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Review article

Advances in understanding physical and biological controls on eggs and larval distribution in Pacific fisheries: A review

Md Afsar Ahmed Sumon [1], **Sugeng Hartono** [2], **Ramzi H. Amran** [2], **Muhammad Browijoyo Santanumurti** [2], **Saadullah Jan Khan** [3], **Sajia Akther** [1], **Mohamed Hosny Gabr** [2], **Nguyen Vu Linh** [1, 4, *], **Hien Van Doan** [1, 4, *]

[1] Department of Animal and Aquatic Sciences, Faculty of Agriculture, Chiang Mai University, Chiang Mai 50200, Thailand.

[2] Department of Marine Biology, Faculty of Marine Sciences, King Abdulaziz University, Jeddah 21589, Saudi Arabia.

[3] Research Institute for Health Sciences, Chiang Mai University, Chiang Mai 50200, Thailand.

[4] Functional Feed Innovation Center (FuncFeed), Faculty of Agriculture, Chiang Mai University, Chiang Mai 50200, Thailand.

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***Correspondence**:
Nguyen Vu Linh
e-mail: linhvu.n@cmu.ac.th
Hien Van Doan
e-mail: hien.d@cmu.ac.th

Abstract

The early stages of fish, comprising eggs and larvae, are exceptionally fragile and sensitive to environmental dynamics and climate change. Pacific Ocean (PO) currents play an important role in shaping the distribution of marine organisms, influencing global climate patterns, heat distribution, coastal temperatures, and nutrient redistribution. These currents reveal significant changes within the climate system. Their variability across different timescales can be attributed to the complex interplay of physical forces. These currents are subjected to diverse anthropogenic factors, exerting detrimental effects on the dispersal of fish larvae. Furthermore, climate change variables, including alterations in tropical PO temperature associated with the ENSO cycle, Atlantic *Niño* modes influencing equatorial Atlantic temperature, changes in ocean salinity, polar ice cap melting, increasing greenhouse gases, marine heatwaves, and fluctuations in subsurface flows, directly impact the distribution, abundance, and species composition of early life stages. Major Pacific fisheries, such as those targeting Pacific sardines, saury, and anchovies, undergo population booms and declines due to significant alterations in the current dynamics of currents and fronts within the PO. The anticipated intensification of the ENSO cycle, characterized by more frequent and severe *El Niño* (warm) and *La Niña* (cold) events as a result of climate change, is expected to significantly impact the early developmental stages of important commercial fish stocks regularly. This review synthesizes the current understanding of the physical and biological parameters driving changes in ocean currents and their implications for early fish dispersion, emphasizing the critical need for research in this area to inform global conservation efforts, fisheries management, and food security.

Keywords: Pacific Ocean, climate change, dispersal, fish eggs and larvae, ocean dynamics

Abbreviations

BC: Benguela Current; CC: California Current; ENSO: *El Niño*-Southern Oscillation; EC: Equatorial Currents; Et: Ekman transport; KC: Kuroshio Current; MHWs: Marine Heatwaves; NP: North Pole; NPC: North Pacific Ocean; NEC: North Equatorial Current; NOAA: National Oceanic and Atmospheric Administration; OC: Oyashio Current; PO: Pacific Ocean; PC: Peru Current; SP: South Pole; SPG: South Pacific Gyre; SCB: Southern California Bight: SEC: South Equatorial Current.

Introduction

Ocean currents are defined as the motion of water masses flowing within and between ocean basins (Wulandari et al., 2023). These currents arise from the complex interplay of internal and external forces driving overall ocean circulation patterns (Stewart, 2008). The currents and interactions between them lead to various ocean dynamics and circulations, which are vital for marine organisms and the overall health of the ocean ecosystem (Hays, 2017). Lalli and Parson (Lalli & Parsons, 1997) emphasized the crucial role of ocean currents in distributing water masses that contain specific chemical and physical properties necessary for marine organisms. Furthermore, ocean currents distribute nutrients and food over large water areas, facilitating the migration of some species adapted to these currents (Gaspar et al., 2006). Marine fish, perhaps more than any other species of vertebrates, shows remarkable connectivity over great distances through ocean currents (Ramesh et al., 2019). Global fish populations form a small-world network with complex relationships between populations and significant productivity centers, with significant implications for conservation, management, and global food supplies (Barange et al., 2018b). Most fish spawning occurs in or near gyral, upwelling, or other current-directed circulation systems that are generally connected with major current systems (Richardson et al., 2009).

Pacific Ocean (PO) currents are crucial in regulating global climate patterns, distributing heat, affecting coastal temperatures, and redistributing nutrients (Morioka et al., 2019). They also reveal climate system changes by transporting water properties that influence terrestrial and marine organism dispersal, including critical stages, including fish eggs and larvae (Merino & Monreal-Gómez, 2009). Major currents such as the Oyashio Current (OC) impact the dispersal of migrating species like Pacific saury, influencing migration routes and fishing grounds. Meanwhile, the Kuroshio Current (KC) delivers nutrients to regions supporting fishing and diverse marine food webs (Liu et al., 2022). The largest spawning biomass of Pacific sardines in California occurs in the transition zone between the California Current (CC) and inshore upwelled waters (Lo et al., 2005). Moreover, the PO is a central player in the *El Niño*/Southern Oscillation (ENSO), which is recognized as a major driver of global climate variability. The ENSO phenomenon disrupts weather patterns across the globe, affecting precipitation, temperature, and even the frequency of extreme weather events (Hu et al., 2015). This variability extends to oceanic processes, where changes in sea surface temperatures can lead to significant alterations in marine ecosystems and nutrient cycling (Chenillat et al., 2012).

The dispersal of eggs and larvae concentrates populations in key areas to generate abundant fish communities. Fish larvae depend on optimal currents for transport and adequate food during travel to reach suitable nursery habitat at the right time, size, and condition (Norcross & Shaw, 1984). Understanding the influence of ocean currents on the dispersal of fish eggs and larvae is critical, given their fragility and sensitivity to environmental dynamics during early stages (Arellano & Rivas, 2019). Water movement emerges as a crucial variable controlling fish larvae dispersal and distribution. During their initial stages, larvae, with a substantial yolk sac and limited swimming ability, may be passively carried by the water currents. Their small-sized makes them susceptible to being easily swept away by the ocean circulation, potentially leading them to ecosystem that is suitable or unsuitable for their survival. Even if they successfully hatch or grow, ocean currents play a role in directing them to safe areas where they are not preyed on by predators (Osse & Van den Boogaart, 1999).

