



Navigating the future: Advancing fisheries predictions with a front-to-fish approach

D M Lal^{*a}, Harisha^a, N Nagaswetha^a, A Samanta^a, S K Baliarsingh^a, C Sathish^a, R Premkumar^a, S Jha^a, S Raulo^a, S Joseph^a, T M B Nair^a, M N Kumar^a, D Shenoy^b & A K Warrierc

^aOcean Modeling, Applied Research & Services Group, Indian National Centre for Ocean Information Services, Hyderabad, Telangana – 500 090, India

^bChemical Oceanography Division, CSIR-National Institute of Oceanography, Dona Paula, Goa – 403 004, India

^cDepartment of Civil Engineering, Manipal Institute of Technology, Manipal Academy of Higher Education, Manipal, Karnataka – 576 104, India

*[E-mail: dhanya.ml@incois.gov.in]

Received 30 March 2024; revised 15 May 2024

Oceans, vast reservoirs of abundant fish and marine life, exhibit varying exploitation and utilisation potential across space and time. A comprehensive understanding of the complex interaction between the environment, biology, and fish movements is crucial for accurately predicting fishing grounds, a key prerequisite for sustainable fisheries. The application of remote sensing technology has significantly enhanced the predictive capabilities on fisheries. It can portray environmental variables linked to productivity across the ocean, effectively identifying potential fishing grounds. Fishing grounds around the world are often found along current boundaries, upwelling zones, eddies, continental shelves, and reef banks. Oceanic fronts typically mark these boundaries or areas of upwelling and eddies, where favourable conditions for food webs are established due to the high nutrient levels, increased primary productivity, and abundance of prey organisms. The Indian National Centre for Ocean Information Services (INCOIS) offers fisheries advisories such as Potential Fishing Zones (PFZs), aiding fishers in locating areas with fish abundance, thereby saving fuel and time. INCOIS is progressing towards upgrading its services through habitat suitability studies and ecosystem modelling. The approach involves tracking oceanic front persistence and studying productivity scaling over time, utilizing environmental data from remote sensing, field observations, and food web studies. Anticipated outcomes include a deeper understanding of ocean biochemical phenomena in fronts, leading to improved predictions of fishing grounds, species, and fish catch. These advancements aim to contribute to sustainable fisheries management and promote more economical and fuel-efficient fishing.

[**Keywords:** Fisheries predictions, Indian ocean, Ocean fronts, Productivity scaling]

Introduction

Fishing dates back to time immemorial, initially serving as a means of subsistence for ancient human populations settled along riverbanks. Early fishing activities in marine waters primarily occurred in intertidal zones and near islands¹. Through observations and experience over time, ancestors developed insights into the distribution and seasonal variations of fish populations, thus laying the foundation for the concept of fishing grounds. As science and technology progressed, fishing methods and tools evolved, and humans were able to venture further offshore and into deeper waters. Consequently, fishing grounds expanded to include shallow seas, open oceans, and deep-sea regions, facilitated by advancements in fishing capacity.

While the evolution of the science of fishing ground detection spans across ages and continents, a notable technical breakthrough occurred only

in the recent past, spanning a mere 50 to 70 years. Since the 70s, advancements in ocean remote sensing technology have complemented the efforts in fisheries forecasting. Countries like the United States, Japan, France, and India have utilized data from ocean remote sensing, such as Sea Surface Temperature (SST) and chlorophyll-*a* (chl-*a*) concentration, to enhance their forecasting capabilities for commercial and recreational fisheries applications. Furthermore, the continuous development of fisheries forecasting technology, coupled with innovations in information technology, space technology, artificial intelligence, and big data analytics, has led to significant improvements in forecasting accuracy (Fig. 1). Over several decades of refinement, a comprehensive fishery forecasting discipline and technical framework was established^{1,2}.

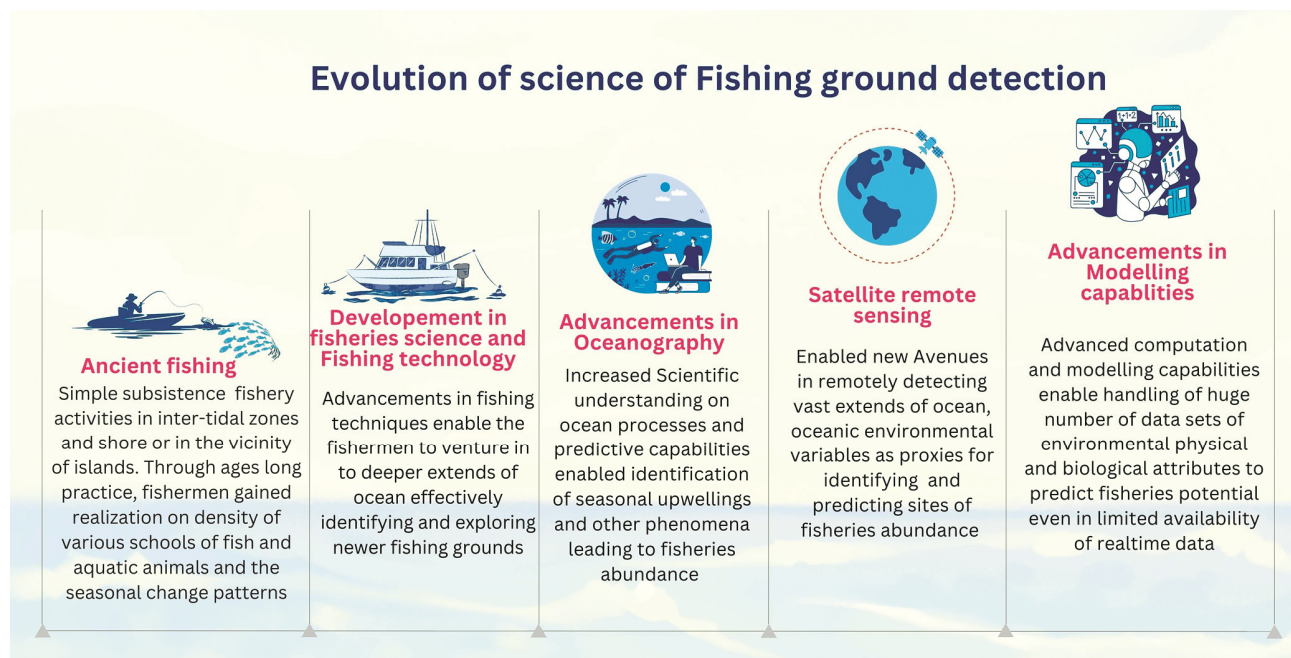


Fig. 1 — Evolution of the science of fishing ground detection

In India, The Indian National Centre for Ocean Information Services (INCOIS) delivers daily Potential Fishing Zone (PFZ) advisories to fishermen, utilizing remotely sensed SST and chl-*a* data obtained from various satellite sensors *viz.* Advanced Very High-Resolution Radiometer (AVHRR), MODIS-Aqua and Oceansat. This operational service is suspended only during regional fishing ban periods. The advisories are generated based on the thermal front detection and Chl-*a* data, following the methodology outlined by Solanki *et al.*^{3,4}. Research efforts are underway to enhance existing services, as evidenced by a recent study that used a coupled physical-biogeochemical model on a regional scale that is able to adequately simulate the state of the ocean's biogeochemistry within the marine ecosystem⁵. Such advancements aim to address operational challenges in producing PFZ advisories caused by satellite data unavailability and transitioning these advisories into PFZ forecasts. INCOIS is currently focused on enhancing fisheries-related services through research efforts aimed at species-specific forecasts, ecosystem modelling, and refining the spatio-temporal accuracy of these forecasts. Front-to-fish is an approach to study the dynamic frontal features for their productivity scaling towards fisheries production using in-situ, satellite data sets, and advanced modelling approaches. With this background, this paper exclusively discusses the

science of fishing ground formation along the ocean fronts, its dynamics, concepts, and the future prospects in research towards improving fisheries prediction.

Concept of fishing ground prediction

While fish and other marine living resources dwell throughout the oceans, shallow seas, bays, and estuaries, fishing grounds do not form ubiquitously, nor do the seasons for fishing align universally throughout the year. The formation of fishing grounds requires several primary conditions. Firstly, large schools of fish must migrate and pass through or gather in a specific habitat. Second, both biotic and abiotic environmental factors must support fish aggregation and habitation. Thirdly, there should be availability of suitable fishing gear and methods, since the lack of which can limit an area's scope to be an ideal fishing ground, even with abundant fish and favourable conditions¹.

Forecasting of fishery is the backbone of fishery oceanography research, which focuses on predicting fish abundance in specific areas or seasons. Combined with the resource sustainability principles, this can also be the prediction of the quantity of fishery resources or advocate the sustainable harvest of a particular species within a specific time and place. The foundation of forecasting lies in understanding the intricate relationships and patterns between fish movement, feeding and breeding, biological conditions, and

environmental factors. One can gain an understanding of this from diverse data, including catch statistics, oceanographic variables, abundance indices, and environmental parameters, often collected from historical catch data, field surveys, and remotely sensed data^{1,2}.

Ocean fronts and variability on a global scale

As mentioned earlier, marine fishery resources in the vast extent of the ocean prefer to aggregate around specific habitats for vital activities such as feeding, reproduction, and migration, forming their fishing grounds, and such relationships are being extensively studied in coastal environments⁶. In the oceans, features such as eddies and fronts serve as essential habitats for trophic transfer, facilitating migration, foraging, and reproduction for pelagic species of commercial importance⁷.

