International Council for the
Exploration of the Sea

C.M. 1991/L:43
Session V

THE SARDINE-ANCHOVY RECRUITMENT PROJECT (SARP): RATIONALE, DESIGN AND DEVELOPMENT

Andrew Bakun*, Jürgen Alheit** and Gunnar Kullenberg***

* Pacific Fisheries Environmental Group, NMFS, NOAA, P.O. Box 831,
Monterey, CA 93942
U.S.A.

** POLARMAR, Columbus-Center, Bürger 20, 2850 Bremerhaven,
Germany

*** Intergovernmental Oceanographic Commission, Unesco, 7 Place de
Fontenoy, 75700
Paris, France

ABSTRACT

The SARP species complex is a major factor in world fisheries production, a key trophic basis for other valuable stocks, and notoriously variable and prone to population collapse. SARP was selected as the initial focal project of the International Recruitment Project, which is part of the Ocean Science and Living Resources Program of IOC and FAO because of (1) the need to address within-year variability in survival and (2) the opportunity provided by newly developed technologies. The comparative method is a major element in the SARP project design. SARP projects have been implemented in European waters, in the Southwest Atlantic, in the upwelling region of the Southeast Pacific, off California and off Japan.

INTRODUCTION - OSLR

There is growing concern that various trends of global change (accumulation of atmospheric greenhouse gases and other anthropogenic effects such as pollution, overfishing, coastal development, etc.) may have major effects on marine ecosystems and the living resources that they contain. In any particular region, evidence of subtle trends tends to be submerged in large-amplitude natural interyear and inter-decadal local variability. However, greenhouse gases accumulate on a global scale and the other major anthropogenic trends are also occurring globally. It thus makes sense to look for effects globally. Part of the rationale behind the development of the IOC - FAO Program of Ocean Science in Relation to Living Resources (OSLR) is that by analyzing events in similarly functioning marine ecosystems distributed around the world, global patterns of events related to significant global trends must ultimately appear from within the "noise level" of naturally-occurring regional climatic variability. In fact, certain regional ecosystems (e.g., the Mediterranean, etc.) appear to be in advance of certain of the global trends and can provide early case histories. Once such patterns are identified, and credibly linked to progressive trends, they can constitute a basis for real prognostic capability with which to guide adaptive actions by governments, industries, and individuals. This rationale also supports the goal of developing enhanced marine scientific capabilities around the world with which to deal with the challenges ahead.

Variability in "recruitment" of younger fish into an exploited population has been recognized as the key unsolved problem hindering more effective management of living marine resources. Accordingly, an International Recruitment Program (IREP) was established as the initial subprogram of OSLR.

More recently a new OSLR subprogram on Harmful Algal Blooms has been established in response to the rapid global increase in economic and public health problems associated with toxic and anoxic algal-related phenomena. Many scientists believe that a worldwide epidemic of harmful species may be fostered by growing incidence of marine eutrophication and spread by human activities such as ships' ballast water discharges (Anon. 1990).

At the most recent meeting of the OSLR Guiding Group of Experts (February 1990) a third OSLR subprogram, Ecosystem Dynamics and Living Resources (EDLR), was proposed. This was in recognition of the evolution of OSLR activities toward system integration and to provide a natural interface with such programs as IGBP, GLOBEC, ECOMONOC (Russian), BICED (Brazilian), etc., and with other major IOC programs:

Ocean Dynamics and Climate, Marine Pollution, etc. The potential effects of Global Climate Change on living marine resources are intended to be a major focus of EDLR.

IREP

Lack of scientific understanding of the mechanisms controlling recruitment variability is widely recognized as the key problem area in fishery science at the present time (the term "recruitment" refers 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 varies erratically from year to year in ways that cannot presently be explained or predicted. The unexplained large-amplitude variance obscures the essential underlying signals needed to manage and preserve the populations over longer time scales. These signals include the functional form of the relationship of expected recruitment to stock size, declines in stock productivity, effects of interspecies interactions, and reactions to habitat alterations, pollution, climate change, 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 that control these outcomes. Collapses of important fishery stocks around the world continue to occur, with serious socioeconomic consequences. Moreover, as we now seem to be facing the prospect of unprecedented monotonic trends in ecosystem processes, associated with atmospheric greenhouse effects and other anthropogenic impacts, management schemes based on the old assumptions (quasi-random variation about some stable mean state, etc.) which have not worked well in the past can be expected to be even less effective in the future. Proclaiming the need for holistic management of our marine ecosystems is a very popular activity at the present time. However most would agree that a sound scientific basis on which to proceed is far from in place. Real improvement in the situation does not appear likely until significant advances in scientific understanding of mechanisms controlling recruitment variability can be realized.

