

RECRUITMENT IN FISHERY RESOURCES AND ITS RELATIONSHIP TO ENVIRONMENT: ACCESSIBLE PATHWAYS TO GREATER INSIGHT

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Abstract

Scientific progress in the resistant problem area of recruitment variability in exploited fish populations may depend on the ability to move beyond the restrictive paradigm that has provided the framework for many previous advances in fisheries science. Rather than aggregating information temporally and spatially into composite annual data points, it appears necessary to specifically address the richly detailed temporal and spatial patterns which exist within seasonal periods and within the same, and among different, regional habitats.

Coherent conceptual frameworks, within which generic questions can be posed, are needed. Well-posed high resolution studies, such as the SARP "within-year" exercises along with complementary high spatial resolution observational exercises, offer rational approaches to addressing certain key questions. Broad application of the comparative method of science is advocated. Interpretation of behavioral adaptations to environmental circumstances potentially constitutes a powerful inferential tool. It is suggested that particularly amenable fish population and habitat settings be utilized in addressing key generic questions in order to support broadly-based multilateral scientific progress.

INTRODUCTION

Lack of scientific understanding of the mechanisms controlling recruitment variability constitutes the key problem area in fishery science at the present time (the term "recruitment" referring to the quantity of younger fish surviving the various egg, larval, and juvenile stages to begin to be captured in a fishery). Recruitment in most fish populations is found to vary erratically from year to year in ways that presently cannot be explained or predicted. The problem remains largely unsolved after many decades of dedicated scientific effort by highly capable scientists in a number of nations around the world.

The result is a situation in which those involved in fishing and associated industries must deal with chronic uncertainties as to the year-to-year fluctuations in the abundance of the fish populations on which they depend. However, even more importantly, the unexplained large-amplitude interyear variability obscures the essential underlying signals needed to foresee and manage the effects of fishery exploitation over longer

time scales. These signals include the functional form of the relationship of expected recruitment to stock size, trends in stock productivity, interspecies interactions, effects of climatic change or habitat alterations, etc. Lacking the ability to resolve these signals, the methodologies of fishery science must rely on arbitrary assumptions and extreme simplifications concerning the very factors which control the important long term outcomes (such as the possibility of eventual displacement of a fished species from a position in the biological community wherein it constitutes an economically viable resource). The smooth functional curves drawn through erratic scatters of data points, which are often the products of these conventional methodologies, tend to be neither intellectually convincing nor operationally reliable. Collapses of important fishery stocks around the world continue to occur, with attendant socio-economic consequences. Real improvement in the situation does not appear likely until significant advances in scientific understanding of the mechanisms controlling recruitment variability can be realized.

Since "recruitment" is the net result of a chain of life cycle events extending from the formation of reproductive product within the adult fishes, through the various egg, larval, and juvenile stages, it typically reflects not a single process but a large number of interacting processes by which huge numbers of tiny eggs undergo drastic reduction to very much smaller numbers of surviving recruits. In passing through these stages, an individual grows through a great range in size, and so an identical process may affect its survival in different ways at different stages in its development. During this period, the organisms are essentially invisible to humans because they are not taken by any fishery. Thus it is undeniably expedient, in an operational sense, to treat this entire period in terms of the single aggregate quantity, "recruitment". However it is not surprising that this approach has not generally yielded simple, constant relationships either to parental stock size or to environmental conditions.

Straightforward step-by-step application of the experimental method, in the classical scientific tradition, has not yielded major penetration of the problem. Valid experiments on the processes regulating survival of larval or juvenile fishes tend to be very difficult to accomplish. This is because conditions in the ambient ocean environment are not amenable to experimental controls and also because the mixture of scales of motion in the ocean makes it impossible to maintain the integrity of the volume of water in which an experiment is taking place unless it is contained in some way. However, any sort of artificial containment restricts the scales of the processes, and also imposes unrealistic interfaces and substrates, such that essential mechanisms tend to be altered. But of all the experimental difficulties, probably the most serious is the fact that, because of the enormous reduction in numbers that occurs, survival of any individual to the stage at which recruitment takes place is a very rare event with respect to the fate of the overwhelming majority of hatchlings. Thus, the circumstances affecting a given sample of quite typical larvae may be quite irrelevant to eventual recruitment to the population; that is, it may well be that only very small subgroups of quite non-typical larvae that find themselves in very special circumstances are the only ones with any prospect at all of survival. Thus even if valid result could be obtained for an experimental sample, these are likely to bear no relationship at all to the net recruitment observed at the population level. Thus, in order to achieve unequivocal results, experiments need to be performed at the population level; and if experiments on sample segments of a population are difficult, the problems involved in addressing a population as a whole tend to be overwhelming. For these reasons, most recruitment research in the past has followed the empirical approach, whereby

statistical relationships are sought between the total integrated result, i.e. "recruitment", and various indices of aggregate environmental circumstances or population size.

