

# LIFE ON THE EDGE: MARINE LIFE AND FRONTS

By Donald B. Olson, Gary L. Hitchcock,  
Arthur J. Mariano, Carin J. Ashjian,  
Ge Peng, Redwood W. Nero and  
Guillermo P. Podestá

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*"Pelagic plant life draws its principal supply of dissolved or undissolved nitrogen either from the coasts or from localities where warm and cold currents meet."*

J. Hjort

*"Where cold and warm currents meet at the surface of the ocean there is a rise of temperature for the animals of the cold current and a fall of temperature for the animals of the warm current, which results in a plentiful destruction of organisms."*

Sir John Murray

*"We are well acquainted with the stream in our pursuit of whales, which keep to the sides of it but are not met within it."*

Capt. Timothy Folger\*

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There are still many questions . . . concerning the nature of biological response to fronts.

THE CONCEPT that ocean fronts are important features in oceanic biology has a long history, as noted by the quotations cited above. The example of a functional understanding of fronts provided by a common fisherman is an example of scientific knowledge lagging behind common knowledge (see Franklin, 1786). The modern situation has seen major advances in our understanding of frontal dynamics and the basic processes that influence biota in fronts. There are still many questions, however, concerning the nature of biological response to fronts. In fact, just as the physical oceanographer still asks whether the Gulf Stream front is an area of strong mixing or a barrier to exchange (Bower *et al.*, 1985), the biological response can be thought of as enrichment (Murray and Hjort, 1912; Hitchcock, 1988; McClain *et al.*, 1988) or as a region of stress and death (Murray and Hjort, 1912; Dutkiewicz *et al.*, 1993). In relationship to Folger's observation on whales, it is possible to say that many large free-swimming animals seek out fronts for forage and mi-

gration but in a preferential way, i.e., they seek out definite subdomains of the frontal zone environment. The nature of fisheries, regrettably, makes it very difficult to test these hypotheses because of inadequate data and lack of control samples; fishermen do not fish where they expect to find no prey (Podestá *et al.*, 1993). In modern fisheries where fishing is often guided by the same satellite remote sensing charts of frontal locations that are available to scientists, the control samples are indeed rare.

The present work will consider the response of four trophic levels: primary producers, secondary herbivores, tertiary consumers, and apex predators, to the presence of ocean fronts. The goal is to explore the basic processes that produce oceanic fronts and make them important ecosystem features. The discussion highlights both the historical aspects of the problem and recent field work in western boundary current fronts. References to other frontal regimes are included where they add to certain points, but the reader should be aware that a similar paper could focus on eastern boundary current fronts or any number of other frontal systems.

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D.B. Olson, G.L. Hitchcock, A.J. Mariano, C. J. Ashjian, G. Peng, G.P. Podestá, RSMAS University of Miami, 4600 Rickenbacker Cswy., Miami, Florida 33149, USA; R.W. Nero, NRL CODE 7174, Stennis Space Flight Center, Bay St. Louis, Mississippi 39529, USA.

\* The first two quotes are from Murray and Hjort (1912) while the last is from Franklin (1786) (see Stommel, 1966). Note all of these predate the definition of a front.

## Fronts as Physical Entities

The concept of what a front is demands some definition and historical background. The general tendency is to define any region of large spatial change in any variable as a front. This leads to a wide variety of possible fronts: i.e., temperature

fronts, salinity fronts, color fronts, etc. Under this nomenclature any high gradient region becomes a front. This makes sense in the observational sense, but is not adequate in terms of the temporal evolution, i.e., the kinetics (movement) and dynamics (development) of fronts. From a historical view, the term front has a meteorological source. It is clear that the current usage comes from the Bergen (Norway) school definition of a weather front (Bjerknes and Solberg, 1922). Their choice of terminology is debatable—the front of the storm, as denoted by Fitzroy in the 1880s, or as an analog to World War I battle fronts. Considering the times, we suspect the war analog was in mind. Whichever history one accepts for the name, the classical meteorological usage involves dynamic features. In particular, it is the zone of high vertical shear (increase in velocity in the vertical) coupled with the strong horizontal density gradient that marks the front (cf. Palmén and Newton, 1969). The coupling of a horizontal density gradient and rapid wind changes in the vertical is known as the thermal wind and is a fundamental manifestation of the geostrophic balance, i.e., the balance between pressure gradients and Coriolis acceleration. A front, so defined, is then a maximum in the intensity of both the pressure gradient force and the acceleration tied to momentum in the presence of a rotating earth. It is relevant to understanding the dynamics associated with the formation, mature structure, and decay of these features. It is also important to contrast these dynamics with the formation of high gradients in passive quantities, i.e., environmental properties that do not influence the future history of the flow field.

