

The Comparative Approach: Latitude-dependence and Effects of Wind Forcing on Reproductive Success

Andrew Bakun*, Claude Roy**, Philippe Cury**

* Pacific Fisheries Environmental Group, Southwest Fisheries Science Center, NMFS, NOAA, P.O. Box 831, Monterey, California 93942, U.S.A.

** Institut Français de Recherche Scientifique pour le Développement en Coopération (ORSTOM)
Temporary address: Pacific Fisheries Environmental Group*

Abstract

Recent findings concerning the effects of wind forcing on reproductive success of coastal pelagic fishes are surveyed, including several intriguing results that invite explanation. These include (1) the remarkable apparent constancy, among widely differing geographical settings, of the "ideal" wind condition (or "optimal environmental window") yielded by empirical time series analysis, (2) a tendency for peak reproductive activity to coincide with the seasonal upwelling peak in low latitude locations but to be out of phase with the upwelling at higher latitudes, and (3) the remarkable capacity of the Peruvian ecosystem to support particularly massive pelagic fish populations. The latitudinal dependence of certain of the processes is introduced as a means of drawing conclusions via the comparative method. The importance of vertical and offshore scales is indicated. The concept of "scaled offshore velocity" is introduced. The interaction of latitudinal-varying factors with ~~latitudinally-constant~~ factors in near-equatorial latitudes is proposed as a hypothetical explanation of the ~~special capacity~~ of the Peru Current ecosystem with respect to pelagic fishes.

Résumé

De récents résultats concernant les effets du vent sur le succès de la reproduction des poissons pélagiques côtiers sont examinés et notamment certains faits curieux qui font l'objet d'un examen plus approfondi. On s'intéressera tout d'abord à la valeur de vent optimale pour le recrutement (ou "fenêtre environnementale optimale") qui apparaît constante quelque soit la région considérée; le second point concerne le calendrier de la reproduction qui semble être en phase avec la saison d'upwelling aux basses latitudes et décalé de quelques mois aux latitudes plus élevées. Pour terminer, une hypothèse concernant la capacité de l'écosystème péruvien à soutenir des populations de poissons pélagiques côtiers particulièrement importantes sera émise. La variation suivant la latitude de certains paramètres est ensuite envisagée comme un moyen permettant d'extraire des informations à partir d'une approche comparative. L'importance des échelles verticale et horizontale est soulignée. Le concept de "vitesse standardisée vers le large" est introduit. L'interaction entre des paramètres dépendant et indépendant de la latitude dans une zone proche de l'équateur est proposée comme hypothèse pour rendre compte de l'abondance des populations de poissons pélagiques devant les côtes du Pérou.

Introduction

Traditionally, temperature has been the variable of first choice in addressing environmental effects on fish populations. However, particularly with respect to the small pelagic-spawning clupeoid fishes that are the focus of the SARP project, recent findings have tended most often to implicate effects of wind acting on the sea surface. For example, a wind-based index of coastal upwelling (Bakun 1973) has been empirically related to population dynamics of a substantial number of commercial fish stocks of the California Current and other eastern ocean upwelling systems (Bakun and Parrish 1980; Shepard *et al.* 1984; Bakun 1985; Bakun in press). The work of Lasker (1975, 1978, 1988) has drawn attention to the detrimental effects of wind-induced turbulent mixing of the water column in dispersing fine-scale concentrations of food particles necessary for adequate larval nutrition. Peterman and Bradford (1987) have added support to Lasker's findings by empirically relating interyear variability in larval anchovy mortality rate off California to frequency of calm periods of sufficient duration for fine scale strata of food organisms to form. On the other hand, Rothschild and Osborn (1988) suggest that certain levels of turbulence could actually enhance feeding efficiency of small marine organisms. In a variant of Sinclair's (1988) "member/vagrant" hypothesis, Parrish *et al.* (1981) implicate detrimental effects of wind-induced offshore Ekman transport, which would carry eggs and larvae away from the favorable coastal habitat; Parrish *et al.* (1983) show a pervasive tendency for both offshore transport and exposure to turbulence to

be minimized in reproductive habits of eastern ocean coastal pelagic fishes. Cury and Roy (1989) have extended these results by comparative time series analysis, employing new nonlinear methods (Mendelssohn and Cury 1987), and have empirically demonstrated a consistent "optimal environmental window", where reproductive success is favored at an intermediate range of wind speed, neither too low for adequate upwelling-based enrichment nor so high that excessive offshore transport and turbulent mixing occurs. Roy (1990) showed the same pattern of apparent selection for an intermediate ideal characteristic wind speed in a survey of the reproductive habits of West African coastal pelagic fishes.

The emergence of wind effects as perhaps the key environmental variable to be considered in the SARP context is particularly interesting with respect to the climate change problem. The need for insight as to consequences of global climate change has emerged as a key scientific issue throughout the world, and potential effects on marine ecosystems and resources are important and particularly uncertain issues. One "greenhouse effect" about which we can be rather certain is an increase in temperature contrast between the heated continental land masses and the oceans during the warmer seasons of the year. This would lead to amplified sea breeze circulations and alongshore coastal winds, correspondingly enhanced offshore Ekman transport in the ocean surface layer, and intensified coastal upwelling (Bakun, 1990).