A major problem with the empirical approach is the fact that the lack of understanding of the causal mechanisms presents far too many choices of variables and formulations to be effectively sorted out with the relatively short lengths of available data series. There are always a multiplicity of potential linkages of environmental processes and conditions to survival of young fish available for consideration. A variety of oceanographic, meteorological, or proxy time series can be constructed and associated with one or more of these linkages. Various uncertainties as to appropriate time scale, temporal lag between cause and effect, etc., multiply the possibilities for constructing explanatory data series. By searching through the range or possibilities, some degree of correlation with short (usually autocorrelated) time series of annual data points can often be found and then readily justified according to one or another ecological mechanism. When such a correlation happens to be high enough to meet standard significance criteria, it becomes "publishable" as an advance in scientific understanding, whereas slightly weaker correlations do not. This happens even though given the multitude of possible interactions with growth, predation, transport, physiological stress, etc., occurring at various life cycle stages, it may seem nearly inconceivable that any one mechanism could so dominate survival as to yield a strong univariate correlation that was not at least to some degree spurious. Even if the search through the possibilities of explanatory variable formulations proceeds over a period of time via independent efforts of a number of different researchers, each with a separate *a priori* hypothesis, and each scrupulously limiting himself to a single *a priori* choice of explanatory variables, the problem is not alleviated. Only successes are generally published, and so the ratio of successes to non-successes is unknown. Therefore, a statistical basis for judging the likelihood that a particular reported "relationship" may be spurious, is lacking. Thus, we have the situation that most of the empirical environment/recruitment relationships published in the scientific literature are probably at least to some degree spurious, with others that may have represented realistic degrees of actual linkage having been discarded as not meeting significance criteria (Bakun, 1985).

As a result of the respective difficulties involved in the experimental and empirical approaches, fishery-environmental science is not well-developed at the present time. Perceiving this less than satisfactory situation, fish population dynamicists have tended either to

ignore environmental variation altogether or to treat it in unrealistic ways (e.g., as merely random variability about some steady base level, etc.). Indeed, some (e.g., Walters, 1984; Butterworth et al.¹) have become sufficiently discouraged to suggest that studying the causes of recruitment variation may ultimately turn out to be futile and that research funds might be better spent on other problem areas.

Such a lack of optimism is disconcerting in its apparent implication that what we call "fishery science" is somehow fundamentally different from other sciences wherein the existence of generalizable laws and principles, capable of being identified through application of the scientific method, is taken for granted. And it would seem to relegate fishery science to a somewhat permanent status of being more in the nature of an operational "craft" than of a true prognostic science. Nevertheless, it is a fair question and these authors can in no way be faulted for posing it. And, it should be acknowledged that by "futile" they undoubtedly mean to imply "futile at any justifiable level of research funding".

In fact, the analyses of Walters and of Butterworth et al. present compelling arguments under the conventional paradigm within which they are posed. An axiom of that paradigm is the idea that each "unit stock" exists in such a unique biological and environmental setting that the only information useful for analysis and prediction is that derived directly and exclusively from the particular stock in question. In addition, fish are mobile and live in a moving fluid environment, thereby blurring spatial distinctions within the stock habitat. Also the seasonal variation is of such dominance in most biological processes that interference of seasonal effects tends to distort subannual time series. As a result the conventional practice has been to aggregate all the data of a given type that may be available within a particular year into a single annual data point. This paradigmatic view has served as the primary conceptual framework for fishery science for a number of decades, providing the basis for its major operational accomplishments (e.g., yield-per-recruit estimation, surplus-productions models, stock-recruitment relationships, etc.). So it is not surprising that there is a strong inclination among fishery scientists to couch the recruitment variability issue within the same frame of reference.