The various means of creating a physical front, as outlined by Hoskins and Bretherton (1972), involve the following: 1) differential advection, either convergence or normal and shear deformation in the horizontal flow, or 2) differential vertical mixing. At the very large scales in both the ocean and atmosphere, these act to create *frontal zones* such as the polar front in the atmosphere or western boundary currents such as the Gulf Stream in the ocean. For example, the western intensification of the subtropical gyres leads to regions rich in frontal phenomena in the Kuroshio, Gulf Stream, and Brazil Current. It is the nature of the wind forcing off the west coasts of continents that induces large scale upwelling on eastern ocean boundaries and creates the complex frontal regimes such as the California and Benguela currents. The primary biological response, however, is tied to the dynamics of the smaller scale features, i.e., individual fronts, that are characteristic of these broader frontal zones.

The large scale biogeography of marine life follows the basic geometry provided by frontal zonation. This includes subtropical and subpolar gyre edges as boundaries but adds distinct transition

fauna and flora that take advantage of frontal zones (Reid *et al.*, 1978; Backus, 1986). A good example of an organism's use of a frontal zone ecotone (Brandt and Wadely, 1981) is the distribution of the euphausiid *Nematoscelis megalops* along the Kuroshio extension across the Pacific and then down the California current (Fig. 1). Maintenance of a population in a unidirectional large-scale flow demands population dynamics that utilize counter-flows and the structure of the eddy field (cf. Olson, 1991; Hogg, 1993) to provide a steady seed population or recruitment to the upstream end of the domain. The dynamic tendency for the large scale flow in frontal zones to become hydrodynamically unstable, in the sense that it tends to break down into meanders and eddies, provides an appropriate physical setting that allows this recruitment.

Oceanic organisms are strongly influenced by intense eddy fields associated with frontal jets and isolated eddies that form an integral part of fronts. Meandering, as shown schematically in Figure 2a, alternatively produces *frontogenesis* (frontal intensification) and *frontolysis* (frontal weakening). Individual eddies are formed as meanders grow and become occluded or closed. Each eddy then has a distinct front around its core. The energy flux and self-induced translation of such eddies can create counterflows much like those observed on either side of the Gulf Stream (Hogg, 1993). In addition, eddy fields themselves can act to rectify flows and create small scale fronts. For example, eddy processes are responsible for the structure of the subtropical front (Halliwell *et al.*, 1994). In other cases different factors such as wind or surface buoyancy fluxes act to create small scale fronts. Examples include coastal upwelling (Peterson *et al.*, 1979) and intense fronts associated with edges of deep convective events.

### Biological Fields in Fronts

The basic biological distributions in proximity to fronts typically involve higher biomass on the higher density side of the front. For example, the Slope Water is enriched (eutrophic) in comparison with the highly impoverished (oligotrophic) northern Sargasso Sea to the south of the Gulf Stream. This is in part just a consequence of the uplifted thermocline as one crosses the front, which brings high nutrient deep waters in closer proximity to the euphotic zone than on the southern side. The attendant difference in permanent near-surface stratification also concentrates euphotic zone nutrients in the Slope Water as compared with the influence of deep wintertime convection in the Sargasso, which limits production by limiting light in the classical Sverdrup (1953) sense. In many fronts the dense side of the front is a site of direct wind driven upwelling of nutrients. This is, of course, the situation in coastal upwelling fronts. Although both the Gulf Stream and Kuroshio are