The paradigm that has provided the framework for most of the previous advances in fishery science generally involves aggregation of information, temporally and spatially, into composite annual data points. The IREP rationale is to attempt to move beyond the restrictive conventional paradigm to address the richly detailed temporal and spatial patterns which exist within seasonal periods and both within and among regional habitats. A key goal is to develop coherent conceptual frameworks within which generic questions can be posed. Broad intra- and inter- regional application of the comparative method is seen as a means to develop the multiple differing realizations needed to draw scientific inference in a problem area where experimental controls are unavailable. Well-posed high resolution studies, both high temporal resolution "within year" exercises, along with complementary high spatial resolution studies, offer rational approaches to addressing key questions. Developmental activity within IREP has been oriented mainly toward two major projects: The Sardine - Anchovy Recruitment Project (SARP) and the Tropical Demersal Recruitment Project (TRODERP).

THE COMPARATIVE METHOD AND SARP

The experimental method and the comparative method have been called the two great methods of science (Mayr 1982). The experimental method is the method of choice when experiment al conditions can be readily controlled. The comparative method offers an alternative in cases where experimental controls may be impractical. As an example of its power, Mayr credits "nearly all the revolutionary advances in evolutionary biology" to the comparative method.

Bakun (1989) provides an overview of the problems involved in applying the experimental method to the recruitment problem. The ocean-atmosphere system is largely uncontrollable. Moreover, the mixture of scales of motion in the ocean makes it virtually impossible to maintain the integrity of the volume of water in which an experiment is taking place unless it is artificially contained in some manner. However, artificial containment restricts the scales of crucial dynamic processes and also presents anomalous interfaces and substrates which can alter essential mechanisms. Most importantly, because of the enormous reduction in numbers that occurs, survival of an individual to the age at which recruitment occurs is a very rare event compared to the fates of the overwhelming majority of hatchlings. The results obtained for most samples of larvae may be quite irrelevant to eventual recruitment at the population level. Thus experiments should ideally be performed at the population level. And if experiments on small population segments are difficult, the problems of performing experiments at the population level are overwhelming.

Although it is undeniably useful for certain issues (such as physiological requirements and responses of individuals, etc.) which may be validly be addressed in small controlled volumes, the experimental method has only limited utility with respect to the general problem of recruitment variability in marine populations. Thus the comparative method is the available, and logical, alternative. Accordingly, the comparative approach has become a key element in the design of SARP project activities.

THE SARP CONCEPTUAL DESIGN

The SARP "within-year" exercise

The SARP high temporal resolution "within-year" exercise, developed under the leadership of Ruben Lasker and his colleagues at Southwest Fisheries Center, has been identified as a uniquely promising process-oriented approach for addressing the mechanisms and impact of short term temporal variability in larval survival (Anon. 1983,1984,1987). The within-year exercise consists basically of three operational elements: (i) a determination of short-period (ideally two weeks or less) variation in the production of larvae within a spawning season, (ii) the establishment of a birthdate distribution of juveniles originating from that production, and (iii) an observational program to specify simultaneous variation in potential explanatory variables, which may include physical, chemical, and biological processes and properties. The ratio between the curves developed in elements "i" and "ii"constitutes a "survival index" which identifies periods (cohorts) with particularly good survival or particularly high mortality. A particular attribute of this approach is that it addresses the problem at the population level, rather than addressing the fate of typical or "average" larvae which, as discussed above, may be irrelevant to net reproductive success. It does this by relying on the capture of survivors, i.e., members of the successful subset, at a later life cycle stage and then reconstructing its birth date from daily marks carried in the bony structures (Pannela 1971, Methot 1983, Campana and Neilson 1985). Comparison of the survival index to short term variability in environmental processes and conditions developed in element "iii" may reveal linkages and causal mechanisms. Another key ingredient in the formulation of the SARP within-year exercise is application of newly-developed technological tools such as the larval birthdating methodology, histological measures of starvation (Theilacker 1986) and immunoassays of predator stomach contents (Theilacker et al. 1986).

Implicit in the concept is a loss of spatial resolution within the larval habitat because the animals may undergo substantial movements during the period between birth and capture. This may not be a crucial drawback because the most energetic sources of short-term environmental variability (atmospheric storms, etc.) have large spatial scales. Actually, any source of increased mortality that did have both a short temporal scale and a small spatial scale, could not have any substantial effect on net annual recruitment to fish populations whose spawning is distributed on a regional scale over an extended spawning season.

In order to produce a valid "survival index" from larval or juvenile birthdate frequencies it is necessary to adjust for short term variability in larval production. Since larval production can vary on small spatial scales as well as on small temporal scales, a full SARP "within-year" exercise requires detailed monitoring of larval production over the entire habitat at short intervals over an extended period. This is one of the most demanding aspects of the operation. Because of the extensive ship time and other operational resources required, no fully elaborated SARP "within year" exercise, incorporating a full suite of environmental and biological (histological, etc.) diagnostic procedures, has been completed to date.

Broadening the concept (high spatial resolution, etc.)

In view of this, participants in the Ad Hoc SARP Consultation (Anon. 1989b) have recommended that the SARP concept should be broadened to include other types of high-resolution (both temporal and spatial) studies. The original SARP "key phrases": high-resolution, new technologies, and inter-regional comparative studies would continue to characterize SARP activities.