The arguments of Walters (1984) and Butterworth et al.¹ provide the valuable service of clearly pointing out

¹Butterworth D.S., Bergh M.O., Sparks R. Prospects for incorporating environmental and species interaction effects in Benguela pelagic resource projections - presented at the Symposium on Population and Community Ecology in the Benguela Upwelling Region and Comparable Frontal Systems, Cape Town, South Africa, 8-12 September, 1986

that in order to develop crucially-needed improved insight into the recruitment question it may be inescapable that this restrictive paradigm must be relinquished and legitimate ways to move beyond it found. Actually, this broadening of viewpoint is already well underway. There have been recent indications of the utility of the comparative method of science, as applied to appropriate groupings of different stocks and environmental setting (e.g., Bakun, 1985). And recent technological developments have led to the development of high-resolution (both temporal and spatial) approaches to the problem (e.g., Lasker, 1988; Buckley and Lough, 1987) thereby resolving the "single aggregate data point per year" dilemma. We have a new global scientific program, the International Recruitment Program (IREP), established within the Program of Ocean Science in Relation to Living Resources (OSLR) which is co-sponsored by the Intergovernmental Oceanographic Commission (IOC) and the Food and Agriculture Organization of the United Nations (FAO). IREP is being specifically designed to facilitate multinational collaboration in, and to thereby maximize effectiveness of, both the comparative and the high temporal/spatial resolution approaches. One of the focal projects within IREP, the Sardine-Anchovy Recruitment Project (SARP), has been established to focus particular attention on the high-resolution aspect, although the interregional comparative approach is also incorporated as an important element of the SARP project design.

POSING GENERIC QUESTIONS

It appears that the route to progress may lie, rather than in attempting to solve the recruitment question completely and independently in any one regional system, in being able to find ways to break the problem down to certain key generic questions, as well-posed and amenable to multilateral scientific effort as possible, that will facilitate a broadly based step-by-step accumulation of insight. As such increases in insight might accrue, they would not only be available for direct application to management concerns but could provide guidance as to proper design and allocations of subsequent research effort.

I would here like to cite two recent studies. The first is the recent paper by Peterman and Bradford (1987) which suggests that early stage survival of anchovy larvae off California is related to the frequency of periods of calm winds during the spawning season (Fig. 1). The conclusion one would draw is that reproductive success may be related to rather short-term, somewhat random events in the manner or the hypotheses developed by Reuben Lasker and his co-workers at La Jolla (e.g., Lasker, 1978, 1981a, 1981b, 1988). In such a case, a

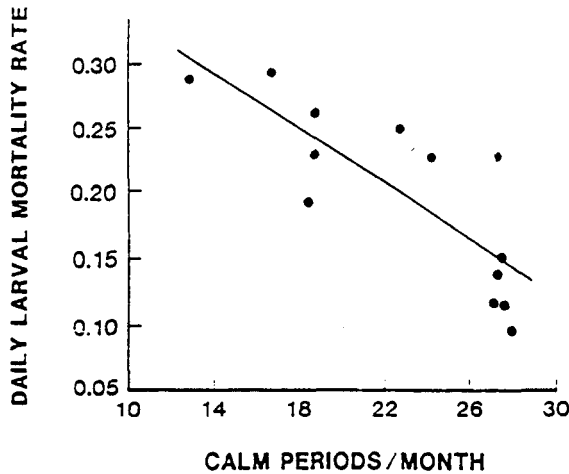


Fig -1 Correlation between frequency of calm periods and mortality rate of recently hatched northern anchovy larvae (*Engraulis mordax*) off California (after Peterman and Bradford, 1987, reprinted with permission of Science. Copyright 1987 by AAAS)

single annual composite environmental descriptor would obviously be inadequate to demonstrate the linkage; moreover, where more than one type of short term effect might be acting at different times within a season, aggregating the information in annual composites would tend to hopelessly confound the analysis.

Next I would like to cite Kawasaki's (1983) paper which called attention to the fact that sardine populations off California, off Chile, and off Japan seem to have grown and collapsed in synchrony (Fig. 2a,b,c). Kawasaki suggested subtle, very long-term, oceanwide environmental changes which must somehow affect these very widely separated populations similarly. In this case, the suggested oceanwide environmental changes must have been quite subtle, since no clear evidence of directly corresponding fluctuations has (to the knowledge of this author) yet been reported in the available marine climatic data. Therefore, one would think that they would have to be too subtle to control such explosive population expansions and collapses by direct effects on the sardines themselves. And so one would tend to think of complex reorganizations of the biological community structure in the ocean perhaps in response to chronic, long-term, low-level environmental changes.