Ocean fronts represent narrow regions with pronounced gradients of physical and biochemical properties, separating areas of different vertical structures^{8,9}. They usually form between warm and cold waters, with higher horizontal temperature gradients associated with substantial vertical velocities, mixing^{10,11}, and enhanced biological production¹².

Studies reported remarkable variation in the precursors, features (including gradients and extent), periodicity, and persistence between high- medium altitude and tropical fronts¹³. Based on the process that causes its formation, ocean fronts can be water mass convergence fronts, shelf fronts, tidal mixing fronts, shelf break fronts, coastal upwelling fronts, and equatorial upwelling fronts¹⁴. Kumar *et al.*¹⁵ also demonstrated important types of fronts like Plume fronts, Shelf breakfronts, diverging fronts, converging fronts, and coastal upwelling fronts with varying fisheries significance.

The cross-frontal temperature and salinity along the strongest fronts could be as high as 10 to 15 °C and 2 to 3 psu in temperate waters. Whereas, the strongest reported cross-frontal temperature gradient in the tropics is around 5 °C^(refs. 14,17). Certain fronts, known as frontal systems, span several hundred kilometres in width, such as the transition zone between the Oyashio and Kuroshio currents in the northern Pacific. These zones are crucial habitats for fish species like albacore and other tunas¹⁶. Conversely, other fronts vary in width from tens of kilometres to mere metres, with smaller fronts being less permanent and more prone to variability in position¹².

Several seasonally and perennially persistent fronts exist in the world's oceans, in both temperate and sub-

tropical regions along Florida current, Gulf stream, California current system, and the Southern Ocean¹⁷⁻²⁰. Belkin *et al.*¹⁷ undertook the pioneering attempt to map and characterize the major fronts within the Large Marine Ecosystems (LMEs) of the World Ocean. Their work provided valuable insights into the origins and persistence of these fronts across the LMEs. They documented the primary spatial patterns of 64 LME fronts using a specialized global database. This database relied on thermal front data derived from AVHRR-SST for the period 1985 – 1996 utilizing the front detection algorithm by Cayula-Cornillon²¹. These maps provide a global reference for studying subsurface oceanographic features like thermohaline fronts using hydrographic data and satellite-detected thermal signatures from the ocean surface.

Formation and dynamics of ocean fronts and productivity in the Arabian Sea and Bay of Bengal

The Arabian Sea (AS) and Bay of Bengal (BoB), key LMEs in the Indian Ocean, hold significant ecological and fisheries importance for India. Belkin *et al.*¹⁷ categorized the AS LME to be dominant with upwelling and water mass convergence fronts in their work. In contrast, the BoB LME is characterised by the dominance of fronts formed by freshwater inflows. As this work explores the connection between ocean fronts and productivity, and since variations in frontal features can significantly affect the productivity they support, it would be relevant to highlight the differences in oceanographic features and productivity across these LMEs.

Various studies have focused on the upwelling phenomenon in the AS, providing essential insights into its biologically significant frontal features. Among those, Kumar & Prasad²² and Madhupratap *et al.*²³ are notable. These studies documented the influence of the monsoon winds and their seasonal reversal on the phenomenon of upwelling in the northeastern AS. The dry and cold air blowing from the continent, transported by northeasterly trade winds during the winter monsoon season (December to February), intensifies evaporation, which leads to cooling of the surface and convective mixing. Consequently, the subsurface water, which is nutrient-rich and dense, intrudes to the surface, fostering higher productivity.

Conversely, during the summer monsoon (June to September), southwest winds drive upwelling along the northeastern AS coast, stimulating high

productivity along the coast and shelf. Building on these findings, Belkin *et al.*¹⁷ identified several fronts of varying gradients, extent, and persistence in the AS, shaped by the seasonal monsoon winds and their reversals. Among these fronts, the most stable and seasonally persistent one develops in the Gulf of Aden, exhibiting a cross-frontal temperature range of up to 5 °C. Additionally, upwelling fronts are widespread off the coast of Pakistan and off the western coast of India, displaying seasonal patterns similar to major upwelling frontal zones observed off Northwest Africa and the US west coast within the California current system¹⁷.

Freshwater convergence by major river systems, weak coastal upwelling, and numerous eddies influence productivity in the northwestern BoB. Upwelling occurs in this region from March to September, weakening from south to north due to intense runoff from the rivers in the northern Bay²⁴. Eddies in this area exhibit significant variability in intensity and location inter-annually, serving as a primary driver for changes in the coast's biogeochemical and physical properties, driving rapid shifts of thermal gradients²⁵⁻²⁹. This area features cold-core eddies that serve as vital nutrient sources, triggering phytoplankton blooms in the BoB³⁰. Additionally, solar radiation, which is constrained during summer due to extensive cloud coverage compared to winter, also significantly impacts the productivity in the western BoB^{31,32}.

However, the BoB is considered less productive compared to the AS. Despite upwelling, eddies, and freshwater inputs, the significantly lower productivity in the BoB is well explained by Kumar *et al.*³⁰. The study illustrates that the low productivity is primarily due to strong upper-ocean stratification. During the summer months, the freshwater plume flowing equator-ward along the BoB's western boundary suppresses upwelling despite the presence of southwesterly winds that are considered to be upwelling-favorable³³. During this time, the surface waters in the BoB are nutrient-depleted, notably lacking in nitrate, and wind-driven mixing is insufficient to introduce nutrients into the euphotic zone. This condition arises from increased surface buoyancy from warmer, fresher waters (less dense), which creates a strong stratification that prevents dense, nutrient-rich waters from reaching the surface.

In contrast, the AS benefits from summer monsoon winds that induce various processes like Ekman pumping, wind-driven mixing, and advection (lateral)

of upwelled waters, bringing nutrient-rich water into the upper layers. However, in the BoB, the same kind of winds fail to disrupt stratification, and the absence of strong coastal upwelling further limits nutrient input³⁰. These phenomena better explain why the freshwater front-dominated BoB is less productive compared to upwelling front-dominated AS.

Persistence of frontal features in the Indian Ocean

Sarkar *et al.*³⁴ contributed valuable insights into the persistence of frontal features along the Indian Ocean, utilizing SST data sets of 14 years to calculate a monthly Frontal Probability Index (FPI). They identified 17 persistent SST fronts in the north Indian Ocean, including eight linked to the shelf-slope boundary and five associated with water masses mixing. Prominent among them are the West India Shelf Slope Front (WISSF), West India Mid Shelf Front (WIMSF), and Gulf of Mannar Front (GMF), all hold significance for Indian coastal fisheries due to their seasonal variability and habitat characteristics. The WISSF is observed from November to April, with peak FPI observed from December to March along the shelf break (~200 m isobath) in the north eastern AS. The WIMSF comprises two sections, with one near the coast and the other along the 200 m isobath in the northeastern AS, visible from November to April. The GMF is an intermittent front with a high FPI along the northern boundary of the Gulf of Mannar between India and Sri Lanka, peaking from August to September and reappearing from December to January. Mohanty *et al.*³⁵ also reported prominent thermal fronts in the northeastern AS between the 50 m to 200 m isobath (up to the continental shelf break). The study found that, out of all thermal fronts, 45 – 75 % occurred annually, while 20 – 30 % appeared semi-annually. The study by Chakraborty *et al.*⁵ also observed a higher persistence of frontal features during the winter months in the Indian Ocean.

Ocean fronts and pelagic predators

Several studies worldwide established the fact that the pelagic species' habitats are liable to shift with respect to ocean climate changes, as their distribution is closely linked to oceanic primary production, frontal systems, and water masses³⁶⁻³⁸. Early scientific investigations into fishing grounds naturally took an objective approach, seeking to understand the conditions favoring the presence of target species.

Due to the high demand for large predators like tuna, marlins, and billfishes in global fisheries, much research in the late 20th century focused on these species rather than the more abundant small pelagic fish that sustain subsistence fisheries. This is particularly evident in studies focusing on frontal productivity, with many observing significant aggregations and higher Catch Per Unit Effort (CPUE) of large pelagic predators near or within frontal structures^{12,39-43}. Laurs & Lynn³⁹ described the movements of tagged albacore tracked with ultrasonic equipment. The study revealed that the fish tended to remain close to the 'upwelling fronts' when present but moved away when upwelling ceased, which indicated that frontal boundaries and temperature preferences highly influence the albacore migration. Sund *et al.*¹² also observed the significant influence of temperature in the distribution of tuna species such as skipjack, albacore, and yellowfin tuna. Roffer⁴⁴ suggested that young bluefin tuna in the Northwestern Atlantic migrate north seasonally along with preferable SST bands.

Similarly, Palko *et al.*⁴⁵ suggested temperature's significance in swordfish distributions across oceans. Bigelow *et al.*⁴⁶ studied the association between the CPUE of swordfish and blue sharks and specific oceanic environments. They recorded significantly higher catch rates associated with frontal systems than those in other areas. Several other researchers also reported the zones of high fish concentrations coinciding with current rips and tropical fronts⁴⁷⁻⁴⁹.

Ocean fronts and aerial predators

In addition to focusing on predatory fish and ocean fronts, researchers have also explored the link between aerial predators and ocean fronts, considering seabirds as indicators of productive ocean zones and potential fishing grounds. Studies have revealed that seabirds, being one of the apex consumers in marine food webs, exhibit parallel responses to lower trophic levels that are associated with fronts and eddies formed by western boundary currents and upwelling. Various works, including those focused on the Gulf stream fronts in the North Atlantic⁵⁰, the East Australian current^{51,52}, and the North Pacific⁵³, have documented short-term segregation of seabird species around fronts and eddies. These findings suggest that the segregation of seabirds at eddies may stem from variations in the types, abundance, or size classes of their prey.

