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# 1 History of international co-operation in research

*Jürgen Alheit and Andrew Bakun*

Over the last 25 years, since about 1980, international co-operation in research on small pelagic schooling fish with pelagic eggs, such as anchovy, sardine, sprat, and sardinella focused, first on processes determining recruitment variability and, then, since the mid 1990s, on the impact of climate variability on ecosystems dominated by small pelagics. Recruitment research was carried out to a large extent under the umbrella of the Sardine–Anchovy–Recruitment Program (SARP) within the Ocean Science in Relation to Living Resources Program (OSLR) run jointly by IOC[1] and FAO[2] and the Climate and Eastern Ocean Systems project (CEOS) conducted by a variety of research institutions.

Lack of scientific understanding of the mechanisms regulating recruitment was widely recognized in the 1980s (and still is) as the key unsolved scientific problem currently hindering effective management of small pelagic fish populations. Their collapses such as the Californian sardine or the Peruvian anchovy have had enormous negative economic and social effects on fishing nations which might have been avoided had there been the opportunity to predict recruitment. Consequently, several international and national initiatives were started in the 1980s to understand the relationship between environmental processes and fish recruitment. At this point, Reuben Lasker's "stable ocean hypothesis" (Lasker, 1975, 1978) had suddenly caught the attention of the fisheries scientific community, and provided a major conceptual basis for motivating and planning the early activity. Simultaneously, two new technologies, the "Daily Egg Production Method" (DEPM) (Lasker, 1985) and a technique for daily age and growth estimates based on measuring and counting daily marks laid down on larval fish otoliths (Methot, 1983), were under development in Lasker's laboratory. By increasing the temporal resolution of demographic studies on fish larvae, these appeared to offer promising new ways to seek improved understanding of fish recruitment variability.

At its 11th Assembly in 1979, the IOC passed resolution XI-17 to promote development of plans for major oceanographic studies of the physical–ecological interactions of importance to fishery resource-related problems, including the formation of a "Group of Four" experts (Bakun *et al.*, 1982) to advise on program formulation. FAO and SCOR[3] were asked in the resolution to develop a comprehensive scientific program for OSLR. SCOR and the ACMRR[4] of FAO responded to the IOC request forming Working Group 67 on "Oceanography, Marine Ecology and Living Resources." This group was formed with the aim to develop a proposal for an international recruitment experiment to investigate the relationships between environmental variability and fluctuations of living resources (Barber *et al.*, 1982). The same year, coincidentally, the "Fish Ecology III Conference" in the USA developed a conceptual framework for REX, a "recruitment experiment" (Rothschild and Rooth, 1982). In the meantime, a "Workshop on the Effects of Environmental Variation on Survival of Larval Pelagic Fishes" (IOC, 1981) was organized in Lima as a contribution to OSLR by FAO and the Peruvian–German technical aid project PROCOPA[5] (Pauly and Tsukayama, 1987) was established at the Peruvian fisheries institute, IMARPE.[6] These efforts finally converged in a joint "Ocean Science in Relation to Living Resources" (OSLR) program, which was co-sponsored by IOC and FAO, the main focus of which was to be the processes governing recruitment to fish populations (IOC, 1983).

The DEPM is a fisheries-independent method to estimate the spawning biomass of small pelagics, including the associated statistical precision of the estimated value. It was developed at the Southwest Fisheries Science Center in La Jolla under the leadership of Reuben Lasker (Lasker, 1985). The breakthrough for its development was the finding of Hunter and Goldberg (1980) that the age of postovulatory follicles can be used to estimate the daily proportion of spawning females. After its first application to the Californian anchovy in 1980, it was successfully carried out for the Peruvian anchovy (Santander *et al.*, 1984) and is now widely used in South America, South Africa and Europe (Alheit, 1993; Stratoudakis *et al.*, 2006). The application of this method for spawning biomass estimates requires extensive knowledge of reproductive parameters such as batch fecundity, spawning frequency and daily egg mortality and, consequently,

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as a by-product, has furthered international co-operation in recruitment research.