Technologies for indicating short term variability in larval growth rates, both biochemically (Buckley 1984) and by measurement of otolith increment width (Gutierrez and Morales-Ninn 1986) are available. Starvation and predation appear to be the major sources of larval mortality (Hunter 1981). These are both associated with growth rate. Starvation represents the extreme of minimal (negative) growth rate. Vulnerability to predation appears to be size dependent (Hunter 1981) and so growth rate would affect predation mortality. A focus on factors controlling growth rate variation would provide a high temporal resolution verification field without the onerous necessity for the detailed specification of larval production (Bakun, 1989). Also, since the very recent growth may be determined, spatial resolution is restored. The availability of spatial resolution allows many new hypotheses to be addressed. These would include effects of topographically-controlled hydrodynamic structures and frontal formations, effects of eddies and current meanders, etc., and all the associated hypotheses concerning larval retention (Sinclair 1987), local enrichment, convergence, advection, etc.

Participants in the 1989 Ad Hoc SARP Consultation suggested adoption of some particular research "themes" for SARP that could be addressed at a variety of activity levels in various regional settings but could promote a steady accumulation of insight. Some possibilities are listed in the report of that meeting (Anon. 1989). The consensus of the Consultation was that the prototype SARP "Within-year" exercise should continue to be an important aspect of the SARP strategy, but the lack of resources to implement this particular exercise should not preclude valid and valuable participation in SARP.

PRESENT STATE OF ORGANIZATION AND IMPLEMENTATION OF SARP

The SARP project was created at the "Workshop of the IREP Component of the IOC Programme on Ocean Science in relation to Living Resources" in Halifax in 1983 following suggestions by Ruben Lasker (Anon. 1983). It was then initiated at a second workshop in La Jolla in 1984 where detailed proposals for SARP projects in South America and California where formulated. However, perhaps because the SARP rationale is multi-disciplinary and somewhat outside the "mainstream" of conventional fishery science, none of these proposals received funding, and the field work was delayed for several years. Only recently have SARP proposals attracted substantial funding support.

The European SARP (EUROSARP) is a cooperative project of five European laboratories: Lisboa University, Instituto Espanol de Oceanografia, Plymouth Marine Laboratory, Hamburg University, and the Alfred-Wegener Institute of Polar and Marine Science in Bremerhaven. It is receiving the core funding from the Directorate General for Fisheries of the Commission of the European Community. The project was initiated in 1990 and concentrates on North Sea sprat (Sprattus sprattus), the sardine (Sardina pilchardus) off northern Spain and the anchovy (Engraulis encrasicholus) in Portuguese estuaries. The project includes the "high temporal resolution" exercise as well as "high spatial resolution" studies.

The Southwest-Atlantic SARP was initiated in late 1989 by a cooperative multi-national cruise with the German research vessel "METEOR" funded by the German Research Association (DFG), the German Ministry for Research and Technology (BMFT), IOC, the bilateral programmes for marine research between Argentina, Brazil, and Germany, and authorities of the five participating countries. A multi-disciplinary team of biologists and physical oceanographers from Argentina, Brazil, Germany, Sweden, and Uruguay carried out the field work. The samples and data are processed in the laboratories of the five countries. Communication is facilitated by frequent exchanges of scientists between different laboratories. This project has concentrated so far on the high spatial resolution exercise on a single species, the Southwest Atlantic anchovy (Engraulis anchoita) the spawning area of which extends over 2800 km along the shores of southern Brazil, Uruguay , and northern Argentina comprising a whole suite of diverse environments. The rationale of this project is described in Anon. 1989a.

Implementation of operational SARP field activities in the. eastern South Pacific has made only slow progress due to funding difficulties. However, it is expected that the SARP initiatives for anchovies and sardines off Chile, Peru, and Ecuador as suggested in 1984 by the workshop in La Jolla will eventually be funded in view of the pressing problems of the fisheries and fish industry in this region and of the need for insight into effects of predicted global climate changes. In contrast to the status of the operational approach, the inferential approach, as elaborated in the report of the IREP Workshop in Halifax in 1984 (Anon. 1984), has been successfully implemented in a cooperative project on the "Peruvian Anchoveta and its Upwelling Ecosystem" supported by IMARPE/GTZ/ICLARM. This activity presented an example of an innovative way to study recruitment of the Peruvian anchoveta (Engraulis ringens) and other components of the Peru Current ecosystem and also provides a model for assembling and presenting regional data so as to support multilateral progress via the comparative approach. The results are published in two substantial volumes (Pauly and Tsukayama 1987 and Pauly et al.1989).

The Centro de Investigacion Cientifica y Educacion Superior de Ensenada (CICESE) in Baja California initiated a programme on the dynamics of recruitment of Pacific sardine (Sardinops sagax caerulea) in the Gulf of California. Of particular interest are the interactions with the anchovy (Engraulis mordax) population which has recently entered the Gulf. Associated with this research is a study on the historical abundance of sardines and anchovies in the Gulf using fish scales preserved in varves from laminated sediments.