Unlike predatory fish that inhabit the water column, seabirds possess a more remarkable ability to detect changes in their environment due to their aerial perspective, leading to differential attraction and behaviour based on preferences. Aggregation of birds near fronts, which work as natural remote sensors, offer valuable insights into the distribution of their preferred prey items. It is also a long-standing practice among fishers to identify fish aggregations by locating their aerial predators, a technique used since ancient times. Studies indicate that areas with higher chlorophyll concentrations and biomass exhibit high turbidity. Haney⁵⁰ provides a clear illustration of frontal productivity characteristics by examining the occurrence and preference of seabirds in distinct areas formed within and around the Gulf Stream eddy water masses. The study suggests that frontal areas can be delineated by the abundance and distribution of seabirds, with the segregation of species composition influenced by prey preferences and foraging behaviour. The area is conceptualised into three distinct zones based on prevailing physicochemical characteristics: the Gulf Stream, warm filaments, and cold cores. Observations reveal that zooplanktivorous seabirds, such as storm petrels and shearwaters, congregate around the cold core area of Gulf Stream upwellings, feeding on zooplankton while maintaining a constant height above the water surface. Some species within these groups have been observed feeding on small schooling baitfish (family: Carangidae) within the cold core of eddies, which harbour maximum biomass. In contrast, bird species with specific fish preferences, relying more on visual cues, tend to avoid highly turbid cold cores and concentrate around Gulf Stream and warm filaments, foraging over larger areas and seeking out scarce, widely dispersed prey in the oligotrophic marine habitats⁵⁴.

Ocean fronts and migratory and endangered species groups

Exploring how ocean fronts increase the vulnerability of endangered species groups is quite apparent yet interesting. Numerous studies have reported the association between fronts and species such as sea turtles^{55,56} and seabirds^{50,53}. The global decline in leatherback turtle (*Dermochelys coriacea*) populations is attributed mainly to the heightened mortality resulting from their interactions with fisheries, with the majority of such studies stemming from the Atlantic Ocean⁵⁷.

Observations reveal extensive migration patterns of turtles throughout the Atlantic, with their movement dynamics, including diving depths and speed, varying widely in response to environmental variables along their pathways. Satellite telemetric studies have demonstrated that turtles encountering prominent fronts tend to slow down, likely due to enhanced availability of prey. It has also been reported that, apart from leatherbacks, other turtle species, which are pelagic-feeding, also tend to follow mesoscale eddies and frontal features^{58,59}. Additionally, the diving patterns of most individuals studied are shallower than 250 m. Given that frontal areas harbour high fisheries abundance and the depth of turtle movement aligns with the preferred operational depth of most pelagic fishing gears, the likelihood of by-catch increases in these regions. Consequently, fronts indirectly heighten the vulnerability of endangered species to by-catch incidents.

Potential reasons for fish aggregation around ocean fronts

The quest to understand the aggregation of predatory fishes near fronts leads to various interpretations. Sund *et al.*¹² suggested that a temperature front with the isotherm limiting a tuna's range could act as a barrier, where tuna will potentially aggregate⁶⁰⁻⁶³. Similarly, the temperature was identified as a critical factor influencing swordfish size distribution and biomass⁶⁴⁻⁶⁶. Most of these studies primarily focused on SST as the primary limiting factor for commercially important fish distribution due to its measurability and potential as a marker for ocean fronts. However, it is evident that temperature alone might not sustain species abundance, and biogeochemical attributes driven by fronts likely play a crucial role. Podesta *et al.*⁴² suggest that changes in the parameters such as current velocity, water clarity, and salinity are often associated with temperature changes across fronts, influencing fish aggregation.

Sund *et al.*¹², in an early systematic review of the distribution of tuna, also marked the opinion that there can be associations between tuna and the thermal features associated with fronts; however, the attractive property of the front could be purely biological. Several studies reported that ocean fronts delimit the distributions of subtropical and subarctic species by harbouring endemic zooplankton and nekton, hence increasing localized prey availability^{67,68}. The findings

by Varela *et al.*⁶⁹ substantiate the theory of high prey availability around the fronts, as evidenced by fuller stomachs in albacore in frontal areas. Young *et al.*⁷⁰ also reported that local food concentrations near fronts may attract swordfish. Several other studies have reported the influence of the physical gradients at eddies on the community composition of phytoplankton⁷¹⁻⁷³, zooplankton⁷⁴, cephalopods^{75,76}, and mid-water fishes⁷⁷⁻⁷⁹, which probably could be linked to the abundance of the predatory species.

It is clear that prey abundance is the main factor attracting larger fish species near fronts, a conclusion that can be drawn without extensive scientific insight. However, the underlying reasons for this prey abundance still require scientific explanation.

The increased prey abundance near fronts is anticipated as a result of mesoscale oceanic processes like upwelling, stimulating primary productivity, and concentrating production⁸⁰⁻⁸³. Generally, the productivity in the frontal region is expected to dissipate with the cessation of the upwelling. Polovina *et al.*⁸⁴ hypothesized that, despite weak downwelling in the North Pacific frontal region, zooplankton and buoyant organisms like jellyfish can maintain their position and aggregate along the front. These organisms graze on phytoplankton, and hence concentrated in the convergence zone^{7,85}. The concentration of these secondary producers attracts higher predators in the higher trophic levels, and in turn, a pelagic food web is sustained beyond the duration of the upwelling⁸⁵. These findings indicate that some upwelling fronts, while triggering productivity in certain regions, can support prolonged trophic succession under the right background conditions. These fronts can sustain productive fishing grounds for extended periods when ideal conditions are met.

Do all fronts lead to productive fishing grounds?

The notion that fronts could serve as fertile fishing grounds raises the question of whether all fronts can form ideal fishing grounds. We must delve into the fundamental principles of existence and survival to understand this. Simply, for a species to thrive in a particular area, it requires specific environmental conditions, notably temperature, salinity, and dissolved oxygen, crucial for respiration, thermoregulation, and osmotic balance, three pillars of aquatic organism survival⁸⁶. Even if these conditions are met, sustained survival in the area is not guaranteed, which is a prerequisite for designating

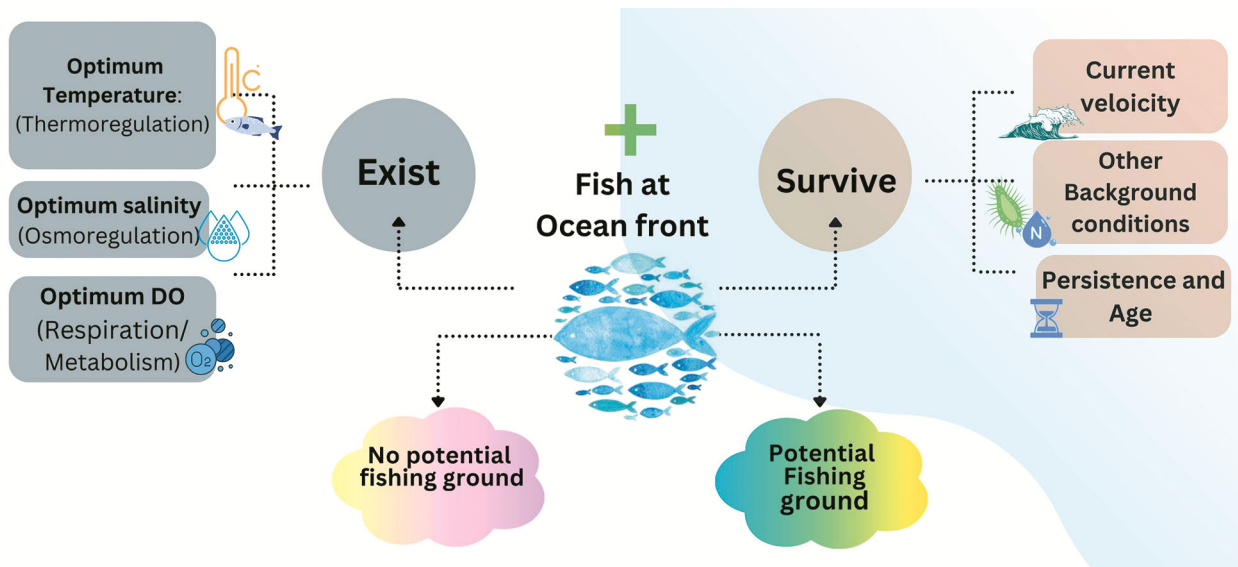


Fig. 2 — Illustration showing major factors influencing fronts to become a fishing ground

it as a potential fishing ground. According to Chen¹, a frontal region can become a fishing ground only when three key parameters align. Firstly, the current velocity at the convergence; secondly, the background conditions; and thirdly, the persistence and age of fronts (Fig. 2).

The current velocity at the convergence holds paramount importance, especially for convergence fronts. Chen¹ explains the fish behaviour in water mass convergence zones, stating that weak convergence leads to a flow rate below the critical velocity necessary for fish positioning, allowing zooplankton and fish to accumulate in these zones gradually. Moderate convergence still permits fish to maintain positioning in the current, though with potentially lower zooplankton accumulation, often leading to fish congregating upstream of the convergence zone. Conversely, strong convergence propels fish to swim in the top current, drifting downstream, resulting in fish accumulation downstream of the convergence zone, while zooplankton struggles to aggregate. In such scenarios, viable fishing grounds fail to materialize¹.

Background conditions include the concentration of limiting nutrients and the precursors necessary for primary producers to flourish. Additionally, there must be a sufficient presence of zooplankton precursors and fish schools in the vicinity to aggregate around, without which the front cannot manifest as a fishing ground. A study by Sarma *et al.*⁸⁷ strongly supports this notion, highlighting the

importance of background conditions in forming a productive front. The authors delineate that background conditions, such as SST, nutrient availability (including nitrate, phosphate, and silicate), and biological prerequisites (phytoplankton, zooplankton, and bacterial biomass), play a crucial role in determining the fate and productivity of the front.

