

7 *Fronts and Eddies in the Sea: Mechanisms, Interactions and Biological Effects*

ROBERT W. OWEN

1 Introduction

This chapter concerns fronts and eddies, two major classes of water motion that create and change patterns of biological distributions. Flow of water across topographic features in the open sea produces patterns of vertical circulation ('fronts') and eddy-like motions which can reorder life processes and distributions in a variety of ways. Such patterns may also arise independently of sea bottom topography from ocean current confluence, from wind stress applied unevenly in space and time, or from heat and water exchange across the sea surface. Frontal and eddy circulations can occur at any depth and affect populations of organisms at all trophic levels, including benthic forms from great depths to the littoral zone. Life forms as diverse as phytoplankton, protozoans, crustaceans, fish, sea snakes, marine mammals and birds are found to alter their distributions in the presence of such flow patterns.

The ocean is widely held to be turbulent upwards of the scale of a few centimeters and seconds, but also to contain quasi-ordered velocity fields. Recent experimental work suggests that such ordered fields may be more prevalent in turbulent fluids than previously believed (Laufer, 1975). Fronts and eddies are two such classes of quasi-ordered velocity fields. We are concerned here with flow patterns that locally alter biological distributions, but it is obvious that various processes causing fronts and eddies can occur at the same place and time. This frequently leads to a degree of complexity that approaches fully turbulent motion, i.e. chaos. To the degree that organisms interact with mixed regimes of physical processes, patchiness of organisms induced by behavioral mechanisms alone may be obliterated.

There is a considerable body of evidence that patterned patchiness frequently arises from patterned circulation. Environmental circumstances under which such patterns arise are often rather unexceptional, and thus may be more widespread than case studies imply. There is also some promise

of prediction of patterning (or de-patterning) circulations, which would be of value in estimating yield of fish stocks affected by patterning of food and supply. Accounting for such patterning of organisms, which is recurrent and widespread in many instances, should also enhance the accuracy of biological production models constructed for organisms at any position in the food web.

Fronts and eddies are engendered by a variety of physical processes and have a variety of biological consequences. The terms 'front' and 'eddy' are used here to denote localised zones where quasi-ordered singularities of lateral flow induce or intensify vertical flow. A front is a line or linear zone that defines an axis of laterally convergent flow, below or above which vertical flow is induced (Fig. 1). A frontal system denotes sets of convergences. These usually produce alternating zones of downwelling and upwelling flow. An eddy denotes an area of closed horizontal streamlines where vertical motion is induced or sustained.

Fronts and eddies are recurrent or persistent singularities in the ocean's usually turbulent flow. They are found singly, in groups, and in combination in all seas and at all depths, although most frequently and to clearest ecological effect in the surface layers. Characteristic motions have been detected on scales that range from 1 to 10^5 m laterally and 1 to 10^3 m in depth, and persist from a few hours to virtual permanence. The magnitude of ecological effects, however, is not necessarily scale-dependent. Time and space scales are related: the smallest fronts and eddies are the most ephemeral and the largest are the most permanent. This relationship holds because driving forces are more ephemeral on small scales, because size of circulations tend to increase where the driving force is maintained, and because when the driving force relaxes, larger circulations persist longer.

A basic and attractive tenet implicit in much of the work in this area is that vertical displacements have greater ecological effects than similar horizontal displacements because environmental gradients, such as light, pressure, temperature, salinity, oxygen, nutrients and flow, are by far the steepest in the vertical (chapter 14). Vertical motion in fronts is often vigorous and highly localised, whereas in eddies it is slow and spread over much larger areas. For this reason, lateral gradients of temperature, salinity and food supply are correspondingly sharper across convergent flows than across eddies. Direct responses of organisms have not often been demonstrated, and causal effects are notoriously difficult to isolate.

Vertical motion in eddies occurs to compensate for lateral flow into or out of the circulation. Such convergent or divergent lateral flow occurs as a result of deflection due to the Coriolis parameter of relative motion on the rotating earth (Von Arx, 1962). Cyclonic eddies of sufficient size exhibit divergent flow due to the Coriolis deflection and compensatory upward movement occurs. Anticyclonic eddies, conversely, exhibit downward

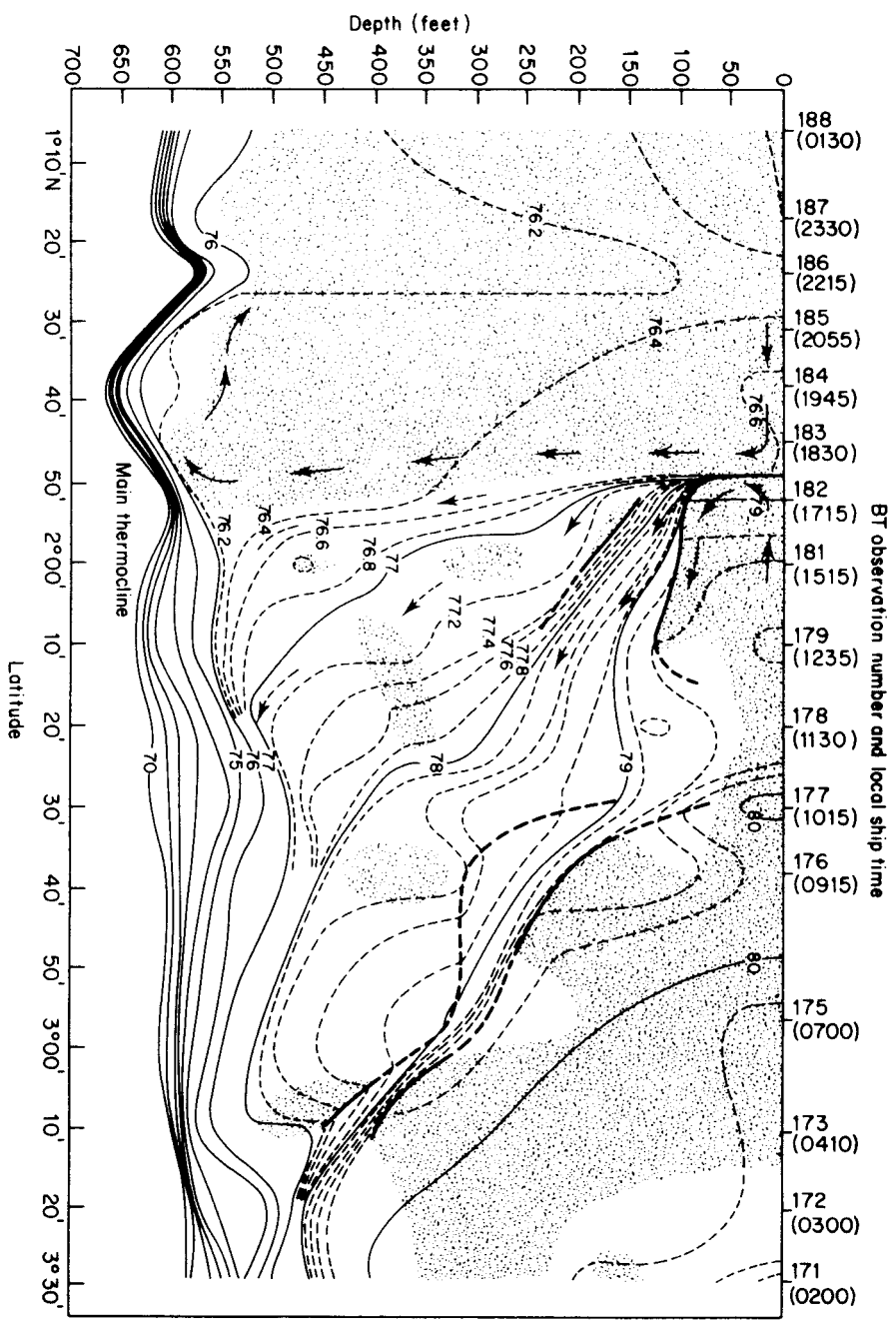


FIG. 1 Thermal structure and inferred circulation in an ocean front along 172°W near the Equator. From Cromwell and Reid (1956)

motion in their interiors. Estimates of upward velocities in large cyclonic eddies (cf. Owen, 1980) are of the same order as sinking rates of some phytoplankton and detrital particles and can also transport substantial nutrient supplies upward (Broenkow, 1965). Whether cyclonic or not, eddies are zones of horizontal recirculation and thus locally maintain and transport their contained populations and substances.

Difficulty of detection and measurement at sea in part accounts for the fact that we can only guess at the full extent, nature and ecological impact of some of the interactions reviewed here. We currently look to advances in instrumentation and observation platforms (especially appropriately equipped and deployed spacecraft) to add needed perspective and we regard the study of such singularities to be in its early stages.

2 Interactive characteristics of organisms and substances

Most macroscopic particles, living or not, have properties that make possible their differential concentration in the presence of fronts or eddies of appropriate scale and intensity. These properties are: differential motion (sinking, floating and swimming) and proliferation (production and reproduction). Characteristics of these properties are more or less specific to the type of particle. They operate interactively with vertical circulations either directly or indirectly as rates and directions of sinking and swimming and on local rates of production. Rates and directions are in turn responsive mainly to food (or nutrient) supply and to environmental gradients, especially light, temperature and food concentrations.

It must be emphasised that a degree of randomness is typical of both water motion and organism characteristics. Sinking and swimming rates vary between organisms of the same species, size or population, and water motion is usually subject to random variations so that trapping efficiency of a particular circulation is accordingly diminished, as is the sharpness of the resulting patterns of organism concentration. It seems clear from case studies, however, that factors creating pattern frequently predominate over those that disrupt it. Vertical movement, for example, tends to be more consistent in rate and direction among individuals of the same types than among individuals of different types.

The same arguments apply to production rates: among plankton species represented at a site, several are likely to respond with similar division rates to a change in, say, nutrients supplied by a front or eddy. Such species become differentially concentrated as a set if their vertical motions are either similar or not important. Production rates tend to be more similar within than between organism types, ranging upward to 2 doublings/day among some phytoplankton populations.

Particle characteristics that determine sinking rates are size, form and density. Volume and density of a particle govern its buoyant forces whereas its surface area and form are the primary determinants of local fluid drag.

Detrital particles of filterable size sink in still water at rates depending primarily on their size and form. Detritus is predominantly microscopic but can exceed 1 m in largest dimension in shapes as diverse as "burst balloons", strings and sheets. These can have occluded bubbles and lumps that make estimates of density and sinking rate uncertain. The bulk of detritus, however, has little apparent potential for passive collection except in the slowest convergences and perhaps in cyclonic (upwelling) eddies. This is because most detrital particles sink slowly: they are either quite small or are in an aggregated form known as 'marine snow'. An important exception is fecal pellets of zooplankton, particularly those of copepods since they are so numerous. Smayda (1969) found still water sinking rates of naturally occurring fecal pellets to range from 1.5 to 15.6 m h⁻¹, mostly about 6 m h⁻¹. Large pellets sank faster than small ones, and shape effects also were discerned. Effects of diet on pellet buoyancy and shape are apparent from observations of Marshall and Orr (1955) and may be expected to influence sinking rate of the pellets. Disintegration and bacterial or fungal growth probably affect sinking rates of older pellets.

Sinking of diatoms, which have little or no other motility, was reviewed comprehensively by Smayda (1970). He cites sinking rates up to 1.26 m h⁻¹ for a large centric diatom and average rates of about 1 m day⁻¹, determined on live cells sinking in still water. Smayda also cites studies of sinking rates derived from field observation of rates at which diatom layers changed depth. These ranged from 1–5 m day⁻¹, greater than still water sinking rates of the same or similar species.

Many diatoms apparently exercise a degree of control over their sinking rate through regulation of their density, size and shape. Changes in sinking rates favorable to the population have been noted to occur in apparent response to environmental factors, notably light and nutrient levels. although sinking predominates widely, diatoms may also become positively buoyant on occasion, changing buoyancy by ionic regulation of cell sap density or by accumulation of fats. Smayda (1970) cites several cases of centric diatom blooms at the sea surface that dramatically demonstrate floating. As would be expected if cell density were independent of its volume, the main influence on still water sinking rates of phytoplankton is cell size (or aggregate size, if colonial). Eppley *et al.* (1967) summarise this effect and also emphasise the physiological condition of cells as a determinant of sinking rate. Cells from senescent cultures sink about four times faster than cells from growth-phase cultures. Increased sinking rates would place

nutrient-deficient or light-blitzed cells at water depths more favorable in either respect.

The determination of sinking rates in dinoflagellates is more complex because most are motile. A passive sinking rate of *Gonyaulax polyedra* in growth phase was reported by Eppley *et al.* (1967) at 2.8 m day^{-1} , whereas swimming at $1 \text{ to } 2 \text{ m h}^{-1}$ is indicated by studies of this and other dinoflagellate species (Hasle, 1950, 1954; Hand *et al.*, 1965). In any case, dinoflagellates move faster by swimming than by sinking.

Phototaxis is not restricted to dinoflagellates, but is widely represented among motile plankton and fish species. The resulting diel patterns of vertical migration thus occur in every phylum represented in the sea and for a wide variety of apparent advantages to the migrants. Longhurst (1976) provides a recent discussion of the mechanisms and advantages of vertical migrations as well as entry to the extensive literature on patterns of vertical movement of zooplankton. In circumstances where phototactic migrants move into or through persistent vertical circulations, patterns due to their interaction must necessarily have diel periodicity. Zones of higher organism concentration in daylight would thus become rarified at night, as the migrators would instead collect, if at all, at convergences of the opposite direction. Diel variation of convective circulation in the surface layer (Woods, in press) also would affect such patterning.