This review describes the effects of major PO currents on dispersion and distribution of fish eggs and larvae, emphasizing their sensitivity to transport mechanisms. It also assesses the related impacts of climate change on altering ocean currents and, consequently, fish distribution.

The major forces which act on the ocean currents

Ocean currents represent the horizontal or vertical flows of surface and deep water that traverse the world's oceans (Neumann, 2014). The term 'wind-driven current' denotes currents generated by the wind, which can occur locally or globally on a planetary scale. Other factors, such as the existence of landmasses and the Earth’s rotation, also exert influence on these phenomena. Examples of different types of currents, such as Ekman transport, boundary currents, surface gyres, and geostrophic currents, illustrate the complexity of ocean dynamics (Segar & Segar, 2018; Stewart, 2008; Webb, 2019). Physical processes, including friction, gravity, and Coriolis force act as dominant drivers of ocean dynamics and circulation across different timescales (Figure 1).

Friction, a significant force shaping ocean currents, arises when one body moves past and contacts another. Wind stress, the most common surface friction force in the ocean, imparts horizontal motion to surface waters through frictional momentum transfer. This wind-driven flow at the surface extends deeper into the upper ocean through Ekman transport processes. Uneven pressure above the surface waves, induced by wind-driven ocean currents, contributes to wave growth (Segar & Segar, 2018).

Gravitational forces, in addition to wind-driven flow, lead to density-driven currents (Abolfazli et al., 2020). The weight of the water in the ocean, influenced by gravitational forces, produces pressure disparities, creating buoyancy and tides. Gravity exerts upward or downward forces on water masses that are more or less dense than nearby water. When cold air blows over the sea, it cools the water on the surface, making it denser than the water below. Gravity then causes the denser

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water to sink, which creates a force-driven by density differences. Contrarily, horizontal pressure gradients arise from distinct water masses throughout the ocean. Water is compelled to flow toward lower pressure areas to attain equilibrium. Furthermore, the gravitational pull of the sun and moon induces oscillating tidal bulges and complex tidal currents, incorporating turbulence and mixing. These tidal flows significantly contribute to coastal and estuarine circulation (Stewart, 2008). Although not directly wind- or density-driven, these recurrent horizontal and vertical tidal flows influence overall circulation through their mixing effects.

Pseudo-forces, as described by Stewart (Stewart, 2008), represent an additional influence shaping ocean currents. Newton's first law stated that a body in motion stays constant unless an external force acts on it. When observed the ocean from a rotating coordinate system, a moving water mass that maintains a constant velocity will seem to change direction due to the Coriolis force. In a rotating, Earth-fixed coordinate system, this force is a dominant fictitious force dictating motion. Ocean currents can be affected by external forces such as atmospheric pressure or seismic disturbance. Atmospheric pressure induces an inverted barometer effect, whereas air from a high-pressure atmosphere flow into the area of lower pressure. This atmospheric pressure, particularly in subtropical to higher latitudes, influences ocean heat and circulation, and vice versa (Fahad & Burls, 2022; Fahad et al., 2020). Wind associated with high and low atmospheric systems can lead to formation of storms that drive masses of ocean water. Simultaneously, seismic activity may result in tsunamis or big waves driven by earthquakes, volcanic eruptions, or other earth vibrations (Webb, 2019). The propagation of seismic waves through the oceans not only induces local flows but also influences overall circulation. Although relatively small compared to wind and density effects, these transient pseudo-forces significantly impact coastal and regional transport .

Pacific Ocean currents and circulations

Boundary currents and surface gyres

Eastern boundary currents represent robust systems along the east side of Earth's major ocean basins, directing water toward the equator and inducing significant upwelling (Yang et al., 2020). These currents are particularly responsible for the Northern Pacific Gyre, a subtropical gyre in the North Pacific Ocean (NPC), and the South Pacific Gyre (SPG). The SPG plays an important role in regulating the climate and ecosystem of the Southern Hemisphere (Strub et al., 2013). The SPG is defined by its clockwise circular pattern formed by four principal ocean currents: the North Pacific Current (northern boundary current), the California Current (eastern boundary current), the North Equatorial Current (southern current), and the Kuroshio Current (western boundary current) (Figure 2). Changes in large-scale wind forcing have contributed to the strengthening of the SPG over the last century. Gyres, such as these, facilitate the transport the solar heat, affecting weather and climate events, and contribute to the dispersion of eggs and larvae throughout the ocean. Especially, there are five coastline currents associated with significant upwelling areas globally, with the four eastern boundary currents representing

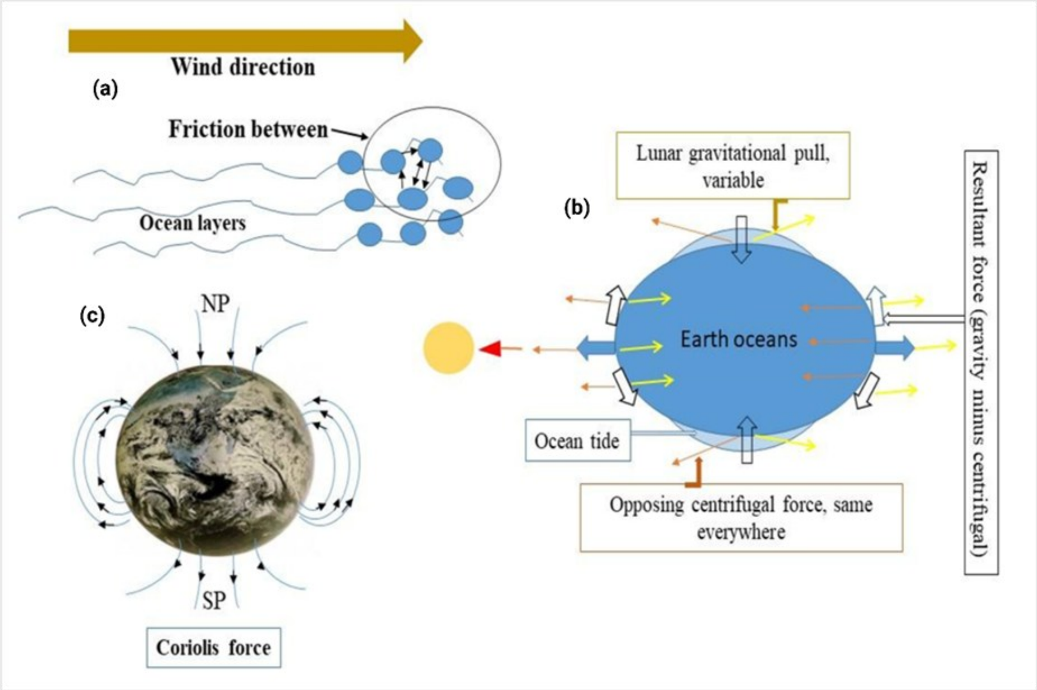

Figure 1. The picture represented different ocean forces; (a) Friction force, (b) Gravity force, and (c) Coriolis force. NP, North Pole and SP, South Pole.