The third, perhaps less explored but equally crucial aspect, is the persistence and age of the feature. Lehahn *et al.*⁸⁸ highlighted a temporal lag in ecosystem development ranging from a few days to several months for aggregation processes and ecosystem maturation to higher production. This temporal delay may also lead to a spatial displacement of foraging sites from regions of primary production. Empirical evidence supporting this phenomenon includes the tracking of elephant seal's migratory routes. Despite the absence of an evident chl-*a* concentration in late summer, the seals intensively foraged on a particular water mass. However, backward tracking of this water mass in time revealed that this water mass had supported a rich phytoplankton bloom months earlier⁸⁹. Remarkably, the water mass had travelled over 1000 km from the bloom site prior to being utilized by the elephant seals. Sarma *et al.*⁸⁷ also offers significant insights into the impact of persistence on the fishery productivity of ocean fronts in the North Eastern AS. Their study on biogeochemistry and plankton associations revealed that plankton response varied according to the age of the front. Specifically, fronts

aged between 9 – 11 days exhibited high zooplankton response and increased fishing activity compared to weaker and short-lived fronts. Such findings underscore the significance of considering temporal dimensions and lag periods in studying plankton blooms, advection, and persistence for understanding frontal productivity.

Scaling productivity: Food web progression at ocean fronts

The study of productivity scaling in ocean food webs, from primary producers to fish, can be approached through two main lenses. Firstly, the biochemical cycling of carbon across its various forms and fate through the food chain. Secondly, the biological perspective focuses on prey-predator dynamics, affinity, and abundance. While the former approach falls outside the scope of this paper.

When conditions favoring productive front formation align, fishing grounds gradually develop. However, understanding how phytoplankton precursors become available at frontal zones to enhance productivity requires a grasp of phytoplankton bloom dynamics in the oceanic realm. Let us briefly overview the evolution of fishing grounds based on various studies worldwide.

According to Prants⁹⁰, plankton precursors, or inoculums, are essential in transforming ocean fronts into affluent areas of biological productivity. Over a span of a few weeks (typically 1 or 2), the spring bloom of phytoplankton can generate a significant phytoplankton reservoir, which is laterally drifted by currents, forming surface features like curls, spirals, and filaments. These passive fronts exhibit high gradients in chlorophyll, shaped by ocean currents. As phytoplankton communities drift from their origin, their composition may change during advection. Moreover, Prants⁹⁰ noted that strong frontal circulation subducts denser, chlorophyll-rich water, creating subsurface chlorophyll layers parallel to the surface. Surface chlorophyll reserves serve as dynamic indicators of vertical gradients, indicating sites of primary production.

Altered by local nutrient injections, post-blooming patches exhibit higher biological richness than surrounding waters. Over time, the biomass from primary producers moves through trophic levels up to the top predators⁸⁸. The phytoplankton aggregation at fronts is typically found with an abundance of zooplankton^{85,91,92}, serving as prey for squid and small pelagic fish. These subsequently draw large

pelagic fish, top predators, and seabirds, demonstrating a bottom-up effect in the food web.

The vertical segregation of the plankton can also affect the structure of food webs at fronts. Some studies around the Kuril Islands in the northwestern Pacific have empirically found that the conditions favourable for saury (commonly known as mackerel pike, a zooplankton feeder) feeding occur at the fronts with a prominent seasonal pycnocline. The area marked with high phytoplankton concentrations in the upper mixed layer attracts zooplankton, which serves as prey for planktivore fishes like saury⁹³. Studies suggest that a thinner upper mixed layer leads to higher zooplankton concentrations. Conversely, when strong stratification is absent, phytoplankton remains evenly distributed throughout the water column rather than concentrating in subsurface layers where zooplankton typically gathers⁹³.

Several authors also studied the influence of the type and size of plankton in developing the food web. Legendre & Rivkin⁹⁴ investigated upper ocean carbon fluxes and the regulation by food-web control models. They outlined two primary food chain progressions: for large phytoplankton with size $> 5 \mu\text{m}$, consumption starts with mesozooplankton to large metazoans (fishes). Conversely, tiny phytoplankton with size $< 5 \mu\text{m}$ are consumed by microbial heterotrophic plankton, leading to mixotrophs and microphagous macrozooplankton (salps, doliolids, appendicularians, pteropods, etc.) to metazoans and results in a much longer food chain, which limits the probability for larger predators to accumulate, as longer food chains typically support fewer top predators due to energy loss at each trophic level. This phenomenon can result in lower biodiversity at higher trophic levels but higher diversity at lower trophic levels. For example, ecosystems with shorter food chains may have fewer species of top predators but more diversity among primary producers and primary consumers⁹⁵.

Studies by Friedland *et al.*⁹⁶ and Krumhardt *et al.*⁹⁷ echoed similar conclusions, noting the dominance of tiny phytoplankton in warmer, nutrient-limited environments. In such oligotrophic regions such as the South Pacific Gyre and Sargasso Sea, small phytoplankton (picoplankton and nanoplankton) dominate, comprising cyanobacteria and picoeukaryotes. The work of Landry & Kirchman⁹⁸ supports this observation, as they demonstrated that interactions among bacteria and flagellates represent

the primary pathways of energy flux (autotrophic and heterotrophic) across vast areas of tropical and subtropical oceans, where the microbial loop prevails. In these regions, primary producers are often resource-limited, with small cells dominating due to their efficiency in competing for limited nutrients⁹⁹. These highly efficient competitors are kept at relatively low and constant biomass levels by microzooplankton (protistan) grazers, and their growth is primarily sustained by the remineralised by-products of grazing⁹⁸.

In nutrient-rich ecosystems influenced by upwelling or substantial terrestrial inputs, larger phytoplankton, such as dinoflagellates and diatoms, dominate, contributing significantly to the biomass of larger predators^{87,97}. Thus, the type and combination of these initial background conditions significantly influence the food web that develops within the frontal region.

Fronts: Applications in fisheries forecasting

Advancing towards a deeper comprehension of frontal productivity, researchers investigated multiple potential factors contributing to enhanced fisheries productivity in the late 1990s and early 2000s^(refs. 42,100). While these studies primarily focus on habitat suitability for commercially significant species, the roles of fronts and productivity dynamics remain an area for further exploration. In India, PFZ advisories by INCOIS utilize the identification of ocean fronts to locate areas likely to have abundant fisheries. This system has evolved from experimental trials to a fully operational model validated by multiple agencies, consistently demonstrating higher catches of commercially important species from frontal sites^{15,101-104}. Other countries also operate fishery forecast systems based on frontal detection, continuously validated through field trials. The validation experiments also similarly reported strong evidences of higher catches near PFZ advisory positions¹⁰⁵.

Although these studies have validated the effectiveness of PFZ advisories, the underlying reasons for variability in species abundance in relation to their trophic niche or other background conditions are yet to be explored extensively. Additionally, the differences in PFZ characteristics, which likely influence the type and nature of fish availability, still need to be investigated. This is particularly relevant for India's fisheries sector, where multi-species, multi-gear fisheries dominate. Understanding the progression of fronts, their productivity, and species-specific forecasts based on favourable frontal features would offer significant advantages beyond conventional PFZ advisories. Such

an approach would enable fishers to conduct more targeted fishing operations and plan fishing activities and markets based on the demand for specific species, thereby reducing the uncertainty in fishing operations and maximizing economic returns. The existing gaps thus highlight the need for further research into the dynamics of ocean fronts to improve predictions of fishery abundance.

Future directions towards front to fish approach

Improving current fisheries forecast services demands a profound understanding of qualitative and quantitative interactions among the living components in areas where fish aggregate. Merely examining the environmental conditions conducive to the existence of a specific species may be insufficient for formulating predictive models, as the species of concern for fishing is just one element in the intricate web of trophic interactions. These interactions extend from phytoplankton to the immediate prey consumed by the target species, highlighting the need for understanding micro-level species diversity in potential fish assemblage sites.

Establishing coexistence matrices for organisms at a micro-level is crucial for developing better fisheries prediction models. However, the complexity of tropical species diversity and spatio-temporal dynamics, especially under climate change and extreme events, presents challenges for developing fisheries prediction models. Ocean warming impacts pelagic food webs from bottom-up and top-down processes¹⁰⁶. In tropical oceans, vertical fluxes like upwelling and nutrient cycling and lateral processes such as eddies and boundary currents are crucial to distributing prey species like micronekton. These processes are more complex in tropical regions due to greater species diversity and variability across trophic levels, directly affecting predator feeding and migration. Indirect impacts include changes in the distribution and composition of phytoplankton, zooplankton as well as micronekton prey communities, causing alterations in the base of the food webs. Basin-wide variations in phytoplankton biomass and zooplankton compositions linked to long-term climatic oscillations have also been reported by various studies^{107,108}. Addressing these challenges within the front-to-fish approach requires well-structured study designs that capture the spatial and temporal variability in the assemblage patterns of plankton and their connections to top predators. This could help unravel the intricacies of tropical food

webs and significantly contribute to more accurate fisheries prediction models in the future.