The Lima Workshop in 1980 (IOC, 1981) brought together an international group of recruitment researchers with scientists working on reproduction and recruitment of the Peruvian anchovy and allowed comparisons of recruitment processes between small pelagics in the Humboldt and California currents. Important outcomes of this meeting were the first quantitative estimate of egg cannibalism (MacCall, 1980) and the first sketch of the "Basin Model," an attempt to explain population dynamics of small pelagics based on an "optimal free distribution" interrelationship between geography, movement, and growth dynamics at the population level (MacCall, 1990). It also produced an early comprehensive review (Bakun and Parrish, 1981) of empirical and conceptual frameworks for applying available environmental data to inferring the primary causative factors in recruitment variability, including the suggestion for the formulation that became known as "Lasker windows" (Peterman and Bradford, 1987; Pauly, 1989).

A most authoritative account on the ecology of marine fish larvae with a focus on anchovy and sardine was published in 1981 by four eminent fish larval researchers from the Southwest Fisheries Center in La Jolla: R. Lasker, J.R. Hunter, H.G. Moser and P.E. Smith (Lasker, 1981). It contains a thorough discussion of the role of larval starvation and predation on fish larvae for recruitment and was a pacemaker for the Sardine–Anchovy Recruitment Program, SARP.

The 12th Assembly of IOC in 1982 adopted the OSLR concept as a long-term program. It promoted coordinated regional research projects to elucidate factors determining recruitment to fish populations with the International Recruitment Project (IREP) as the initial main focus of OSLR. The Assembly established a Guiding Group of Experts for the OSLR Program and initiated the "Workshop on the IREP Component of the IOC Program on Ocean Science in Relation to Living Resources" in Halifax, Canada, in 1983 (IOC, 1983). This workshop, under the chairmanship of R. Beverton, recommended (i) direct investigations of the early life history, particularly SARP, including, *inter alia*, the otolith ring method, the DEPM and relevant oceanographic measurements (IREP Minimum Plan) and (ii) indirect (inferential) approaches by making available the wealth of long-term time series, including relevant information, normally peripheral to the marine field, such as climatic and meteorological data that could help to elucidate the physical and biological coupling controlling recruitment at different scales.

At its first meeting in Paris in 1984, the Guiding Group of Experts for OSLR recommended SARP as the pilot program for IREP. The basic SARP concept involved repeated surveys of larval production during the extended spawning season of small pelagic fish. These surveys were coupled with a comprehensive physical and biological oceanographic sampling program designed to determine variations in conditions related to larval starvation (Lasker, 1981), predation (Lasker, 1981), advection, physiological stress, and other factors leading to mortalities of early life stages. Later in the season, surviving juveniles were to be sampled and their birthdate frequencies determined using daily otolith growth rings (Methot, 1983). These frequencies, when compared with the observed larval production rates corresponding to the various birthdates, provide an index of variation in survival rate of early life stages. This is compared to variations in environmental processes to identify the mechanisms that best explain the observations. The SARP concept therefore, while basically an empirical field approach, offered a major departure from previous empirical approaches to study the recruitment problem in its ability to address higher frequency "within-year" variability. Whereas previous empirical attempts have been defeated by the necessity to combine shorter scale variations, having various causes, into single annual composites, SARP offered the possibility of resolving different causes and effects on the time scales on which they actually act to determine net reproductive success.

Accordingly, a number of regional field-going SARP components (direct investigations) were initiated to test the several recruitment hypotheses (starvation, predation, advection) (Bakun *et al.*, 1991): a US SARP in the California Current on anchovy, an Iberian SARP on anchovy and sardine in a joint Spanish–Portuguese–US project (López-Jamar and Garcia, 1992), a SW Atlantic SARP on anchovy and sardine in a co-operation by Brazil, Uruguay, Argentina, Germany, and Sweden (Alheit *et al.*, 1991) and a EURO-SARP[7] project on anchovy, sardine, and sprat in European waters run by scientists from Germany, Spain, Portugal, and the UK (Alheit and Bakun, 1991; Valenzuela *et al.*, 1991). A major aspect of SARP's scientific rationale was the application of the comparative method of science, whereby the multiple expressions of the problem afforded by various species groups inhabiting different regional ecosystems were considered as "proxy replicates" of similar processes, gaining additional explanatory power (degrees of freedom), to sort out the complex interacting mechanisms involved in recruitment variability. The comparative scientific method (Bakun, 1996) is particularly appropriate to problem areas where experimental controls are unavailable. This is one of the reasons why a coordinated international scientific SARP effort was thought to offer large potential benefits. Whereas all these SARP initiatives provided a wealth of new important information on the life history of small pelagics, it has to be admitted that no breakthrough was made in understanding and predicting recruitment. The main constraint was that no regional initiative had sufficient funding to carry out the complete SARP program. On the other hand, the increase in temporal resolution for the study of larval demography was insufficient by itself to explain differential larval mortality without a comparable increase in resolution in the observation of the potentially causally related oceanographic variables. A serious blow was delivered to the SARP initiative when the most promising US SARP project was stopped suddenly by federal budget restrictions.