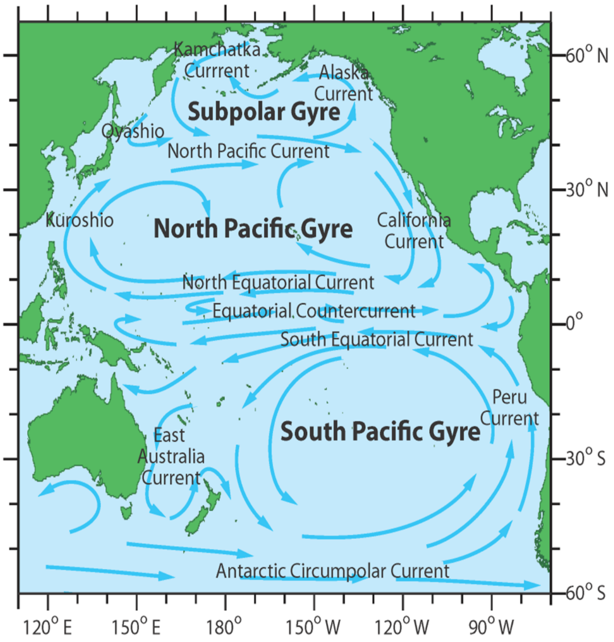

Figure 2. Major Pacific Ocean currents and circulations (source: NOC).

prominent upwelling zones (Hitt et al., 2022; Sousa et al., 2017). The California Current (offshore California and Oregon), the Peru or Humboldt Current (offshore Peru and Chile), the Canary Current (offshore Northwest Africa), and the Benguela Current (offshore western southern Africa) are examples of these currents. Coastal upwelling in these regions introduces nutrient-rich water, making them highly productive and crucial fishing grounds (Fréon et al., 2009). The increased primary production supports diverse fish populations while providing essential food and larval habitat critical for survival during early life stages.

California Current

The California Current (CC) is an ocean surface current originating at 50° N, where the Subarctic Current meets North America continent. It then bifurcates into the Alaska Current (flowing northward) and CC (flowing southward) (Shanks & Eckert, 2005). Extending southward as a broad current (approximately 500 km wide) at a moderate speed (0.05– 0.10 ms^{-1}). It continues until it reaches 20° N, where it turns westward, transforming into the North Equatorial Current (NEC) (Auad et al., 2011). Seasonal variation in temperature and salinity within the CC result from factors such as upwelling, insolation, and water flow (Lynn, 1967).

The CC plays a pivotal role in transporting cold, nutrient-rich waters from higher latitudes to coastal regions, substantially impacting the efficiency of biological production in upwelling systems (Arellano & Rivas, 2019). Fish production is influenced by offshore transport since it affects the coupling between lower and upper trophic levels. Also, the cold upwelling water supports a rich abundance of plankton and marine life, contributing essential nutrients to the ocean surface. The CC exhibits two distinct phases driven by the Subarctic Current: a warm phase, during which the Alaska Current may be intensified while the California Current weakened, and a cold phase, which shows the opposite pattern (Shanks & Eckert, 2005). These changes in oceanography over decades significantly affect the fauna of the Eastern North Pacific. *El Niño*-Southern Oscillation (ENSO) events occur approximately twice or thrice each decade in the CC (Storlazzi & Reid, 2010), further contributing to the dynamic nature of this current. A distinctive California Current region occurs when alongshore winds blow from the north or northwest in spring and summer, while robust winds from the southwest prevail during the winter. This transition occurs between Point Conception and Vancouver Island, where the inshore countercurrent (Davidson Current) replaces the CC (Auad et al., 2011). At the convergence zone, the California and Inshore counter currents meet, forming a corresponding poleward jet. The coastline turns sharply eastward at Point Conception defines the Southern California Bight (SCB) (Shanks & Eckert, 2005).

Peru Current

Peru Current (PC), also known as the Humboldt Current, is characterized by its cold, low-salinity ocean flow (Grados et al., 2018). This current establishes the Equatorial Front and play an essential role in cooling the climates of Ecuador, Peru, and Chile. The periodic disruptions in upwelling events caused by the ENSO event can have significant societal and economic repercussions (Montecino & Lange, 2009). In the PC, a substantial18-20% of the global marine fish catch is derived from pelagic species such as sardines, anchovies, and jack mackerel (van Ginneken, 2019). This current serves as a critical determinant of the abundance and distribution of these key species, consequently influencing fisheries and ecosystems across the region. Understanding of the dynamics of the Peru Current is essential for marine scientists and policymakers, as both play a central role in managing and sustaining these vital marine resources.

Equatorial Currents (EC)

The Pacific Ocean has two equatorial currents are South Equatorial Current (SEC) and North Equatorial Current (NEC). The SEC and NEC in the Pacific Ocean facilitate the redistribution of warm water from the western Pacific towards the central and eastern Pacific (Seidel & Giese, 1999). They contribute to the growth of *El Niño* and *La Niña* phenomena (Yu et al., 2023). Yu *et al.* (2023) (Yu et al., 2023) showed that anomalous zonal and meridional currents close to the equatorial central Pacific produce negative nonlinear zonal and meridional temperature advection anomalies for both *La Niña* and *El Niño* events, favoring *La Niña* events that are stronger than *El Niño* events. Equatorial Currents are primarily driven by winds, propelling westward movement in proximity to the equator (Basu, 2019). The Southeast Trade Winds exert their influence by driving the Pacific SEC westward until approximately longitude 180° E, where it flows approximately between latitudes 5° N and 15°–20° S (Dunxin & Maochang, 1991). At this juncture, the current undergoes a division: one segment heads north to merge with the countercurrent, while the remaining portion bending southward, giving rise to the East Australian Current, which flows east of New Zealand. The Peru Current, which feeds the SEC and West Wind Drift, flows north to the PC, which forms the Pacific SEC (Sirota et al., 2004). Simultaneously, the Pacific NEC is influenced by the Northeast Trade Winds and divides into the KC and the NPC (West Wind Drift) (Wu et al., 2019). The KC initially moves northward towards Japan, then shifts eastward as the NEC and southward as the California Current. The CC, in conjunction with the equatorial countercurrent, combines to form the Pacific NEC (Qiu et al., 2015).