At the present time one really cannot say which is generally more important in controlling fish population dynamics: short term, rather stochastic environmental

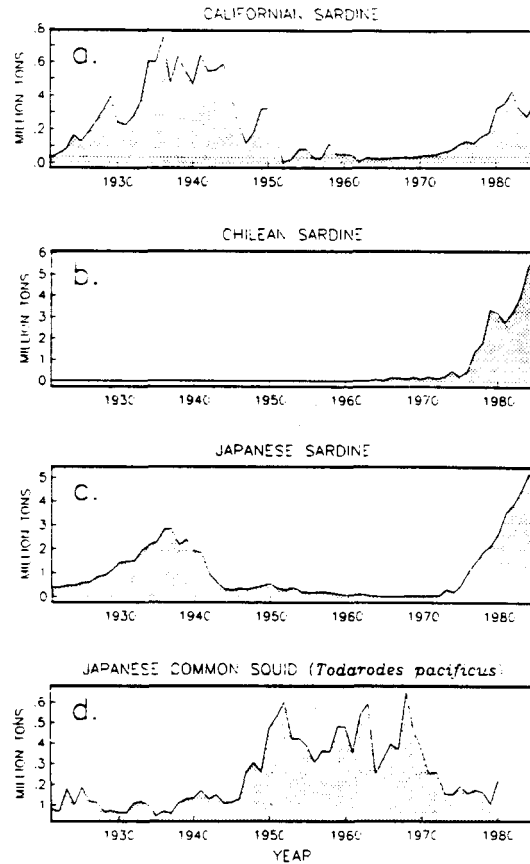


Fig -2 Time series of sardine catches in the (a) northeastern Pacific, (b) southeastern Pacific, and (c) northwestern Pacific Ocean and of catches of (d) *Todarodes pacificus* (winter spawning population) in Japanese waters. (Note that the scales for panels 'a', and 'd' are expanded relative to those of panels 'b' and 'c' by factors of about ten. Also note that in the earlier peak shown in panel 'a', catches were largely from the northern subpopulation inhabiting the region off the western U.S.A., while the recent catches are largely from a subpopulation existing within the Gulf of California and include catches of other pelagic species. Panels 'a', 'b' and 'c' are adapted from Kawasaki, 1983, with the adaption of more recent data kindly provided by Dr. Kawasaki. Panel 'd' is adapted from Hatanaka et al., 1984.)

events directly affecting reproductive success, or longer-term chronic effects, perhaps acting by way of changes in the composite marine biological community structure. The question is certainly a salient one, from both the research and management points of view. If the environmental controls are direct, it might be reasonable to attempt to manage a stock somewhat in isolation, directing effort toward insuring maintenance of sufficient spawning population to take advantage of

rather randomly occurring opportunities for excellent reproductive success. However, where the controls may act through biological community interactions, it might be well to direct some serious study to the possibility of beneficial intervention by purposefully impacting selected components of the interlinked biological system. For example, R.K. O'Dor, of the cephalopod International Advisory Council (CIAC), has pointed out that the explosive rebirth of the Japanese sardine stock directly coincided with the collapse, under heavy fishery pressure, of the very large stock of oceanic squid, *Todarodes pacificus*, in the region (Fig. 2d). Such squids are undoubtedly voracious and efficient predators on small pelagic fishes, growing to full size and completing their entire life cycle within one year (Hatanaka et al., 1985).

The SARP Concept

The SARP temporal-resolution "within-year" exercise (often referred to simply as the "SARP Experiment"), developed under the leadership of Reuben Lasker and his colleagues at Southwest Fisheries Center, has been identified (e.g., Anon., 1983, 1984, 1987) as the most promising experimental approach presently available for addressing the mechanisms and impact of short term temporal variability in larval survival *at the population level*. As mentioned earlier, other types of potential experiments suffer from the fact that because of the enormous reduction in numbers of individuals during the early life stage, recruitment may depend on small subsets of very non-typical larvae; the fate of typical larvae may be quite irrelevant. The key attribute of the SARP concept is its reliance upon capturing survivors, i.e., members of the **successful** subset, at a later life cycle stage and then reconstructing its exact birth date, and also indications of its growth history, from daily marks carried in the bony structures (Pannela, 1971; Methot, 1983; Campana and Neilson, 1985). These would then be compared to short term variability in environmental processes and conditions, utilizing such techniques as histological measures of starvation (Theilacker, 1986) and immunoassays of predator stomach contents (Theilacker et al., 1986) as diagnostic tools, to reveal the causal mechanisms.