Hardy and Bainbridge (1954) measured swimming speeds of various zooplankters by placing individual animals in a water-filled torus, which was then rotated on its horizontal axis at recorded rates to keep the swimmer at the same height. Sustained upward rates of nearly 30 m h^{-1} were achieved by the robust copepod, *Centropages*, and 90 m h^{-1} by the euphausiid, *Meganyctiphanes norvegica*. Downward speeds often exceeded upward speeds: e.g. *Calanus* sustained speeds of 47 m h^{-1} downward versus 15 m h^{-1} upward. Enright (1977), from open ocean catches of the 2–3 mm copepod *Metridia pacifica* in several sets of serial net hauls made vertically above and below the base of the thermocline, determined upward swimming speeds from 30 to 90 m h^{-1} for more than an hour. This was greater by 2 to 10 times than previous field estimates he noted. These values give some idea of the maximum depth range that could be traversed in one or two hours of vertical swimming in the absence of vertical flow.

Sinking rates of zooplankton are usually small compared to their vertical motility, but could be important during periods of inactivity. One such period is at night: after the organisms have completed their main upward migration, passive sinking may occur for several hours before downward migration is induced near dawn (Raymont, 1963). Sinking has been invoked to explain the 'midnight scattering' apparent among various vertical migrants that spend the night in the upper layer. This scattering could as

well be due to random vertical swimming in the absence of light stimulus. Midnight scattering may be followed by upward swimming near dawn just before the migrants swim downward to seek their daytime levels.

Diel vertical migrations of fish usually follow the pattern of most zooplankton migrants; rising to the surface layers around sunset, dispersal during darkness, and returning to deeper layers by sunrise. Adults and larvae of sardine, herring, pilchard, coalfish and plaice have been noted to migrate roughly according to this pattern, and many myctophids and gonostomatids perform regular diel migrations to the sea surface layer from several hundred meters depth. These larger zooplankton and fishes do not necessarily interact directly with patterning circulations, but may find feeding advantages where their prey are so concentrated.

Organisms not directly affected by patterned vertical motions may nevertheless respond to substances or to organisms that are so affected. For example, nutrient salts brought up to the euphotic zone locally stimulate production of phytoplankton, whereas zooplankton patterned by vertical motion may locally graze down phytoplankton or attract predators, producing secondary patterning of either. Similarly, flotsam and surface active materials collect at surface-convergent fronts where they subsequently can attract or affect organisms. Some, if not most, organisms respond selectively to gradients that are created or modified by fronts and eddies.

Attraction to food commonly accounts for aggregation of animals at or near fronts larger than the Langmuir pattern. They may arrive by a variety of ways. Passive floating behavior by *Pelamis platurus*, the sea snake, causes large aggregations at fronts in the eastern tropical Pacific where they feed on small fish (Kropach, 1975). Small fish, in turn, aggregate in these fronts for plankton. Several species arrive with the floating wood and debris to which they are attracted (Hunter and Mitchell, 1967). The phenomenon is commonplace and commonly attracts larger and smaller animals of recurrent species, leading Dunson and Ehlert (1971) to suggest that the fronts create a community. Most often seen nearshore, such assemblages occur in offshore water to sometimes dramatic degrees. In the offshore eastern tropical Pacific, fronts occur that assemble plankton, fishes, birds, whales and porpoises, as well as flotsam with expatriated littoral and neritic animals and plants. Beebe's (1926) classical description of such a front lists several species in each of these categories. They arrived in numbers by every conceivable pathway.

These observations have been since confirmed and extended, e.g. for bird aggregation by Ashmole and Ashmole (1967), and for mammals by Gaskin (1968 and 1976). Food aggregations were the attractants in each case.

3 Patterned flow types, scales and genesis

Where circulation characteristics are determined by the presence of coastlines, islands, banks, seamounts, etc. the pattern is under topographic control. Circulations under dynamic control are relatively independent of topography, and include fronts and eddies arising from atmospheric forcing and from current confluence, meandering, or other flow instabilities. Fronts and eddies of both types occur at all sizes and frequencies important to organisms. Those of the dynamic type occur virtually anywhere in the sea, whereas the topographic type occur most frequently and noticeably along continental margins and in island wakes.

Due to their proximity to external driving forces, the surface layers of the sea tend to be the most energetic, both physically and biologically. Topographic control is thus most pronounced where the bottom is shoal enough to intercept and modify surface layer processes. Although active over far less ocean area than dynamic processes, topographic fronts and eddies operate in zones already high in biological activity. Fronts and frontal systems that affect measurable biological conditions operate on scales as small as meters and hours and as large as 10^3 km and years. On the other hand, eddies of less than a few km in radius and a week in duration have not been noticed to produce biological patterning. Although small eddies transport and perhaps conserve materials, their main effect is to broach or attenuate features of larger scale and thus act more to disrupt than to create pattern.

SMALL-SCALE FRONTAL SYSTEMS

Patterned convergences on the smallest scales at the sea surface are usually accounted for by cellular convections due to wind or to thermocline effects. Such convections take the form of paired, vortical cells of opposing rotation around their horizontal axes. Water downwells where surface flow converges between cells and upwells where subsurface flow converges. Thermohaline convection occurs when denser water forms rapidly at the sea surface and is responsible for the smallest patterns seen to collect organisms. Denser water forms by cooling due to evaporation, back radiation and heat conduction from the very surface. The density increase by cooling may be augmented by the salinity increase from evaporation. Formation of denser water at the sea surface creates vertical instability. At high rates of formation, this water is hydrodynamically most easily discharged by sinking of the dense water along preferred planes rather than by simple diffuse sinking as small filaments. This process has been observed to create patterns of small-scale convection cells which are elongated Bénard cells. Bénard cells may be commonplace under light wind conditions and probably

augment convection at higher wind speeds. Defant (1961) reviewed criteria for such convections and gave evidence that Bénard circulations are frequent and widespread in equatorial and mid-latitudes, extending in depth to 25 m or more in the absence of overriding motions. Instability of surface layers, due mainly to evaporation, is cited to occur in the entire pelagic sector of the Atlantic from 20° N to 50° S and to be most pronounced between 15° S and 20° S.

The smallest coherent frontal patterns that have been noted to collect organisms in the open sea were attributable to the Bénard mechanism. Surface convergences penetrated to less than a meter in depth, extended visibly for more than 30 m in unbroken length, spaced at intervals of about 1.5 m. The patterns persisted in the absence of wind for at least two days (Owen, 1966). Taken singularly, such 'micro-fronts' would have little ecological impact. This particular frontal system, however, extended over several hundred km², so that even such fine-scale patterns can produce widespread alteration of concentration patterns and, presumably, concentration-dependent biological processes. In this instance, the surface convergences were marked by red bands less than 10 cm wide that consisted of upward swimming oikopleurans that had been highly concentrated in the upper 5 cm of the convergence planes. Their still water swimming speed of about 0.2 cm s⁻¹ set an upper limit on downwelling water speed in the convergence planes.

Under freshening and sustained winds, convergence systems of the better known and (usually) larger scale Langmuir circulation either develop extant Bénard cells or create their own patterns, detectable as parallel windrows. Windrows lie along the wind axis and are often marked by assemblages of any floating (i.e. strongly buoyant) substances in the neighborhood. These are swept by convergent surface flow to the frontal zones. Trapping efficiency of buoyant materials is virtually 100% under steady wind direction. Surface convergences can become strong enough on occasion to submerge even highly buoyant *Sargassum* weed, requiring a downwelling circulation of 5–7 cm s⁻¹ (Woodcock, 1950). Organic films on the sea surface also are rapidly collected along such convergences to give windrows their characteristic banded appearance. Under lower winds, collected oils dampen capillary waves to give the windrows the appearance of parallel slicks. At higher wind speeds, the organics are partly frothed and mark convergences by foam lines.

The size and circulation strength of these convection cells increase with time and wind speed. Spacing of convergence lines several meters to over 100 m is typical, and downwelling speeds may exceed 10 cm s⁻¹. Depth of penetration is some fraction of the distance between convergences, usually half or somewhat less.

Extant theories that attempt to account for the Langmuir circulation include instability of vertical shear in the water, forcing by atmospheric vortices, wind-oriented thermal (Bénard) convection, wind profile modification by surface films, lateral radiation pressure on surface films, convergence of wave trains (reviewed by Scott *et al.*, 1969), and vertical decay of surface wave oscillations (Faller, 1969). Failure of their data to support or rule out any single mechanism led Scott *et al.* (*op. cit.*) to conclude that combinations could occur of mechanisms they considered. A subsequent study (Harris and Lott, 1973) lends support to the possibility of development of Bénard cells into Langmuir cells: mean downwelling velocities ranging from 2 to 10 cm s⁻¹ in Langmuir convergences correlated well with wind speed during net surface cooling but not as well during net surface heating. Despite the lack of agreement on mechanisms, Langmuir circulations are now widely held to be the most important mechanism for vertical transfer of heat and substances in surface waters of lakes as well as oceans.

The theoretical and mathematical description of particle trajectories in cellular convections was formulated by Stommel (1949) and subsequently elaborated to include swimming (e.g. Stavn, 1971). Direct observations confirm the applicability of the model to real particles and plankters in such circulations, despite the rather large difficulties of field measurement and the less-than-ideal behavior of both the fluid and plankters.

A number of field studies confirm the effectiveness of the Langmuir circulation in collecting and patterning organisms and substances. The most visible examples involve buoyant animals and substances such as *Physalia* (Woodcock, 1944), *Sargassum* weed (Faller and Woodcock, 1964; Woodcock, 1950) and surface films (Szekielda *et al.*, 1972). Sutcliffe *et al.* (1963) demonstrated that whitecapping and perhaps other wind action converts dissolved organics to particulate form available to zooplankton, and that a Langmuir convection downwelling at 3–6 cm s⁻¹ produced subsurface concentrated zones of these particulates. The soluble inorganic phosphate concentration was also shown to be higher in such particulates. Sutcliffe *et al.* (1971) showed, by detecting an increase in particle concentrations with increase in wind speed, that the process is highly effective. They found peak production to be particles of 6 μm diameter. Higher concentrations of particles 2–13 μm diameter were found below convergence zones.

Patterning of phytoplankton and microzooplankton by Langmuir circulations has been more widely reported than one would expect from the mismatch of their reported rates of vertical motion. Bainbridge (1957) reviews several observations of dinoflagellate concentrations in Langmuir-scale patterns. The mobile and prolific ciliate *Mesodinium rubrum*, which can occur in blooms ('red-water') concentrations, has been reported to gather in Langmuir convergences. Powers (1932) found them in windrows off Maine,

and Bary (1953) found windrows of the same ciliate to orient along a changing wind axis in New Zealand. Packard *et al.* (1978) describe *Mesodinium* windrows spaced at 100 m intervals under 10–20 knot winds, and their dispersion through the water column at winds over 30 knots.

Patterning of zooplankton in Langmuir circulations is less apparent and notoriously difficult to sample. The best examples of Langmuir patterning of zooplankton thus are from lakes, where populations of cladocerans and copepods migrate vertically into Langmuir vortices in the epilimnion and form rows of higher concentration in convergence planes (George and Edwards, 1973).

INTERNAL WAVE PATTERNS

Internal waves generate banded patterns on the sea surface on a range of scales extending from that of the Langmuir circulation. Visible rows spaced 10–100 m apart are common on continental shelves, particularly when insolation produces a thin, light surface layer. Ewing (1950) first identified internal waves as responsible for light-wind band slicks and presented evidence that slicks progressed with and marked convergent displacements on the surface layer, moving at 1–100 cm s⁻¹. They are made visible from collection of surface films in compression zones (Garrett, 1967) or directly from the effect of billow currents of internal waves (Garrett and Hughes, 1972), either of which locally damps surface capillary waves. Rows may extend for several km and lie usually more or less parallel to shore, to isobaths and to one another. Row orientation is independent of wind direction, but rows are erased (or replaced by the Langmuir circulation) when wind speed increases about 3 m s⁻¹ for 30 minutes or more.

Internal waves on the continental shelf are generated remotely by a variety of mechanisms and altered by changes in density stratification, currents and current shear, and proximity to the sea surface and bottom (see review by Garrett and Munk, 1979). Wind storms and tides are the likeliest common source of their generation. Unlike circulations discussed here, there is no net transfer of water or organisms with the passage of internal waves unless they break. Thus there is no actual circulation of substances and organisms are not differentially collected, except perhaps ephemerally at the very surface. Bacteria depending on the surface film for support are sometimes highly concentrated in internal wave slicks, but more often show no particular relation to them (ZoBell, 1946).