Kuroshio Current (KC)

The Kuroshio Current, often referred to as the Japan Current, Black Stream, and Gulf Stream of the Pacific, stand as a significant warm western boundary current within the wind-driven, subtropical, and subarctic circulations of the North Pacific Ocean (Hurlburt et al., 1996). Originating from the Philippine Sea, (Kawai, 1998), the KC asserts its prominence as the largest current in the western Pacific, traveling a remarkable distance of almost 2,000 miles before veering away from coastline (Saito, 2019). Renowned for its heightened productivity, the Kuroshio contributes to the establishment of a distinct subtropical climate in the region (Zheng et al., 2016). Especially, the current gives rise to numerous small and meso-scale eddies, featuring an average sea surface temperature of approximately 24 °C (75 °F) and extending across a width of about 100 kilometers (62 miles) (Qiu & Lukas, 1996).

In the northwestern expanse of the Pacific Ocean, the KC plays a crucial role in the transport of heat, salt, and organic matter. This influence reverberates through the ocean ecosystem and supporting a significant fishing industry in Japanese society, where fish serves as the primary source of protein (Holsman et al., 2019). The interannual variability of the Kuroshio significantly affects biological production, nutrient delivery, and the fishing sector, although the precise mechanisms underlying these linkages remain elusive. Recent studies propose that the Kuroshio operates as a nutrient stream that carries a substantial quantity of nutrients from south to north in the ocean's dark subterranean strata (Nagai et al., 2019). Nagai *et al.* (Nagai et al., 2019) further contend that the region downstream of the Kuroshio, termed the Kuroshio Extension, is the area with the highest net CO_2 absorption. The Kuroshio currents increase the ability of warm waters to absorb CO_2 by cooling them from south to north. This cooling, along with phytoplankton photosynthesis, is crucial for understanding the function of the Kuroshio nutrient stream in developing the CO_2 sink, which can help predict future ocean responses to climate variability (Nagai, 2019).

North Pacific Current

The North Pacific Current (NPC), recognized as a Northern boundary current, is a key component the formation of the North Pacific Subtropical Gyre–a slow-moving warm water current (Cummins & Freeland, 2007). Often referred to as the North Pacific Drift, this current traverses the Pacific Ocean from west to east, coursing between latitudes 30 and 50 degrees north (Sverdrup, 1940). Its primary function involves the transportation of warm water from western Pacific to the coastal regions of North America. Furthermore, the NPC plays a crucial role in conveying warm water across the North Pacific Subpolar Gyre and the upper reaches of the North Pacific Gyre (Zhang et al., 2021). The origin of the NPC can be traced to the confluence of the Kuroshio and Oyashio Currents off the coast of Japan. The Oyashio is a cold subarctic current, extends southward, executing an anticlockwise loop over the western North Pacific Ocean (Ueno et al., 2023). The meeting point of these currents generates the NPC, initiating the conveyance of varying volumes and flows of warm water toward the Gulf of Alaska and the CC (Auad et al., 2011). This divergence of water flow is termed bifurcation. Remarkably, approximately 60% of the NPC water is directed toward the Gulf of Alaska, whereas the remaining 40% contributes to the CC (Freeland, 2006). Despite some fluctuations in these volumes, the resultant variations contribute to increased volumes and velocities of the NPC water entering these currents. The intricate interplay of the NPC with its oceanic counterparts underscores its significance in shaping regional hydrodynamics and temperature distributions within the North Pacific Ocean.

Factors driving Pacific Ocean currents

Ekman transport

Ekman transport (Et), influenced by wind friction and the Coriolis force, plays an important role in driving the PO currents (Santander-Rodríguez et al., 2022). As the wind interacts with the ocean surface, the Ekman transport ensues. The Earth's rotation induces an inertia force opposing the water mass's movement, initiating the Coriolis effect. While the water mass should logically follow the wind's direction, the Coriolis effect causes a deflection. In the Northern Hemisphere, water mass deviates 45 degrees to the right of the wind, whereas in the Southern Hemisphere, the deviation is to the left [10]. The directional angle of mass water transport increases as the depth of water increases. The Coriolis effect creates the curvature that spirals. In the deeper layer, the current direction can reach up to 90 degrees. However, energy dissipation through friction and reduced current speed occur below a depth of approximately 100 meters (330 feet) (Webb, 2019). Webb (2019) noted that ideal conditions rarely exist in the ocean and that this phenomenon happens. While the surface currents generally run parallel to the wind direction, Et in the open ocean typically deviates by around 70 degrees. Similarly, in shallow coastal waters, the alignment may closely follow the wind's direction, showcasing the complexity of Et dynamics in different oceanic settings.

Upwelling and downwelling

Upwelling occurs predominantly along the eastern margins of oceans, with less prevalence on the western margins. Significant coastal upwelling zones are found in the eastern boundary currents of the Pacific oceans (Bakun et al., 2015). The interplay of the Coriolis effect, Ekman transport, and topographic steering of westerly winds contributes to these phenomena. Wind-driven currents and Ekman transport induce vertical movements of subsurface water, leading to the occurrences of upwelling and downwelling (Kämpf et al., 2016).

Upwelling involves the ascent of cold, nutrient-rich deep water to the surface, revitalizing nutrient-depleted coastal areas and stimulating primary production (Matano & Palma, 2008). In contrast, downwelling is the downward movement of surface water, potentially delivering oxygen to deeper waters but simultaneously increasing the depth of the nutrient-poor stratum, thereby reducing productivity (Webb, 2019). According to Stewart *et al.* (Stewart, 2008), upwelling initiates when surface currents split off or diverge. Wind generates surface currents aligned with its direction, and the Coriolis effect induces the Ekman transport, causing water mass divergence. To establish upwelling zones, deeper water must replace the ascending surface water. For instance, in the Equatorial Pacific, the trade winds prompt the westward flow of North and South equatorial currents. The resulting northward and southward movement of surface layers, influenced by Ekman transport, creates a divergence zone and highly productive upwelling areas. Downwelling occurs when surface currents converge, forming a convergence zone. In this scenario, surface currents accumulate and flow downward, leading to the descent of surface water (Stewart, 2008). Downwelling areas do not have abundant marine life because critical nutrients are not constantly replenished from the cold, deep, and nutrient-rich water beneath the surface. Thus, the regions have minimal production (Webb, 2019). Downwelling occurs off the coast of Oregon and Washington during the winter months. It is also found along Alaska's west coast, on the eastern edge of the Gulf of Alaska gyre (Hickey et al., 2001).