Understanding the complexities of ocean food web progression in oceans is highly challenging due to the vast scale of the marine environment. Therefore, approaches focusing on smaller spatial scales hold great potential for studying productivity succession, which is essential for future fisheries models. While the existing knowledge allows us to predict fisheries aggregation near oceanic frontal features, delving into the biological diversity near progressing ocean fronts at different stages is ideal in the present stage for understanding the productivity scaling to fishery production in oceans. Numerous research avenues exist in tropical frontal studies, focusing on improving methods for predicting fishing grounds and species-specific forecasts based on fronts. These opportunities capitalise on significant advancements made in recent decades. Literature suggests that the primary fronts in the AS LME are upwelling fronts. At the same time, those in the BoB are freshwater convergence fronts, which are less persistent than the temperate fronts. Research on tropical waters still needs to be more

extensive, underscoring the need for a systematic approach to understanding frontal features in tropical and temperate waters. This approach should consider the significant variability in physiological phenomena and reference points between regions, even for the same species or species groups. Recent studies have identified seasonally persistent fronts in the Indian Ocean, presenting ample opportunities for intensive research into frontal productivity and its impact on higher trophic levels³⁴.

Critical directions for future research include incorporating properties such as sub-surface chl-*a*, age of the front, and other background conditions into frontal research and predictions^{87,109}. Secondly, exploring the combinations of model-simulated and remotely sensed fronts to provide a comprehensive analysis of frontal dynamics¹⁰⁹. Thirdly, integrating biogeochemical and trophic models with physical models can also significantly enhance fisheries predictions^{5,98}.

The "front to fish" approach represents a unified strategy that encompasses these factors to enhance PFZ predictions (Fig. 3). The endeavours shall also include tracking the persistence of oceanic fronts,

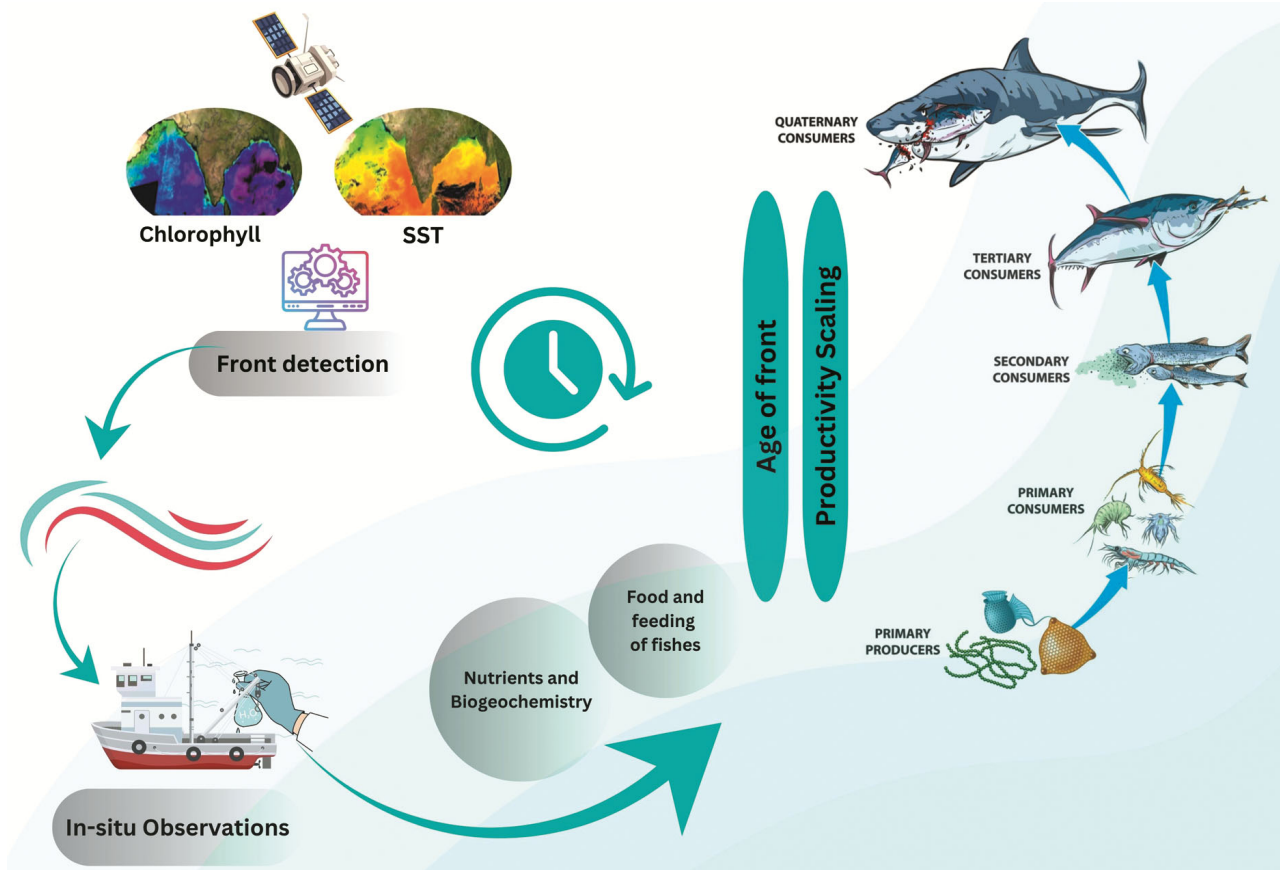


Fig. 3 — Conceptual diagram of front to fish approach for advancing fisheries predictions

studying productivity trends over time, and utilizing environmental data from remote sensing, field observations, and food web studies. Expected outcomes of the approach include a deeper understanding of oceanic biochemical processes near fronts, leading to better predictions of fishing grounds, species distribution, and fisheries catch. Chen¹ highlights that a major challenge in establishing statistical relationships between environmental conditions and fish distribution is the absence of synchronized biochemical and physical data collected at suitable temporal and spatial scales. Hence, strengthening data collection and field observations are the backbone of advancing the "front to fish" program.

Acknowledgments

The authors thank the Ministry of Earth Sciences, Govt. of India, for supporting the marine ecological services and applied research programs of INCOIS. The authors are also thankful to the organizers of the World Ocean Science Congress 2024 for providing an avenue for this manuscript to be included in the conference's special issue. The authors sincerely acknowledge the anonymous reviewers for their insightful comments and suggestions, which greatly contributed to improving the quality of this manuscript. This is INCOIS' contribution number 534.

Conflict of Interest

The authors declare that there are no conflicts of interest in publishing the manuscript in the Indian Journal of Geo-Marine Sciences.

Ethical Statement

This review was conducted in accordance with ethical guidelines and principles for scientific integrity. All data sources and methodologies adhere to ethical standards.

Authors Contributions

DML: Conceptualization, data analysis, investigation, visualization, and writing – original draft; Ha: Writing – original draft; NS, AS & SKB: Formal analysis and writing – original draft; CS, RP, SJh & SR: Writing – review & editing; SJo & TMBN: Supervision, project administration and writing – review & editing; MNK, DS & AKW: Writing – review & editing.

References

- 1 Chen X (ed), *Theory and Method of Fisheries Forecasting*, (Springer, Singapore), 2022, pp. 199. <https://doi.org/10.1007/978-981-19-2956-4>
- 2 Leggett W C & Frank K T, Paradigms in fisheries oceanography, In: *Oceanography and Marine Biology*, 1st edn, edited by Gibson R N, Atkinson R J A & Gordon J D M, (CRC Press, Boca Raton), 2008, pp. 337–370. eBook ISBN: 9780429137259
- 3 Solanki H U, Dwivedi R M, Nayak S R, Naik S K, John M E, *et al.*, Application of remotely sensed closely coupled biological and physical processes for marine fishery resources exploration, *Int J Remote Sens*, 26 (10) (2005) 2029–2034. <https://doi.org/10.1080/01431160310001595028>
- 4 Solanki H U, Mankodi P C, Nayak S R & Somvanshi V S, Evaluation of remote-sensing-based potential fishing zones (PFZs) forecast methodology, *Cont Shelf Res*, 25 (18) (2005) 2163–2173. <https://doi.org/10.1016/j.csr.2005.08.025>
- 5 Chakraborty K, Maity S, Lotliker A A, Samanta A, Ghosh J, *et al.*, Modelling of marine ecosystem in regional scale for short-term prediction of satellite-aided operational fishery advisories, *J Oper Oceanogr*, 12 (sup 2) (2019) S157–S175. <https://doi.org/10.1080/1755876X.2019.1574951>
- 6 Benaka L R, Fish habitat, *Essential Fish Habitat and Rehabilitation: Proceedings of the Sea Grant Symposium, August 26–27* (1998), Hartford, CT (USA), 459 pp. ISBN: 1-888569-12-3
- 7 Bakun A, Babcock E A, Lluch-Cota S E, Santora C & Salvadeo C J, Issues of ecosystem-based management of forage fisheries in “open” non-stationary ecosystems: The example of the sardine fishery in the Gulf of California, *Rev Fish Biol Fish*, 20 (2010) 9–29. <https://doi.org/10.1007/s11160-009-9118-1>
- 8 Fedorov K N, The Physical Nature and Structure of Oceanic Fronts, 1st edn, Series: Coastal and Estuarine Studies, (Springer-Verlag, NY), 1986, pp. 333. ISBN: 978-0-387-96445-4
- 9 Belkin I M & Cornillon P, SST fronts of the Pacific coastal and marginal seas, *Pac Oceanogr*, 1 (2) (2003) 90–113.
- 10 Klein P & Lapeyre G, The oceanic vertical pump induced by mesoscale and submesoscale turbulence, *Ann Rev Mar Sci*, 1 (2009) 351–375. <https://doi.org/10.1146/annurev.marine.010908.163704>
- 11 Schneider N & Qiu B, The atmospheric response to weak sea surface temperature fronts, *J Atmos Sci*, 72 (9) (2015) 3356–3377. <https://doi.org/10.1175/JAS-D-14-0212.1>
- 12 Sund P N, Blackburn M & Williams F, Tunas and their environment in the Pacific Ocean: A review, *Oceanogr Mar Biol: Ann Rev*, 19 (1981) 443–512.
- 13 Lynn R J, The subarctic and northern subtropical fronts in the eastern North Pacific Ocean in spring, *J Phys Oceanogr*, 16 (2) (1986) 209–222.
- 14 Belkin I M & Cornillon P, *Fronts in the world ocean's large marine ecosystems*, ICES CM 2007/D:21, International Council for the Exploration of the Sea: Copenhagen, Denmark, 2007, pp. 33. <https://www.ices.dk/sites/pub/CM%20Documents/CM-2007/D/D2107>
- 15 Kumar S, Kumar N, Padmaja N S, Nayak S, Pillai V N, *et al.*, *Validation of Potential Fishing Zone (PFZ) Advisories (2006–2007)*, Tech Rep, Indian National Centre for Ocean Information Services, Hyderabad, Report No: INCOIS-ASG-PFZ-TR-08-20, 2007, pp. 27.
- 16 Qiu B, Toda T & Imasato N, On Kuroshio front fluctuations in the East China Sea using satellite and in situ observational