Internal waves, however, may interact with current boundaries and shelf-break fronts. Curtin and Mooers (1975) presented measurements that indicated generation of large amplitude, high frequency internal waves by breakdown of the semidiurnal internal tide at the shelf-break front off Oregon. These induced major perturbation of a sonic scattering layer of

organisms inshore of the front. Earlier, Yasui (1961) presented a theoretical framework arguing for generation and propagation of tidal period internal waves along fronts due to current confluence, which are zones of high lateral shear as well as vertical circulation. Localised interaction between internal waves and eddies in mid-ocean also has been detected (Frankignoul, 1976) which may affect rate of vertical diffusion. As yet, these phenomena seem to be unexplored, but may be expected to modify effects of fronts on biota. Kamykowski (1974), for example, presented a reasonable mechanism by which phytoplankton can interact with the semidiurnal internal tide to produce patterns of species and biomass.

Internal waves are sensitive to current shear and to vertical density gradients, both of which are altered at fronts and eddies. It will not be surprising to find evidence of biological responses to these coactive physical processes if adequate sampling techniques can be devised.

4 Coastal fronts and eddies

Topography of the sea floor and obstacles to flow exert locally significant control of convergence systems above the scale of the Langmuir phenomenon and spawn eddies large enough to affect biological processes.

TIDAL FRONTS

Simpson and Pingree (1978), Pingree *et al.* (1977) and Pingree *et al.* (1974) described cases of genesis and maintenance of shallow sea fronts by tidal mixing on the European continental shelf. Surface convergent fronts of considerable physical and biological activity occur in zones where water types of different mixing histories impinge. Where tidally-mixed water contacts stratified water, a convergent front occurs. Thermal images of the Celtic Sea from the NOAA-5 satellite confirm the broad occurrence of tidal fronts and show the genesis of cold eddies from frontal meanders (Fig. 2). These fronts respond to the neap and spring tidal cycle and its effect on phytoplankton chlorophyll concentrations in the stratified water beyond the front. The quoted studies suggest that blooms of a somewhat distant dinoflagellate population were caused by periodic release of nutrients from the destratified side of the front.

Admixture of water types at shelf fronts locally stimulates phytoplankton photosynthesis and thus sustains higher phytoplankton concentrations in the frontal zones. Savidge (1976) and Savidge and Foster (1978) described such a process from surface measurements of chlorophyll, temperature and photosynthesis along transects on the European shelf between Ireland and Wales.

Zooplankton concentrated in shelf fronts is also observed. Pingree *et al.*

1100 BST 18·8·76 1017 BST 19·8·76 1128 BST 20·8·76



FIG. 2 Infrared images from NOAA-5 satellite of thermal patterns in the Celtic Sea from 18 to 20 August 1976. Lighter shades represent cooler surfaces. From Simpson and Pingree (1978)

(1974) described a vigorous tidal front of 15 km extent in the English Channel from temperature, salinity and current measurements and from direct underwater and surface observations of its effects on organisms and substances. Surface net hauls showed much greater frontal concentrations of copepods, crustacean meroplankton, the euphausiid *Nyctiphanes* sp. and (perhaps) young fishes.

Plankton concentrated by the front was confirmed by subsurface visual observation. Underwater observation of motions of plankton and of dye injected at several depths also confirmed the turbulent and convergent character of the fronts that was apparent from temperature and salinity structure and from drogue measurements. The list provided of animals associated with floating macrophytes concentrated at the front consisted of a variety of post-larval fishes and crustacean species. Puffins, shearwaters and terns were seen feeding along the front, which also collected debris and oil lumps. The authors remark on the similarity of this front and its biota to the large, deep-ocean fronts described by Beebe (1926) and Amos *et al.* (1972).

Marine mammals are documented to exploit the biota of tidal and other shelf fronts. Gaskin (1976), for example, cited feeding by minke whales on herring or capelin aggregated in coastal tide slicks of eastern Canada and feeding by fin whales on surface concentrations of the euphausiid *Meganyctiphanes* in a convergence in the Bay of Fundy. Mackerel schools had forced the euphausiids to the surface.

SHELF-BREAK AND UPWELLING FRONTS

Fronts of large extent commonly occur in the general vicinity of the shelf-break, i.e. where the gradient of the continental shelf steepens to become the continental slope, generally at about 100–300 m depth. Mooers *et al.* (1978) usefully distinguished between prograde fronts, those that separate more saline shelf water from offshore water, and retrograde fronts, those that separate less saline shelf water from offshore water (Fig. 3). Shelf waters of both types usually are colder than offshore.

Prograde fronts arise by upwelling on the continental shelf. Seasonal and episodic wind-driven upwelling is characteristic of eastern boundary current systems, but occurs inshore of western boundary currents as well, where upwelling occurs by topographic deflection or trapping of currents. Retrograde fronts are due to shelf-water dilution from terrestrial runoff and thus predominate off large coastal watersheds. Their incidence and intensity usually vary with season.

Prograde shelf-break fronts off upwelling zones bound plankton rich shelf waters. There is a dearth of studies that demonstrate higher plankton concentrations in these fronts than inshore, at least in part because field studies have been concerned more with the upwelling system as a whole and do not sufficiently sample the frontal interface. Packard *et al.* (1978) described the incidence and habitat of the pigmented ciliate, *Mesodinium rubrum*, in an upwelling zone off Baja, California. Characteristics of its environment in combination with its phototactic behavior, rapid reproduction rate and ability to use both inorganics and organics for food, were cited to potentiate surface-layer concentrations of the ciliate at prograde fronts.

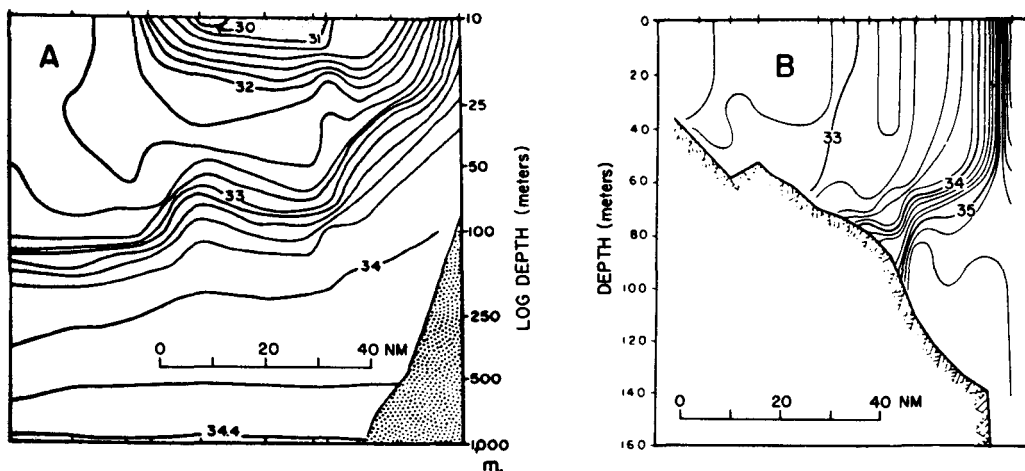


FIG. 3 Structure of prograde (upwelling) fronts and retrograde (estuarine) fronts. Panel A from Owen (1968). Panel B from Mooers *et al.* (1978)

Bang (1973) described measurements showing a strong upwelling front extended northwest off Cape Town in the eastern boundary current of South Africa. Mixing cells occurred and episodic overturn at the front produced subthermocline sheets of homogeneous water. Concentrations of large zooplankton or micronekton were detected at the front by fathometer. The area inshore of this front has begun to support a fishery on the lantern fish *Lampanyctodes hectoris* incidental to the extant anchovy and pilchard fishery of the region (Ahlstrom *et al.*, 1976).

Albacore make annual trans-Pacific migrations to feed on relatively high concentrations of large plankton and small fishes in the California current, seaward of coastal upwelling zones. The offshore extent of these upwelling zones are frequently denoted by prograde (upwelling) fronts. Albacore caught, tagged with ultrasonic transmitters and released were tracked in the vicinity of such a front off Monterey Bay, California (Laurs *et al.*, 1977). Their results showed that such temperature fronts influence local concentration of albacore, with albacore concentrating in the vicinity of the front, moving away with the degradation of the front as upwelling ceased. Albacore also were seen to move more slowly when crossing fronts and to spend little time on the colder side ($t < 15^{\circ}\text{C}$) indicating a thermal barrier effect which would result in their collecting at fronts. The enriching effects of large cyclonic eddies that predominate outside upwelling zones, and eddy transport from upwelling zones described by Owen (1980) may also support higher forage levels beyond such fronts.

An important aspect of upwelling fronts is their periodic relaxation or breaching, and the subsequent release into offshore water of nutrients and plankton previously accumulated in the shelf water. Frontal relaxation occurs upon cessation of upwelling, which can be either seasonal or episodic depending on the wind system. Breaching occurs more locally than does relaxation. The causes of breaching have not been defined but likely involve meanders and eddies due to local instabilities of frontal currents, outside eddy impingement, and perhaps wave interactions with the fronts. When clear weather permits, breaching is clearly evident in thermal images of sea surface temperature fields off California transmitted from satellites. Bernstein *et al.* (1977) demonstrated the possibility of using such infrared images to follow the genesis, lysis and incidence of eddies, fronts and upwelling zones where they involve temperature, as in the California current system.

ESTUARINE FRONTS

Retrograde (estuarine) fronts exhibit salinity gradients, since freshwater sources dilute surface waters on one side of such fronts. Iisuka and Arie (1969) showed concentrations of *Trichodesmium* (flagellate) for 80 km along an estuarine front off Japan. LeFèvre and Grall (1970) showed similar

convergent aggregations of *Noctiluca scintillans* off Brittany, and emphasised local competition for diatoms between *Noctiluca* and copepods.

Owen (1968) studied effects of the Columbia River plume, which albacore encounter in their early summer arrival off Oregon. Based on research vessel catch rates and oceanographic data, results showed that albacore moved through the pronounced outer plume boundary, defined by the $32.2^{\circ}/_{\text{‰}}$ isohaline that demarcated the outer estuarine boundary of the salinity front of the plume-sea interface. Catches were usually lower in mid-plume than in the vicinity of its frontal limits, indicating an attraction to the fronts *per se* or possibly a combined attraction/aversion to the warmer temperatures/lower salinities of the plume core. Catch rates may be seen to be much higher near the outer plume limit than near the inshore limit, where even stronger thermohaline fronts result from combined effects of the plume and coastal upwelling (cf. Fig. 3, panel A).

On smaller scales near shore, Tsujita (1957) showed seasonal on-shore/offshore movements of stocks of the Japanese sardine off western Japan. Spawning and hatching occurs at depth in oceanic water near a retrograde (estuarine) coastal front. Larvae are transported or migrate through the shelf-break front and seek nearshore feeding grounds, growing to 7–10 cm and diffusing seaward in summer in the upper layer of the coastal zone.

A large saline front found spanning the Equator 600 km off Sumatra and south of the Bay of Bengal by Amos *et al.* (1972) was formed at the confluence of the saline Equatorial Countercurrent with water from the north, diluted by effluent of the Ganges, Irrawaddy and Salween rivers. Hardly a shelf-break feature, the front still was of estuarine character and exhibited high biological activity: obviously associated with the front were small sharks and flying fish, and feeding sea birds. The front also collected a large quantity of debris and abundant plankton. Sea snakes and dolphin fish also were seen at the convergence. Under no immediate topographic control, the front was nevertheless of estuarine origin.

5 Deep-sea fronts and eddies

Beyond immediate topographic control, confluenced waters of different mixing histories produce a front or frontal system in the equatorial Pacific (Wyrtki, 1966). Pak and Zaneveld (1974) demonstrated increased particle concentrations associated with a front east of the Galapagos Islands (downstream with respect to the equatorial undercurrent) that was defined by large horizontal gradients of temperature, salinity, density and nitrate concentration. They attributed the front to the confluence of the Peru current with the south equatorial current, and cite earlier physical oceanographic investigations of the same feature that indicate its perma-

nence and the seasonality of its location and intensity. It seems possible that this is the same front described by Beebe (1926) that dramatically assembled a large fauna.

Cromwell and Reid (1956) described such fronts (or the same front) from close-spaced temperature profiles along 120°W and 172°W and suggested cell-like circulation from their data (see Fig. 1). Knauss (1957) described a second front crossing at 120°W with even closer temperature profiles that defined the frontal edge. Knauss mentioned high concentrations at the front of squid, *Pyrosoma*, flying fish (2 species), sauries and lantern fish (2 species), and the absence of floating debris. Water characteristics on the cold sides of these fronts indicated the involvement of the east-flowing equatorial undercurrent in their creation and maintenance.

Murphy and Shomura (1972) documented increased availability of yellow-fin tuna near island groups of the central Pacific, particularly of younger fish in surface schools. Three assessment methods, sightings of surface schools, surface trolling and deep longlining clearly indicated their increased abundance within 100 km of islands. Concentration of tuna forage by topographic fronts and eddies was suggested to account for the effect.

Murphy and Shomura (1972) pointed out that 'the very existence of schools of carnivores would seem to require schools or aggregations of prey, for if prey were distributed at random, it could be most effectively harvested . . . by individual predators'. They showed a close correspondence between the incidence of thermal fronts and tuna school sightings on transects from 10°N to 5°S in the central Pacific beyond influence of islands. They concluded that concentrating mechanisms were more important than overall levels of forage in determining incidence of surface schools, but that the overall forage levels were of more influence on distribution of the much less aggregated deep-swimming tunas.