El Niño and *La Niña*

El Niño is a climatic phenomenon characterized by an abnormal warming of surface waters in the eastern tropical PO (Philander, 1989). This phenomenon induces a shift in rainfall patterns from the western PO and eastern Australia to the central and eastern PO, adversely affecting marine life along the Pacific coast (Grove, 1998). *El Niño* represents the warm phase of the ENSO cycle (Redondo-Rodriguez et al., 2011). Conversely, *La Niña*, the polar opposite of *El Niño*, causes cooler-than-average sea surface temperatures in the eastern and central equatorial PO. Currently, NOAA reports the presence of *El Niño* in the tropical Pacific (NOAA, 2023), with forecasters anticipating its persistence through the spring, potentially intensifying into a strong event with a 75-85% probability. *La Niña*, on the other hand, is the polar opposite of *El Niño*, which refers to cyclical climatic conditions that occur in the equatorial PO (Collins, 2005). The interconnected factors of sea surface temperature, rainfall, air pressure, and atmospheric and ocean circulation contribute to these phenomena (Li et al., 2022; Stewart, 2008). In the typical tropical Pacific, robust trade winds move westward, transporting warm surface water toward the western Pacific adjacent to Asia and Australia (Hu et al., 2015). During *El Niño*, the intensity of these trade winds diminishes along the Equator due to fluctuations in atmospheric pressure and wind velocity (Ordinola, 2002). This reduction allows warmed surface water to move eastward from the western Pacific to the northern coast of South America, deepening the thermocline and impeding normal upwelling. Consequently, the nutrient-rich cold-water upwelling that sustains the generally productive coastal environment in the eastern Pacific's euphotic zone is disrupted (Peña et al., 1994). In *La Niña* conditions, intensified trade winds carry more warm water to Asia, fostering upwelling along the west coast of the Americas. Cold, nutrient-rich water rises to the surface, enhancing the coastal ecosystem's productivity (Anderson & Lucas, 2009; Kämpf & Chapman, 2016; Webb, 2019).

ENSO

In the 17th century, the *El Niño* phenomenon was identified by a group of South American fishermen off the coast of Peru, where they found a warm ocean current, and Peruvian scientists considered it a local event when it was first analyzed (Grove & Adamson, 2018). The *El Niño* phenomena, which occurred in 1957-1958, led scientists to recognise that it was more than just a tropical coastal current, but a linked basin-scale phenomenon involving coupling between the atmosphere and the ocean, known as ENSO (Bertrand et al., 2020). This phenomenon is one of the most prominent fluctuations between years that occur in the tropical climate system, and it has a significant impact on weather patterns all over the world. ENSO originates in the tropical PO, where it consists of two opposite phases: *El Niño*, an irregular warming phase that occurs in the central and eastern tropical Pacific, and La Niña, marked by anomalous cooling subsequent to *El Niño*. During the boreal summer, anomalous developments occur in sea surface temperatures in the tropical Pacific Ocean, which peak during the winter and subside in ocean surface temperatures during the following spring (Bertrand et al., 2020; Philander, 2001). The irregular nature of ENSO events, occurring every two to seven years, poses challenges for precise forecasting (Barnston et al., 2012). The impact of ENSO reverberates across the globe, affecting diverse climatic conditions and necessitating a comprehensive understanding of its dynamics for accurate prediction and mitigation strategies.

Equatorial countercurrents

In the PO, the presence of the Equatorial countercurrent is highly conspicuous (Segar & Segar, 2018). This countercurrent represents a significant surface flow responsible for transporting water eastwards across the Pacific Ocean (Wyrtki, 1967). This region is located near the equator and it is flanked by two westward-moving currents: the North Equatorial Current (NEC) and the South Equatorial Current (SEC). The circulation of NEC and SEC may vary based on general pattern, with a considerable portion of the water mass remaining directed towards lower latitudes. This phenomenon happens because the Coriolis effect is minimal near the equator (Godfrey et al., 2001). The accumulation of water along the western margin of an ocean basin leads to an elevation in the average sea level on the basin's western side, reaching up to 2 metres (6.6 feet) higher than on the basin's eastern side (Webb, 2019). Additionally, it is affected by gravity, which causes the water along the western edges to flow downward. Consequently, small Equatorial countercurrents form moves eastward in opposition to and between the adjacent Equatorial Currents. The Equatorial countercurrent, typically centered near 5 °N in the western Pacific and 7 °N in the central Pacific, serves as a demarcation between the Canary Current and the coastline (Gouriou & Toole, 1993).

The events affecting the distribution of fish early stages

The spatial dispersal, connectivity, and genetic diversity of fish populations are profoundly influenced by ocean currents, particularly within the marine environment (Munguia-Vega et al., 2018). Changes in current magnitude and variation play an essential role in larval dispersal, the transport dynamics of eggs and larvae, and ultimately impacting the recruitment of pelagic fishes (Bashevkin et al., 2020). The strength of currents is a critical factor that can also alter the natural mortality rates of fish eggs and larvae, thereby impacting the recruitment of new generations and overall availability of food resources. Ocean currents serve as navigational aids for various fish species and sea turtles during migration, facilitating the dispersion of their larvae with significant ecological implications (Scott et al., 2014). Several important events that are greatly affected PO fisheries described in below:

Boundary currents and surface gyres

Boundary currents are indicative of the spatial dispersal of fish early stages (Schilling et al., 2020). The influence of trade winds has the potential to transport fish eggs and larvae from equatorial regions along the west coast to open ocean areas (Bakun, 2006). The Equatorial Currents can also bring water masses with fish eggs or larvae from the open ocean at the equator to the coastline upon reaching the continents (John et al., 2000). It is distributed northward in the northern hemisphere and southward in the southern hemisphere. Fish eggs and larvae of coastal waters in subtropical regions are distributed toward the offshore due to the westerlies existence (Rodríguez et al., 2006). The eastward currents generated by winds facilitate the transport of fish eggs and larvae from the open ocean to the western coastal regions of subtropical areas. The distribution pattern of fish larvae and eggs align along the coastline, with the northern hemisphere facing southwards and the southern hemisphere facing northwards. Mann and Lazier (Mann & Lazier, 2005) suggest that the offshore journey may be a part of a gyral circulation that brings larvae back to the shore or involves travel in a shoreward-moving countercurrent. They explain further that these gyres are robust oceanic currents. For instance, the Gulf Stream and the KC are located in the northern subtropical gyres, whereas the Labrador Current and the OC are located in the subarctic gyres. These currents play a vital role in the life cycle of economically significant marine organisms, including salmon, eels, and squid.