Thus, the exercise constitutes a "natural experiment", wherein advantage is taken of naturally-occurring environmental variation rather than relying on controlled manipulation of conditions. Implicit in the procedure is a loss of spatial resolution, because the animals are mobile during the period between birth and capture; this may not be a crucial drawback because the most energetic sources of short term variability (atmospheric storms, etc.) affecting the upper ocean environment tend to be of rather large spatial scale.

In order to produce a valid "survival index" from larval birthdate frequencies it is necessary to adjust for short term variability in larval production, which may occur on rather finely detailed spatial scales; thus a full SARP "within-year" exercise requires detailed monitoring of larval production over the entire reproductive habitat at short (one-to two-week) intervals over the major portion of an extended spawning season. The full exercise therefore implies a sizable commitment of resources for at-sea operations that has been difficult to achieve under the funding constraints of recent years.

This has led to suggestions (by J. Alheit and others) that the SARP context be broadened to include other types of high-resolution (both temporal and spatial) studies. Besides yielding important new insight on their own, such studies would also serve to maximize the scientific value of the relatively few full SARP "within-year" exercises that can be expected to be accomplished, around the world, within the next few years.

Technologies for indicating short term larval growth rates, both biochemically (Buckley, 1984) and by measurement of daily otolith increment width (e.g., Gutiérrez and Morales-Ninn, 1986), appear to be applicable in the SARP context. While not yielding "survival" directly, growth rate probably regulates survival to a large degree. The major sources of larval mortality appear to be starvation and predation (Hunter, 1981). Starvation and growth rate are obviously related. Vulnerability to predation appears to be highly size-dependent (*ibid.*) and so predation mortality can also be considered to be closely linked to growth rate.

If the growth rate history recorded in the daily otolith increments can be appropriately utilized, some of the attributes of the high temporal resolution SARP experiment may be realizable at a fraction of the at-sea survey cost of the full SARP "within-year" exercise. This is because such a growth record does not necessarily require the repeated detailed surveys of larval production that are required to convert birthdate frequencies to an index of survival. It may be possible to draw useful conclusions from as minimal a field effort as collecting several representative samples of late larvae or juveniles, reconstructing the sequence of characteristic growth rate variability (adequately replicated among acceptably independent samples), and simply comparing the sequence to such readily apparent large-scale events as storm occurrences.

An alternate technique for indicating relative differences in growth rate, i.e., which utilizes RNA - DNA ratios (Buckley, 1984), does not yield a temporal record

from any sample. It reflects only very recent growth, on the several-day time scale. However, the necessary close linkage in time also implies a corresponding close linkage in space; and so spatial resolution, lost in the full SARP "within-year" exercise, is recovered. Important habitat structure exists on relatively small scales in both the vertical and horizontal dimensions. Appropriate sampling of larvae with respect to such structure, and determining abundance and nutritional state as reflected in recent growth rate, could yield rich material for drawing mechanistic inferences. Additional diagnostic tools such as the histological and immunoassay techniques mentioned above could also be employed. Satellite imagery would be an aid in defining horizontal structure at the sea surface. This could be related to vertical structure in ocean properties and flow by means of physical oceanographic theory (and by use of sonic or *in situ* profiling techniques, etc., where available, during the sampling operation).

Such high spatial resolution studies are another example of a "natural experiment" which utilizes natural variation, in this case in the spatial dimension, as a substitute for controlled experimental manipulation. Spatial studies of this type could yield valid conclusions concerning mechanisms regulating larval survival without the requirement for repeated detailed characterization of an entire reproductive habitat which is such a demanding feature of the full SARP "within-year" experiment. They could also serve to "fill in" our understanding of spatial aspects needed to derive the maximum insight from those temporal SARP studies (wherein spatial resolution is lost) that can be implemented.

THE COMPARATIVE METHOD

"Natural experiments" such as discussed above, which take advantage of natural variability to produce distinct realizations of the processes being investigated, actually constitute applications of the comparative method of science. Mayr (1982) identifies the experimental method and the comparative method as "the two great methods of science" and in fact bases the distinction between them on whether or not there is controlled manipulation of the experimental conditions. He cites the revolutionary advances in evolutionary biology, based nearly entirely on the comparative method, as an example of its power. Since the ocean environment is basically uncontrollable, and certainly so on scales affecting important fishery species at the population level, it would seem to make sense to look to the comparative method as one clearly operable route toward scientific progress on the recruitment question.