At higher latitudes, front-prone zones correspond with transition zones of the atmosphere between the easterly tradewinds and westerlies. The region between 22°N and 32°N in the Atlantic appears particularly active in late winter and spring (Voorhis and Hersey, 1964). Voorhis (1969) described shipboard physical measurements of a large, meandering thermal front extending east-west for nearly 1000 km at 27–30°N in the Sargasso Sea. A similar front was later found to persist for 3 months by repeated surface temperature surveys from low-flying aircraft equipped with an infrared detector.

Biological sampling across the Sargasso Sea at other times has shown north-south discontinuities at the front of small particles (Spilhaus, 1968), phytoplankton production (Ryther and Menzel, 1960), species composition and standing stock of phytoplankton (Hulbert, 1964), zooplankton (Colton *et al.*, 1975) and mesopelagic fishes (Backus *et al.*, 1969).

In the Pacific, the annual feeding migration pattern of albacore tuna from

waters off Japan to the American west coast appears to be bounded by fronts defining the northern and southern limits of the transition zone separating Pacific central and subarctic water masses. Shomura and Otsu (1956) and Graham (1957) found that mid-Pacific albacore catches were characteristically associated with the subarctic front and transition zone. This zone is probably a consistent source of surface layer enrichment (McGary and Stroup, 1956) indicated by elevated phosphate levels and reduced water transparency due to plankton production. Laurs and Lynn (1977) studied albacore catch rates in relation to transition zone fronts, both under intensive coverage as the fish approached the west coast feeding grounds in late spring. Large catch rates did not persist in any one area for more than a few days, indicating movement of the schools; their degree of constraint between oceanographically-defined frontal zones is apparent in Fig. 4.

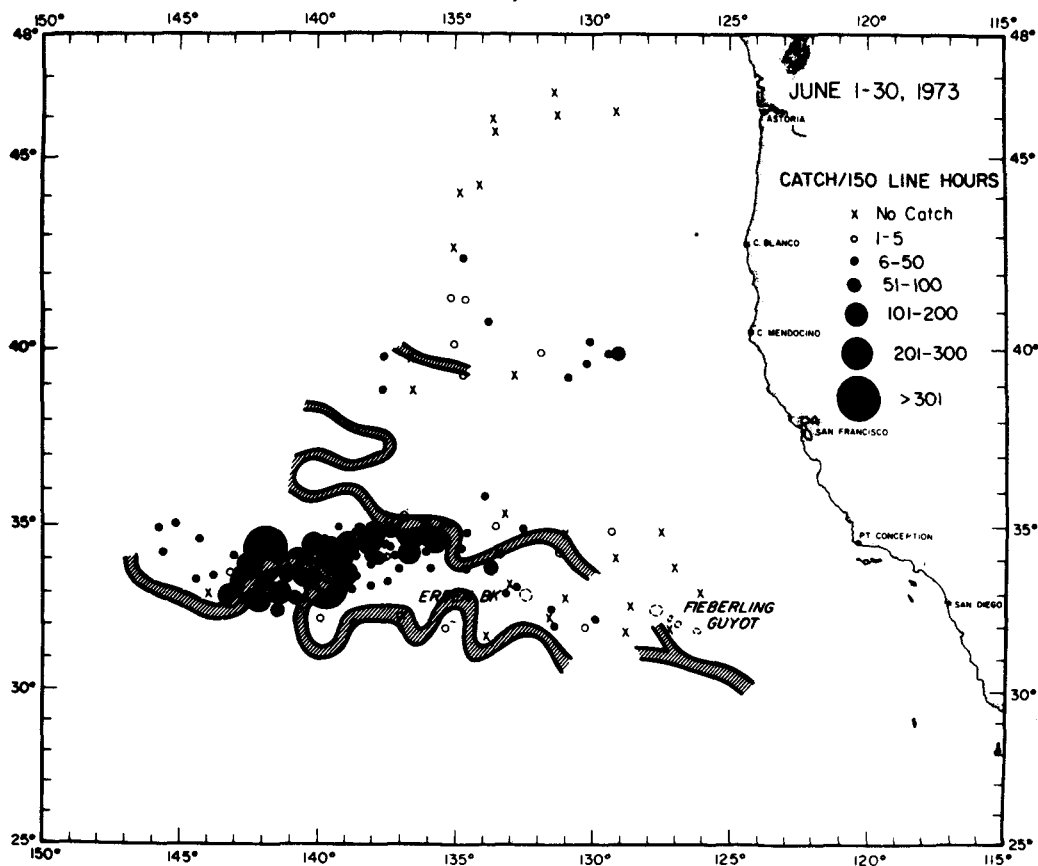


FIG. 4 Albacore tuna catch rate in relation to fronts (shaded) of the transition zone in June 1973. From Laurs and Lynn (1977)

Although not clear from the limited direct measurements available, this transition zone and its fronts probably furnish more food to migrators than waters beyond. Albacore have a fondness for saury and squid, which have been noted to concentrate at frontal structures elsewhere (Uda, 1938, 1952; Han and Gong, 1970). The subtlety of temperature and salinity gradients that define transition zone fronts make it seem unlikely that albacore respond directly to these gradients to determine their movements, although Neill *et al.* (1976) suggested a mechanism by which tunas may orient to temperature gradients as small as $0.1^{\circ} \text{ km}^{-1}$.

Seckel (1972) suggested that convergent flow along the large-scale saline front between North Pacific central and equatorial water masses may operate directly to concentrate skipjack tunas as well as their food. This front is demarcated by a horizontal salinity gradient that periodically reaches or passes the Hawaiian Islands; the abundance of skipjack, indicated by skipjack catch by local fishing, increases at these times. This suggests at least a bounding effect on the fish. The northward passage of the front is detected by the sharp decrease (here, in May) of salinity at a shore station on Oahu.

A growing body of evidence suggests that topographically independent baroclinic instabilities (wavelike motions in large-scale flows with vertical shear in which Coriolis and buoyancy forces are important) are significant in large-scale ocean circulations. Hart (1979) reviewed the theoretical basis of this large eddy-producing phenomenon and Hide and Mason (1975) reviewed annulus convection experiments in laboratory flows. In addition to the meanders and eddies of the Gulf Stream and Polar Front cited below, examples of such activity are apparent in the central North Pacific. Bernstein and White (1974), from four sets of temperature observations, verified the existence of a mosaic of baroclinic eddies well removed from islands, ocean boundaries and the Kuroshio.

TOPOGRAPHIC CONTROL OF DEEP-SEA EDDIES

It is equally apparent that continental margins dissipate energy through generation of large eddies. Even in the weak and diffused eastern boundary currents, evidence of boundary effects extend well past continental margins (shelf and slope areas). These are evidenced by thermal patterns from satellites (Bernstein *et al.*, 1977) (Fig. 5). Owen (1980) reviewed eddy genesis and incidence in the California current system and demonstrated the preponderance of cyclonicity among large eddies detected in geostrophic flow by extensive surveys of the California Cooperative Oceanic Fisheries Investigations (Wyllie, 1966). One particularly persistent feature is the southern California Eddy which appears to collect and recirculate biota from the upwelling zone north of Pt. Conception. Owen (1980) indicated

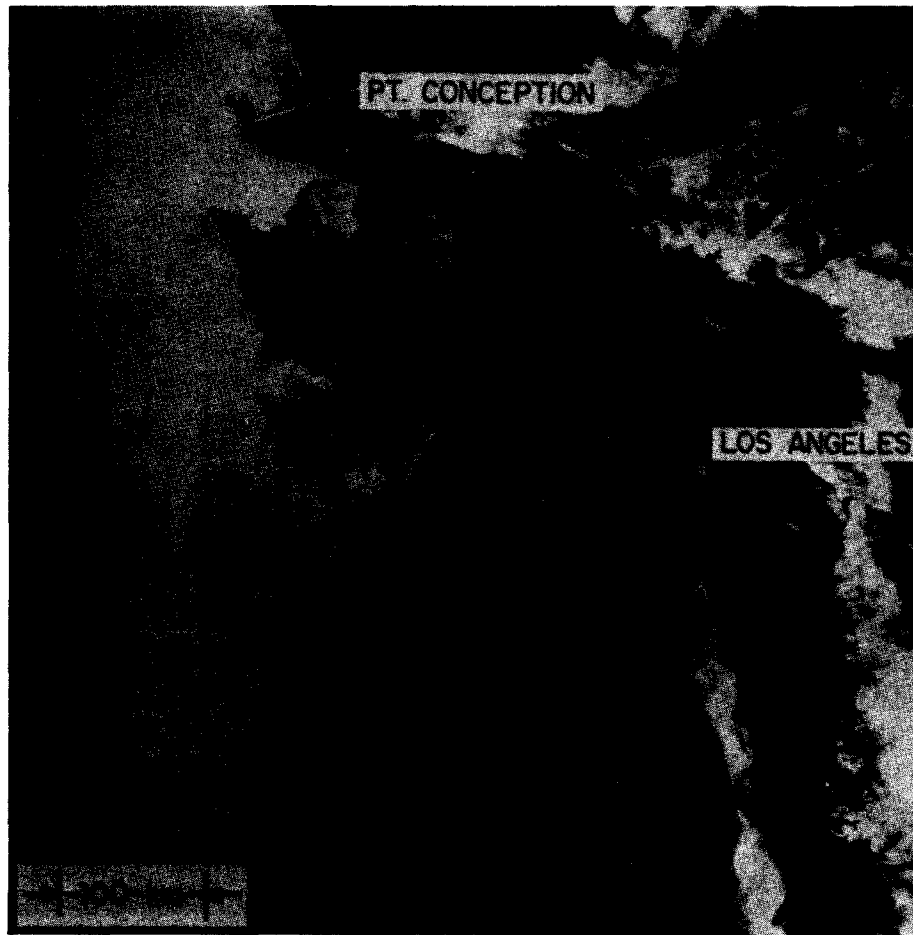


FIG. 5 Infrared image from NOAA-6 satellite of thermal patterns in the southern California Bight, September 1979. Point Conception and the Channel Islands are visible in the upper left quadrant. Lighter shades represent cooler surfaces. Photo courtesy of Remote Sensing Facility, Scripps Institution of Oceanography

the role of the Eddy in nutrient enrichment of the surface layer by upward flow and nutricline displacement. Washdown of diatom assemblages was indicated by Allen (1945) and higher chlorophyll concentrations in the Eddy were shown by Owen (1980). Brinton (1976) examined life history and local distribution of *Euphausia pacifica* which suggested the Eddy to be a reproductive refuge for the population. The correspondence is unmistakable between the Eddy and patterns of concentration of both sardine eggs (Sette and Ahlstrom, 1948) and diatom concentrations (Sargent and Walker, 1948) in spring of 1941.

Another large, stationary eddy is even more isolated; the Costa Rica Dome

is produced by topographic deflection of the north equatorial countercurrent. The Dome, named for its upward bulging thermocline layer, centers in the bight of this deflection (Fig. 6). Upward displacement and active upwelling in the core region cause nutrient enrichment of the photic zone (Broenkow, 1965). This sustains detectably higher stocks of phytoplankton, zooplankton and small nekton according to authors cited by Owen (1980).

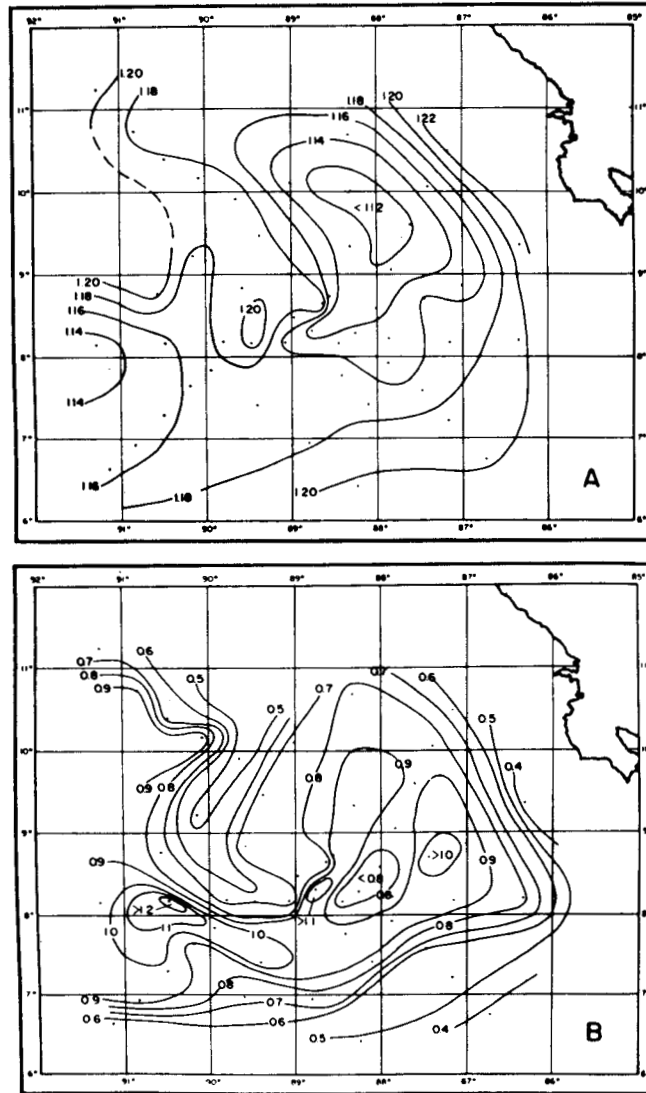


FIG. 6 (A) Flow represented by geopotential topography of the Costa Rica Dome at about 50 m depth relative to 1000 m. (B) Phosphate concentration ($\mu\text{g atoms l}^{-1}$) at 50 m depth. From Broenkow (1965)