The California Current, as one of the Eastern boundary currents, which has great influence on the dispersal and abundance of a major Pacific sardine fishery, *Sardinops sagax* (Nevárez-Martınez et al., 2001). It is the largest Pacific sardine fishery area, with 15-25°C average temperatures, and 160,000 tons of landed fish each year (Petatán-Ramírez et al., 2019). S. *sagax*, is a coastal pelagic fish found in the CC, which runs from the tip of Baja California to the Gulf of Alaska, and in the Gulf of California. Northern Ensenada has the lowest temperature range and Magdalena Bay (central fishery) has the highest, influenced by the CC. The Pacific sardine, crucial for the northeastern Pacific Ocean's fishing industry, experiences fluctuations in juvenile recruitment due to spawning stock biomass and California Current system conditions (Galindo-Cortes et al., 2010). Sardine eggs, buoyant and accumulating near the surface, have a significant vertical distribution, primarily in the upper 20 m. They develop into larvae within days and have experienced significant variations in distribution and abundance over time due to environmental fluctuations. Sardine abundance changes over 30 years, attributed to temperature and upwelling patterns along the CC, particularly during *El Niño*, which shifts Pacific sardines to the northern range of the current (Morales-Bojorquez & Nevarez-Martinez, 2005).

Anchovy and sardine (*S. sagax* and *Sardina pilchardus*) populations have been extensively studied in upwelling and boundary current systems worldwide using different methods such as the daily egg production method and the Continuous Underway Fish Egg Sampler (Bernal et al., 2007; Lo et al., 2005; Twatwa et al., 2005). The study found that Sardine recruited more readily than anchovy in the Kuroshio-Oyashio and the California Currents, while anchovy recruited more readily in the northeast Atlantic, Humboldt, and Benguela Currents (Salvatteci et al., 2018; Siple et al., 2020). As a result of late twentieth-century fish landings, current paradigms suggest that anchovies and sardines alternate regularly, with fluctuations influenced by profound changes of the PO dynamics (Salvatteci et al., 2018). The Gulf of California pelagic fishery experienced a significant decline in the Pacific sardine catch in 1989-90, leading to economic crisis and job loss. However, recovery began in 1993-94, with catch improvements to 128,000 t and 215,000 t. To find out the cause of this great variability, Nevárez-Martınez *et al.* (Nevárez-Martınez et al., 2001) investigated the distribution and abundance of Pacific sardines in the Gulf of California, which were determined by wind patterns (upwelling) and sea surface temperature. The results showed that moderate upwelling (13-18 m^3 s^{-1} per 10 m of shoreline) and sea surface temperatures between 19°C and 25°C produce the greatest abundance. In another study, Farach-Espinoza *et al.* (Farach-Espinoza et al., 2022) studied the catch variability of *S. sagax* in the Gulf of California by studying ocean mesoscale phenomena such as eddies, costal upwelling, thermal fronts, and cold filaments. The study reveals that eddies significantly impact seasons with anomalous catches, with optimal durations leading to high catches. There is a significant increase in catches associated with coastal upwelling and a declining trend associated with Tropical Surface Sea Water (TSW) intrusion northward.

Ekman transport, upwelling, and downwelling effects

The dispersion of fish eggs and larvae is influenced by the transportation of water mass through Ekman transport (Et). This phenomenon may manifest in either the offshore or nearshore regions. In the equator of the open ocean of the northern hemisphere, Et pushes the water mass northward, while it moves southward in the southern hemisphere. Fish eggs and larvae in equatorial regions may align with these currents, as they are easily carried away by them. Research by John and Erasmi (John et al., 2000) on the distribution of fish larvae, especially *Bathylagus argyrogaster* and *Hygophum macrochir*, supports the hypothesis that equatorial Et's are interconnected and can drag plankton from the equatorial regions towards temperate latitudes. This result is supported by historical and newly gathered data on the distribution of adults and larvae of primarily *Bathylagus argyrogaster* and *Hygophum macrochir*, as well as hydrographic information. Along the continental slope, their larvae are found 440 to 920 kilometres poleward of their adult reproductive areas. Fish larvae of *B. argyrogaster* occur mainly below the thermocline and reach further poleward than fish larvae of *H. macrochir*, which dwell mostly at thermocline depths. However, the equatorial regions are also the most productive due to their status as the upwelling zones. This condition can attract fish larvae to gather in the regions in search for food (Lett et al., 2007; Segar & Segar, 2018). Fish eggs and larvae can be also brought by the transport to be far from coastal area toward offshore (Lett et al., 2007; Smith & Suthers, 1999). It is caused by the existence of Et in the coastal areas of equatorial regions, such as west coast area in the northern hemisphere and the east coast area in the southern hemisphere. Norcross and Shaw (Norcross & Shaw, 1984) also stated that these waters are also productive due to its upwelling zones, thus it also can assemble fish larvae to come for nursery. Meanwhile, in the coastal areas of subtropical regions, Et tends to move water masses toward the land due to westerlies. It generates downwelling zones in the coastal area, which results in low productivity of the waters, making these areas unfavourable for early-stage larvae nurseries. Nevertheless, the onshore water movement can accumulate fish larvae in the coastal area (Ings et al., 2008; Segar & Segar, 2018).

In the Kuroshio-Oyashio confluence zone, sardines have adapted to highly productive ocean environments, particularly eastern ocean upwelling systems (Yatsu et al., 2013). As adults, they frequently travel to graze on phytoplankton in the intense upwelling core regions. Strong upwelling events can wash salmon larvae far offshore, which can endanger their survival (Wells et al., 2016). While a review found that early-season upwelling is positively associated with the growth and survival of salmon (Wells et al., 2016), a regional climate model suggests potential shifts in upwelling-favourable wind stress in northern California due to increased CO_2 concentrations, impacting larvae's survival (Snyder et al., 2003). For instance, Rockfish release young in winter to avoid turbulent periods, potentially reducing survival due to temporal mismatches (Bakun et al., 2015).