Bakun (1985) presented a rationale for addressing the

recruitment issue by means of interregional comparative studies of two particular types: (1) comparisons of environmental characteristics of reproductive habitats of stocks of the same or similar species in order to infer the dominant common factors affecting reproductive success, and (2) comparisons of empirical model formulations as a means to enhance confidence in statistically-weak relationships and to detect spurious ones.

Parrish et al. (1983) provide an example of the first type of approach; in examining the seasonal and geographical characteristics of the four major subtropical eastern boundary current regions of the world's oceans, they found a general pattern of avoidance of intense wind-induced turbulent mixing and of strong offshore-directed surface Ekman transport in the spawning habits of anchovies and sardines. Temperature at which spawning takes place showed a much less coherent pattern, suggesting that selection of spawning habitat on the basis of a particular optimum temperature is less important than minimizing turbulent mixing (dissipation of food particle concentrations) or offshore transport (loss of larvae from the coastal habitat).

Cury and Roy (in press) provide a most illuminating example of the power of the second type of approach. They investigate the empirical response of interyear variation in recruitment success of pelagic fishes to interyear variation in alongshore wind intensity in several different regional settings (Peru, California, Morocco, Senegal, and Ivory Coast) and find a characteristic "dome" shape in the response, such that very low wind speeds (too little upwelling) and high wind speeds (too much offshore Ekman transport and turbulent mixing) are unfavorable, with optimal survival tending to occur at intermediate wind speed values (peaking at a root-mean-square value of about 5-6 m/sec). In the case of the Ivory Coast, where the upwelling is not substantially wind-induced on the local scale and therefore not linked to local offshore Ekman transport, Cury and Roy found recruitment success to increase monotonically with upwelling intensity.

Certainly, additional types of comparative approaches are available. The crucial ingredient is an appropriate conceptual framework within which the data can be arrayed in ways that reveal informative patterns (i.e., so as to constitute reasonable "natural experiments"). Cushing's (1975) "match-mismatch" hypothesis has been useful in this regard. Lasker's (1981b) "stable ocean" hypothesis has provided conceptual underpinning to many of the examples cited in this paper, as has the "offshore transport" hypothesis of Parrish et al. (1981), Sinclair's (1988) "member/vagrant" hypothesis presents a rich set of ideas concerning population pattern, size, and temporal variability.

Bakun (in press) advanced a particular hypothetical view of trophic interaction in the ocean, wherein large-amplitude interyear variability in reproductive success, largely due to "weak links" in the life cycle, constitutes an integral component of the time-space pattern a fish population presents in order to maintain its "living space" within the trophic pyramid. Such a "high-risk" strategy, which might result in frequent reproductive failure when conditions are not highly favorable (i.e., indice large-amplitude interyear variability), may allow a species to establish itself as a dominant component of an ecosystem under particular favorable circumstances and then persist in its dominance over longer time scales through the action of several density-dependent mechanisms that may favor it over less abundant, suppressed species.

The point to be made is that such hypothetical statements and conceptual views, while they are undeniably speculative and necessarily oversimplified, offer guides for structuring available information in narrowed, more focussed contexts so that a comparative study can to a lesser degree constitute an exercise in circular reasoning (i.e., avoiding falsification by continually adjusting the premise to accommodate conflicting data) and to a greater degree represent a well-posed "natural experiment". Because of the predilections of fishery scientists to view each regional situation as unique, examples of such focused comparative analysis are rare in this field. It seems likely that substantial insights could accrue from simply assembling the various fragments of data and experience that are already available, arraying these according to specific conceptual frameworks, and looking for informative patterns of consistency and disparity.

We have an impressive recent example of cooperative assembly and integrative analysis of various types of data series in the IMARPE/GTZ/ICLARM Anchoveta Ecosystem Study (Pauly and Tsukayama, 1987). It seems that this study can serve as a model for similar efforts in other areas around the world. If so, one effect would be to encourage and facilitate broad application of the comparative method. By offering its experience and results for incorporation in a wider comparative context each such effort could thereby realize enhanced scientific utility in terms of its own local fishery concerns, while in turn expanding the available suite of potential comparative analogues and thereby contributing to the general scientific benefit all of the associated regional efforts.

