclonic eddy dynamics are nearly identical in terms of biological significance.

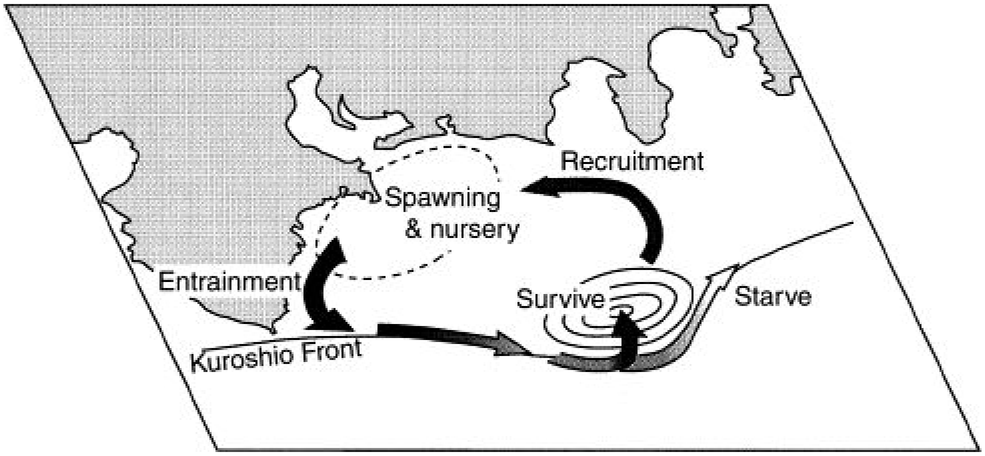

Figure 2 from Kasai's 2002 paper 'Entrainment of coastal water into a frontal eddy of the Kuroshio and its biological significance', showing how eddies breaking off to the north of the Kuroshio plays a role in the life cycle of fish and their egg larvae. Larvae are able to survive on nutrients upwelled within an eddy while not being carried away by the Kuroshio Current itself. When grown, the fish can move towards the coast of Japan to live out their adult lives and continue the cycle.

Warm core eddies of the Kuroshio rotate in an anticyclonic fashion and typically are areas of positive temperature anomalies, just like in the Gulf Stream. In terms of biology, a warm core eddy is indistinguishable from the surrounding waters during the first parts of its lifetime. Chiang and Taniguchi (2000) verified these findings, identifying very little difference in diatom concentrations between the surface layer of a warm core ring and the surrounding waters. Due to the lack of biological variation between warm core rings and the surrounding ocean, research on this phenomena has been limited and current understanding assumes that the mechanisms are analogous to Gulf Stream warm core rings, where upwelling can be found on the peripheries. As a warm core eddy infringes on the continental shelf, upwelling is induced on that particular boundary, and if a significant portion of the eddy breaches the shelf, upwelling can take over (Kimura, 2000) .

The last western boundary current discussed is the East Australian Current. Just as the Gulf Stream and Kuroshio Current, the East Australian Current, referred to as EAC from now, sees great eddy activity (Suthers et al., 2011). The mesoscale variability is extremely large so that sometimes a continuous current does not appear to exist. According to a Suthers et. al (2011), much of this has to do with the geometry of the coast, bottom topography, as well as high baroclinic instabilities in the current. Following the east coast of Australia, the EAC brings warm water poleward, allowing tropical reef fish to live outside of their normal habitat zones (Suthers et al., 2011). The EAC has also been found to exhibit the same positive benefit to fish larvae in cyclonic coastal eddies as seen in other currents (Oke, 2011).

Coastal water has been shown to be entrained into cyclonic eddies, but the Oke (2011) study on a particular EAC eddy takes this a step further. Between December 2006 and February 2007, a very significant cyclonic, cold core eddy formed in the Tasman Sea after weeks of upwelling favorable winds. Nutrient enrichment of surface waters and an increase in phytoplankton biomass surrounding the cyclonic eddy center was reported as the wind stress allowed for upwelling (Oke, 2011). Additionally, the eddy encroached the continental shelf, a topographical barrier which allowed for the water to be forced up the continental shelf, enhancing upwelling (Oke, 2011). Although cyclonic eddies propagate south once they break off of the mean flow, the meandering EAC took a path extremely close to the coast before the eddy could break off (Oke, 2011). This eddy propagated at 1.2 meters per second towards the coast and was found to be tilted towards the land with depth, coined an ‘eddy lean’ (Oke, 2011). Tilting with depth is typical with baroclinic instability, but it was not anticipated that an eddy would be so efficient at baroclinic energy conversion (Oke, 2011). Currents associated with this eddy were found to extend from the surface to the ocean floor (Oke, 2011). The initial theory was that the eddy was simply accumulated cold water that had been upwelled, but the available potential energy associated with the existing gradient as a result was an order of magnitude smaller than the eddy kinetic energy over the course of the eddy’s life (Oke, 2011). This particularly strong eddy was found to have barotropic and baroclinic components, a combination of the density gradient from the cold upwelled water as well as the energy from the wind stress (Oke, 2011). This particularly strong eddy indicated an additional pathway for eddy formation by introducing high barotropic as well as baroclinic conversions of energy. This anomalous energy conversion was associated with anomalous biological productivity, but these events happen on a smaller scale across western boundary currents every day (Oke, 2011).