ENSO

The ENSO phenomenon is one of the most important indicators of climatic and environmental changes, which have significant effects on the distribution and productivity of fish in the oceans (Anderson & Rodhouse, 2001). The phenomenon of ENSO (*El Niño* and *La Niña*) may induce environmental changes on across various parameters on both temporal and spatial scales (Glynn et al., 2017; Muñoz et al., 2023). During two ENSO events between 2015–2016 and 2019–2020, Cataldo *et al.* (Cataldo et al., 2022) observed a decrease in ichthyoplankton density, affecting abundance due to the extent and density of the events. Notably, during *La Niña* periods, the average density of eggs and larvae decreased by 65% and 85%, respectively. Mesopelagic fish larval assemblages exhibit seasonal variation, with a north-south gradient influenced by the CC's seasonal pattern. *El Niño* episodes significantly impact on marine food webs in the Peru-Humboldt current and CC ecosystems, leading to a decline in primary productivity, zooplankton abundance, and fish populations. The Peruvian anchoveta and salmon, for instance, return to rivers in emaciated condition during *El Niño* events (Espinoza-Morriberón et al., 2017). Moreover, *El Niño* negatively impacts marine organisms in the eastern Pacific, including tiny prey on sardine larvae such as medusas, ctenophores, and predatory copepods, which may experience multiple reproductive failures during an *El Niño* episode. The ENSO phenomenon enhances the diversity, number of species, and abundance of tropical warm-water species further north in the Ensenada and Punta Baja regions (Funes-Rodríguez et al., 2011). However, it was discovered that the strong *El Niño* and *La Niña* events had an impact on the dispersal and abundance of fish populations in the Beibu Gulf. These communities composition and distribution vary before

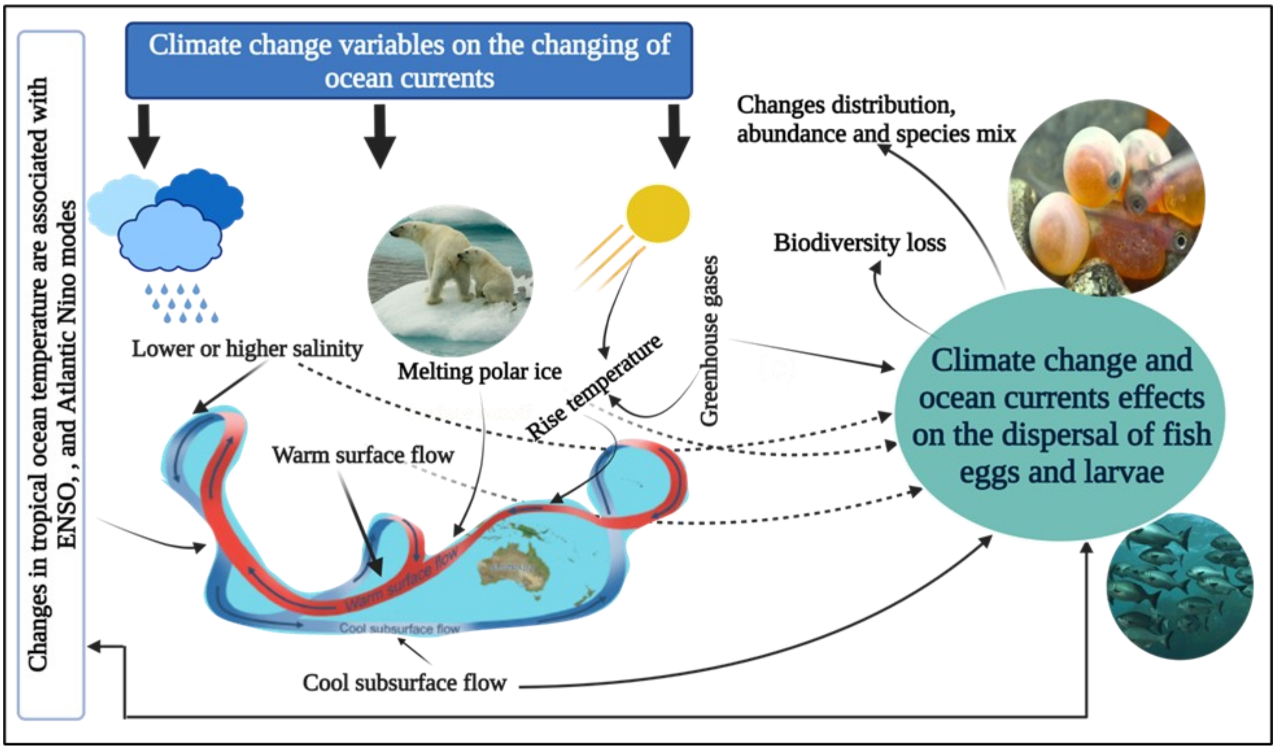

Figure 3. Climate change factors affecting ocean currents and the distribution of early stages of fish eggs and larvae.

and after these events, which caused more severe damage to Japanese jack mackerel (*Trachurus japonicus*) and scad (*Decapterus maruadsi*) (Li et al., 2023).

Marine heatwaves

Marine heatwaves (MHWs) are severe climatic phenomenon that can have catastrophic consequences for an ecosystem (Guo et al., 2022). MHWs are caused by a combination of oceanic and atmospheric processes, including changes in ocean currents, temporary wind weakening, reduced cloud cover, and increased air and water temperatures (Zhang et al., 2023). MHWs have become more frequent, prolonged, and intense in recent decades, and this pattern is likely to contribute with an increase in global warming to 1.5 °C (Simon et al., 2023). It has been shown that MHWs can have considerable impacts on marine communities and ecosystems, including biodiversity, fisheries, and aquaculture (Brown et al., 2024; Cavole et al., 2016; Jones et al., 2018; Oliver et al., 2017). Due to MHWs, mobile marine species (fish and marine mammals) have relocated to alternative habitats, disrupting their previously thriving ecosystems (Jacox et al., 2020). The Pacific Ocean and its fisheries have seen significant changes owing to climatic variability, particularly ENSO, which is the primary cause of MHWs in this region (Holbrook et al., 2022). Current assessments suggest that by 2050, the majority of the Pacific area could face increased intensities of MHW (Holbrook et al., 2022). Northeast Pacific has experienced a large MHW (known as “Warm Blob”), which originated off Alaska's coast and expanded south to Baja California, persisting from 2013 to 2015 (Bond et al., 2015; Cheung & Frölicher, 2020). MHWs at the scale of the Blob are anticipated to occur every ten years under current level of global warming. There have been several observational studies that report ecological changes in the Northeast Pacific region, such as shifts in the vertical and horizontal distributions of marine fish species like Pacific cod (*Gadus macrocephalus*), arrowtooth flounder (*Atheresthes stomias*), walleye pollock (*G. chalcogrammus*), Pacific ocean perch (*Sebastes alutus*) (Brodeur et al., 2019; Li et al., 2019; Yang et al., 2019). According to Laurel & Rogers (Laurel & Rogers, 2020), further warming may reduce Pacific cod spawning duration and spatial extent in the Gulf of Alaska.