The Japanese BIOCOSMOS (SARP) project on population dynamics of the Japanese sardine (Sardinops melanostica) was initiated in 1989 and funded for ten years. The ultimate goal of this multi-disciplinary project, in which a number of different laboratories is involved, is to forecast future population variations.

In addition, several Mediterranean countries are considering initiating SARP on their anchovy or sardine stocks. A scheme of the structure of the OSLR programme including the SARP initiatives is given in Fig. 1. The SARP programme since 1984 has been under the auspices of the Guiding Group of Experts for OSLR. Recently, to cope with the needs for coordinating an expanding SARP programme, particularly in view of the increased levels of activity in other OSLR elements due to the addition of the EDLR and HAB sub-programmes, a special Guiding Committee for SARP was established in 1990.

Over the last 18 months, activity in the regional SARP projects has increased considerably. SARP has clearly shifted from the phase of implementation into a second phase which is characterized by continuous sampling at sea, processing of samples, analysis of data in different regions of the world, and integration of the results generated by the various operational and inferential approaches.

EMERGING GENERALIZATIONS

The various studies completed within the SARP project and within associated scientific programmes appear to be converging toward a general pattern wherein a combination of three general factors is associated with favorable reproductive habitat for anchovies and sardines. These factors are:

1. Enrichment of the food web by physical processes (upwelling, mixing, etc.);
2. Opportunity for concentrated patch structure of food particles to accumulate (stability, lack of active turbulent mixing, and/or strong convergence in frontal structures);
3. Availability of mechanisms promoting retention of larvae within (or transport of larvae to) appropriate habitat.

The processes involved in these three factors are not generally mutually compatible. For example, upwelling is a response to divergent horizontal flow. Upwelling and convergence therefore cannot directly coincide. Likewise mixing may lead to enrichment but destroy vital small scale structure in food particle distributions. Coastal upwelling, being induced by offshore surface transport, is directly linked to loss of larvae from the coastal habitat. The wind that drives the upwelling also mixes the upper ocean layer, destroying its structural stability. Thus, the three factors can combine favorably only in special environmental configurations. Each factor must be present to a sufficient degree, but not to so overwhelming a degree as to preclude the others. Alternatively, the favorable configurations may involve temporal and spatial lags that allow effects of opposing processes to be mutually supportive

For example, applying the comparative method to seasonal and geographical aspects of habitat climatology Bakun and Parrish (1991) have diagnosed three separate configurations used by a single extended anchovy (Engraulis anchoita) population off the coasts of Argentina, Uruguay, and southeastern Brazil. The recent multinational SARP cruise in the Southwest Atlantic by the German vessel METEOR has tended to corroborate these findings (Anon. 1989a, Alheit et al. 1991). The most common favorable configuration for eastern ocean coastal regions (Parrish et al., 1983) appears to be that of a coastal bight downstream of an upwelling center (Fig. 2a). This is apparently the configuration used by the clupeoid fish populations, Engraulis anchoita and Sardinella brasiliensis, spawning within the Southeastern Brazilian Bight. However, southward along the coast of South America, conditions change and Engraulis anchoita uses two distinctly different environmental configurations to extend its reproductive habitat.

Off Uruguay and adjacent regions of Argentina and Brazil, Surface Ekman transport tends to be directed onshore, which is opposite to the direction that would induce coastal upwelling. However, the hydrographic situation of this wide, abruptly-breaking continental shelf generates substantial upwelling at the shelf break. The onshore Ekman transport would serve to carry the upwelling-based nutrients and enriched production onto the inner shelf habitat, where the continent itself serves as a shield from the large-scale westerly winds and relatively low wind- mixing rates result. Relatively strong water column stability is favored by confluence of different water masses associated with the various alongshore boundary flows, by strong seasonal surface heating in the wind sheltered region, and by substantial fresh water input. The areas of water mass confluence, including fronts associated with the freshwater outflows, represent convergence zones which may serve to concentrate distributions of larval food particles. Certainly the onshore-directed surface Ekman transport facilitates the retention of eggs and larvae within the shelf habitat. This second configuration (Fig. 2b) would seem to have a strong analog in the spawning grounds of the South African anchovy population (Parrish et al., 1983).

On the Patagonian Shelf off Argentina, strong tidal mixing over the inner continental shelf results in a third configuration (Fig. 2c). In some shallower locations the water column is homogenized from surface to bottom. The result is that surface water in the mixed areas is of greater density than the surface water of the adjacent stratified areas. Similarly, the bottom water is of lesser density than that of the stratified areas. Thus the less dense surface water of the stratified offshore zone tends to override the denser mixed water, leading to onshore flow in the surface layer toward a convergent surface front. The heavier bottom water of the stratified zone tends to wedge under the lighter mixed water, leading to onshore flow also in the bottom layer. To balance these gravity-driven onshore flows at the surface and bottom, the mixed waters find their equivalent density level within the stratified water column and move offshore in the mid-depth thermocline. The upward mixing of deeper waters in the mixed water column injects dissolved plant nutrients into the illuminated surface layers. Resulting phytoplankton growth may be further concentrated in the convergent frontal zones. Also the rather stable situation within the thermocline, shielded from surface mixing processes by the lighter waters above and from bottom generated turbulence by the heavier layer below, may favor patch formation, swarming, and other processes leading to concentration of small organisms in the trophically-enriched waters moving offshore from the mixed zone (Valenzuela et al. 1991). Retention of larvae near the frontal zone could be ensured by appropriate vertical migratory behavior to utilize the onshore flow in the surface or bottom layers. And on the larger scale, the general onshore wind-driven surface Ekman transport would serve to prevent major loss of larvae from the shelf habitat. Association of anchovy larvae with the frontal structures has been demonstrated on the recent SARP Cruise of the METEOR.