Islands, seamounts and headlands act as obstacles to sea and air flow and induce instabilities that can develop into eddies. Eddies may be stationary, "attached" to the obstacle or, with increased flow or obstacle size, may be shed in series. Barkley (1972) found remarkable agreement between observed current patterns downstream of Johnson Atoll and an adaptation of

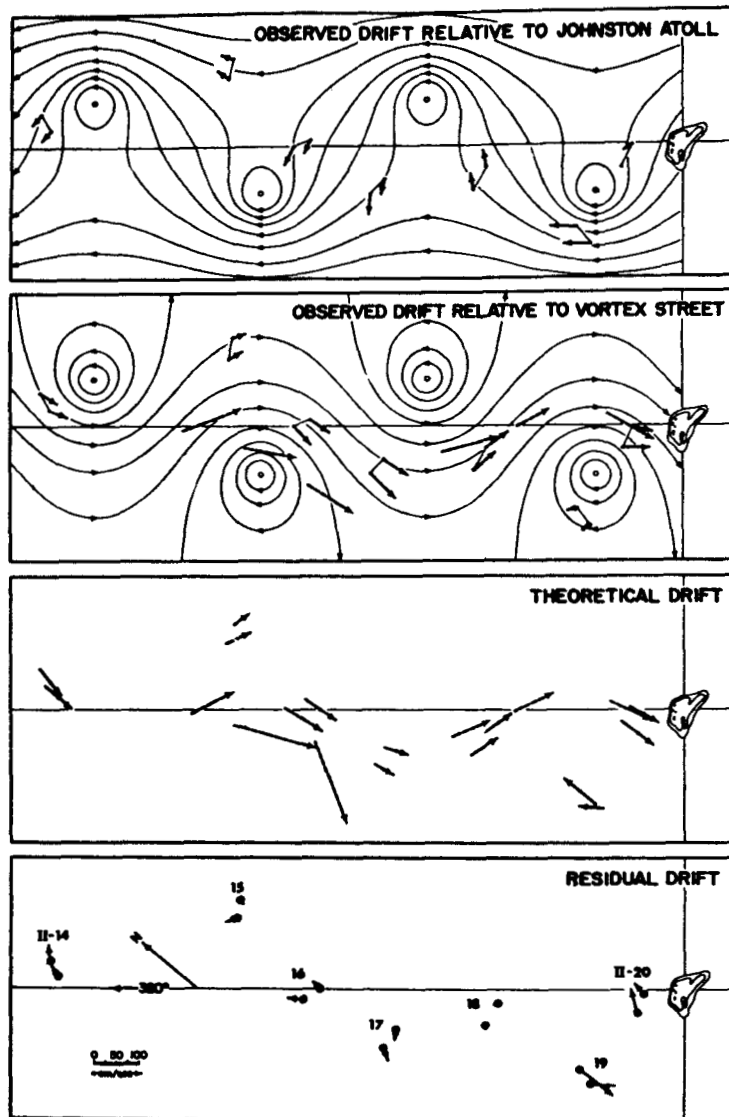


FIG. 7 Eddies in the wake of Johnston Atoll. Streamlines in upper panels derived from von Kármán model of vortex street, fitted to current measurements. Degree of fit is apparent from the lower panels; residual drift values are small compared with theoretical and observed values. From Barkley (1972)

Von Kármán's model of flow past cylinders (Fig. 7). Patzert (1970) described eddy systems in the lee of the Hawaiian group, where eddies appeared to form by local wind forcing. White (1973) detected eddy patterns east of the Galapagos, with respect to the equatorial undercurrent. Wind or current effects at headlands produce eddies, perhaps acting as half an island. Arthur (1965) identified the importance of flow vorticity at headlands of west coastlines. Where the thermocline and nutricline are shallow, the eddy formation produces cool, enriched water at the surface equatorward of such promontories (Reid *et al.*, 1958).

Boden (1952) and Boden and Kampa (1953) determined summer and winter circulation patterns over the submerged platform of the seamount from which Bermuda emerges. Distribution of density in both seasons indicated a cyclonic eddy spanning the entire seamount, and convergent fronts at its margins. The planktonic larvae of benthic animals sampled in summer were considered to be returned to and retained on the platform by both eddy and frontal circulations, enhancing their eventual recruitment to the bottom fauna. Intense mixing zones close to the platform sides were indicated by local vertical instabilities as density inversions.

Hogg *et al.* (1978) detected eddies near the Bermuda Platform (Fig. 8). Fine-structure of temperature variation on intervals from 0.2 to 25 m indicated a large degree of vertical mixing in patches close to the island, a consequence they felt due to strong longshore flow between the eddies. Hogg *et al.* (1978) attribute one of the eddies to a meander in the Polar Front. Intense mixing zones occurred on small scales (0.2–1 m variances) next to the platform walls (note Boden and Kampa's result above) and on larger scales (5–25 m) at about 10 miles distance. Velocity profiles showed that the vertical scales of mixing increased with distance from the island. Internal waves were discounted as a source of the mixing. Osborn (1978), using measurements of velocity shear microvariation, found zones of high energy dissipation (by mixing) within 5 km of the island of Santa Maria in the Azores. Mixing zones were as much as 45 m thick, at the base of the upper mixed layer. At 80 km distance, maximum dissipation zones were below the thermocline at depths over 250 m.

Emery (1972) described evidence from drift bottle and current meter data favoring a persistent system of shed eddies in the wake downstream of Barbados Island (West Indies). Weekly evening plankton tows made 3 km off Barbados for over a year indicated that retention or return of meroplankton near the shelf of the island was enhanced by the eddies.

Jones (1962) cited evidence for effects of the Marquesas Islands in the equatorial Pacific. He found significantly higher zooplankton volumes in quantitative net tows approaching the islands from any direction in the zone from 10 to 180 miles. The higher plankton concentrations were not due to

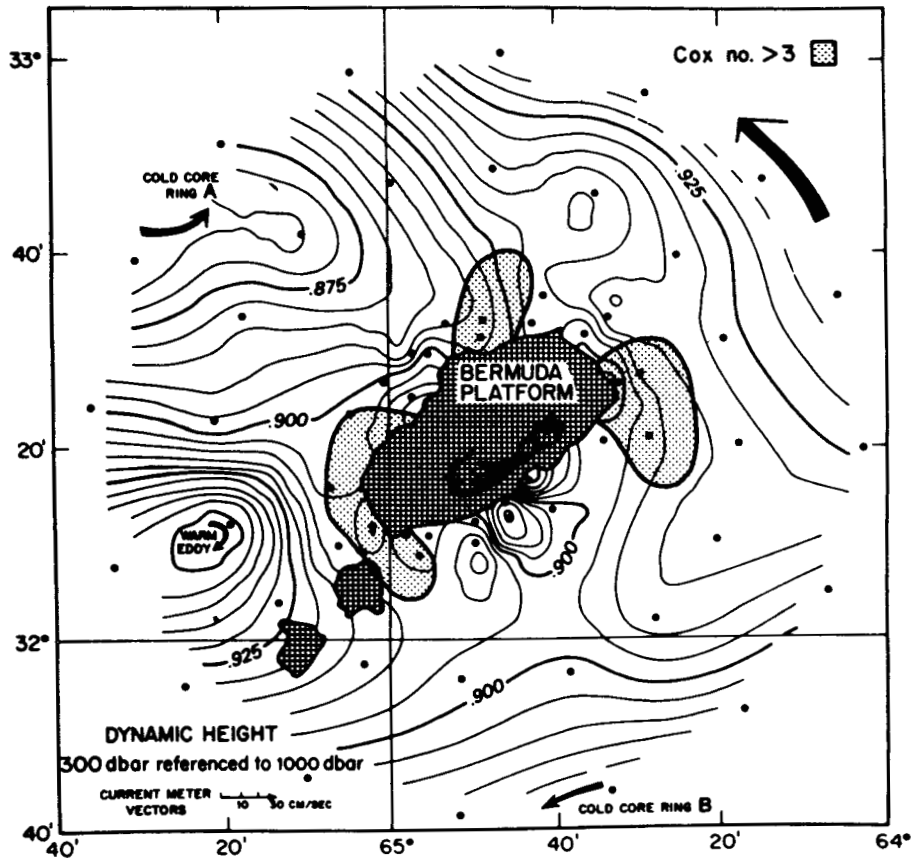


FIG. 8 Flow represented by geopotential topography and intense small-scale mixing zones at about 300 m depth near the Bermuda Platform, according to Hogg *et al.* (1978)

washout of island plankton as most were dominated by euphausiids and siphonophores. Neither group is considered land dependent. The decrease in water transparency approaching the island zone is consistent with higher phytoplankton stocks.

FRONT-EDDY INTERACTIONS

Large-scale associations of fronts and eddies are apparent from several examples. Where fronts are vigorous for their size or meet an obstacle, flow becomes unstable and frontal meanders may pinch off and become eddies as shown in Fig. 9 (Fuglister and Worthington, 1951). Western boundary currents and their seaward extensions produce large intense fronts and eddies. A well-documented example is spawning of eddies from the North

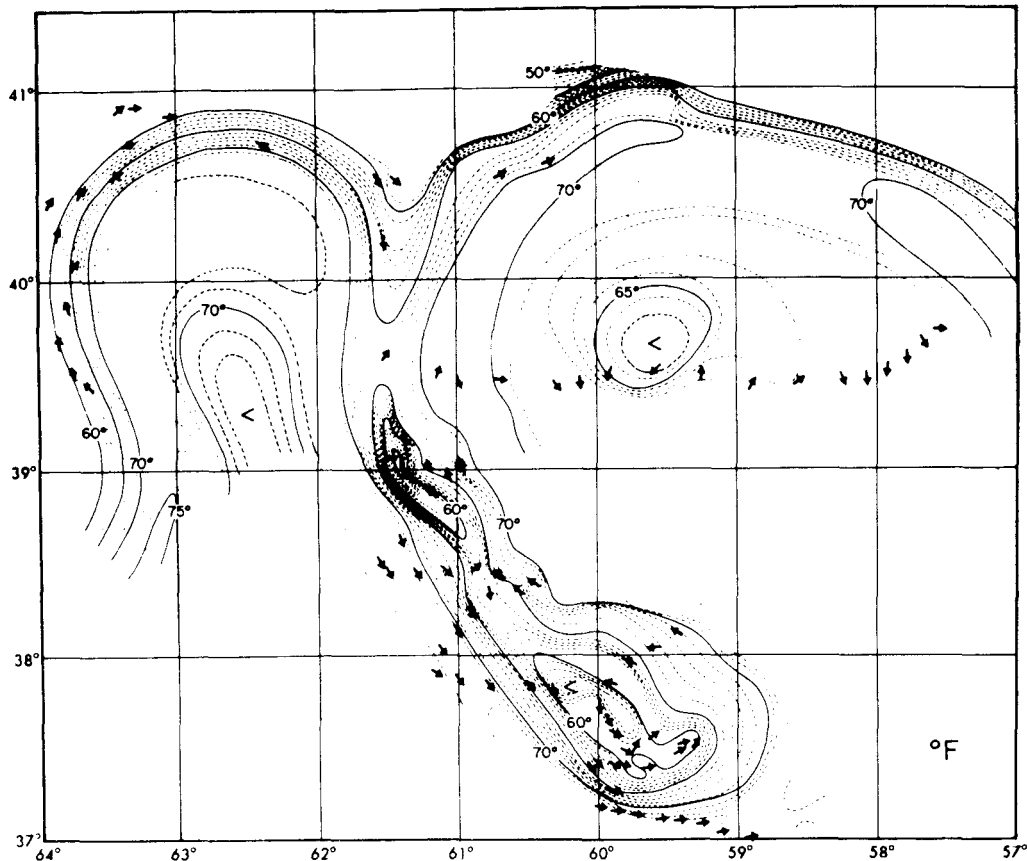


FIG. 9 Cyclonic eddy genesis from a Polar Front meander. Temperature pattern at 200 m depth and measured current vectors (\rightarrow) delimit a cold core meander and eddy pattern. From Fuglister and Worthington (1951)

Atlantic Polar Front. The front is a product of the seaward extension of the Gulf Stream axis into mid-Atlantic and is defined by the large temperature gradient between cold shelf or subarctic water to the north and warm Sargasso Sea water to the south. Flow instability periodically produces a large meander of the Front that is subsequently shed as an eddy. If shed south or east of the front, the eddy contains colder water from the north side and is cyclonic, whereas warm-core, anticyclonic eddies spin off into colder water to the north and west (Fig. 10). Cyclonic eddies so form several times a year and are physically identifiable for as much as 2 years (Parker, 1971). Initially, they range to 300 km diameter laterally and extend from the sea surface to 3 km in depth. Such eddies do not always extend to the sea surface. Howe and Tait (1967) detected a sub-thermocline eddy generated