The comparative method has been identified as a key component of the international SARP research strategy. In the following sections of this paper, we discuss certain recent results concerning wind-related effects on reproductive success of small coastal pelagic fishes. We use this discussion to introduce certain concepts and terminology that may be useful in drawing comparative inferences and in integrating the operational and "inferential" (Anon. 1983) approaches within the SARP project.

Latitude-Dependent Dynamics and Comparative Ecology

Many dynamic characteristics of the ocean-atmosphere system are dependent on latitude. This certainly applies to upwelling ecosystems. For example, eastern ocean coastal upwelling seasons continue essentially through the entire year near the tropics, but with increasing latitude they become increasingly restricted to a narrowing period in the "high sun" portion of the year (Wooster and Reid 1963; Parrish *et al.* 1983). Within the upwelling season, the upwelling process which is rather steady in the tropics becomes increasingly variable and episodic with increasing latitude (Parrish *et al.* 1981). Since the local horizontal plane (i.e., tangent to the earth's surface) makes different angles to the earth's axis of rotation at different latitudes, the Coriolis constraint, which controls the observed effects of large-scale hydrodynamical linkages, depends very strongly on latitude. In fact, the Coriolis constraint vanishes at the equator, creating singularities in several crucial processes which have dynamic expressions with Coriolis effect in the denominator. Very significantly, the quantitative coupling of the momentum transferred from wind stress on the sea surface to transport of ocean surface water is very strongly a function of latitude, i.e.

$$\mathcal{E} = \frac{\tau}{f} \quad (1)$$

where \mathcal{E} represents the surface ocean Ekman transport (Ekman 1905), τ is the stress of the wind on the sea surface and f is the Coriolis parameter ($f = 2\Omega\sin\phi$, where Ω is the angular velocity of the earth and ϕ is the latitude; for convenience, we define $\underline{f} = f/2\Omega = \sin\phi$; thus $\underline{f} \sim f$, where " \sim " signifies "proportional to"). Thus $\mathcal{E} \sim \underline{f}^{-1}$ (curve "D" in Fig. 1), and the Ekman transport responding to a given intensity of wind stress becomes exponentially large as the equator is approached. Note that when the wind stress is alongshore (equatorward on an eastern ocean coastal boundary, poleward on a western ocean boundary), \mathcal{E} represents both the large-scale offshore transport of the ocean surface layer (and entrained larvae, etc.) and the locally wind-driven coastal upwelling.

Such strong dependences on latitude should be useful in sorting out the processes controlling spawning strategies and, by implication, reproductive success. For example, the latitude dependence might provide insight into the relative roles of turbulence and offshore transport in regulating larval survival, since the input of turbulent mixing energy at a given wind intensity is not believed to be dependent on latitude (Fig. 2).

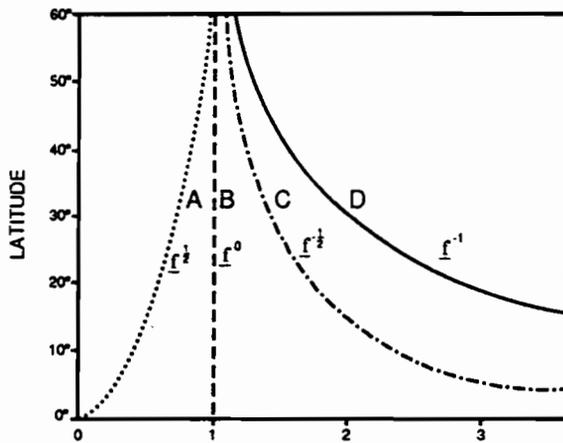


Figure 1. Latitude dependences: Powers of f (where $f = \sin\phi$; ϕ = latitude).

A: $f^{1/2}$, B: f^0 , C: $f^{-1/2}$, D: f^{-1} .

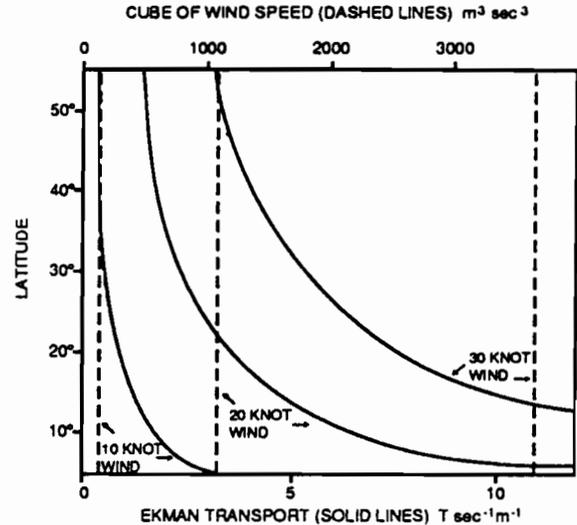


Figure 2. Turbulent mixing energy production (proportional to the third power of the wind speed), for several values of wind speed.