Cury and Roy and their collaborators have combined the comparative approach with sophisticated time series analysis to further bolster the general pattern that is emerging. Roy et al. (1989) explain the gross seasonal and geographical aspects of the spawning strategies of African clupeoid stocks north of the Equator in terms of two limiting factors, planktonic production (related to enrichment processes) and environmental stability (which they associate with both larval retention and lack of turbulent mixing). In fact, Roy (1990) points out that the observed spawning habits of that group of stocks fall into a pattern wherein the spatial locations of spawning grounds appear to particularly optimize larval retention while the seasonal aspects of spawning appear to be tuned in a way that particularly limits exposure to turbulent mixing of the water column. Cury and Roy (1989) have analyzed recruitment time series for various clupeoid stocks of West Africa, Peru, and California; their time-series analysis, utilizing new nonlinear empirical techniques, indicates a consistent "optimal environmental window" (i.e., an intermediate band of wind speeds, neither so high as to cause undue turbulent mixing and offshore transport nor so low as to yield insufficient trophic enrichment via upwelling and mixing) wherein reproductive success is favored. Very recent extention of their analysis to additional stocks (California anchovy, Moroccan sardine) continue to consistently yield the dome-shaped "optimal environmental window" pattern (Roy et al. 1991).

Various univariate correlative relationships between recruitment and one or another of the three primary factors have been published over the years. In view of the new insights now being developed, it is not surprising that a specific environmental configuration and a specific biological life style could combine to make variability in a particular single factor stand out from the others in its correspondence to year class survival. But it is also not surprising that such relationships, which only reflect part of the causal "equation", often break down unexpectedly. For example, an increasing trend in wind speed, by increasing upwelling, might favor good recruitment up to a point where the concentration and the retention factors are unduly disrupted. Continued increases in wind may then become detrimental.

Increased upwelling and mixing are generally reflected in lower sea surface temperatures, as is increased offshore transport due to its linkage to upwelling. Increased stability, or onshore transport of oceanic surface waters in a coastal upwelling region, tends to be reflected in warmer sea surface temperature. Thus, temperature is often found to be correlated with year class success. However the recent results call attention to the fact that the relationship may not be direct but only a reflection of the interaction of dynamic processes. Certainly, a pelagic fish would generally be able to compensate for any direct detrimental effects of anomalous temperatures merely by adjusting its depth level. For example, the anchovy inhabits the surface layer off Patagonia, which is toward the poleward end of its range. However, in the Southeastern Brazilian Bight, which is toward the tropical end of its range, it is found within or beneath a shallow thermocline and at the surface only within cool plumes of recently upwelled water (Matsuura et al., 1985). Thus temperature alone appears to be an uncertain and somewhat precarious indicator of environmental effects on year class success.

We are finding that tropical outbreaks (e.g, El Nino) and other instances of anomalous dominance of tropical waters and conditions (e.g., lack of normal penetration of productive temperate water masses into the coastal habitat off Southeastern Brazil) appear to be generally detrimental to local reproductive success. However, rather than being attributable to direct effects of the associated warm temperatures, the detrimental effects are most often ascribed to suppression of the enrichment factor during these episodes. Other types of warm anomaly often appear to favor reproductive success of anchovies and sardines (Bakun, in press).

REFERENCES CITED

Alheit, J., J. de Ciechomski, C. Ebel, M. Ehrlich, J.-C. Elgue, L. Djurfeldt, G. Mantero, Y. Matsuura, H. Mianzan, W. Nellen, C. Odebrecht, F. Ramirez, R. Sanchez, G. Shaffer and M.D. Vinas 1991. SARP studies on Southwest Atlantic anchovy, Engraulis anchoita, off Argentina, Uruguay and Brazil. ICES C.M. 1991 / L:46

Anon. 1983. Workshop on the IREP Component of the IOC Programme on Ocean Science in Relation to Living Resources (OSLR). IOC Workshop Rep. 33. Intergovernmental Oceanographic Commission, Unesco, Paris. 51pp.

Anon. 1984. IOC-FAO Guiding Group of Experts on the Programme of Ocean Science in Relation to Living Resources, First Session. Reports of Meetings of Experts and Equivalent Bodies SC-84/WS/18. Intergovernmental Oceanographic Commission, Unesco, Paris. 34pp.