- data, *J Geophys Res: Oceans*, 95 (C10) (1990) 18191–204. <https://doi.org/10.1029/JC095iC10p18191>
- 17 Belkin I M, Cornillon P C & Sherman K, Fronts in large marine ecosystems, *Prog Oceanogr*, 81 (1-4) (2009) 223–236. <https://doi.org/10.1016/j.pocean.2009.04.015>
 - 18 Miller A J & Cornuelle B D, Forecasts from fits of frontal fluctuations, *Dyn Atmos Oceans*, 29 (2-4) (1999) 305–333. [https://doi.org/10.1016/S0377-0265\(99\)00009-3](https://doi.org/10.1016/S0377-0265(99)00009-3)
 - 19 Nagai T, Tandon A, Yamazaki H, Doubell M J & Gallagher S, Direct observations of microscale turbulence and thermohaline structure in the Kuroshio Front, *J Geophys Res*, 117 (2012) 1-21. <https://doi.org/10.1029/2011JC007228>
 - 20 Boutin J, Merlivat L, Hénocq C, Martin N & Sallee J B, Air-sea CO₂ flux variability in frontal regions of the Southern Ocean from Carbon Interface Ocean Atmosphere drifters, *Limn Oceanogr*, 53 (5 Part 2) (2008) 2062–2079. https://doi.org/10.4319/lo.2008.53.5_part_2.2062
 - 21 Cayula J F & Cornillon P, Edge detection algorithm for SST images, *J Atmos Ocean Tech*, 9 (1) (1992) 67–80. [https://doi.org/10.1175/1520-0426\(1992\)009%3C0067:EDAFSI%3E2.0.CO;2](https://doi.org/10.1175/1520-0426(1992)009%3C0067:EDAFSI%3E2.0.CO;2)
 - 22 Kumar S P & Prasad T G, Winter cooling in the northern Arabian Sea, *Curr Sci*, 10 (1996) 834–841. <https://www.jstor.org/stable/24098555>
 - 23 Madhupratap M, Kumar S P, Bhattathiri P M, Kumar M D, Raghukumar S, *et al.*, Mechanism of the biological response to winter cooling in the northeastern Arabian Sea, *Nature*, 384 (6609) (1996) 549–552. <https://doi.org/10.1038/384549a0>
 - 24 Shetye S R, Shenoi S S, Gouveia A D, Michael G S, Sundar D, *et al.*, Wind-driven coastal upwelling along the western boundary of the Bay of Bengal during the southwest monsoon, *Cont Shel Res*, 11 (11) (1991) 1397–408. [https://doi.org/10.1016/0278-4343\(91\)90042-5](https://doi.org/10.1016/0278-4343(91)90042-5)
 - 25 Gopalan A K, Krishna V V, Ali M M & Sharma R, Detection of Bay of Bengal eddies from TOPEX and in situ observations, *J Mar Res*, 58 (5) (2000) 721–734. <https://doi.org/10.1357/002224000321358873>
 - 26 Jyothibabu R, Maheswaran P A, Madhu N V, Ashraf T M, Gerson V J, *et al.*, Differential response of winter cooling on biological production in the northeastern Arabian Sea and northwestern Bay of Bengal, *Curr Sci*, 25 (2004) 783–791. <https://www.jstor.org/stable/24109357>
 - 27 Kumar S P, Ramesh R, Sardesai S & Sheshshayee M S, High new production in the Bay of Bengal: Possible causes and implications, *Geophys Res Lett*, 31 (18) (2004) 1-4. <https://doi.org/10.1029/2004GL021005>
 - 28 Chen B, Landry M R, Huang B & Liu H, Does warming enhance the effect of microzooplankton grazing on marine phytoplankton in the ocean? *Limnol Oceanogr*, 57 (2) (2012) 519–526. <https://doi.org/10.4319/lo.2012.57.2.0519>
 - 29 Nuncio M & Kumar S P, Life cycle of eddies along the western boundary of the Bay of Bengal and their implications, *J Mar Syst*, 94 (2012) 9-17. <https://doi.org/10.1016/j.jmarsys.2011.10.002>
 - 30 Kumar S P, Muraleedharan P M, Prasad T G, Gauns M, Ramaiah N, *et al.*, Why is the Bay of Bengal less productive during summer monsoon compared to the Arabian Sea? *Geophys Res Lett*, 29 (24) (2002) 1-4. <https://doi.org/10.1029/2002GL016013>
 - 31 Gomes H R, Goes J I & Saino T, Influence of physical processes and freshwater discharge on the seasonality of phytoplankton regime in the Bay of Bengal, *Cont Shelf Res*, 20 (3) (2000) 313–330. [https://doi.org/10.1016/S0278-4343\(99\)00072-2](https://doi.org/10.1016/S0278-4343(99)00072-2)
 - 32 Madhupratap M, Gauns M, Ramaiah N, Kumar S P, Muraleedharan P M, *et al.*, Biogeochemistry of the Bay of Bengal: physical, chemical and primary productivity characteristics of the central and western Bay of Bengal during summer monsoon 2001, *Deep Sea Res Part II: Top Stud Oceanogr*, 50 (5) (2003) 881–896. [https://doi.org/10.1016/S0967-0645\(02\)00611-2](https://doi.org/10.1016/S0967-0645(02)00611-2)
 - 33 Gopalakrishna V V & Sastry J S, Surface circulation over the shelf off the east coast of India during the south west monsoon, *Indian J Geo-Mar Sci*, 14 (1985) 62–66.
 - 34 Sarkar K, Aparna S G, Dora S & Shankar D, Seasonal variability of sea-surface temperature fronts associated with large marine ecosystems in the north Indian Ocean, *J Ear Syst Sci*, 128 (1) (2019) p. 20. <https://doi.org/10.1007/s12040-018-1045-x>
 - 35 Mohanty P C, Mahendra R S, Nayak R K, Kumar N, Kumar T S, *et al.*, Persistence of productive surface thermal fronts in the northeast Arabian Sea, *Reg Stud Mar Sci*, 16 (2017) 216–224. <https://doi.org/10.1016/j.rsma.2017.09.010>
 - 36 Wahl T R, Ainley D G, Benedict A H & DeGange A R, Associations between seabirds and water-masses in the northern Pacific Ocean in summer, *Mar Biol*, 103 (1989) 1-11. <https://doi.org/10.1007/BF00391059>
 - 37 McGowan J A, Chelton D B & Conversi A, Plankton patterns, climate, and change in the California Current, *Cal Coop Ocean Fish Invest Rep*, (1996) 45–68.
 - 38 Lehodey P, Andre J M, Bertignac M, Hampton J, Stoens A, *et al.*, Predicting skipjack tuna forage distributions in the equatorial Pacific using a coupled dynamical biogeochemical model, *Fish Oceanogr*, 7 (3-4) (1998) 317–325. <https://doi.org/10.1046/j.1365-2419.1998.00063.x>
 - 39 Laurs M R & Lynn J, Seasonal migration of North Pacific albacore, *Thunnus alalunga*, into North American coastal waters: distribution, relative abundance, and association with Transition Zone waters, *Fish Bull*, 75 (4) (1977) 795-822.
 - 40 Laurs R M, Fiedler P C & Montgomery D R, Albacore tuna catch distributions relative to environmental features observed from satellites, *Deep Sea Res Part A: Oceanogr Res Pap*, 31 (9) (1984) 1085–1099. [https://doi.org/10.1016/0198-0149\(84\)90014-1](https://doi.org/10.1016/0198-0149(84)90014-1)
 - 41 Maul G A, Williams F, Roffer M & Sousa F M, Remotely sensed oceanographic patterns and variability of bluefin tuna catch in the Gulf of Mexico, *Oceanol Acta*, 7 (4) (1984) 469–479.
 - 42 Podesta G P, Browder J A & Hoey J J, Exploring the association between swordfish catch rates and thermal fronts on US longline grounds in the western North Atlantic, *Cont Shelf Res*, 13 (2-3) (1993) 253-277. [https://doi.org/10.1016/0278-4343\(93\)90109-B](https://doi.org/10.1016/0278-4343(93)90109-B)
 - 43 Worm B, Sandow M, Oschlies A, Lotze H K & Myers R A, Global patterns of predator diversity in the open oceans, *Science*, 309 (5739) (2005) 1365-1369. <https://doi.org/10.1126/science.1113399>
 - 44 Roffer M A, *Influence of the environment on the distribution and relative apparent abundance of juvenile Atlantic bluefin tuna along the United States east coast*, Ph. D. thesis, University of Miami, Coral Gables, Florida, 1987, pp. 154.