The optimal environmental window

Over the past several decades, empirical analyses of the relationships between local wind effects and recruitment variability in different eastern ocean pelagic fish populations have often yielded differing and, therefore, rather unsatisfying results (Bakun and Parrish 1980). Over the recent period of development of fishery-environmental science, reliance on linear statistics and empirical methods has been very much the fashion. Recently, effective nonlinear methods of empirical analysis have been introduced to fisheries science (Mendelsohn and Cury 1987; Mendelsohn and Mendo 1987). These methods were applied by Cury and Roy (1989) to the Peruvian anchoveta (*Engraulis ringens*), the California sardine (*Sardinops sagax caerulea*), the Moroccan sardine (*Sardina pilchardus*), and the Senegalese and Ivorian sardinellas (*Sardinella aurita*). The result was a consistently domed-shaped relationship (Fig. 3, bottom) where reproductive success appeared highest at an intermediate wind strength which whether expressed as " W^3 " rate of turbulent mixing energy input) or " \mathcal{E} " (wind stress, Ekman transport, upwelling index, etc.), consistently decomposed to a characteristic wind speed near 5 - 6 $m\ s^{-1}$. It is thus no mystery that the previous results may have been inconsistent. In cases in which most of the data may have been on the "left flank" (low wind speed side) of the optimal environmental window, an increasing relationship with wind speed would be found. Conversely, if most of the data were on the "right flank" (high wind speed side), a decreasing relationship with wind speed would be found. If the data were rather evenly distributed across both flanks of the window, linear methods could pick up no relationship at all.

Very recently, expansion of the analysis to additional stocks or data sets has yielded the same result. The California anchovy (*Engraulis mordax*) can be added to the list of "optimal environmental window" stocks (Roy *et al.* 1991). New recruitment estimates for the Moroccan sardine (Kifani 1991; Roy *et al.* 1991) and an analysis of pre-1945 data for the California sardine (Ware and Thomson, in press) showed the same characteristic "window" feature of maximum recruitment corresponding to an intermediate wind intensity during the larval period.

Constructing an interpretation of the optimal environmental window result is quite straightforward. It readily conforms to, and incorporates, the most prominent current hypotheses concerning variability in larval survival. The control on the "right flank", i.e., the "high wind" side, could come about either through (1) excessive offshore transport leading to offshore loss of pelagic larvae from the favorable coastal habitat (e.g. Parrish *et al.* 1981; Sinclair 1988) or through (2) overly intense turbulent mixing which could disperse fine-scale concentrations of appropriately sized and nutritious food particles needed for successful first feeding (Lasker 1975, 1978). An obvious explanation for the "left flank", or "low wind" side, is a lack of nutrient-enrichment by wind-induced upwelling or mixing, leading to inadequate production of

appropriate larval food (Cushing 1969). Also, it is possible that under conditions where the interaction of feeding behavior with stable fine-scale food particle structure may be less important than the energy savings produced by turbulent diffusion of food particles toward feeding larvae, the mechanism of Rothschild and Osborn (1988) may exert some control on the "left flank" by increasing larval survival toward the slightly higher wind speeds within the "window".

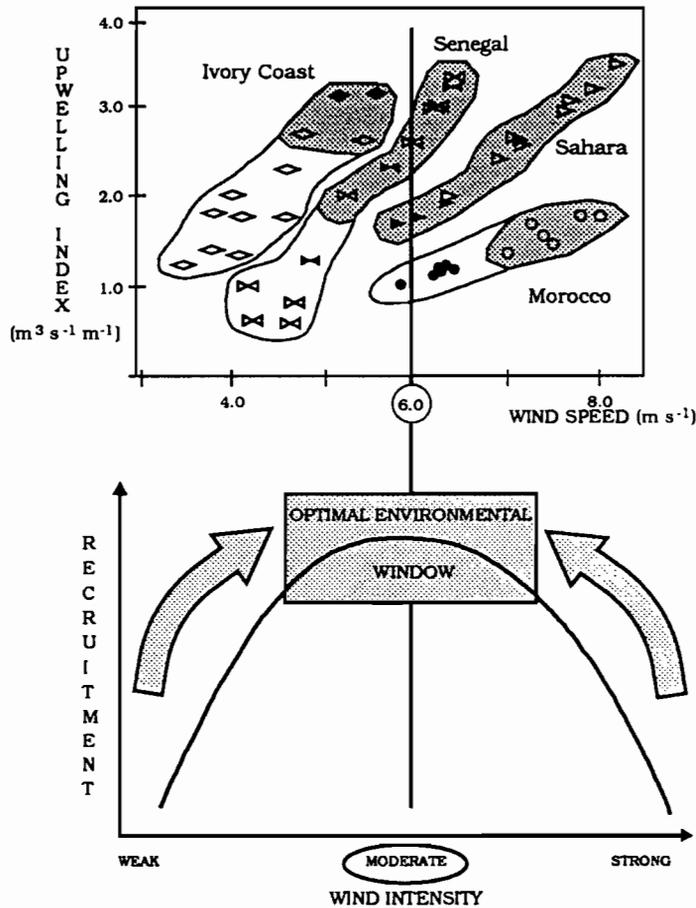


Figure 3 : Upper : annual monthly mean values of wind speed ($m \cdot s^{-1}$) and upwelling indices ($m^3 \cdot s^{-1} \cdot m^{-1}$) in the main West-African upwelling areas (Morocco, Sahara, Senegal and Ivory-Coast). A bold sign represents the months when reproduction is active and a shaded area represents the months when upwelling is active (from Roy et al., 1991).

Lower : theoretical relationship between recruitment and environmental factors in upwelling areas (from Cury and Roy, 1989).