Anon. 1987. IOC-FAO Guiding Group of Experts on the Programme of Ocean Science in Relation to Living Resources, Second Session.Reports of Meetings of Experts and Equivalent Bodies SC-87/WS/41. Intergovernmental Oceanographic Commission, Unesco, Paris. 37pp.

Anon. 1989a. Second IOC Workshop on Sardine / Anchovy Recruitment Project (SARP) in the Southwest Atlantic. IOC Workshop Report No. 65. Intergovernmental Oceanographic Commission, Unesco, Montevideo, Uruguay 21-23.August 1989.

Anon. 1989b. IOC Workshop Report of the Expert Consultation on the Sardine/Anchovy Recruitment Programme (SARP). IOC Workshop Rep. 66. Intergovernmental Oceanographic Commission, Unesco, Paris.

Anon. 1990. IOC-FAO/OSLR Ad hoc Group of Experts on Harmful Algal Blooms, Paris, 31 January - 2 February 1990. IOC/INF-817. Intergovernmental Oceanographic Commission, Unesco, Paris. 23 pp. + 4 annexes.

Bakun, A. 1989. Recruitment in fishery resources and its relation to environment: Accessible pathways to greater insight. pp. 25-34. In: Memorias del Simposio International de los Recursos Vivos y las Pesquerias en el Pacifico Sudeste, Via del Mar, 9-13 mayo, 1988. Rev, Pacifico Sur (Numero Especial). Comision Permanente del Pacifico Sur (CPPS).

Bakun. A. In press. The California Current, Benguela Current, and Southwestern Atlantic Shelf ecosystems: a comparative approach to identifying factors regulating biomass yields. In: K. Sherman, L.M. Alexander and B. Gold (eds.) Stress Mitigation and Preservation of Large Marine Ecosystems. American Association for the Advancement of Science.

Bakun, A. and R.H. Parrish. 1990. Comparative studies of coastal pelagic fish reproductive habitats: the Brazilian sardine (Sardinella aurita). J. Cons. Explor. Mer. 46: 269-283.

Bakun, A. and R.H. Parrish. 1991. Comparative studies of coastal pelagic fish reproductive habitats: the anchovy (Engraulis anchoita) of the southwestern Atlantic. J. Cons. int. Explor. Mer. (In press, August 1991 issue).

Buckley, L.J. 1984. RNA-DNA ratio an index of larval fish growth in the sea. Mar. Biol. 80: 291-298.

Campana, S.E. and Neilson, J.D. 1985. Microstucture of fish otoliths. Can. J. Fish. Aquat. Sci. 42, 1014-1032.

Cury, P. and Roy, C. 1989. Optimal Environmental window and pelagic fish reproductive success in upwelling areas.Can. J. Fish. Aquat. Sci. 46, 670-680.

Gutierrez, E. and Morales-Nin, B. 1986. Time series of daily growth in Dicentrarchus labrax L. otoliths. J. Exp. Mar. Biol. Ecol. 103: 163-179.

Hunter, J.R.1981. Feeding ecology and predation of marine fish larvae, p. 33-79. In R. Lasker (ed.) Marine Fish Larvae. Wash. Sea Grant. Program, Univ. Washington Press, Seattle, London. 131 p.

Matsuura, Y., Amaral, J.C., Sato, G., and Tamassia, S.T.J. 1985. Ocorrencia de peixes pelagicos e a estrutura oceanografica da regiao entre o Cabo de Sao Tome (RJ) e Cananeia (SP), em Jan-Fev/1979. Ser. Doc. Tec., PDP/SUDEPE, Brasilia, no.33, p3-70.

Mayr, E. 1982. The Growth of Biological Thought. Harvard Univ. Press, Cambridge, Mass. 974pp.

Mendelssohn, R. and Mendo, J. 1987. Exploratory analysis of anchoveta recruitment off Peru and related environmental series, p. 294-306. In D. Pauly and I. Tsukayama (eds.) The Peruvian Anchoveta and Its Upwelling Ecosystem: three Decades of Change. ICLARM Studies and Reviews 15. Instituto del Mar del Peru (IMARPE), Callao, Peru; Deutsche Gesellschaft fur Technische Zusammenarbeit (GTZ), GmbH, Eschborn, Federal Republic of Germany; and International Center for Living Aquatic Resources Management (ICLARM), Manila, Philippines. 351 pp.

Methot, R.D., Jr. Seasonal variation insurvival of larval northern anchovy (Engraulis mordax) estimated from the age distribution of juveniles. Fish. Bull., U.S. 81: 741-750.

Pannella, G. 1971. Fish otoliths: daily growth rings and periodical patterns. Science 173: 1124-1127.

Parrish, R.H., Bakun, A., Husby, D.M. and Nelson, C.S.1983. Comparative climatology of selected environmental processes in relation to eastern boundary current pelagic fish reproduction. p.731-778. In: G.D. Sharp and J. Csirke (eds.) Proceedings of the Expert Consultation to Examine Changes in Abundance and Species Composition of Neritic Fish Resources. FAO Fish. Rep. 291. 1224pp.