LOOK AT THE ORGANISMS AND WATCH WHAT THEY DO

Active movement within the liquid ocean envi-

ronment exacts a significant caloric cost; moreover this cost is relatively higher for smaller organisms because of size-dependent hydrodynamic factors. A fish population occupying a dominant position within its particular trophic level would tend to be one that could excel at dealing energetically with the spatial and temporal pattern presented by its food sources, while presenting a pattern to its predators that imposes a sufficient energetic cost to defeat growth of intolerable levels of predation pressure (Bakun, in press). Certainly, since vulnerability to predation may decrease with increasing size (Hunter, 1981), a great premium must be placed on conserving energy so that as much as possible can be used in maximizing growth rate, particularly in the case of early stages. Likewise, it will be important for mature adults to conserve energy for maximizing production of gonadal material.

Since survival and reproductive success are the factors which drive natural selection, it is logical that any observed adaptations which involve substantial energy expenditures must be strongly linked to mechanisms exerting major control on these factors. Thus, one can argue that consistent behavior patterns involving directed active movement by the organism must in no way be mere capricious quirks, but are reflective of adaptive responses to processes or conditions which regulate recruitment (i.e. net reproductive success and survival to adulthood of the progeny, at the population level). Thus it is reasonable to look to such behavior patterns as clear indicators of the identity of the predominant processes controlling recruitment variability.

For example, Parrish et al. (1981) noted that coastal pelagic fishes of the California Current, which feed as adults in the upwelling region off northern California and in the richly productive regions even further to the north, migrate long distances to the Southern California Bight to spawn. By contrasting the conditions in the reproductive habitat and in the distant feeding grounds, and by utilizing certain other evidence, they arrived at the conclusion that avoidance of offshore transport and associated loss of larvae from the coastal habitat was a major factor controlling reproductive success (i.e., important enough to be worth the long migration). This finding has provided an independent rational basis for some successful empirical tests of recruitment success against indices of offshore transport in the larval habitat; these tests are cited by Shepard et al. (1984) as one of the few indications to date of positive progress in linking variations in fish stocks to environmental effects.

On a much smaller spatial scale, the high spatial resolution studies discussed earlier in relation to the SARP

project could involve a similar inferential rationale in cases where active swimming may be deemed to account for spatial patterning in the concentration of larvae. However, because of the limited swimming ability of early life stages, their ability to exert control on their location by directed swimming behavior in the horizontal plane, except on the very smallest scales, tends to be slight. Thus, the horizontal distribution of larvae may be largely reflective of random, somewhat accidental displacements, rather than of adaptive behavioral responses. Therefore the horizontal larval distribution in itself may offer limited unequivocal information as to mechanisms regulating survival on the population level. This is the reason that a high spatial resolution study may need other criteria in addition to the distribution of larval abundance, such as afforded by the various techniques to indicate recent growth and nutritional state cited earlier, to yield informative inferences from horizontal pattern in environmental and biological processes.

However, if the focus is shifted to address pattern in the vertical dimension, the situation is quite different. Even small, feebly swimming organisms can exert substantial control on their vertical position in the water column. Thus directed behavioral adaptations can significantly counter fortuitous displacements in the vertical, with the result that vertical pattern in larval distribution may represent a quite clear signal that is relatively free of unrelated random noise that could obscure evidence of adaptive conformity to environmental mechanisms. Most flow processes affecting larval transport in the ocean are characterized by significant vertical shears. The hydrodynamical mechanisms involved are fairly well understood by physical oceanographers. Bakun (1986) surveys these mechanisms and provides references for more detailed treatment; also see additional discussion by Bakun (in press). These hydrodynamic mechanisms afford a ready conceptual framework for analyzing the function of vertical migratory behavior, concentrations in vertical strata, etc., by larvae. And to reiterate, evident adaptive conformity to one of these mechanisms may be taken as indication that the particular mechanism is important to reproductive success and therefore a factor in recruitment variability.

In the past, sampling of fish larvae has been often directed primarily toward estimating gross abundance or toward general delineation of spawning grounds, and so vertical structure in the distribution of larvae has commonly been viewed merely as irrelevant detail and an unwanted source of sampling error. As a result, a standard practice in fisheries work has been to integrate this structure by use of vertical or oblique net tows. For this reason, there is presently relatively little informa-

tion available on vertical pattern in larval distributions, even for well studied fish stocks. However, the necessary sampling gear and techniques are available, as are new sonic techniques for describing vertical profiles of current velocity. And there is growing recognition that fish larvae commonly manage to undergo drift trajectories that are distinctly different from those which inert drifting particles must follow (Bakun, 1986; Sinclair, 1988). The conclusion is that vertical migratory behavior, interacting with vertical structure in the flow field, often constitutes a key ingredient in life cycle closure and, to the extent that this closure is dependent on a varying flow field, in recruitment variability. Thus, mere assembly of a set of observations of vertical distribution of larvae, covering a range of conditions which might affect flow characteristics, might provide a basis for an inferential process leading to important insights into factors controlling both interyear and spatial scale of recruitment (Bakun, 1986).