Intriguing findings

Several intriguing findings invite explanation. The "optimal environmental window" appears to be remarkably stable among widely separated regions. It is nearly always centered very near an index value that, whether expressed as offshore Ekman transport or as turbulent mixing index, decomposes to a wind speed of about $6 m \cdot s^{-1}$ (Cury and Roy 1989, Roy et al. 1991). This seems to hold in upwelling systems located quite near the equator (Peru, Senegal), in mid-latitude upwelling ecosystems (California, Morocco), and at various points between (Op. cit.).

Another intriguing finding is the demonstration (Roy 1990; Roy et al. 1991) of a striking difference in the seasonal relationship of peak reproductive activity to peak upwelling intensity between low latitude and mid-latitude habitats along the North Atlantic coast of Africa. In low latitude systems, the spawning peak tends to directly coincide with the period of maximum upwelling intensity. Conversely, in higher latitude systems, the peak spawning tends to be well before the seasonal upwelling peak, occurring in late

winter to early spring. However, in both low and mid-latitude situations, the spawning peak does occur at a seasonal period typified by a mean wind speed very near the 6 m s^{-1} value (Fig. 3, upper panel) that consistently appears as the "optimal environmental window" in time series analysis.

A third intriguing finding, not particularly new but in fact a subject of conjecture for over two decades, is the apparently unique capacity of the Peru Current Ecosystem to support massive populations of coastal pelagic fishes. The anchoveta (*Engraulis ringens*) population of the Peru Current, was, prior to its collapse in the early 1970s, by far the largest neritic fish population ever recorded (e.g. Paulik, 1971). And in the subsequent period, the combined Peruvian and Chilean landings of sardine (*Sardinops sagax*) have reached the largest annual totals ever recorded for any eastern ocean sardine population. The intensity of the upwelling that occurs does not seem in itself to be the answer. On a year round basis, the intensity of the upwelling occurring off Peru appears to be no greater than that near Cap Blanc in the Canary Current system and to be substantially less than off Namibia (Lüderitz) in the Benguela system (Parrish *et al.*, 1983). What is it about the Peru Current ecosystem that makes it such a good place for giant populations of these fishes to develop?

Physical scales

In considering the balances of processes leading to the "optimal environmental window" and other attributes of favorable reproductive conditions, it is useful to specify significant horizontal and vertical physical scales. In deep waters, two different vertical scales appear to be of particular interest. One is the *mixed layer depth* (MLD). The MLD is the depth of the relatively homogeneous ocean surface layer above the seasonal thermocline. In general, even in the absence of active erosion of the thermocline by wind-generated turbulence, nocturnal cooling at the ocean surface would increase the surface water density enough to cause the waters within this mixed layer to be "turned over" at least once each day (otherwise, a discernable thermocline would build up, determining a new, shallower MLD). Thus larvae or other organisms that do not oppose this mixing by actively behaving so as to maintain themselves within a constant depth increment would tend, on average, to be rather evenly distributed over the MLD.

The second important vertical scale is the *Ekman depth*, \mathcal{D} . This is the depth to which significant wind-induced Ekman transport extends. An expression for the Ekman depth is (Ekman 1905):

$$\mathcal{D} = \pi \sqrt{\frac{2A_z}{\rho f}} \sim f^{-1/2} \quad (2)$$

where A_z is the vertical eddy viscosity coefficient, and ρ is the density of sea water. \mathcal{D} is generally thought to be of the order of 10 - 50 m, and probably does not extend significantly into stable density stratification. Thus, in general, $\mathcal{D} \leq \text{MLD}$.

The offshore scale for dynamic ocean processes such as coastal upwelling is the Rossby radius of deformation, \mathcal{R} . We can thus think of \mathcal{R} as the intrinsic scale for the coastal pelagic habitat. An expression for \mathcal{R} applicable to coastal upwelling ecosystems is (Mooers and Allen 1973):

$$\mathcal{R} = \frac{HN}{f} \sim f^{-1} \quad (3)$$

where H is the water depth and N is the Brunt-Vaisala frequency. Estimates of \mathcal{R} are generally of the order of 10 - 20 km in mid-latitude eastern ocean coastal habitats. \mathcal{R} obviously becomes much wider in tropical regions, due to the inverse dependence on f (curve "D", Fig. 1); eq. (3) becomes infinite at the equator itself.

A second dynamically-important offshore scale is the width of the continental shelf. The shelf width has been cited as being important for primary and secondary production (Binet 1991) and fish reproduction (Parrish *et al.* 1983; Nelson and Hutchings 1987). The upwelling region off Senegal provides an illustrative example. To the north of Cap Vert the continental shelf is rather narrow, sea surface temperature increases rather monotonically offshore and chlorophyll is rather uniform (Fig. 4, left panels). However, south of Cap Vert where the shelf abruptly widens, the lowest sea surface temperature is not at the coast but over the continental shelf break (Fig. 4, left panels) and high phytoplankton biomass and productivity, indicated by chlorophyll concentration (Fig 4) is apparently retained over the inner shelf (Gning *et al.* 1990), suggesting a double-celled upwelling circulation (Jacques and Tréguer 1986) which may provide an area of retention inshore of the most intense upwelling.