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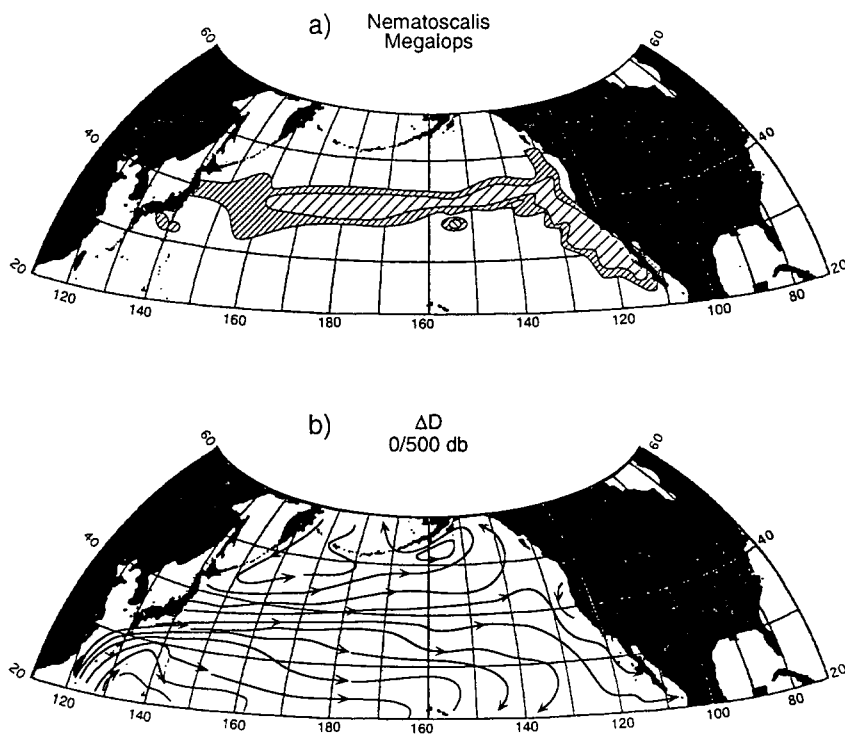


Fig. 1: (a) The distribution of *Nematoscalis megalops*, or in some works a closely related species *N. difficilis* (Brinton, 1962), in the North Pacific. The distributions are such that each shading indicates a factor of ten in abundance with the inner contour being 50–500 individuals per thousand cubic meters and the outer being 1 to 50. Unshaded areas indicate no catch. Distribution is redrawn from McGowan (1971). Original data is from Brinton (1962). (b) Surface current patterns in the North Pacific based on 0/500 dbar dynamic heights from Wyrki (1974). Note that the large scale current patterns are from west to east across the entire Kuroshio extension that this species inhabits.

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favorable in terms of wind driven upwelling, this tendency is masked by the strong upwelling associated with meanders and eddies (cf. Bower and Rossby, 1989; Lee *et al.*, 1989). Here the direct wind driven influence is neglected and the focus is placed on the meander and eddy driven components of frontal enhancement.

### Phytoplankton

Frontal enhancement of primary producers has been reported by numerous authors (Bainbridge, 1957; Olson, 1986; Strass, 1992; to name a few). Primary production is modified within fronts through four possible routes: 1) vertical motion of fluid leading to changes in the light field seen by phytoplankton (Lillibridge *et al.*, 1990); 2) mixing of phytoplankton and nutrients along the frontal interface (Yoder *et al.*, 1983; McClain *et al.*, 1990); 3) death and remineralization of expatriate populations inducing endemic species growth; and 4) along-front advection of populations in the presence of an along-front gradient in environmental factors. The first influence can be viewed as an adiabatic effect following fluid parcels as they

move along a front as compared with the diabatic nature of mixing. Phytoplankton brought into higher light as they move into a meander crest can potentially increase their photosynthetic rate given nutrients brought up with them from depth. This of course assumes that the increase in light levels is not sufficient to induce inhibition. Similarly, cells adapted to surface light conditions will typically not do well if they are moved deep in the euphotic zone by downwelling in meander troughs (Fig. 2). This influence was hypothesized to be a major contribution to changes in the edge of a meander by Hitchcock (1988). This was not borne out in synoptic biological mapping of Gulf Stream meanders in 1988–89 as part of the Navy funded BIOSYNOP experiment. Instead the results of these surveys suggest that vertical movement of phytoplankton communities in the light field only contributes a small amount to growth over the length of a single meander (Hitchcock *et al.*, 1993; Lohrenz *et al.*, 1993).

Here it is useful to introduce a comparison between models of fronts and observations. In the BIOSYNOP case models and observations suggest large vertical velocities,  $\sim 200 \text{ m d}^{-1}$ , which occur over very narrow regions, and only affect a parcel for a matter of hours. Thus the net observed shift in depth of the chlorophyll field in both observations and models is only 50 m transiting through a meander; i.e., small as noted above. While a change in depth of 25 m in a typical exponential light field ( $k = 17 \text{ m}^{-1}$ ) can lead to a response in production of  $-80$  to  $+300\%$ , the time scale for passage through a single meander,  $\sim 2\text{--}4 \text{ d}$ , does not allow significant response in phytoplankton with doubling times,  $\sim 1 \text{ d}^{-1}$ . Both observations and models suggest that phytoplankton enhancement in the front is more closely tied to the overall development of meanders and the frontogenesis/frontolysis associated with it (Fig. 2b), which have time scales of  $\sim 30 \text{ d}$ —time scales associated with the development of the frontal zone eddy field rather than with individual frontal elements.