Pauly, D. and Tsukayama, I., (eds.) 1987. The Peruvian Anchoveta and Its Upwelling Ecosystem: Three Decades of Change.ICLARM Studies and Reviews 15. Instituto del Mar del Peru (IMARPE), Callao, Peru; Deutsche Gesellschaft fur Technische Zusammenarbeit (GTZ) GmbH, Eschborn, Federal Republic of Germany; and International Centerfor Living Aquatic ResourcesManagement (ICLARM), Manila, Philippines. 351pp.

Pauly, D., Muck, P., Mendo, J., and Tsukayama, I., (eds.) 1989. The Peruvian Upwelling Ecosystem: Dynamics and Interactions. ICLARM Conference Proceedings 8. Instituto del Mar del Per (IMARPE), Callao, Peru; Deutsche Gesellschaft fr Technische Zusammenarbeit (GTZ), GmbH, Eschborn, Federal Republic of Germany; and International Center for Living Aquatic Resources Management (ICLARM), Manila, Philippines. 438pp.

Roy, C. 1990. Reponses des stocks de poissons pelagiques a la dynamique des upwellings en Afrique de L'Ouest: analyse et modelisation. These de Doctorat. Universite de Bretagne Occidentale, Brest, France. 149 pp.

Roy, C., Cury, P., Fontana, A. and Belveze, H. 1989. Statgies spatio-emporelles de la reproduction des clupids des zones d'upwelling d'Afrique de l'Ouest. Aquat. Living Resour. 2: 21-29.

Roy, C., Cury, P. and Kifani, S. 1991. Optimal environmental window and pelagic fish reproductive strategy in upwelling areas. International Symposium on Benguela Trophic Functioning. Capetown, 8-13 September 1991. 26 pp. (in manuscript form).

Sinclair, M. 1987. Marine Populations. Univ. Washington Press, Seattle and London. 252 pp.

Theilhacker, G.H. 1986. Starvation-induced mortality of young sea-caught jack mackerel, Trachurus symetricus, determined with histological and morphological methods. Fish. Bull., U.S.

Theilhacker, G.H., Kimball, A.S. and Trimmer, J.S. 1986. Use of ELISPOT immunoassay to detect euphasid predation on larval anchovy. Mar Ecol. Prog. Ser. 30: 127-131.

Valenzuela, G., J. Alheit, S.H. Coombs and R. Knust. 1991 Spawning patterns of sprat and survival chances of sprat larvae in relation to frontal systems in the German Bight.
ICES C.M.1991/L:45