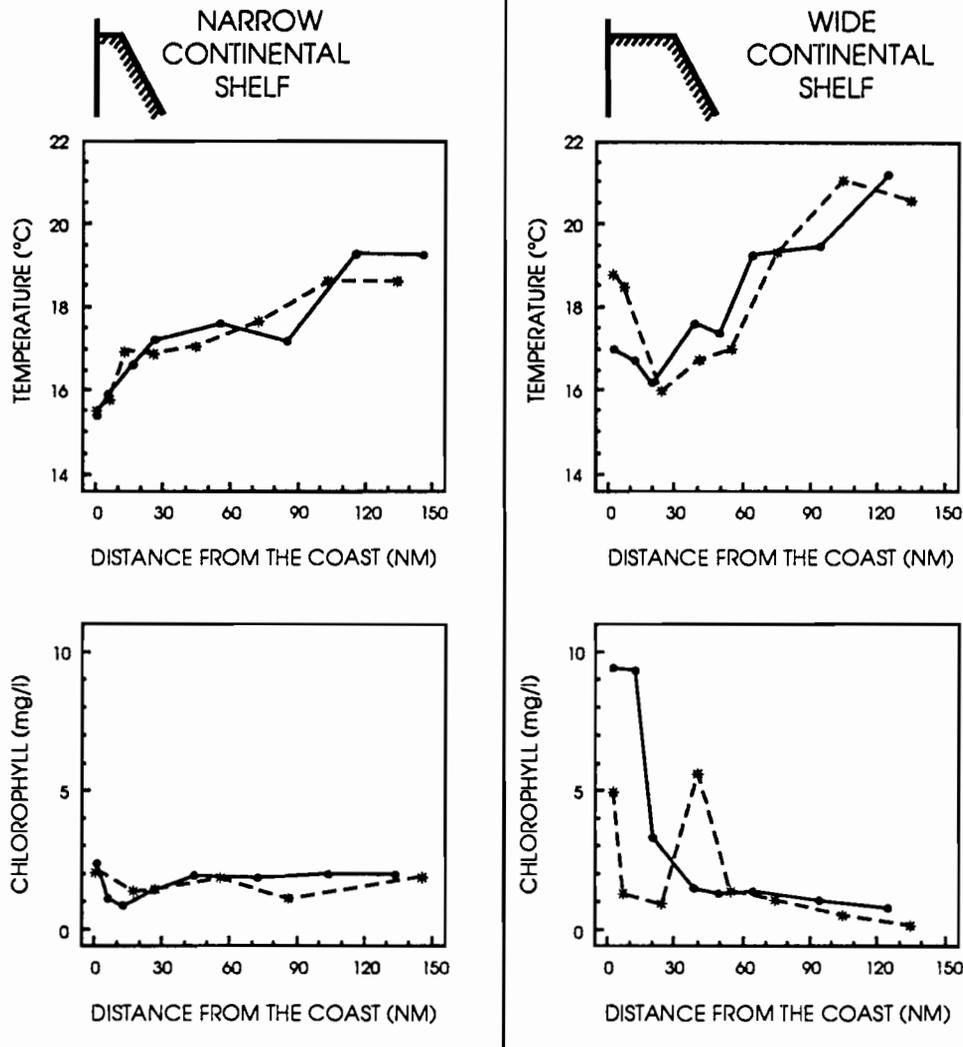


Figure 4 : Surface distribution of temperature (°C) (upper) and chlorophyll ($\text{mg}\cdot\text{l}^{-1}$) (lower) along two transects off the Senegalese coast, for a narrow continental shelf (left) and a wide continental shelf (right), (from Gning et al., 1990).

Scaled offshore velocity

The Ekman volume transport of water can be approximated from an estimate of wind stress on the sea surface. However, it is not the magnitude of the transport (i.e., the number of m^3 per day per unit width of coastline) that determines the proportion of larvae that may be carried so far offshore that their chances of survival are severely impacted. Rather, it is the *speed* at which larvae are, on average, carried offshore that is the determining factor. This speed is determined by dividing the offshore volume transport by the appropriate depth scale to yield units of velocity ($\text{km}\cdot\text{day}^{-1}$, for example).

Further, the speed of offshore larval movement is only significant in relation to the offshore width of the favorable coastal habitat. For example, if the offshore habitat width is wider in one situation than in another, a greater offshore velocity may have less detrimental effect. To adjust for differences in habitat width, the speed can be divided by the appropriate offshore habitat scale. This finally yields what we will call the "scaled offshore (Ekman) velocity" or "SOV". Thus

$$\text{SOV} = \frac{\mathcal{E}}{\text{depth scale} \times \text{offshore scale}} \quad (4)$$

The SOV thus expresses, in relative terms, the fraction of the offshore habitat scale that is traversed per unit time by the "average" larvae due to offshore directed Ekman transport. We suggest SOV as the appropriate quantity for inter-regional or inter-seasonal comparisons of apparent effects of directly wind-driven offshore larval transport on reproductive success.

The qualification "in relative terms" is required in the previous paragraph because of uncertainties as to exact relationships of the physical scales to the "behavior-scales" of the organisms. This point may be illustrated by studying two different cases, each based on a different assumption concerning the manner in which active behavior of the organisms themselves might affect their depth distribution within the upper mixed layer of the ocean.