The patterns observed in boundary current extensions show enhanced phytoplankton biomass along meandering fronts. The conditions in both model and observations for a well developed BIOSYNOP meander are displayed in Figure 3. Both observations and the model show a maximum in phytoplankton biomass in the region between the crest and trough. Both imply that formation requires at least 6–8 d and that the feature is nearly frozen in space relative to the meander; the feature is not in the core of the Gulf Stream where it would be rapidly carried down stream. The response to upward advection in the meander crest is for phytoplankton to increase in the recirculations in meander troughs. This involves a combination of direct advection from the crest into the trough and mixing of fluid from the crest into the north-east portion of the meander trough (Bower, 1991;

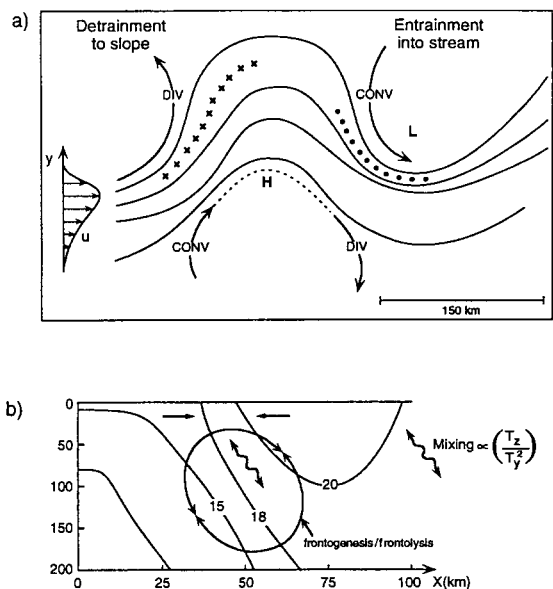


Fig. 2: (a) Schematic of a western boundary current meander. The profile at the left indicates the current profile in an incoming jet. The contours indicate depth to a thermocline isotherm or isopycnal. The entire regime is a frontal zone in that it has high density gradients. Divergence/convergence patterns associated with the meandering create alternate frontolysis/frontogenesis patterns going from north to south in the meander crest as denoted in the  $x$  (downstream) direction by an  $H$  for high dynamic height or pressure. This is reversed in the meander trough as denoted by the  $L$  for low pressure. Also note the locations of detrainment and entrainment into the stream denoted by arrows leaving the meander pattern (cf. Bower and Rossby, 1989; Bower, 1991; Dutkiewicz *et al.*, 1993). Crosses indicate upwelling while dots going into the meander trough denote downwelling. The basic schematic was originally put together by the lead author based on the atmospheric analog, but the reader should also consider Robinson and Niiler (1967, Fig. 10). (b) Cross stream representation of frontogenesis/frontolysis in the front. These are pictured through the action of a secondary circulation indicated by the oval arrow pattern. The major impact can be visualized as an upward tilting of the isotherm pattern shown to increase frontal intensity (frontogenesis) or a flattening tendency to create frontolysis. Surface convergence is shown in the center of the figure. Mixing is indicated by a wavy line along with its rough scaling in terms of thermal gradients.

Dutkiewicz *et al.*, 1993; Fig. 4). The downwelling along the outer edges of meander troughs (Fig. 3) through similar advective/diffusive paths leads to increased oligotrophy on the Sargasso side of meander crests. This leads to a pattern in which downstream meanders slowly accrete higher pig-

ment patterns in their troughs (cf. the NASA poster series). In fact in the most oligotrophic season (August) the Gulf Stream can have marked high chlorophyll features along its front (Fig. 4). Other fronts such as the Brazil/Malvinas and Agulhas extensions also show up as pigment maxima as seen in Coastal Zone Color Scanner data.

### Zooplankton

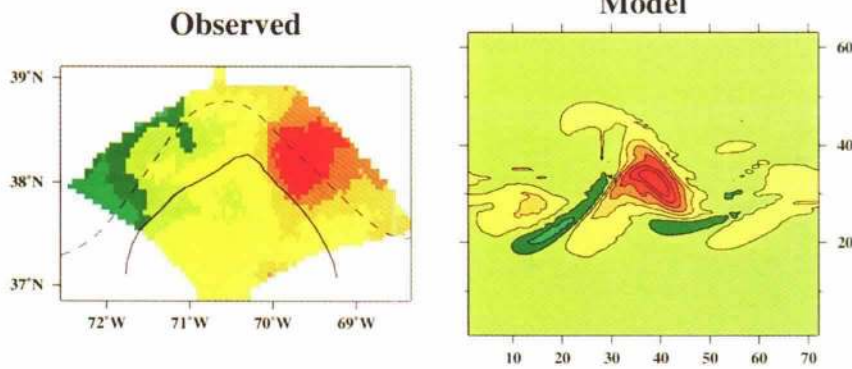
While phytoplankton patterns have scales similar to salinity and other physical variables in the Gulf Stream front (Hitchcock *et al.*, 1993), zooplankton distributions are more variable and patterned at smaller scales. This implies different controls at the two trophic levels. While microzooplankton can respond rapidly to increased phytoplankton availability, the macrozooplankton measured acoustically in Figure 3 can not have resulted from population growth because the time scales for such a response exceed the time course of advection.