In summary, the adaptive responses which we observe in the behaviors and life cycle activities of marine organisms may be viewed as the integrated result of a great number of "trial and error experiments" performed by their populations. As such, they may represent rather clear signals of the primary mechanisms affecting reproductive success which are relatively uncontaminated by short term, large amplitude, quasi-random "noise" imposed by environmental fluctuations or by associated transients in the biological community structure. Thus, by looking at what the organisms habitually do under various circumstances, assuming we have an adequate conceptual framework for appropriately sorting out the circumstances, it may be possible to infer much about the nature and causes of population variability that might be very difficult to develop using more direct empirical or experimental approaches.

Multilateral collaborative effort

As indicated above, the salient question is not whether the recruitment problem is intrinsically solvable (i.e., with unlimited research resources), but rather how to achieve badly needed progress under the stringent funding constraints generated by current economic circumstances. It has been argued above that there are certain reasonable directions for productive research that might be followed at reasonable cost; these can generally be expected to be most illuminating when pursued multilaterally in a number of systems of differing degrees of similarity. Key process-oriented at-sea exercises, such as the SARP "within-year experiment" are relatively expensive; obviously these cannot be duplicated in every major ecosystem of the world ocean.

We have recently applied the same methods previously used in our comparative study of eastern ocean boundary systems presented at the FAO Costa Rica Workshop (Parrish et al., 1983), to the western boundary areas of the South Atlantic^{2,3}. One finding of interest is that the sardinella of southeastern Brazil seems to be employing an identical strategy in its seasonal and locational adaptations, to solve a very similar set of environmental problems, to that of the sardine which spawns in the Southern California Bight. This is in spite of the very different environmental contexts represented by tropical versus temperate water temperatures and by the very different western boundary current versus eastern boundary current dynamical situations, and in spite of the separate genera (*Sardinella* versus *Sardinops*) involved. In our previous paper we found strong analogies between the reproductive strategies of the Southern California stock, and other eastern boundary current stocks which chose spawning habitats within coastal bights downstream of upwelling centers. Thus the Brazilian population would also appear to be quite analogous, with respect to environmental-reproductive linkages, to such other important sardine stocks as the spawning in the large coastal bight off northern Chile and southern Peru, and the Canary Current stocks spawning in coastal indentations near Casablanca, and near Sidi Ifni, Morocco.

The moderate size of the Brazilian population, and its relatively confined habitat located near ports and scientific institutions, may make it a particularly amenable setting for population-level recruitment experiments such as the "SARP Within-year" experiment. The recruitment question has certainly proven to be very resistant to scientific solution when addressed, in the conventional manner, in the context of any single autonomous fish stock and habitat. The idea, that a few well-posed process-oriented experimental efforts mounted in particularly amenable habitat settings could support and progressively advance a framework of comparative scientific insight, is undeniably attractive.

There is a question of motivation and coordination and of such an altruistic multinational scientific attack on a common scientific problem area. The OSLR Programme being co-sponsored by IOC and FAO, and the International Recruitment Programme (IREP) established as its primary initial focus, have been

2. Bakun A., Parrish R.H. Comparative studies of coastal pelagic fish reproductive habitats: the Brazilian sardine (*Sardinella aurita*) -MS
3. Bakun A., Parrish R.H. Comparative studies of coastal pelagic fish reproductive habitats: the anchovy (*Engraulis anchoita*) of the southwestern Atlantic -MS.

mentioned earlier. Recently, the International Council for the Exploration of the Sea (ICES) has constituted an IREP Steering Group to promote collaborative action. France has established a National Recruitment Programme (PNDR). The U.S. National Marine Fisheries Service is in the process of re-orienting to an "ecosystem" research focus. A variety of other efforts by organizations such as SCOR, CPPS, Unesco, and various other international and national scientific agencies and institutions bear on the general problem area. The OSLR-IREP structure can potentially constitute a global collaborative framework of coordination of multilateral effort. Whether this can lead to tangible scientific progress may ultimately depend on the motivation of individual nations to commit resources to scientific project supportive of a broadly-based accumulation of generalized insight, rather than adhering to the conventional practice of viewing the problem exclusively within the restricted context of one's own particular regional marine ecosystem and fish stocks of local economic concern.

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