Warm core eddies of the EAC have been studied even more extensively than cold core eddies (Dietze, 2009). Low productivity is typical of warm core eddies in other western boundary currents, where there is typically a decrease in biomass. According to Tranter et al., (1983), copepods were found to be smaller in warm core eddies in southwest Australia due to either the warmer temperatures or the lack of productivity, or both. Upwelling occurs around the boundaries of the eddy, and species of lobster were found to be abundant in these areas as well according to Tranter et al., (1983). Warm core eddies of the EAC have a seasonality, which can allow for relatively productive Springs when colder, winter water is entrained into the eddy (Baird et al., 2010). Study of EAC warm core eddies has led to the description of a mechanism called ‘surface flooding’, or the sinking of warm core rings (Baird et al., 2010). The drop of air surface temperature due to cold outbreaks has been determined to cool off warm core rings, increasing their density (Baird et al., 2010). As the ring sinks, the water that overwhelms the surface of the ring is initially from water found below the eddy itself (Baird et al., 2010). ‘Surface flooding’ in this case becomes an upwelling mechanism across a warm core eddy that can lead to phytoplankton growth as a mixed layer develops on top of the eddy (Baird et al., 2010). Previously, the warm core eddy acted as a cap to primary productivity, but as nutrient rich water is upwelled to the euphotic zone, blooms can occur, especially in late winter and the spring (Suthers et al., 2011). Ultimately, warm core rings can become productive as well under the right conditions.

Eddies have been typically explored through the lens of western boundary currents, but their effects on eastern boundary currents which are typically more productive on average, are important to discuss (Chen, 2014). Individual eddies may have the opposite effect, but on a large scale there is mostly a positive relationship between eddies and productivity, determined by eddy kinetic energy and surface chlorophyll (Gruber et al., 2011). The opposite is true for eastern boundary currents. According to Gruber et al (2011), individual eddies in eastern boundary currents do have higher biomasses and productivity, yet there is a negative correlation between eddy kinetic energy(EKE) and biological productivity. The explanation for this hypothesis is that eddy activity shifts limiting nutrients from coastal waters to the more open ocean. The EKE and biological productivity relationship does not hold at low levels of EKE, but this is explained after a model simulation that can resolve eddies in eastern boundary currents was performed. Gruber (2011) studied the California Current System (referred to as CalCS from now on) to uncover the relationship between eddies and productivity.

The model simulations done by Gruber et al. (2011) showed a reduction in net primary production by 50 to 70% in eastern boundary upwelling systems. Eastern boundary currents are the eastern part of the subtropical gyre, flowing much slower than western boundary currents. They are in areas with upwelling favorable winds, so that Ekman transport is offshore and upwelling of cold, nutrient rich water from below can occur (Gruber et al., 2011). With the introduction of eddies to the system, offshore production increases, implying some type of offshore transport of nutrients. A decrease in nitrate and organic carbon concentration is found near the shore of the CalCS (Gruber et al., 2011). Offshore, nitrate and organic carbon concentrations increase by amounts on the same order that they are lost nearshore (Gruber et al., 2011). In eastern boundary current systems, eddies have a tendency to advect heat towards the shore as well as buoyancy (Gruber et al., 2011). These characteristics are not limited to California and are found in the Peru Current, Humboldt, and other eastern boundary currents (Plattner, 2011).

The area of upwelling decreases significantly as a result of the thermocline flattening out from the advection of heat (Grubet et al., 2011). Nearly every factor contributing to an upwelling environment is affected by the introduction of eddies. At high levels of EKE, nearshore primary production is extremely low, but these areas of high EKE have far reaching effects (Gruber et al., 2011). These effects are so far reaching that a spatial statistical analysis of areas with EKE and areas of productivity indicates no strong relationship between areas of low EKE and areas of high productivity (Gruber et al., 2011). It has been observed that low productivity will exist within large areas surrounding an area of high EKE, leading to a misleading EKE-productivity relationship (Gruber et al., 2011).

Stramma et al. 2013 confirms the hypothesis in the Peru Current with observational data that coastal eddies act as a mechanism for transport of nutrients, specifically nitrogen, offshore and away from the upwelling front. Additionally, eddies in eastern boundary currents supply the oxygen minimum zone with even more oxygen poor water, increasing the size of this zone and negatively impacting organisms (Stramma et al., 2013). Typically eastern boundary currents supply oxygen rich water to these zones (Stramma et a., 2013) The advection of nutrients away from the upwelling front appears to be the mechanism detrimental to the productivity of the entire system. These dynamics are found in both the California Current and the Peru Current, and can be applied to productive eastern boundary upwelling currents.

Based on research that has been done already, eddies have the role of redistributing heat, salinity, and nutrients across the boundary currents that act as fronts between cold and warm, or high and low density waterse. Eddy activity in western boundary currents has its own unique dynamics depending on whether or not the eddy is anticyclonic or cyclonic, but the sum effect of all eddies is a positive one. The cyclonic cold core eddy's positive effects on biological productivity overwhelms the anticylonic warm core eddy's negative effects on biological productivity. This had to do with the more oligotrophic nature of western boundary currents. Eddies, as a redistributor of nutrients, allows for more biological productivity in the Sargasso Sea than there otherwise would be. Additionally, the periphery of anticylonic eddies in western boundary currents see upwelling, especially when the eddy infringes on the continental shelf, sparking phytoplankton blooms.

Eastern boundary currents thrive with very high levels of biological productivity, both primary and secondary. Eddies, serving as the redistributor, have a net negative effect on eastern boundary currents due to the redistribution of nutrient rich water towards the open ocean away from the upwelling front near the shore. Although an individual cold core and warm core eddy may have similar effects on local production, large scale dynamics are quite different between east and west boundary currents. The upwelling front is the main mechanism driving biological productivity in eastern boundary currents. Experiencing high eddy activity is akin to driving a car while its gas tank is nearing empty. The sputtering and stalling due to a lack of energy is comparable to an eastern boundary current with high eddy kinetic energy. Nutrients are not made available to the upwelling front in an eastern boundary current with high EKE.

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