The observed zooplankton enhancement must then arise through behaviorally mediated concentration in the presence of convergence, through changes in vertical migration behavior, as a consequence of strong gradients in habitat, or by advection of high concentrations out of the Slope Water or even off the shelf. The net result of these interactions leads to strong cross-frontal gradients in species composition, depth distributions, and zooplankton biomass (e.g., Grice and Hart, 1962; Ashjian and Wishner, 1993a). The physiological effects of thermal and food changes, including those tied to the enhanced food supply induced by the meandering Gulf Stream, have also been postulated to influence zooplankton distributions through differential mortality of expatriate species (Boyd *et al.*, 1978) or changes in reproductive status (e.g., Ashjian, 1993; Ashjian and Wishner, 1993b).

Indeed the model (Fig. 3) without zooplankton behavior only shows a modest response. The observed zooplankton distribution must then arise through behaviorally mediated concentration in the presence of convergence in the front (Okubo, 1978; Olson and Backus, 1985; Franks, 1992; Govoni and Grimes, 1992) or by preferential advection of high concentrations out of the northern Slope Water or even off the shelf. The net result of this behaviorally modified effect of advection and diffusion in the presence of strong gradients in habitat leads to strong cross frontal gradients in species composition. This is associated with strong gradients in physiological status tied to temperature and food changes (Ashjian, 1991; Ashjian and Wishner, 1993a). The latter involve increased mortality, which is assumed to be at least partly responsible for maintaining the sharp cross-stream species gradients and enhanced reproductive status in at least one cosmopolitan copepod (*Nannocalanus minor*; Ashjian

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# Phytoplankton



# Zooplankton

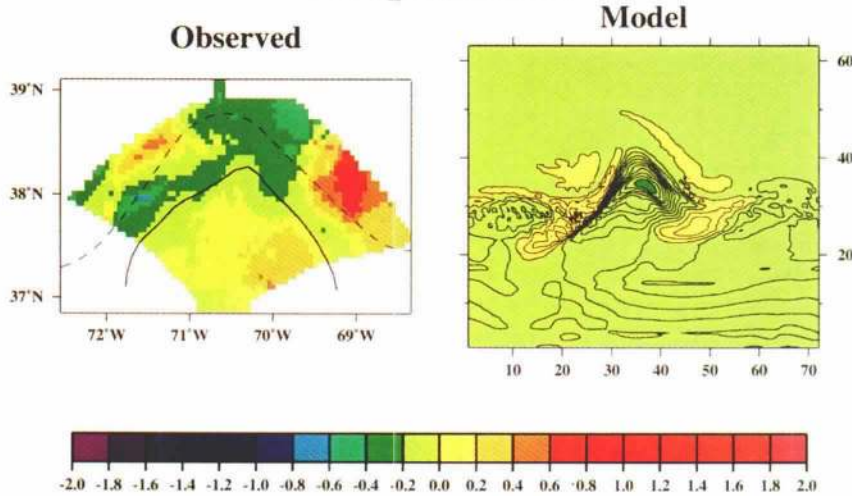


Fig. 3: Observations (left) and model (right) depictions of the phytoplankton and zooplankton response in the BIOSYNOP meander. The phytoplankton observations are from chlorophyll samples taken on the CTD casts in fall 1988 (Hitchcock *et al.*, 1993). The zooplankton data are from acoustic Doppler derived estimates calibrated to MOCNESS tows (Ashjian *et al.*, 1994). Displayed in both observation sets is the first principal component of an objective analysis of the data set after the mean cross-stream variations have been removed. Model results are for a four component nutrient, phytoplankton, zooplankton, detritus model (NPZD) run in a three-layer isopycnic channel model of the Gulf Stream. The model is initialized with the Halkin and Rossby (1985) Gulf Stream cross section and a small localized perturbation. The biology is initially set to an equilibrium state for given nutrient and light levels. Shown are anomalies for the eighth day of the simulation. The meander is well depicted by the high gradient in zooplankton, which is dominated by the cross-stream difference in populations. The model axes are in tens of kilometers. In all of the panels, reds denote high concentrations and greens and blues, low.

and Wishner, 1993b). The improved reproductive state of this copepod is presumably tied to enhanced food supply induced by the meandering Gulf Stream (Ashjian and Wishner, 1993b).