Case 1 (Fig. 5, upper panel) represents a case where a planktonic organism, such as larvae of a fish species, maintains its vertical position to remain within a shallow depth increment (not exceeding the Ekman depth) near the sea surface through active swimming behavior. In this case, the actual speed of offshore movement will depend on the details of the average vertical profile of Ekman velocity within the Ekman layer. These details are not well known or understood and are nearly impossible to measure, constituting large time and space averages of smaller-scale motions. However, for comparing different situations the Ekman depth, \mathcal{E} , may be the appropriate scale. This is because the speed of offshore movement should remain inversely proportional to the Ekman depth, assuming other factors are equal. For example, for a given rate of Ekman volume transport, a deeper Ekman layer will spread the depth distribution of Ekman velocity and cause each fixed depth increment to move at a slower speed. Thus for Case 1 (choosing the Rossby radius as the appropriate offshore habitat scale):

$$\text{SOV} = \frac{\mathcal{E}}{\mathcal{D} \times \mathcal{R}} = \frac{\sim f^{-1}}{\sim f^{1/2} \times \sim f^{-1}} \sim f^{1/2} \quad (5)$$

Thus, for a given magnitude of wind stress, even though the Ekman transport increases toward the equator, under the assumptions of Case 1, the scaled offshore velocity (SOV) decreases toward the equator (curve "A", Fig. 1).

Case 2 (Fig. 5, lower panel) represents a case where the organisms exert no active control on their depth level within the mixed layer, but act approximately as neutrally-bouyant passive drifters. In such a case the organisms would, on average, be rather evenly distributed through the mixed layer. Here the depth of the Ekman layer is irrelevant, since the average offshore velocity of the mixed layer will be the total offshore volume transport of mixed layer water, regardless of its depth distribution within the mixed layer ($\mathcal{D} \leq \text{MLD}$), divided by the depth of the mixed layer. Neutrally-bouyant passive drifters, mixed through the mixed layer, would experience the same average offshore velocity as the water particles within the mixed layer. Thus for Case 2:

$$\text{SOV} = \frac{\mathcal{E}}{\text{MLD} \times \mathcal{R}} = \frac{\sim f^{-1}}{\sim f^0 \times \sim f^{-1}} \sim f^0 \quad (6)$$

In this case the SOV has no latitude dependence at all (curve "B", Fig. 1).

Presently there exists little basis for confidently choosing between Cases 1 and 2 (and other cases that might be constructed on the basis of slightly different assumptions). The primary purpose of most of the larval sampling of coastal pelagic fishes has been quantitative estimation of larval biomass, etc. Thus vertical structure in larval distributions has been regarded as an unwanted source of sampling variance. For this reason, sampling has often been designed with the intention of integrating such structure (e.g., by utilizing vertical or oblique net tows). As a result, we have relatively little information as to details of vertical larval distribution and behavior.

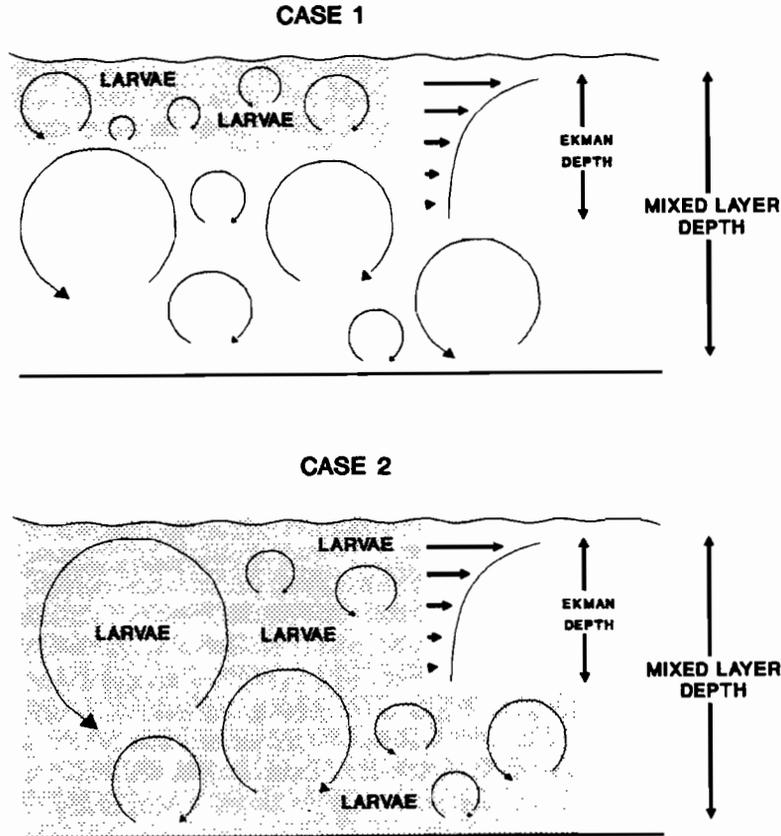


Figure 5. Schematic representations of the upper mixed layer of the ocean. The Ekman depth is represented by the exponentially-decreasing horizontal arrows. The depth of the larval distribution is represented by shading. Case 1: Larvae counter turbulent mixing and maintain their depth distribution within the upper Ekman layer by active behavior. Case 2: Larvae are passively mixed through the mixed layer.