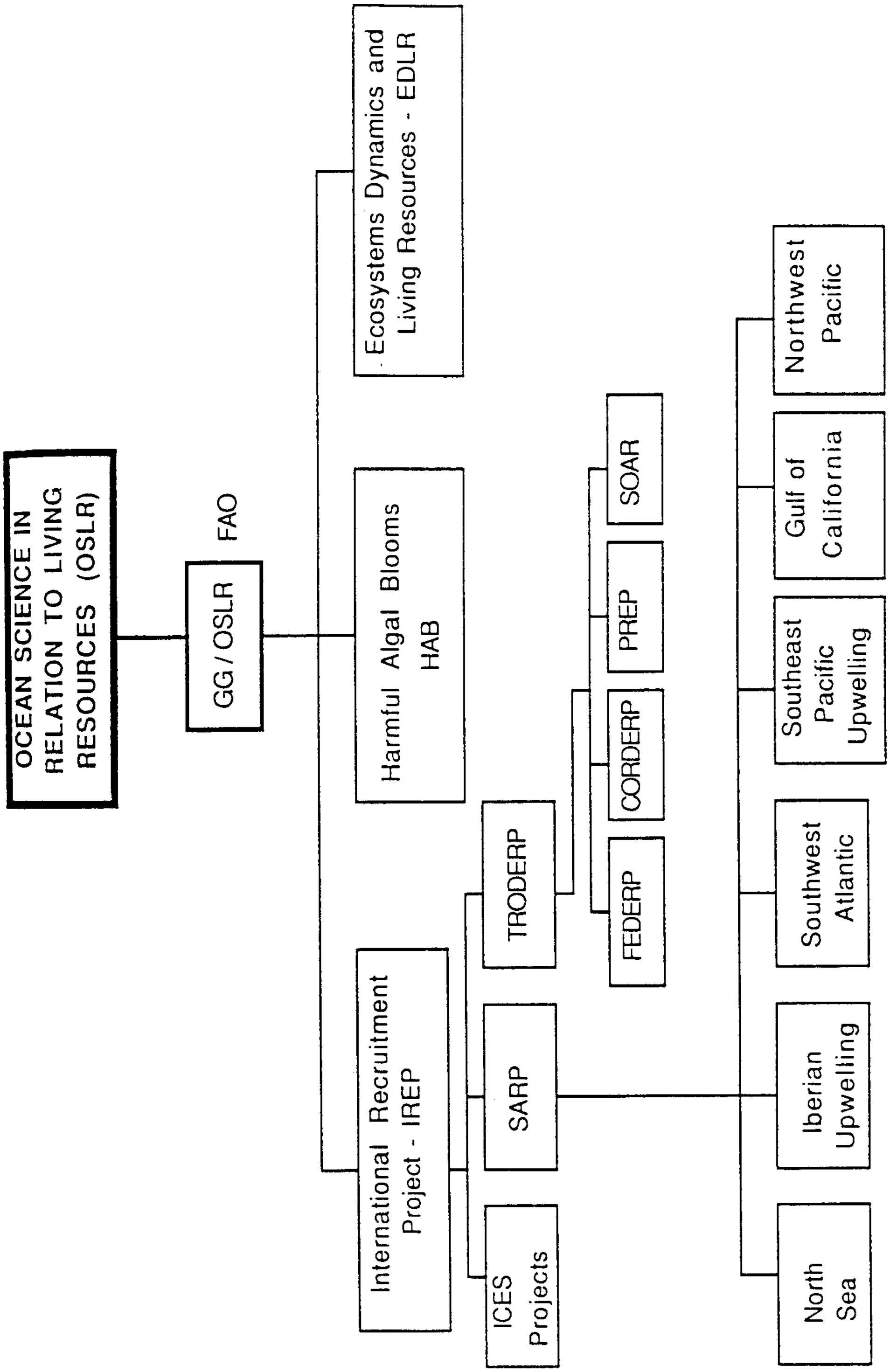

Fig.1 OSLR and its components

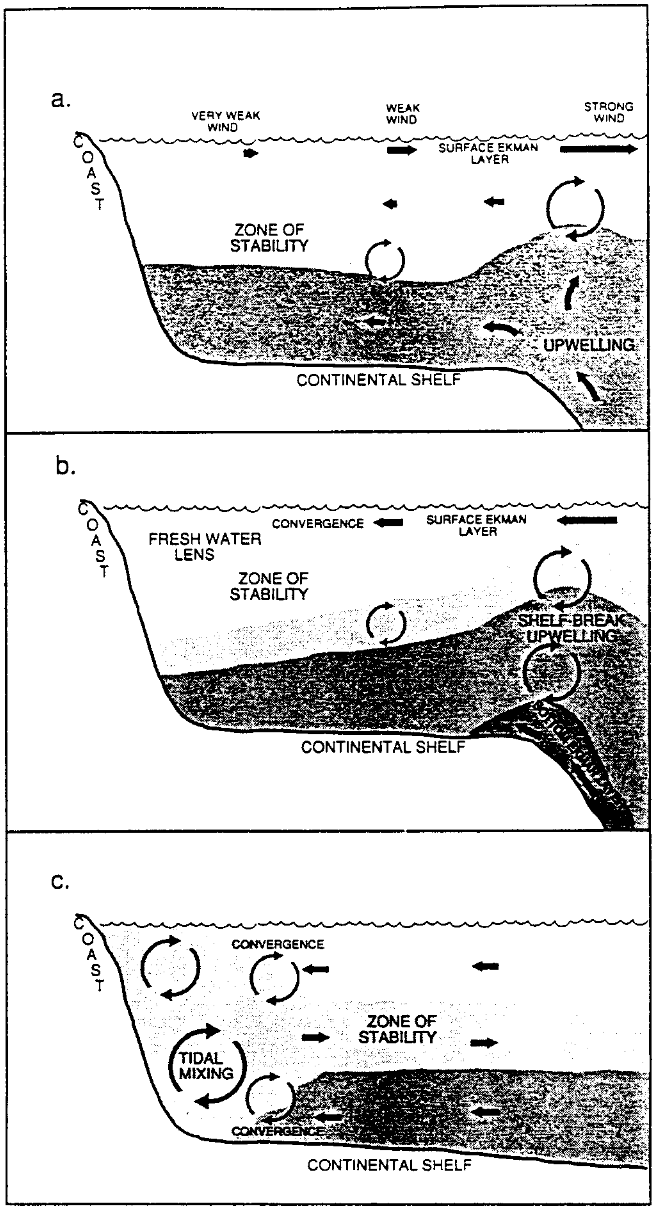

Figure 2. Schematic diagrams of environmental configurations prominent in reproductive strategies of *Engraulis anchoita*. Heavier shading connotes greater water density. Wider arrows indicate mean water transport; lengths are scaled to suggest relative magnitudes. Linked circlular pairs of arrows indicate mixing processes; their sizes are scaled to suggest relative intensities of mixing: (a) Within a coastal indentation in a wind-driven coastal upwelling regime (i.e., the Brazilian Bight; also descriptive of the Southern California Bight in the northeastern Pacific and other eastern ocean anchovy habitats.). (b) Onshore wind-driven transport over a wide continental shelf with upwelling at the shelf break and fresh water runoff rom the continent (i.e., extreme north coast of Argentina, coast of Uruguay and Brazilian coast to north of Rio Grande). (c) A shelf-sea front system driven by tidal mixing (i.e., the Patagonian shelf in the vicinity of Península Valdés; also descriptive of similar frontal systems in the North Sea, the Gulf of Maine, etc.).