It is not possible to sort out simple advection versus behaviorally modified advective concentration as causal factors for the patterns in Figure 3. The concentration of photo- or geo-tactic organisms whose upward swimming cancels out the downward

velocities associated with convergence into the front is capable of producing major aggregations of zooplankton in fronts (Olson and Backus, 1985; Govoni and Grimes, 1992). The basic principle behind this involves a swimming behavior whose effect cancels that of the vertical motions depicted in Figure 2b. These organisms enter the front under frontogenetic convergence but are not carried downward and therefore accumulate on the frontal axis. This effect may be enhanced for vertically migrating species for which the strong cross-frontal environmental gradients have constricted the depth range of the preferred habitat (see Wishner and Allison, 1986; Ashjian and Wishner, 1993a), modifying the vertical extent of their migration and confining populations to a narrower depth range in the water column. A steady state occurs on time scales of days due to a balance between aggregation into the front and outward diffusion. Under frontolysis, dilution of organisms displaying this behavior will also eventually be balanced by inward diffusion to form an equilibrium if time permits. The question in both cases is the following: What do the effects of individual frontal elements produce in the frontal zone as a whole?

Using the model of Olson and Backus (1985), and convergence estimates from either Flierl and Davis (1993) or the model in Figure 3, it is possible to estimate the frontogenetic concentration of organisms. Both of the models produce horizontal divergence on the order of  $3 \times 10^{-5} \text{ s}^{-1}$  in the most intense frontogenesis zones. This can be compared with the  $\sim 5 \times 10^{-6}$  estimate from warm core ring 82B observations (Olson and Backus, 1985). From the analytical model the Gulf Stream should induce hundred fold concentrations in vertically mobile species on spatial scales between 1 and 10 km and on time scales of 1 to 12 d. These concentrations should reach approximate advective/diffusive equilibrium on time scales of 3 to 30 d. All of these calculations assume a diffusion coefficient of  $50 \text{ m}^2 \text{ s}^{-1}$  (Olson, 1986). This sort of response is more than capable of producing the pattern seen in Figure 3. Finer detailed distributions of small nekton in the front in Figure 5 also support this sort of behaviorally coupled dynamics in the stream front. The figure shows an overall increase in scattering on spatial scales of 10 km or less along the stream edge. In the trough (convergence) the maximum scattering is only 5 km across while the maximum is wider and shifted both into the surface and the Slope Water side of the stream in the meander crest. The total set of sections (Arnone *et al.*, 1990) suggests some continuity along the front in these patterns, long-front advection or entrainment are, of course, possible contributors to the overall patterns observed.

Advection of fluid off the coastline and into the Gulf Stream depicted in the inset of Figure 4 is well documented both from the stream separation at Cape Hatteras (Ford *et al.*, 1952; Lillibrige *et al.*,

1990) and around warm core rings. This addition to the stream edge, however, involves organisms that are not well adapted to the open ocean ecosystem. Presumably these populations add to the death pictured by Murray and, through remineralization, a chain of offshore nutrient recycling (old production). In either case, the front is enhanced for those organisms positioned to take advantage of the situation. In other words, transition species adapted to these frontal zone environments may make use of either the enhancements in the environment tied to frontal processes, as detailed above, or of resources advected down-front to them or entrained into the transition environment from the sides. Much of this of course will be mediated by the phytoplankton dynamics. This leads one to a hypothesis that transition zooplankters are adapted to use frontal convergence to aggregate with prey of either origin.

### Fish Populations

There are numerous suggestions that mobile species aggregate in fronts. Reports range from tuna (Dufour and Stretta, 1973; Laurs *et al.*, 1984) and other fishes, to birds (Ainley and Jacobs, 1981; Kinder *et al.*, 1983), and some whales from distributional maps (cf. sperm whale distributions in Bannister and Mitchell, 1980). In some cases the aggregations are caused by feeding behavior and/or migration. Sperm whales, for example, do not seem to use fronts as pathways, but may use them as forage grounds, while some tuna seem to migrate along fronts (Laurs and Lynn, 1977; Maul *et al.*, 1984). There is also evidence for enhanced tuna foraging in fronts (Fiedler and Bernard, 1987). Finally, there is the debate as to whether tuna are really specific to thermal ranges (Blackburn, 1965; Rothschild, 1965; Roffer, 1987) and may only be associated with fronts as a secondary consequence of this (Blackburn, 1965).