Scaled enrichment factor

Nutrition-dependence of larval survival involves both avoidance of starvation and also the opportunity for rapid growth through the various size-dependent predation fields. Both starvation and growth depend on the energy balance between the caloric value of ingested food particles and the energy expended in locating and capturing those food particles. For small organisms such as larvae, the viscosity of sea water is substantial and active movement through it to find food exacts substantial energy costs. And each larva must strike that balance within the particular cubic meter of water in which it finds itself. Thus the nutrition-dependent component of larval survival rate depends not on the total quantity of appropriate food in the habitat but rather on its local concentration (quantity per unit habitat volume). Consequently, for the purpose of inter-regional or inter-seasonal comparisons of apparent effects of upwelling-based enrichment, the offshore Ekman transport (i.e., the upwelling index (Wooster and Reid 1963; Bakun 1973)) should be scaled according to the habitat volume by dividing \mathcal{E} by the effective depth of larval habitat and by the offshore habitat scale. The larval habitat depth scale may be the MLD, as in "Case 2", above, or the behaviorally-maintained depth of larval incidence, as in "Case 1". Neither is a direct function of latitude. Thus if we choose the Rossby radius, \mathcal{R} , as the offshore scale, a "scaled enrichment factor" can be written:

$$\text{Scaled enrichment factor} = \frac{\mathcal{E}}{\text{larval depth scale} \times \mathcal{R}} = \frac{\sim f^{-1}}{\sim f^0 \times \sim f^{-1}} \sim f^0 \quad (7)$$

i.e., a constant with respect to latitude (curve "B" in Fig. 1).

Discussion

With these concepts in hand, we now return to expand the discussion of the three intriguing findings pointed out earlier.

Latitudinal constancy of the "ideal" wind speed

The apparent constancy, over a range of latitudes, of the ideal wind intensity around which the empirically-determined optimal environmental window (Cury and Roy 1989; Roy *et al.* 1991) is centered has seemed remarkable in view of the strong latitudinal dependences of some of the key processes and scales that are expected to be involved. However, if we apply proper scaling to the upwelling-based enrichment effect which is thought (Cury and Roy 1989) to be the primary mechanism controlling the low wind side of the "window", it may in fact be latitude-independent (eq. 7). Wind-generated turbulent mixing is not in itself latitude-dependent (Fig. 2). If turbulent mixing (Lasker 1975, 1978) controls the high wind side, a lack of latitude dependence in the "window" thus follows logically. In addition, a latitude-independent detrimental effect of offshore transport could also be involved on the high wind side of the "window" under the "Case 2" set of circumstances (larvae being rather haphazardly distributed mixed throughout the mixed layer and the Rossby radius being the appropriate offshore habitat scale) reflected in eq. 6.

Seasonal timing: spawning peak and upwelling peak -- in phase or out of phase?

Roy (1990) and Roy *et al.* (1991) report that in the low latitude systems off northwestern Africa, the spawning peak tends to directly coincide with the seasonal period of maximum upwelling intensity (Fréon 1988). Conversely, in the higher latitude coastal pelagic habitats of that region, the peak spawning tends to be well before the upwelling peak, occurring in late winter to early spring (Belvèze and Erzini 1983). However, in both low and mid-latitude situations, the spawning peak occurs within a seasonal period typified by a mean wind speed very near the $5 - 6 \text{ m s}^{-1}$ value (Fig. 3, upper panel) that consistently appears as the "optimal environmental window" in time series analysis.

Since the observed spawning habits reflect the net adaptive response to a history of annual successes or failures in reproduction, one may not be surprised that spawning habits would be geographically and seasonally "tuned" to provide a successful match to the same optimal conditions that has apparently favored reproductive success in the set of recent years incorporated in the empirical time series analysis. We assume that upwelling-based nutrient enrichment of the local trophic system supports reproductive success. Thus the only reason for spawning to occur previous to a seasonal upwelling peak would be if upwelling turned out to have detrimental effects overbalancing the positive effects (e.g., increased offshore larval transport, destruction of stability and increased turbulent dispersion of food particle concentrations, changes of dominance from more nutritious flagellates to less nutritious diatoms, increased incidence of predators, etc.). With respect to offshore larval transport, we have shown that under certain likely sets of circumstances (e.g., "Case 1", discussed above) the SOV, which we have suggested as an appropriate interpretive measure of potential detrimental effects of offshore transport, decreases with decreased latitude (\sim curve "A", in Fig. 1). Thus at lower latitudes, the stocks might be better able to experience the positive effects of spawning within a seasonal upwelling, while experiencing less negative effects from the associated offshore transport.

In the case of a different set of circumstances (e.g., "Case 2", discussed above) the SOV has no intrinsic latitudinal dependence. However, it is dependent on MLD (eq. 6) which may or may not have latitude dependence, but will probably have distinct seasonal dependence. For example, Parrish *et al.* (1983) note that the Peruvian anchoveta spawns during the winter upwelling peak. However, Bakun (1985) used the seasonal cycle of MLD, reported by Parrish *et al.* (1983), to show that the MLD deepened sufficiently during winter that the offshore velocity of the mixed layer was typically at a minimum during the upwelling peak. In fact, eq. (6) shows that when the seasonal cycle of MLD and \mathcal{E} are in phase, in cases where the seasonal cycle of MLD has greater relative amplitude than that of \mathcal{E} , the seasonal cycles of \mathcal{E} and SOV will be in opposite phase.

Here it is well to be reminded that other factors may also interact in determining optimal seasonal timing for peak reproductive effort. As seen in figure 4, high chlorophyll concentration exists along the Senegalese coast during the peak of the upwelling season. This implies a retention area where larvae could benefit from being kept near the coast within a highly productive area and season. Such a structure

could explain the ability of fish to reproduce during the season of highest offshore transport. Roy (1990) has pointed out that the fish may solve the problem of offshore transport of their reproductive products by spawning habits which select locations for spawning where such physical retention mechanisms exist, leaving adjustment of seasonality as an available means for dealing with other factors (e.g., detrimental effects of turbulence).