- 45 Palko B J, Beardsley G L & Richards W J, Synopsis of the biology of the swordfish, *Xiphias gladius* Linnaeus, US Department of Commerce, NOAA Tech Rep, 1981, pp. 28.
- 46 Bigelow K A, Boggs C H & He X I, Environmental effects on swordfish and blue shark catch rates in the US North Pacific longline fishery, *Fish Oceanogr*, 3 (1999) 178–198. <https://doi.org/10.1046/j.1365-2419.1999.00105.x>
- 47 Hidaka K, A theoretical study on the general circulation of the Pacific Ocean, *Pacific Sci*, LX, (1955) 183-220.
- 48 Yamanaka I, *The fisheries forecasting system in Japan for coastal pelagic fish*, FAO Fisheries Tech Paper No. 301, 1988, pp. 72.
- 49 Nimit K, Masuluri N K, Berger A M, Bright R P, Prakash S, *et al.*, Oceanographic preferences of yellowfin tuna (*Thunnus albacares*) in warm stratified oceans: A remote sensing approach, *Int J Remote Sens*, 41 (15) (2020) 5785-5805. <https://doi.org/10.1080/01431161.2019.1707903>
- 50 Haney J C, Seabird segregation at Gulf Stream frontal eddies, *Mar Ecol Prog Ser*, 28 (3) (1986) 279–285.
- 51 Griffiths F B & Brandt S B, Mesopelagic crustacea in and around a warm-core eddy in the Tasman Sea off eastern Australia, *Mar Freshw Res*, 34 (4) (1983) 609–623. <https://doi.org/10.1071/MF9830609>
- 52 Tranter D J, Tafe D J & Sandland R L, Some zooplankton characteristics of warm-core eddies shed by the East Australian Current, with particular reference to copepods, *Mar Freshw Res*, 34 (4) (1983) 587-607. <https://doi.org/10.1071/MF9830587>
- 53 Hyrenbach K D & Veit R R, Ocean warming and seabird communities of the southern California Current System (1987–1998): Response at multiple temporal scales, *Deep Sea Res Part II: Topical Stud Oceanogr*, 50 (14–16) (2003) 2537–2565. [https://doi.org/10.1016/S0967-0645\(03\)00123-1](https://doi.org/10.1016/S0967-0645(03)00123-1)
- 54 Haury L R, McGowan J A & Wiebe P H, Patterns and processes in the time-space scales of plankton distributions, In: *Spatial pattern in plankton communities*, NATO Conf Ser, Vol 3, (Springer, Boston, MA), 1978, pp. 277–327. https://doi.org/10.1007/978-1-4899-2195-6_12
- 55 Ferraroli S, Georges J Y, Gaspar P & Maho Y L, Where leatherback turtles meet fisheries, *Nature*, 429 (6991) (2004) 521–522. <https://doi.org/10.1038/429521a>
- 56 Graham T R, Harvey J T, Benson S R, Renfree J S & Demer D A, The acoustic identification and enumeration of scyphozoan jellyfish, prey for leatherback sea turtles (*Dermochelys coriacea*), off central California, *ICES J Mar Sci*, 67 (8) (2010) 1739–1748. <https://doi.org/10.1093/icesjms/fsq112>
- 57 Hays G C, Houghton J D & Myers A E, Pan-Atlantic leatherback turtle movements, *Nature*, 429 (6991) (2004) p. 522. <https://doi.org/10.1038/429522a>
- 58 Luschi P, Hays G C & Papi F, A review of long-distance movements by marine turtles, and the possible role of ocean currents, *Oikos*, 103 (2) (2003) 293–302. <https://doi.org/10.1034/j.1600-0706.2003.12123.x>
- 59 Polovina J J, Balazs G H, Howell E A, Parker D M, Seki M P, *et al.*, Forage and migration habitat of loggerhead (*Caretta caretta*) and olive ridley (*Lepidochelys olivacea*) sea turtles in the central North Pacific Ocean, *Fish Oceanogr*, 13 (1) (2004) 36-51. <https://doi.org/10.1046/j.1365-2419.2003.00270.x>
- 60 Williams K F, Sea-surface temperature maps to assist tuna fisheries off New South Wales, Australia, In: *Environmental Analysis in Marine Fisheries Research—Fisheries Environmental Services*, edited by Tomczak G H, FAO Fisheries Technical Paper No. 170, 1977, pp. 38-55.
- 61 Syamsuddin M, Saitoh S I, Hirawake T, Syamsudin F & Zainuddin M, Interannual variation of bigeye tuna (*Thunnus obesus*) hotspots in the eastern Indian Ocean off Java, *Int J Rem Sens*, 37 (9) (2016) 2087-2100. <https://doi.org/10.1080/01431161.2015.1136451>
- 62 Sambah A B, Muamanah A, Harlyan L I, Lelono T D, Iranawati F, *et al.*, Sea surface temperature and chlorophyll-a distribution from Himawari satellite and its relation to yellowfin tuna in the Indian Ocean, *Aquacul Aquar Conser Leg*, 14 (2) (2021) 897–909.
- 63 Mediodia H J, Kahui V & Noy I, Sea surface temperature and tuna catch in the Eastern Pacific Ocean under climate change, *Mar Resour Econ*, 38 (4) (2023) 329–351. <https://hdl.handle.net/10419/226235>
- 64 Sbarros P S, Romanov E, Le Foulgoc L, Richard E, Dagorne D, *et al.*, Exploratory analysis of relationships between swordfish captures and environmental features in the southwest Indian Ocean, 11th IOTC Working Party on Billfish, (La Réunion, France), IOTC–2013–WPB11–30 Rev_1, 2013, pp. 17.
- 65 Bandaranayake K H K, Weerasekera S J W W M M P, Jayathilaka R M R M & Haputhantri S S K, Monsoon and temperature effects on swordfish (*Xiphias gladius*) catches in the high seas of the Indian Ocean: A case study in high seas longline fishery of Sri Lanka, IOTC Sixteenth Working Party on Bill Fish, (Cape Town, South Africa), 2018, pp. 10.
- 66 Elepathage T S, Tang D & Oey L, The pelagic habitat of swordfish (*Xiphias gladius*) in the changing environment of the North Indian Ocean, *Sustainability*, 11 (24) (2019) p. 7070. <https://doi.org/10.3390/su11247070>
- 67 Fager E W & McGowan J A, Zooplankton species groups in the North Pacific: Co-occurrences of species can be used to derive groups whose members react similarly to water-mass types, *Science*, 140 (3566) (1963) 453–460. <https://doi.org/10.1126/science.140.3566.453>
- 68 Brodeur R D, Wilson M T, Ciannelli L, Doyle M & Napp J M, Interannual and regional variability in distribution and ecology of juvenile pollock and their prey in frontal structures of the Bering Sea, *Deep Sea Res Part II: Top Stud Oceanogr*, 49 (26) (2002) 6051–6067. [https://doi.org/10.1016/S0967-0645\(02\)00333-8](https://doi.org/10.1016/S0967-0645(02)00333-8)
- 69 Varela J L, Intriago K M, Flores J C & Lucas-Pilozo C R, Feeding habits of juvenile yellowfin tuna (*Thunnus albacares*) in Ecuadorian waters assessed from stomach content and stable isotope analysis, *Fish Res*, 194 (2017) 89-98. <https://doi.org/10.1016/j.fishres.2017.05.017>
- 70 Young J, Drake A, Farley J, Carter T, Brickhill M, Reproductive dynamics of broadbill swordfish (*Xiphias gladius*) in the domestic longline fishery off eastern Australia, (CSIRO Marine Laboratories, Tasmania, Australia), 2002, pp. 121. [https://doi.org/10.1016/0278-4343\(93\)90109-B](https://doi.org/10.1016/0278-4343(93)90109-B)
- 71 Clayton S, Dutkiewicz S, Jahn O & Follows M J, Dispersal, eddies, and the diversity of marine phytoplankton, *Limnol Oceanogr Fluids Environ*, 3 (1) (2013) 182–197. <https://doi.org/10.1215/21573689-2373515>
- 72 Gaube P, Chelton D B, Strutton P G & Behrenfeld M J, Satellite observations of chlorophyll, phytoplankton biomass, and Ekman pumping in nonlinear mesoscale eddies,