From Folger's (Franklin, 1786) observation that sperm whales aggregate in proximity to but not in the Gulf Stream, to more recent attempts to understand the relationship between swordfish catch and fronts south of New England (Podestá *et al.*, 1993), the relationship of large free-swimming animals to frontal zones has proven difficult to quantify. Nowhere is this better illustrated than in the debate between Nakamura and Blackburn (Nakamura and Yamanaka, 1959; Blackburn, 1965; Nakamura, 1969) on the distribution and migration of tuna with respect to "discontinuities in ocean structure" (Nakamura, 1969). Tuna and swordfish are distributed relative to preferred thermal habitats (Blackburn, 1965; Nakamura, 1969; Carey and Robison, 1981). The question is whether these preferences lead the fish to "pile up" on the border of a preferred thermal regime, i.e., in fronts, or whether they actually use fronts as cues in migration and/or as regions where they gain energetically by riding on currents or making use of en-

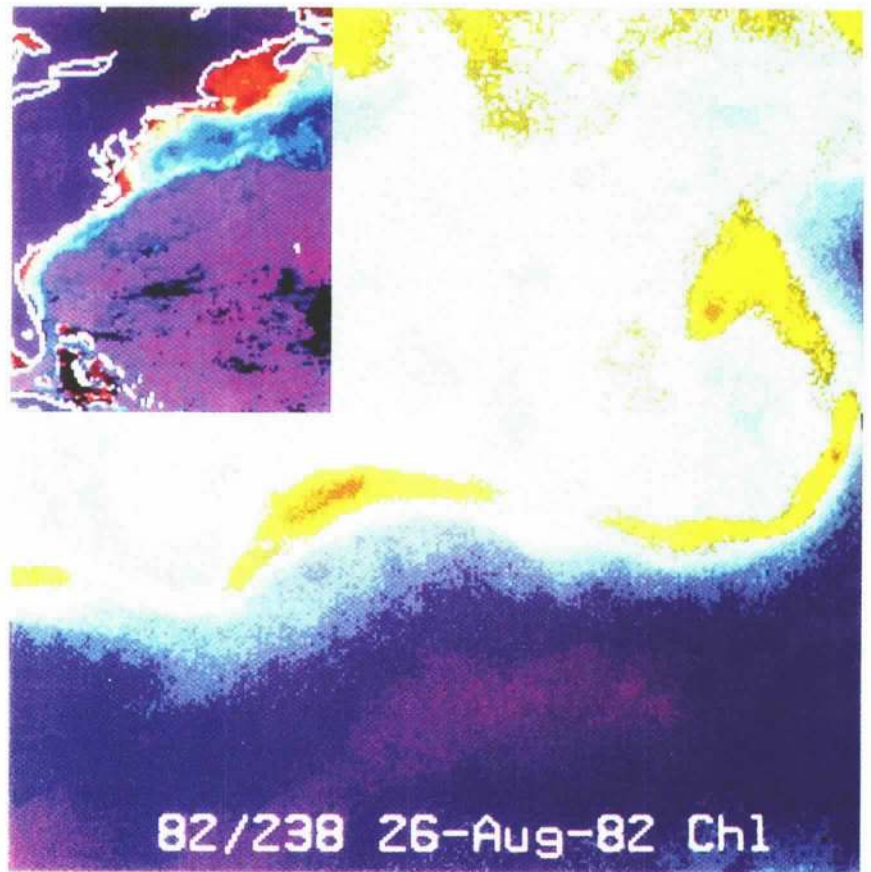


Fig. 4: Satellite derived near surface chlorophyll patterns associated with the Gulf Stream in the highly oligotrophic season (August 1979 for inset and August 1982 for detailed image). In both, the stream shows enhanced phytoplankton biomass. As the inset shows, some of this may result in the entrainment of high chlorophyll waters off the continental shelf (cf. Lillibridge, 1990). In both, however, there is also a response to the meandering itself. The small amplitude meander in the detailed image indicates a high biomass near the meander crest as originally predicted by Hitchcock (1988). Proceeding downstream, streamers of high near surface biomass are progressively swept into the troughs and eventually concentrate there.

hanced forage opportunities (Olson and Podestá, 1987). This brings up the question of whether various species use fronts as migratory pathways either by swimming along them or using them as road signs in an otherwise homogeneous ocean.