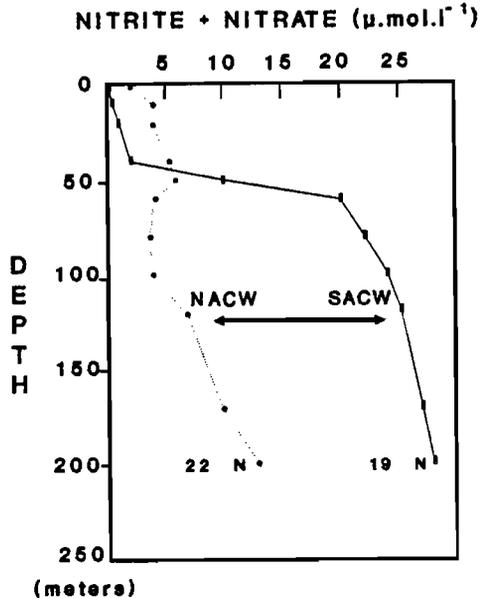


Figure 6 : Vertical profiles of nitrite and nitrate at 22N and 19N, showing the higher nutrient concentration of SACW compared to NACW, (adapted from Llinas *et al.*, 1985).

Also, part of the trade-off between positive effects of upwelling and negative effects of associated offshore transport involves qualitative aspects such as both the nutrient content of the upwelled water and the larval food value of the particular types of organisms that might utilize these nutrients. For example, the North Atlantic Central Water acting as the primary upwelling source north of Cap Blanc (20° N) has a much lower NO₃ content than the South Atlantic Central Water to the south of Cap Blanc (Fig. 6); thus equal intensities of upwelling could result in greater actual upward nutrient transfer to the south of Cap Blanc than to the north.

A basis for the unique pelagic fish productivity of the Peru Current Ecosystem

The considerations presented herein perhaps shed some useful light on the remarkable capacity of the Peru Current Ecosystem to support particularly massive populations of coastal pelagic fishes. Since this habitat is located much nearer the equator than most of the other coastal upwelling habitats in which these fishes have been studied, the Rossby radius (\mathcal{R}), Ekman depth (\mathcal{D}) and Ekman transport (\mathcal{E}) all are large. Under the "Case 1" scenario, the SOV thus is small. And even if the "Case 2" scenario should be more apt, the MLD is very deep off Peru, during the winter spawning peak at least (Parrish *et al.* 1983), again yielding a relatively small SOV. The continental shelf width, which we discussed as an alternate scale for offshore extent of the coastal habitat, is also much wider off north-central Peru than in other eastern ocean coastal upwelling centers (see Table 6 in Parrish *et al.*, 1983.). Turbulence generation by the wind is independent of f ; and thus a given level of wind-driven offshore transport would tend to be accompanied by a much lower level of turbulence than in the other systems (Fig. 2). These considerations present a picture of a particularly benign environment off Peru where relatively weak winds result in strong offshore-directed surface Ekman transport ($1.5 - 2.0 T s^{-1} m^{-1}$) and an associated high volume rate of upwelling which continually enriches a very wide, deep, relative non-turbulent upper ocean habitat (i.e., mixing index values well within the $250 m^3 s^{-3}$ contour (Parrish *et al.*, 1983)). In the case of such a thick surface Ekman layer, the associated average offshore transport of larvae distributed through this layer would be relatively small, and their loss from a very wide coastal habitat would be minimized (i.e. a very low SOV). This same ease in maintaining standing stock in the upwelling-enriched environment and lack of exposure to intense turbulent mixing would be of similar benefit to primary producers, leading to high

concentrations of food organisms for both larval and adult fishes. Note that as long as larval survival (per unit volume) is substantial, a large aggregate quantity of surviving larvae is favored by the latitude-dependent scaling factors which act to determine a very large total habitat volume per unit width of Peruvian coastline.

Concluding remarks

The considerations discussed in this paper are based on the class of "inferential approaches" (Anon. 1983), which includes comparative studies and analyses of interyear time series of temporally- and spatially-aggregated annual data points. Clearly, such approaches have only limited ability to sort out the types of interactions discussed above. Part of this limitation is due to the aggregation of energetic smaller-scale events into the annual temporal and spatial composites. This "smears together" separate causes and effects, that are determining the outcomes on the smaller scales, in a way that makes it very difficult to differentiate them by retrospective analysis. The problem of lack of resolution in our knowledge of processes and distributions in the vertical dimension, discussed above with respect to formulation of the SOV, is perhaps even more serious in the horizontal and temporal dimensions.

This is the reason that the operational approach within SARP is vital. High-resolution studies, both in time and space, are key elements of the SARP operational rationale (Bakun, Alheit, and Kullenberg, this session). The inferential and operational approaches should proceed together, continually feeding back and reinforcing one another. One of the purposes of this paper is to provide some conceptual framework and language that may help to integrate the two approaches. The considerations presented in this paper may suggest certain key issues to the designers of operational field exercises. Certainly, one is the question of scale. We need to define the dominant scales, horizontal, vertical, and temporal, involved in the recruitment problem. Once better insight into these scales is available, the inferential process can proceed with much greater confidence and benefit.

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