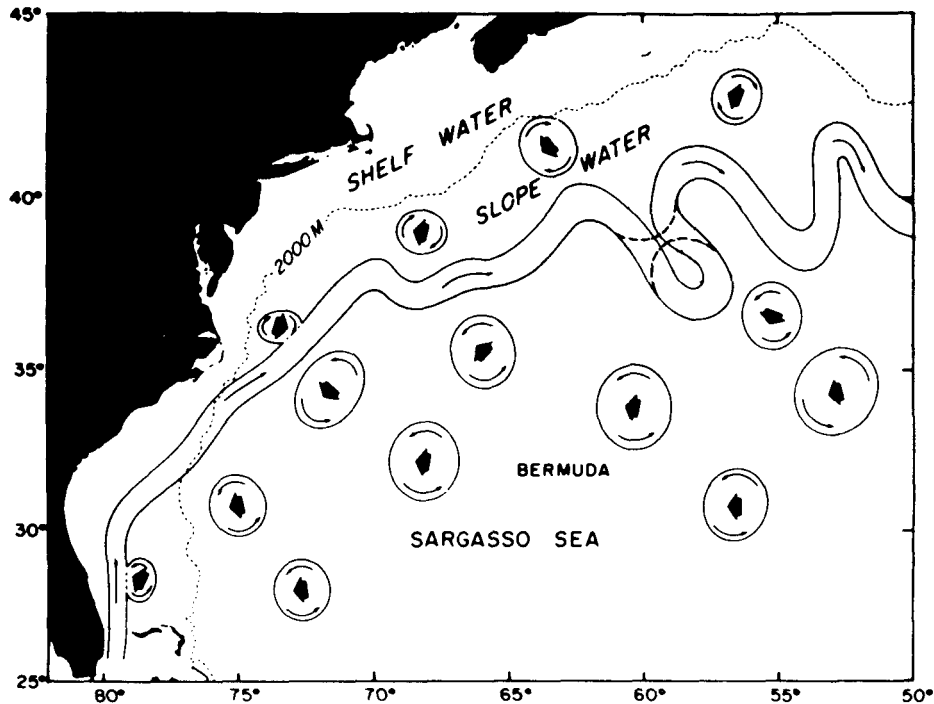


FIG. 10 A schematic representation of the path of the Gulf Stream and the distribution and movement of ring eddies by Richardson (1976)

by a meander of the Polar Front. This eddy centered at about 650 m depth and extended from 150 m to perhaps 1200 m. Circulation strength at the core depth was about 10 cm s^{-1} and the eddy extended laterally about 60 n.mi. Surface layer involvement may have been eradicated by local processes (e.g. wind-induced transport) prior to its detection and measurement. Biological effects peculiar to subsurface eddies are easily imagined but were not assessed.

Predominantly under dynamic control, both the Polar Front and eddy genesis appear to be under local topographic control where the front crosses the mid-Atlantic Ridge. From detailed oceanographic station patterns, Dietrich (1964) noted marked weakening at the Ridge of the temperature and salinity gradients that define the Polar Front at 200 m depth. A major dislocation of the front also occurred at its Ridge crossing: the dislocation took the form of a meander of the type that is a cold-core eddy precursor (Fig. 11, Panel A). Flow direction and speed of the sea surface relative to that at about 1000 m show this meander as well as the blocking or dissipative effect on the Front of the Ridge (weaker gradients of dynamic height east of the Ridge in Fig. 11, right). Topography of the sea floor is

elsewhere unlikely to affect the Polar Front and its eddies, once clear of the American continental slope.

Eddies from the Gulf Stream and Polar Front tend to conserve the biomass and community structure of plankton isolated when they form. Noting their potential for biological interaction, Wiebe *et al.* (1976) summarised biological measurements in several cold-core eddies from the Polar Front. Initially containing plankton stocks of cold-side origin, young cold-core eddies exhibited relatively higher plankton biomass and species assemblages that were distinguishable from surrounding Sargasso Sea waters. With increasing age, such eddies attenuate and assume the physical and biological character of the surrounding water, but may be biologically distinguishable for more than a year.

Phytoplankton biomass and species composition differences in the eddies usually attenuated in about 6 months, or less in one case when storm mixing of the phytoplankton habitat occurred. One young eddy may have generated its own phytoplankton assemblage. Phytoplankton composition in this eddy was shown to differ from that of the source waters as well as from that of Sargasso Sea waters.

Zooplankton biomass and species ensembles of cold-core eddies took considerably longer to attenuate. Consistently higher zooplankton stocks and distinctive euphausiid species were evident in eddies as old as a year. Diel migration patterns of several zooplankton species also appear to have been affected by the presence of the eddies. Daytime depths reached by warm-water euphausiid species that migrate was consistently and markedly deeper beyond than within a cold-core meander of the Polar Front.

Weibe and Boyd (1978) later examined distribution limits of one of the cold-water euphausiids, *Nematoscelis megalops*, involved in the Polar Front and eddy complex. The study illustrates a compound front-eddy effect. The Polar Front (like other western boundary currents) is shown to be an effective thermal barrier to some oceanic plankton species, including *Nematoscelis*. Cold-core eddies shed from the front, however, violate the barrier by transporting *Nematoscelis* far south of where they would otherwise occur. Reduced numbers and nutritional condition of individuals in older eddies indicated that expatriate populations attenuate in time by starvation.

Haedrich (1972) reported midwater trawl catches of myctophids and gonostomatid fishes in the Northwest Atlantic. Much reduced numbers of species and fish biomass were noted in catches at a station in a newborn warm-core eddy on the continental slope north of the Polar Front, compared with species diversity and biomass of catches made at four slope and six warm-water stations.

Dynamic generation of large-scale fronts and eddies is not confined to the

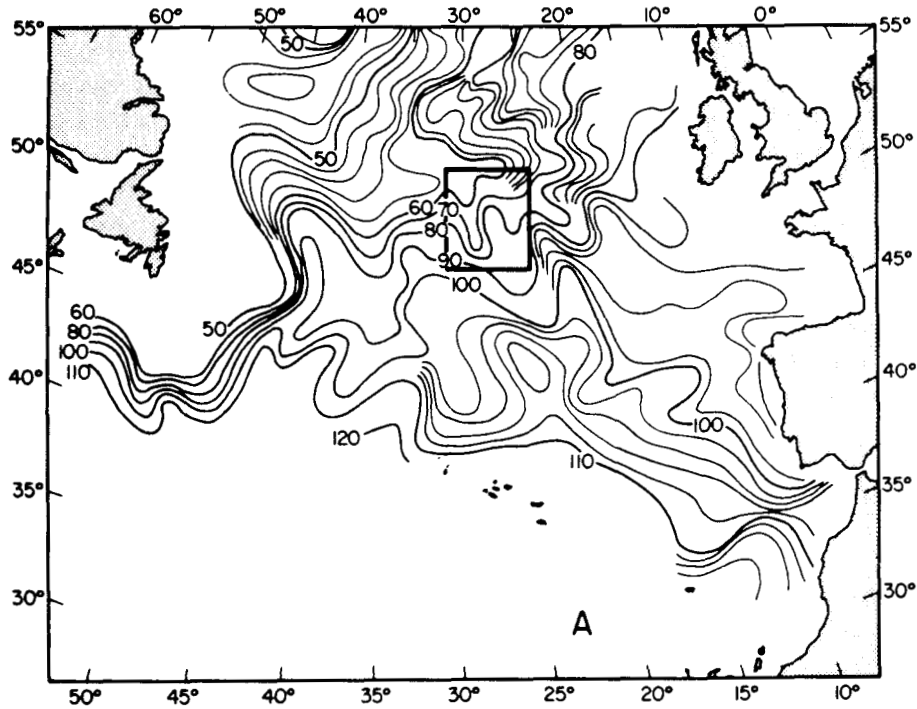


FIG. 11 (A) Flow represented by geopotential topography of the sea surface (relative to that at about 1000 m) in the northern North Atlantic in late summer 1958.

Gulf Stream extension but appears to be characteristic of extensions of other western boundary currents as well. The zone of departure from the South African coast of the Agulhas Current is characterised by complex patterns of vigorous fronts and eddies (Fig. 12). Bang (1970) described the cyclonic eddy 'K' of 50 n.mi. diameter circulating at as much as 6.6 kt at the surface and extending to more than 1600 m depth. Eddy induced vertical displacements of about 500 m were measured in the temperature field. Retroflexion of Agulhas Current water (temp. $> 25^{\circ}\text{C}$) is seen from the shaded part of the figure, as this water is redirected eastward by the West Wind Drift. The narrow strip of cold surface water ($14\text{--}20^{\circ}\text{C}$) above the 'north wall' of the Agulhas Current emphasises the locally divergent nature of what is characterised by Bang as a strongly convergent and eddy-prone frontal system.

Bass (1970) identified the role of the Agulhas retroflexion zone (Agulhas Bank) and the Natal coast as nursery areas for sharks. Four species use Agulhas Bank, 8 other species use the Natal coast. Nursery grounds are on fringes of adult distribution.

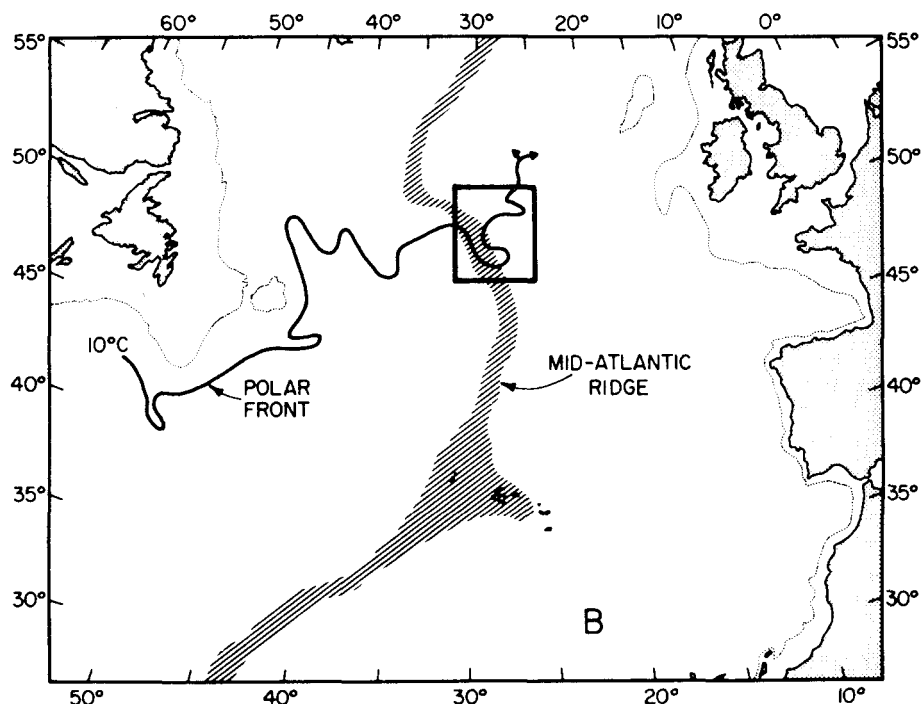


FIG. 11 (B) The oceanic Polar Front axis at 200 m depth in late summer 1958 in relation to the axis of the mid-Atlantic Ridge. Both panels from Dietrich (1964)

Western boundary currents of the Pacific also are well-known to produce fronts and eddies. Strong flow south and flow along the Australian east coast produce large and persistent eddy circulations (e.g. Nilsson *et al.*, 1977). Some of these may be recurrent, or quasi-stationary, suggesting topographic control. Anticyclonic eddies greater than 250 km diameter are particularly common southeast of Sydney. Sufficiently intense biological investigation of the anticyclonic eddies has only recently begun.

The Kuroshio Current off Japan's east coast and its confluence with the south-flowing Oyashio Current are also active generators of large pulsative fronts and eddies. These have long been recognised by Japanese fishermen to attract squids, fishes and mammals (Uda, 1938). Regularity of the eddy patterns along the Oyashio Front, which defines the axis of confluence, led Barkley (1968) to note that these patterns take the form of two vortex streets lying side by side. This mechanism suggests that the Front acts as a perturbing obstacle to the flow of both impinging currents. Because much of the energy of both currents is expended in eddy formation in the confluence region, the Polar and subtropical fronts extending eastward therefore are weaker than the topographically deflected Gulf Stream.