The distribution of tuna and sword fisheries (Nakamura, 1969; Palko *et al.*, 1981) and capture of larval forms imply a connection between these fish and major frontal zones. In particular, spawning of bluefin tuna and swordfish in the North Atlantic reaches a peak in the eastern Caribbean and Florida Straits (Rivas, 1978; Grall *et al.*, 1983). This tendency places the zero-age fish in a position where they will be introduced to the forage grounds off the northeast coast of North America by advection in the Gulf Stream. Distribution of catch and tagging of adults in both species suggest that large adults follow the western boundary current at least through a portion of their migration. As pointed out by Blackburn (1965), however,

there are clearly times when this is not the case with some tuna actually swimming against major currents. Blackburn (1965) also points out that fronts offer lethal conditions in many cases and therefore do not necessarily form optimal pathways for dispersal of young or migration in adults.

For adult fish frontal zones have many advantages if the fish can make use of them. For example, a 1–2 m s<sup>-1</sup> Gulf Stream can make a major energetic contribution to migrations such as those in bluefin, which have typical migration rates of 1.8 m s<sup>-1</sup> (Rivas, 1978). Such a use is consistent with Atlantic bluefin tuna migration. There are further gains if the fish can make use of forage concentrations of the type suggested in Figure 5. Frontal zones have a number of cues associated with them that might be used to orient a large nektonic animal within them. Briefly these include temperature either sensed as a temporal change while swimming or as absolute temperature tied to thermal preference, photic environment changes associated with phytoplankton distributions, and finally behavior associated with the presence of prey (cf. Olson and Podestá, 1987 and references therein). Proof of tuna and swordfish actually using these to aggregate in the stream, however, is not definitive (Podestá *et al.*, 1993) and will demand a concentrated effort to achieve.

### Conclusions

The picture that develops is that frontal zones are complex regions that can either lead to enhanced growth in adapted populations or prove lethal to those not so equipped. Some organisms can make use of fronts through tolerances to variable environmental conditions. These particular behaviors act to optimize their interaction with the frontal domain and can make frontal zones viable niches for part or all of the life cycle. The gain of these species is probably in some part tied to the demise of other lesser adapted forms which add their remains to the frontal environment. Finally, there is much that is unknown concerning the problems of life on frontal edges. In particular there are no data sets that currently allow a definitive assessment of trophic interactions in fronts. This is especially true in the relationship between large pelagic fish such as tuna or swordfish and frontal zones.

### Acknowledgements

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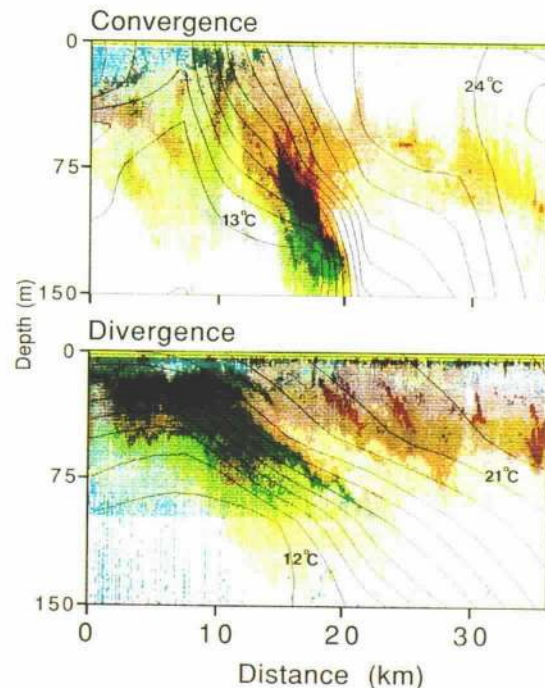


Fig. 5: Acoustic imagery illustrating the distribution of nekton through the trough (convergent, downwelling) and crest (divergent, upwelling) of a Gulf Stream meander. Both cross sections are from night tows of a surface transducer across the stream. Each image is a color composite of red (38 kHz), yellow (70 kHz) and blue (200 kHz) with color intensity proportional to volume backscattering strength. Equal strengths of all three colors represent weak through intense scattering and appear as white (< -70 dB) through grey (-70 to -65 dB) to black (> -65 dB). Higher acoustic frequencies have the potential to detect smaller organisms than lower ones. The approximate cross-sectional diameters of nekton "seen" by each frequency are as follows: red, >1.2 cm; yellow, >0.6 cm; and blue, >0.2 cm. The isotherms from XBT's taken along the transect demonstrate the changes in the near surface thermal structure under the alternate influences of frontogenesis (convergence) and frontolysis (divergence).

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