- J Geophys Res: Oceans*, 118 (12) (2013) 6349–6370. <https://doi.org/10.1002/2013JC009027>
- 73 Chang Y L, Miyazawa Y, Oey L Y, Kodaira T & Huang S, The formation processes of phytoplankton growth and decline in mesoscale eddies in the western North Pacific Ocean, *J Geophys Res: Oceans*, 122 (5) (2017) 4444–4455. <https://doi.org/10.1002/2017JC012722>
- 74 Mackas D L & Galbraith M D, Zooplankton distribution and dynamics in a North Pacific eddy of coastal origin: I. Transport and loss of continental margin species, *J Oceanogr*, 58 (2002) 725–738. <https://doi.org/10.1023/A:1022802625242>
- 75 Roberts M J, Zemplak T & Connell A, Cyclonic eddies reveal Oegopsida squid egg balloon masses in the Agulhas Current, South Africa, *Afri J Mar Sci*, 33 (2) (2011) 239–246. <https://doi.org/10.2989/1814232X.2011.600294>
- 76 Ruvalcaba-Aroche E D, Sánchez-Velasco L, Beier E, Godínez V M, Barton E D, *et al.*, Effects of mesoscale structures on the distribution of cephalopod paralarvae in the Gulf of California and adjacent Pacific, *Deep Sea Res Part I: Oceanogr Res Paps*, 131 (2018) 62–74. <https://doi.org/10.1016/j.dsr.2017.11.005>
- 77 Nishimoto M M & Washburn L, Patterns of coastal eddy circulation and abundance of pelagic juvenile fish in the Santa Barbara Channel, California, USA, *Mar Ecol Prog Ser*, 241 (2002) 183–199. <https://doi.org/10.3354/meps241183>
- 78 Godø O R, Samuelsen A, Macaulay G J, Patel R, Hjøllø S S, *et al.*, Mesoscale eddies are oases for higher trophic marine life, *PLoS One*, 7 (1) (2012) p. e30161. <https://doi.org/10.1371/journal.pone.0030161>
- 79 Devine B, Fennell S, Themelis D & Fisher J A, Influence of anticyclonic, warm-core eddies on mesopelagic fish assemblages in the Northwest Atlantic Ocean, *Deep Sea Res Part I: Oceanogr Res Pap*, 173 (2021) p. <https://doi.org/10.1016/j.dsr.2021.103555>
- 80 Morgan C A, De Robertis A & Zabel R W, Columbia River plume fronts, I: Hydrography, zooplankton distribution, and community composition, *Mar Ecol Prog Ser*, 299 (2005) 19–31. <https://doi.org/10.3354/meps299019>
- 81 Acha E M, Piola A, Iribarne O & Mianzan H, Biology of fronts, In: *Ecological Processes at Marine Fronts: Oases in the Ocean*, (Springer, Cham), 2015, pp. 68. https://doi.org/10.1007/978-3-319-15479-4_3
- 82 Woodson C B & Litvin S Y, Ocean fronts drive marine fishery production and biogeochemical cycling, *Proc Nat Acad Sci*, 112 (6) (2015) 1710–1715. <https://doi.org/10.1073/pnas.1417143112>
- 83 Sato M, Barth J A, Benoit-Bird K J, Pierce S D, Cowles T J, *et al.*, Coastal upwelling fronts as a boundary for planktivorous fish distributions, *Mar Ecol Prog Ser*, 595 (2018) 171–86. <https://doi.org/10.3354/meps12553>
- 84 Polovina J J, Howell E A, Kobayashi D R & Seki M P, The transition zone chlorophyll front, a dynamic global feature defining migration and forage habitat for marine resources, *Prog Oceanogr*, 49 (1-4) (2001) 469–483. [https://doi.org/10.1016/S0079-6611\(01\)00036-2](https://doi.org/10.1016/S0079-6611(01)00036-2)
- 85 Olson M B & Strom S L, Phytoplankton growth, microzooplankton herbivory and community structure in the southeast Bering Sea: Insight into the formation and temporal persistence of an *Emiliania huxleyi* bloom, *Deep Sea Res Part II: Top Stud Oceanogr*, 49 (26) (2002) 5969–5990. [https://doi.org/10.1016/S0967-0645\(02\)00329-6](https://doi.org/10.1016/S0967-0645(02)00329-6)
- 86 Cooper C & Withers P, General ecology: Animal physiology, In: *Encyclopedia of Ecology*, 2008, pp. 181–189. <https://doi.org/10.1016/B978-008045405-4.00456-0>
- 87 Sarma V V S S, Desai D V, Patil J S, Khandeparker L, Aparna S G, *et al.*, Ecosystem response in temperature fronts in the northeastern Arabian Sea, *Prog Oceanogr*, 165 (2018) 317–331. <https://doi.org/10.1016/j.pocean.2018.02.004>
- 88 Lehahn Y, d'Ovidio F & Koren I, A satellite-based Lagrangian view on phytoplankton dynamics, *Ann Rev Mar Sci*, 10 (2018) 99–119. <https://doi.org/10.1146/annurev-marine-121916-063204>
- 89 Cotté C, d'Ovidio F, Dragon A C, Guinet C & Lévy M, Flexible preference of southern elephant seals for distinct mesoscale features within the Antarctic Circumpolar Current, *Prog Oceanogr*, 131 (2015) 46–58. <https://doi.org/10.1016/j.pocean.2014.11.011>
- 90 Prants S V, Marine life at Lagrangian fronts, *Prog Oceanogr*, 204 (1) (2022) p. 102770. <https://doi.org/10.1016/j.pocean.2022.102770>
- 91 Yamamoto T & Nishizawa S, Small-scale zooplankton aggregations at the front of a Kuroshio warm-core ring, *Deep Sea Res Part A: Oceanogr Res Pap*, 33 (11-12) (1986) 1729–40. [https://doi.org/10.1016/0198-0149\(86\)90076-2](https://doi.org/10.1016/0198-0149(86)90076-2)
- 92 Genin A, Jaffe J S, Reef R, Richter C & Franks P J, Swimming against the flow: A mechanism of zooplankton aggregation, *Science*, 308 (5723) (2005) 860–862. <https://doi.org/10.1126/science.110783>
- 93 Filatov N, Johannessen O M, Pozdnyakov D, Bobylev L P, Pettersson L, *et al.*, *Oceanographic regime, White Sea: Its Marine Environment and Ecosystem Dynamics Influenced by Global Change*, (Praxis Publishing Limited, Chichester, UK), 2005, pp. 476.
- 94 Legendre L & Rivkin R B, Fluxes of carbon in the upper ocean: regulation by food-web control nodes, *Mar Ecol Prog Ser*, 242 (2002) 95–109. <https://doi.org/10.3354/meps242095>
- 95 Price A R, The marine food chain in relation to biodiversity, *Sci World J*, 1 (2001) 579–587. <https://doi.org/10.1100/tsw.2001.85>
- 96 Friedland K D, Stock C, Drinkwater K F, Link J S, Leaf R T, *et al.*, Pathways between primary production and fisheries yields of large marine ecosystems, *PLoS One*, 7 (1) (2012) p. e28945. <https://doi.org/10.1371/journal.pone.0028945>
- 97 Krumhardt K M, Long M C, Sylvester Z T & Petrik C M, Climate drivers of Southern Ocean phytoplankton community composition and potential impacts on higher trophic levels, *Front Mar Sci*, 9 (2022) p. 916140. <https://doi.org/10.3389/fmars.2022.916140>
- 98 Landry M R & Kirchman D L, Microbial community structure and variability in the tropical Pacific, *Deep Sea Res Part II: Top Stud Oceanogr*, 49 (13–14) (2002) 2669–2693. [https://doi.org/10.1016/S0967-0645\(02\)00053-X](https://doi.org/10.1016/S0967-0645(02)00053-X)
- 99 Morel F M, Hudson R J & Price N M, Limitation of productivity by trace metals in the sea, *Limnol Oceanogr*, 36 (8) (1991) 1742–1755. <https://doi.org/10.4319/lo.1991.36.8.1742>
- 100 Nimit K, Nagaraja Kumar M, Swetha N, Nayak J, Rose P B, *et al.*, *Utility of sea surface height anomaly (SSHa) in determination of potential fishing zones*, Technical Report, Report No.: ESSO/INCOIS/ASG/TR(02)2015, Indian

- National Centre for Ocean Information Services, Hyderabad, India, 2015, pp. 37.
- 101 Solanki H U, Dwivedi R M, Nayak S R, Jadeja J V, Thakar D B, *et al.*, Application of Ocean Colour Monitor chlorophyll and AVHRR SST for fishery forecast: Preliminary validation results off Gujarat coast, northwest coast of India, *Indian J Geo-Mar Sci*, 30 (3) (2001) 132–138. <http://nopr.niscpr.res.in/handle/123456789/4613>
- 102 Dwivedi R M, Solanki H U, Nayak S R, Gulati D K & Somvamshi V S, Exploration of fishery resources through integration of ocean colour with sea surface temperature: Indian experience, *Indian J Geo-Mar Sci*, 34 (4) (2005) 430–440. <http://nopr.niscpr.res.in/handle/123456789/1577>
- 103 Pillai V N & Nair P G, Potential fishing zone (PFZ) advisories—Are they beneficial to the coastal fisherfolk? A case study along Kerala coast, South India, *Biol Forum*, 2 (2) (2010) 46–55.
- 104 George G, Krishnan P, Dam Roy S, Sarma K, Bharathi M P G, *et al.*, Validation of potential fishing zone (PFZ) forecasts from Andaman and Nicobar Islands, *Fish Technol*, 50 (2013) 1–5.
- 105 Rintaka W E & Susilo E, Validation of potential fishing zone forecast using experimental fishing method in Tolo Bay, Central Sulawesi Province, *IOP Conf Ser: Earth Environ Sci*, 137 (1) (2018) p. 012041.
- 106 Young J W, Hunt B P, Cook T R, Llopiz J K, Hazen E L, *et al.*, The trophodynamics of marine top predators: current knowledge, recent advances and challenges, *Deep Sea Res Part II: Top Stud Oceanogr*, 113 (2015) 170–187. <https://doi.org/10.1016/j.dsr2.2014.05.015>
- 107 Boyce D G, Lewis M R & Worm B, Global phytoplankton decline over the past century, *Nature*, 466 (7306) (2010) 591–596. <https://doi.org/10.1038/nature09268>
- 108 Olonscheck D, Hofmann M, Worm B & Schellnhuber H J, Decomposing the effects of ocean warming on chlorophyll a concentrations into physically and biologically driven contributions, *Environ Res Lett*, 8 (1) (2013) p. 014043. <https://doi.org/10.1088/1748-9326/8/1/014043>
- 109 Miller P I & Christodoulou S, Frequent locations of oceanic fronts as an indicator of pelagic diversity: Application to marine protected areas and renewables, *Mar Policy*, 45 (2014) 318–329. <https://doi.org/10.1016/j.marpol.2013.09.009>