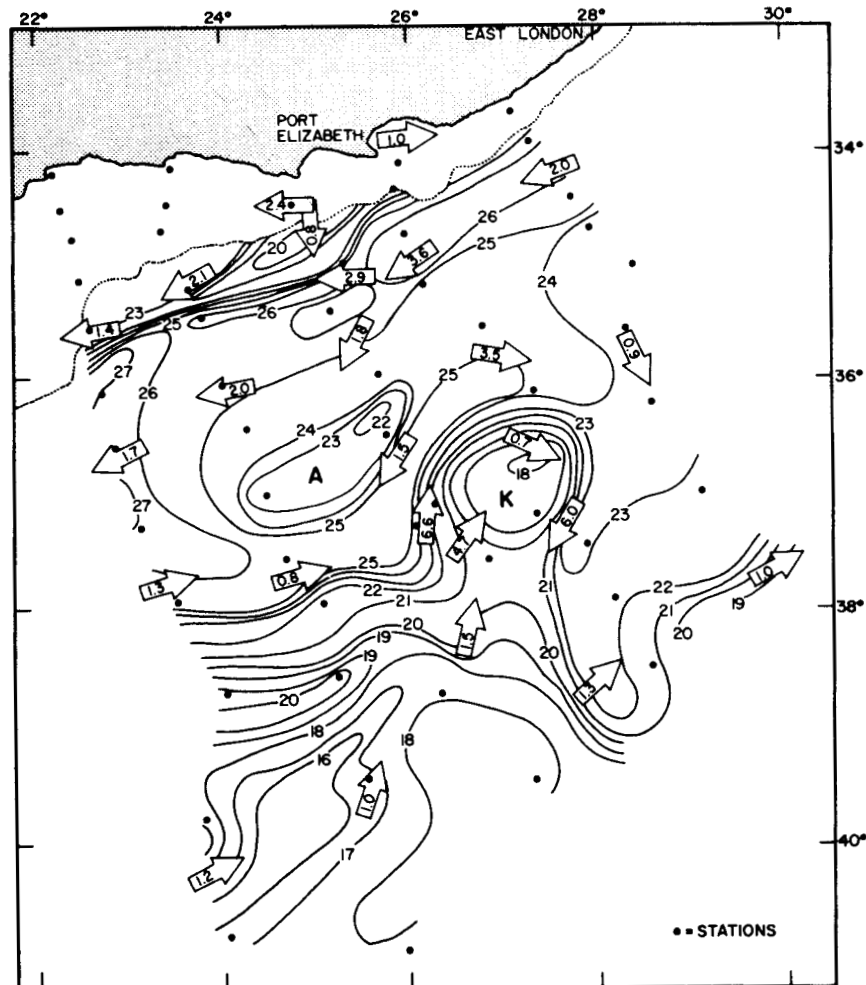


FIG. 12 Surface temperatures, navigation set vectors in knots, and station positions in the Agulhas retroflexion area (southeast tip of Africa) in March 1969. 'A' and 'K' designate adjacent cold-core eddies. From Bang (1970)

Eddy generation also appears to be mediated by flow of air from land masses. Worthington (1972), noting great mixed layer depths and high pressure zones associated with outbreaks of continental polar air over the Pacific south of Japan and over the Atlantic south of New England and east of Newfoundland, believes that convergent sinking of surface water occurs as a result, generating anticyclonic eddies. Anderson *et al.* (1970) consider that flow instabilities of the Agulhas Current off Durban are induced by offshore wind components indicated by local pressure variations.

Since Uda's (1938) comprehensive study of fronts off Japan and their genesis of eddies, the relation of both to the regional Japanese fisheries has received wide attention. Particularly well documented is the effect of the Kurile Front on saury fishing. The Kurile Front is the northernmost of a series of fronts usually found in the Oyashio (Uda, 1938) and is probably analogous to the Polar Front since it forms the southern limit of subarctic water. The most productive saury fishing areas in the northwest Pacific occur in series of eddies along the Kurile Front in summer and fall. This front extends only to 50 m depth. Han and Gong (1970) confirmed this association, showing sensitivity of the saury fishery off the east coast of Korea to the local equivalent of the Polar Front.

Uda (1938, 1952, 1973) and Uda and Ishino (1958) described various associations with fronts and frontal eddies of albacore, yellowfin, skipjack and bluefin tunas, mackerel, salmon, whale species and squid. Feeding, or spawning and feeding provide the biological driving forces for their interaction with fronts and eddies.

6 Summary and conclusion

Combination of physical characteristics of fronts and eddies with interactive characteristics of organisms leads to the following catalog of ecological effects. Many of these have been shown to occur or to account for observed phenomena. Through organisms' sinking, swimming and production, as dictated by food needs and environmental gradients, such quasi-ordered velocity fields have accounted for quasi-ordered patchiness of marine organisms on widely different time and space scales. Fronts and eddies can:

- mechanically affect local concentrations of organisms,
- juxtapose populations that would not otherwise interact,
- create new 'communities',
- conserve and translocate selected species ensembles and concentrations,
- attract and sustain large motile animals,
- serve as reproduction refuges,
- mechanically limit dispersal of meroplankton or neritic populations,
- selectivity pattern components of populations or communities (quasi-ordered patchiness),
- induce/sustain higher local production of organisms,
- modify migration patterns as diverse as annual, trans-oceanic fish movements and diel vertical migrations of motile phytoplankton,
- collect surface active and particulate substances.

We see that on every scale of frontal and eddy activity in the open sea, there are examples of ecologically significant effects operating through food

web stability, community structure, local population dynamics, phytoplankton production and standing stocks, etc. This creates the increasingly distinct view that life forms tend to tessellate the environment in horizontal patterns that are partly governed by vertical exchange due to a variety of physical processes. The scale of the phenomenon and its ecological effect depend on the type and scale of the driving mechanisms, but the resulting biological pattern is also controlled by the organism, its own physical characteristics, behavior, food requirements and response to environmental change.

References

- Ahlstrom, E. H., Moser, H. G. and O'Toole, M. J. (1976). Development and distribution of larvae and early juveniles of the commercial lanternfish, *Lampanyctodes hectoris* (Gunther), off the west coast of southern Africa with a discussion of phylogenetic relationships of the genus. *Bull. So. Cal. Acad. Sci.* **75**, 138-152
- Allen, W. E. (1945). Vernal distribution of marine plankton diatoms offshore in southern California in 1940. *Bull. Scripps Inst. Oceanogr.* **5**, 335-369
- Amos, A. F., Langseth, M. G. Jr. and Markl, R. G. (1972). Visible oceanic saline fronts, p. 49-62. In "Studies in Physical Oceanography" (A. L. Gordon, ed.) Vol. 1. Gordon and Breach, New York
- Anderson, F. P., Sharp, S. O. and Oliff, W. D. (1970). The reaction of coastal waters off Durban to changes in atmospheric pressure. In "Collected Proceedings of the SANCOR Symposium, Oceanography in South Africa 1970", Paper H-2
- Arthur, R. S. (1965). On the calculation of vertical motion from determinations of horizontal motion. *J. Geophys. Res.* **70**, 2799-2803
- Ashmole, N. P. and Ashmole, M. J. (1967). Comparative feeding ecology of sea birds of a tropical oceanic island. *Bull. Peabody Mus. Nat. Hist.* **24**, 1-131
- Backus, R. H., Craddock, J. E., Haedrich, R. L. and Shores, D. L. (1969). Mesopelagic fishes and thermal fronts in the western Sargasso Sea. *Mar. Biol.* **3**, 87-106
- Bainbridge, R. (1957). The size, shape and density of marine phytoplankton concentrations. *Biol. Rev.* **32**, 91-115
- Bang, N. D. (1970). Major eddies and frontal structures in the Agulhas Current retroflexion area in March 1969. In "Collected Proceedings of the SANCOR Symposium, Oceanography in South Africa 1970", Paper B-2
- Bang, N. D. (1973). Characteristics of an intense ocean frontal system in the upwelling region west of Cape Town. *Tellus* **25**: 256-265
- Barkley, R. A. (1968). The Kuroshio-Oyashio front as a compound vortex street. *J. Mar. Res.* **26**, 83-104
- Barkley, R. A. (1972). Johnston Atoll's wake. *J. Mar. Res.* **30**, 201-216
- Bary, B. M. (1953). Sea-water discoloration by living organisms. *N.Z.J. Sci. Technol.* **34**, 393-407
- Bass, A. J. (1970). Shark distribution and movements along the eastern coast of South Africa. In "Collected Proceedings of the SANCOR Symposium, Oceanography in South Africa 1970", Paper G-5
- Beebe, W. (1926). "The Arcturus Adventure". Putnam and Sons, New York
- Bernstein, R. L. and White, W. B. (1974). Time and length scales of baroclinic eddies in the central North Pacific Ocean. *J. Phys. Oceanogr.* **4**, 613-624
-

- Bernstein, R. L., Breaker, L. and Whritner, R. (1977). California Current eddy formation: ship, air and satellite results. *Science* **195**, 353-359
- Boden, B. P. (1952). Natural conservation of insular plankton. *Nature* **169**, 697-699
- Boden, P. B. and Kampa, E. M. (1953). Winter cascading from an oceanic island and its biological implications. *Nature* **171**, 426-427
- Brinton, E. (1976). Population biology of *Euphausia pacifica* off southern California. *Fish. Bull. U.S.* **74**, 733-762
- Broenkow, W. W. (1965). The distribution of nutrients in the Costa Rica Dome in the eastern tropical Pacific Ocean. *Limnol. Oceanogr.* **10**, 40-52
- Colton, J. B. Jr., Smith, D. E. and Jossi, J. W. (1975). Further observations on a thermal front in the Sargasso Sea. *Deep-Sea Res.* **22**, 433-439
- Cromwell, T. and Reid, J. L. Jr. (1956). A study of oceanic fronts. *Tellus* **8**, 94-101
- Curtin, T. B. and Mooers, C. N. K. (1975). Observations and interpretation of a high-frequency internal wave packet and surface slick pattern. *J. Geophys. Res.* **80**, 882-894
- Defant, A. (1961). "Physical Oceanography", Vol. 1, p. 199. Pergamon Press, New York
- Dietrich, G. (1964). Oceanic polar front survey in the North Atlantic. In "Research in Geophysics" (H. Odishaw, ed.) Ch. 12. MIT Press, Cambridge, Mass.
- Dunson, W. A. and Ehlert, G. W. (1971). Effects of temperature, salinity and surface water flow on distribution of the sea snake *Pelamis*. *Limnol. Oceanogr.* **16**, 845-853
- Emery, A. R. (1972). Eddy formation from an oceanic island: Ecological effects. *Carrib. J. Sci.* **12**, 121-128
- Enright, J. T. (1977). Copepods in a hurry: sustained high-speed upward migration. *Limnol. Oceanogr.* **22**, 118-125
- Eppley, R. W., Holmes, R. W. and Strickland, J. D. H. (1967). Sinking rates of marine phytoplankton measured with a fluorometer. *J. exp. mar. Biol. Ecol.* **1**, 191-208
- Eppley, R. W., Holm-Hansen, O. and Strickland, J. D. H. (1968). Some observations on the vertical migration of dinoflagellates. *J. Phycol.* **4**, 333-340
- Ewing, G. C. (1950). Slicks, surface films and internal waves. *J. Mar. Res.* **9**, 161-187
- Faller, A. J. (1969). The generation of Langmuir circulations by eddy pressure of surface waves. *Limnol. Oceanogr.* **14**, 504-513
- Faller, A. J. and Woodcock, A. H. (1964). The spacing of windrows of *Sargassum* in the ocean. *J. Mar. Res.* **22**, 22-29
- Frankignoul, C. (1976). Observed interaction between oceanic internal waves and mesoscale eddies. *Deep-Sea Res.* **23**, 805-820
- Fuglister, F. C. and Worthington, L. V. (1951). Some results of a multiple ship survey of the Gulf Stream. *Tellus* **3**, 1-14
- Gargett, A. E. and Hughes, B. A. (1972). On the interaction of surface and internal waves. *J. Fluid Mech.* **52**, 179-191
- Garrett, W. D. (1967). The organic chemical composition of the ocean surface. *Deep-Sea Res.* **14**, 221-227
- Garrett, C. and Munk, W. (1979). Internal waves in the ocean. *Ann. Rev. Fluid Mech.* **11**, 339-369
- Gaskin, D. E. (1968). Distribution of *Delphinidae* (Cetacea) in relation to sea surface temperatures off eastern and southern New Zealand. *N.Z.J. mar. Sci. Freshw. Res.* **2**, 527-534
- Gaskin, D. E. (1976). The evolution, zoogeography and ecology of *Cetacea*. In "Oceanogr. Mar. Biol. Ann. Rev." (H. Barnes, ed.) Vol. 14, pp. 247-346
-