Climate change impacts

Climate change continues to disproportionately affect the distribution and abundance of aquatic species through rising temperatures, sea level rise, extreme weather events, ocean currents, ocean acidification, and rainfall patterns (Hanich et al., 2018). The FAO predicts that by 2030, 23% of shared fish stocks may move from their historical habitats, and by the end of the century, it could reach 45% (Barange et al., 2018a). International studies and modelling conducted over the last ten years indicate that fisheries in the Pacific region are particularly vulnerable to climate change impacts (Lehodey et al., 2013). Fish species that rely on planktonic food are more likely to respond rapidly to climate change, while highly mobile migratory species like mackerel, blue whiting, and sardines may experience distributional changes (Heath et al., 2012). Locally affected species like the pelagic sandeel (*Ammodytes marinus*) also experience changes (Frederiksen et al., 2006).

Petatán-Ramírez et al. (Petatán-Ramírez et al., 2019) highlight the Pacific sardine's susceptibility to environmental changes, which results in fluctuations in catch. The Gulf of California is the most affected, with raised sea surface temperature and reduced net primary productivity and habitat availability. The species is anticipated to lose up to 50% of its suitable habitat by the century's end. Ocean mesoscale events such as eddies and thermal fronts, impact marine species survival and climate change, potentially altering Gulf of California trophic dynamics due to rising sea surface temperatures (Farach-Espinoza et al., 2022). A stock-recruitment model analysis reveals that warm episodes in Magdalena Bay negatively impact sardine recruitment in the CC system, while in Ensenada and north Pacific regions, it is positive (Galindo-Cortes et al., 2010). According to Valencia-Gasti et al. (Valencia-Gasti et al., 2015), small pelagic fishes within the California Current System are significantly affected by ocean climate change and fishing. Large-scale climate episodes may impact upwelling, stratification, and thermocline depths. Pelagic fish resources may be affected, and marine mammals and seabirds may face challenges in obtaining prey or adapt to favorable biogeographic regions (Bakun et al., 2015). Increased food supplies from coastal upwelling nutrients may enhance fisheries productivity. The surface ocean currents associated with the Ekman transport will also intensify, leading to increased allocation of fish in the early stages to higher latitudes from the equatorial region. Figure 3 shows the various climate change factors affecting ocean currents and the distribution of early fish stages. The tropical ocean consists of internal variability modes such as ENSO in the tropical PO that influences associated with ocean current strength and temperature on year-to-decadal timescales (Johnson et al., 2000; Nnamchi et al., 2015; Schott et al., 2009). Climate change is projected to increase the frequency of tropical ocean interannual variability, impacting fish early stages significantly (Cai et al., 2015). In the tropical Pacific Ocean, currents such as the SEC and the North Equatorial Countercurrent fluctuate significantly in response to ENSO. As the fish eggs and larvae can be more distributed to deeper ocean during an *El Niño* year, whereas opposite during a *La Niña* year, the processes will be more frequent in smaller timescale in future climate due to global warming (Figure 2). The western boundary currents are integral component of the global oceanic circulation system, which is anticipated to undergo alterations in response to the phenomenon of global warming (Bakun et al., 2015). These currents include the KC, the Gulf Stream, the Brazil Current, the East Australian Current, and the Agulhas Current (Yang et al., 2016). Western boundary currents such as KC intensified in past decades and are projected to strengthen further with increased sea surface temperature (Deser et al., 1999; Sato et al., 2006; Yang et al., 2016). With the increase of green-house gas in the atmosphere, the western boundary currents are projected to be shifted towards pole in both hemispheres. Due to extension of subtropical ocean currents to pole, the distribution, abundance, and mixing of species to region will be changed under climate change. Subtropical and tropical fish species are likely to migrate poleward in response to intensified currents and elevated ocean temperatures near the poleward flank of subtropical oceans (Figure 2). However, the Gulf Stream is projected to be weaker in future climate associated with the Atlantic Meridional Ocean Circulation (Yang et al., 2016). This means, in the subtropical Atlantic Ocean, there will be less transportation of fish species over northern latitudes and less nutrients available for them.

Conclusions

The variability of ocean currents exerts a profound influence on the trajectories and eventual destinations of fish eggs and larvae, presenting significant challenges in tracking these early life stages compared to adult fish. Many species release vast quantities of eggs that float near the ocean's surface, while the larvae, measuring only a few millimeters at hatching, continue to drift as plankton until they attain a size that allows for independent swimming (Whitney et al., 2021). During these critical stages of their life cycle, ocean currents transport fish across diverse marine environments, which is particularly evident in the case of pelagic fish larvae such as Pacific sardine and anchovy, whose dispersal is significantly shaped by ocean currents (Thiaw et al., 2017). The relationship between wind patterns (upwelling) and sea surface temperature has greatly impacted on the distribution and abundance of pelagic fish. Predictions indicate a potential increase in coastal upwelling in north-eastern waters and a decrease in southern waters, as outlined in future annual projections (Sousa et al., 2017; Wang et al., 2015). Nutrient-rich subsurface water upwelling along the ocean's eastern boundary currents sustains high fish productivity and contribute substantially to global marine catch with an estimated 20% share (Santora et al., 2017). Despite fluctuations in biomass attributed to environmental variability, the underlying mechanisms remain elusive.

The current impacts the dispersion of eggs and larvae by transporting them to various marine regions and indirectly affects on their survival. Locations with insufficient feeding conditions can lead to a high mortality rate among the brood. Ocean currents and early stages of fish eggs and larval distribution are both affected by climate change. It is projected that the frequency of tropical ocean interannual variability, including *El Niño* and *La Niña*, will increase, thereby significantly affecting the crucial early stages of fish (Farach-Espinoza et al., 2022). In conclusion, further research on ocean currents and their interactions with the early life stages of fish, in conjunction with an understanding of climate change impacts, is essential for global conservation efforts, effective fisheries management strategies, and the sustainability of food supplies worldwide. Addressing these challenges will require an integrated approach that combines ecological, oceanographic, and climatic data to inform policy and management decisions aimed at preserving marine biodiversity and ensuring the resilience of fisheries in the face of ongoing environmental changes.

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Authorship contribution

Md Afsar Ahmed Sumon, Sugeng Hartono, Ramzi H. Amran: Conceptualization; Writing – original draft; Writing – review and editing. **Muhammad Browijoyo Santanumurti, Saadullah Jan Khan, Sajia Akther, Mohamed Hosny Gabr:** Writing – original draft; Writing – review and editing. **Nguyen Vu Linh**: Conceptualization; Writing – original draft; Writing – review and editing. **Hien Van Doan:** Writing – original draft; Writing – review and editing; Supervision; Project administration. All authors gave final approval for publication and agreed to be held accountable for the work performed therein.

Data availability

All data are available in the references cited; no original data are presented here.

Conflict of interest

The authors declare no conflict of interest.

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