- George, D. G. and Edwards, R. W. (1973). *Daphnia* distribution within Langmuir circulations. *Limnol. Oceanogr.* **18**, 798–800
- Graham, J. J. (1957). Central North Pacific albacore surveys, May to November 1955. *U.S. Fish. Wildl. Svc. SSR-Fisheries* No. 212
- Haedrich, R. L. (1972). Midwater fishes from a warm-core eddy. *Deep-Sea Res.* **19**, 903–906
- Han, Hi Soo and Gong, Yeong (1970). Relation between oceanographical conditions and catch of saury in the eastern sea of Korea. In "The Kuroshio – A Symposium on the Japan Current" (J. Marr, ed.) pp. 585–592. East-West Center Press, Honolulu
- Hand, W. G., Collard, P. A. and Davenport, D. (1965). The effects of temperature and salinity change on the swimming rate in dinoflagellates, *Goniaulax* and *Gymnodinium*. *Biol. Bull.* **128**, 90–101
- Hardy, A. C. and Bainbridge, R. (1954). Experimental observation of the vertical migrations of plankton animals. *J. Mar. Biol. Ass. U.K.* **33**, 409–448
- Harris, G. P. and Lott, J. N. A. (1973). Observations of Langmuir circulations in Lake Ontario. *Limnol. Oceanogr.* **18**, 584–589
- Hart, J. E. (1979). Finite amplitude baroclinic instability. *Ann. Rev. Fluid. Mech.* **11**, 147–172
- Hasle, G. R. (1950). Phototactic vertical migration in marine dinoflagellates. *Oikos* **2**, 162–175
- Hasle, G. R. (1954). More on phototactic diurnal migration in marine dinoflagellates. *Nytt. Mag. Biol.* **2**, 139–147
- Hide, R. and Mason, P. J. (1975). Sloping convection in a rotating fluid. *Adv. Phys.* **24**, 57–100
- Hogg, N. G., Katz, E. J. and Sanford, T. B. (1978). Eddies, islands and mixing. *J. Geophys. Res.* **83**, 2921–2938
- Howe, M. R. and Tait, R. I. (1967). A subsurface cold-core cyclonic eddy. *Deep-Sea Res.* **14**, 373–378
- Hulbert, E. M. (1964). Succession and diversity in the planktonic flora of the western North Atlantic. *Bull. Mar. Sci. Gulf and Caribbean* **14**, 33–44
- Hunter, J. R. and Mitchell, C. T. (1967). Association of fishes with flotsam in the offshore waters of central America. *Fish. Bull. U.S.* **66**, 13–29
- Iisuka, S. and Irie, H. (1969). Anoxic status of bottom waters and occurrences of *Gymnodinium* red water in Omura Bay. *Bull. Plankton-Soc. Japan* **16**, 99–115
- Jones, E. C. (1962). Evidence of an island effect upon the standing crop of zooplankton near the Marquesas Islands, central Pacific. *J. Cons. perm. explor. Mer.* **27**, 223–231
- Kamykowski, D. (1974). Possible interactions between phytoplankton and semi-diurnal internal tides. *J. Mar. Res.* **32**, 67–89
- Knauss, J. A. (1957). An observation of an oceanic front. *Tellus* **9**, 234–237
- Kropach, C. (1975). The yellow-bellied sea snake, *Pelamis*, in the eastern Pacific. In "The Biology of Sea Snakes" (W. A. Dunson, ed.) pp. 185–213. University Park Press, Baltimore
- Laufer, J. (1975). New trends in turbulence research. *Ann. Rev. Fluid Mech.* **7**, 307–326
- Laurs, R. M., Yuen, H. S. H. and Johnson, J. H. (1977). Small-scale movements of albacore, *Thunnus alalunga*, in relation to ocean features as indicated by ultrasonic tracking and oceanographic sampling. *Fish. Bull. U.S.* **75**, 347–355
- Laurs, R. M. and Lynn, R. J. (1977). Seasonal migration of north Pacific albacore,
-

- Thunnus alalunga*, into North American coastal waters: distribution, relative abundance, and association with transition zone waters. *Fish. Bull. U.S.* **75**, 795–822.
- LeFèvre, J. and Grall, J. R. (1970). On the relationships of *Noctiluca* swarming off the western coast of Brittany with hydrological features and plankton characteristics of the environment. *J. exp. mar. Biol. Ecol.* **4**, 287–306
- Longhurst, A. R. (1976). Vertical migration. In "The Ecology of the Seas" (D. H. Cushing and J. J. Walsh, eds) pp. 116–137. W. B. Saunders, Philadelphia
- Marshall, S. M. and Orr, A. P. (1955). "The Biology of a Marine Copepod". Oliver and Boyd, London
- McGary, J. W. and Stroup, E. D. (1956). Mid-Pacific oceanographic, mid-latitude waters, January–March 1954. *U.S. Fish. Wildl. Svc. SSR-Fisheries* No. 180
- Mooers, C. N. K., Flagg, C. N. and Boicourt, W. C. (1978). Prograde and retrograde fronts. In "Oceanic Fronts in Coastal Processes" (M. J. Bowman and W. E. Esaias, eds). Springer-Verlag, Berlin
- Murphy, G. I. and Shomura, R. S. (1972). Pre-exploitation abundance of tunas in the equatorial central Pacific. *Fish. Bull. U.S.* **72**, 875–913
- Neill, W. H., Chang, R. K. C. and Dizon, A. E. (1976). Magnitude and ecological implications of thermal inertia in skipjack tuna, *Katsuwonus pelamis* (Linnaeus). *Env. Biol. Fish.* **1**, 61–80
- Nilsson, C. S., Andrews, J. C. and Scully-Power, P. (1977). Observations of eddy formation off east Australia. *J. Phys. Oceanogr.* **7**, 659–669
- Osborn, T. R. (1978). Measurements of energy dissipation adjacent to an island. *J. Geophys. Res.* **83**, 2939–2957
- Owen, R. W. (1966). Horizontal vortices in the surface layer of the sea. *J. Mar. Res.* **24**, 56–66
- Owen, R. W. (1968). Oceanographic conditions in the northeast Pacific and their relation to the albacore fishery. *Fish. Bull. U.S.* **66**, 503–526.
- Owen, R. W. (1980). Eddies of the California Current System: physical and ecological characteristics. In "The California Islands" (D. Power, ed.) Mus. Nat. Hist., Santa Barbara, California
- Packard, T. T., Blasco, D. and Barber, R. T. (1978). *Mesodinium rubrum* in the Baja California upwelling system. In "Upwelling Ecosystems" (R. Boje and M. Tomczak, eds). Springer-Verlag, Berlin
- Pak, H. and Zaneveld, J. R. V. (1974). Equatorial front in the eastern Pacific Ocean. *J. Phys. Oceanogr.* **4**, 570–578
- Parker, C. E. (1971). Gulf Stream rings in the Sargasso Sea. *Deep-Sea Res.* **18**, 981–993
- Patzert, W. C. (1970). Eddies in Hawaiian waters. *Hawaii Inst. Geophys. Rep.* 69–8
- Pingree, R. D., Forster, G. R. and Morrison, G. K. (1974). Turbulent convergent tidal fronts. *J. mar. biol. Assoc. U.K.* **54**, 469–479.
- Pingree, R. D., Holligan, P. M. and Head, R. N. (1977). Survival of dinoflagellate blooms in the western English Channel. *Nature* **265**, 266–269
- Powers, P. B. A. (1932). *Cyclotrichium meunieri* sp. nov. (protozoa, ciliata); cause of red water in the Gulf of Maine. *Biol. Bull.* **63**, 74–80
- Raymont, J. E. G. (1963). "Plankton and Productivity in the Oceans". Pergamon Press, New York
- Reid, J. L. Jr., Roden, G. I. and Wyllie, J. G. (1958). Studies of the California Current System. *Calif. Coop. Oceanic Fish. Invest. Rep.* 1 July 1956 to 1 Jan. 1958
- Richardson, P. (1976). Gulf Stream rings. *Oceanus.* **19** (3), 65–68
-

- Ryther, J. H. and Menzel, D. W. (1960). The seasonal and geographic range of primary production in the western Sargasso Sea. *Deep-Sea Res.* **6**, 235–238
- Sargent, M. C. and Walker, T. J. (1948). Diatom populations associated with eddies off southern California in 1941. *J. Mar. Res.* **7**, 490–505
- Savidge, G. (1976). A preliminary study of the distribution of chlorophyll *a* in the Celtic and Western Irish Seas. *Estuarine & Coastal Mar. Sci.* **4**, 617–625
- Savidge, G. and Foster, P. (1978). Phytoplankton biology of a thermal front in the Celtic Sea. *Nature* **271**, 155–157
- Scott, J. T., Myer, G. E., Stewart, R. and Walther, E. G. (1969). On the mechanism of Langmuir circulations and their role in epilimnion mixing. *Limnol. Oceanogr.* **14**, 493–503
- Seckel, G. (1972). Hawaiian-caught skipjack tuna and their physical environment. *Fish. Bull. U.S.* **70**, 763–787
- Sette, O. E. and Ahlstrom, E. H. (1948). Estimations of abundance of the eggs of the Pacific pilchard (*Sardinops caerulea*) off southern California during 1940 and 1941. *J. Mar. Res.* **7**, 511–542
- Shomura, R. S. and Otsu, T. (1956). Central North Pacific albacore surveys, January 1954–February 1955. *U.S. Fish Wildl. Soc. SSR-Fisheries* No. 173
- Simpson, J. H. and Pingree, R. D. (1978). Shallow sea fronts produced by tidal stirring. In “Oceanic Fronts in Coastal Processes” (M. J. Bowman and W. E. Esias, eds). Springer-Verlag, Berlin
- Smayda, T. (1969). Some measurements of the sinking rate of fecal pellets. *Limnol. Oceanogr.* **14**, 621–625
- Smayda, T. (1970). The suspension and sinking of phytoplankton in the sea. In “Oceanogr. Mar. Biol. Ann. Rev.” (H. Barnes, ed.) Vol. 8, pp. 353–414
- Spilhaus, A. F. Jr. (1968). Observations of light scattering in sea water. *Limnol. Oceanogr.* **13**, 418–422
- Stavn, R. H. (1971). The horizontal-vertical distribution hypothesis: Langmuir circulations and *Daphnia* distributions. *Limnol. Oceanogr.* **16**, 453–466
- Stommel, H. (1949). Trajectories of small bodies sinking slowly through convection cells. *J. Mar. Res.* **8**, 24–29
- Sutcliffe, J. H. Jr., Baylor, E. R. and Menzel, D. W. (1963). Sea surface chemistry and Langmuir circulation. *Deep-Sea Res.* **10**, 233–243
- Sutcliffe, W. H. Jr., Sheldon, R. W., Prakash, A. and Gordon, D. C. Jr. (1971). Relations between wind speeds, Langmuir circulation and particle concentration in the ocean. *Deep-Sea Res.* **18**, 639–643
- Szekielda, K. H., Kupferman, S. L., Klemas, V. and Polis, D. F. (1972). Element enrichment in organic films and foam associated with aquatic frontal systems. *J. Geophys. Res.* **77**, 5278–5282
- Tsujita, T. (1957). The fisheries oceanography of the East China Sea and Tsuchima Strait. 1. The structure and ecological character of the fishing grounds. *Bull. Seikai Reg. Fish. Res. Lab.* **13**, 1–47
- Uda, M. (1938). Researches on “Siome” or current rip in the seas and oceans. *Geophys. Mag.* **11**, 307–372
- Uda, M. (1952). On the relation between the variation of important fisheries conditions and the oceanographical conditions in the adjacent waters of Japan. 1. *J. Tokyo Univ. Fish.* **38**, 376–381
- Uda, M. (1973). Pulsative fluctuation of oceanic fronts with tuna fishing grounds and fisheries. *J. Fac. Mar. Sci. Technol., Tokai Univ.* **7**, 245–265
- Uda, M. and Ishino, M. (1958). Enrichment pattern resulting from eddy systems in relation to fishing grounds. *J. Tokyo Univ. Fish.* **44**, 105–129
-

- Von Arx, W. S. (1962). "An Introduction to Physical Oceanography". Addison-Wesley, London
- Voorhis, A. D. (1969). The horizontal extent and persistence of thermal fronts in the Sargasso Sea. *Deep-Sea Res.* **16** (suppl.), 331-337
- Voorhis, A. D. and Hersey, J. B. (1964). Oceanic thermal fronts in the Sargasso Sea. *J. Geophys. Res.* **69**, 3809-3814
- White, W. B. (1973). An oceanic wake in the equatorial undercurrent downstream from the Galapagos Archipelago. *J. Phys. Oceanogr.* **3**, 156-161
- Wiebe, P. H. and Boyd, S. H. (1978). Limits of *Nematoscelis megalops* in the Northwestern Atlantic in relation to Gulf Stream cold core rings. I. Horizontal and vertical distributions. *J. Mar. Res.* **36**, 119-142
- Wiebe, P. H., Hulbert, E. M., Carpenter, E. J., Jahn, A. E., Knapp III, G. P., Boyd, S. H., Ortner, P. B. and Cox, J. L. (1976). Gulf Stream cold core rings: large-scale interaction sites for open ocean plankton communities. *Deep-Sea Res.* **23**, 695-710
- Woodcock, A. H. (1944). A theory of surface water motion deduced from the wind-induced motion of the *Physalia*. *J. Mar. Res.* **5**, 196-205
- Woodcock, A. H. (1950). Subsurface pelagic *Sargassum*. *J. Mar. Res.* **9**, 77-92
- Woods, J. D. Diurnal and seasonal variation of convection in the wind mixed layer of the ocean. *Q.J. Roy. Met. Soc.* (In press.)
- Worthington, L. V. (1972). Anticyclogenesis in the oceans as a result of outbreaks of continental polar air. In "Studies in Physical Oceanography" (A. L. Gordon, ed.) Vol. 1, pp. 169-178. Gordon and Breach, New York
- Wyllie, J. (1966). Geostrophic flow of the California Current at the surface and at 200 m. *Calif. Coop. Oceanic Fish. Invest. Atlas* No. 4
- Wyrki, K. (1966). Oceanography of the eastern equatorial Pacific ocean. *Oceanogr. Mar. Biol. Ann. Rev.* **4**, 33-68
- Yasui, M. (1961). Internal waves in the open sea. *Oceanogr. Mag.* **12**, 157-183
- Zaneveld, J. R., Andrade, M. and Beardsley, G. F. Jr. (1969). Measurements of optical properties at an oceanic front observed near the Galapagos Islands. *J. Geophys. Res.* **74**, 5540-5541
- ZoBell, C. E. (1946). "Marine Microbiology". Chronica Botanica, Waltham, Mass.
-