Progress was made using inferential methods as suggested by the Guiding Group of Experts. Scientists from the Peruvian–German aid project PROCOPA teamed up in 1981 with an international group to rescue, assemble, and analyze on a monthly basis long-term time series from the period 1953–1982 of all measured variables likely to have affected the Peruvian anchovy and its ecosystem. This resulted in an extremely rich data archive captured in two books (Pauly and Tsukayama, 1987; Pauly *et al*., 1989), which have served as an important source in later studies on the impact of climate variability on the Humboldt Current and its small pelagic fish resources (e.g. Alheit and Bernal, 1993; Alheit and Niquen, 2004).

A meeting which proved to be a milestone in small pelagics research was the "Expert Consultation to Examine Changes in Abundance and Species Composition of Neritic Fish Resources" organized by G. Sharp and J. Csirke of FAO in 1983 in San José, Costa Rica (FAO, 1983). This meeting gathered most of the information on ecology and fisheries of the large stocks of small pelagics relevant then for SARP and later for Small Pelagic Fish and Climate Change, SPACC, a regional project of the GLOBEC[8] program, particularly from developing countries, and still serves as a rich source of information. A key paper which was an enormous stimulus for climate variability research within SPACC even 20 years thereafter was given by T. Kawasaki (1983) on synchronous large-scale fluctuations of the three sardine stocks in the Pacific.

The CEOS project (Durand *et al*., 1998) was an international collaborative study of potential effects of global climate change on the living resources of the highly productive eastern ocean upwelling ecosystems and on the ecological and economic issues directly associated with such effects. CEOS involved a variety of research institutions, notably NOAA/NMFS,[9] ORSTOM,[10] and ICLARM,[11] and was devoted to a study of the potential effects of global change on the resources of upwelling systems through identification of global and local effects impacting on these systems. A major focus of the study was the clupeoid fishes (such as anchovy and sardine). The main objectives were: (1) to assemble, summarize, and analyze the data record of the four decades since 1960 regarding the four eastern boundary upwelling ecosystems and other upwelling areas, (2) to apply the comparative method to identify key physical processes and ecosystem responses, and (3) to resolve underlying global-scale trends that in each individual regional system may be obscured by local interannual and interdecadal variability. Major ideas emanating from the CEOS project are (i) the "Ocean Triad Concept" of Bakun (1996) which suggests that an optimal combination of three physical processes (enrichment, concentration, retention) provides an optimal situation for successful fish recruitment and (ii) the "Optimal Environmental Window" hypothesis (Cury and Roy, 1989), which is a dome-shaped response curve of population growth to increasing intensity of wind stress-associated mixing and transport. The CEOS project paved the way for SPACC, as it started to look not only at recruitment, but also at climatic effects on the dynamics of small pelagics.

SARP had established itself in the international science community so much that it opened access to national funding to carry out recruitment research. Although the large international funding hoped for in the mid 1980s never materialized, several SARP projects were established successfully using national funding. However, due to its complexity the recruitment problem could not be solved by SARP. It became clear in the early 1990s that (i) recruitment studies must be conducted from an ecosystem point of view and that (ii) climatic effects play a major role in population fluctuations of small pelagics leading to so-called regimes (Lluch-Belda *et al*., 1992).

Consequently, SARP and CEOS researchers widened the scope of their investigations accordingly and jointly created in 1994 the SPACC (Small Pelagic Fishes and Climate Change) project which became one of the four core projects of GLOBEC of the IGBP (International Geosphere Bioshere) Program. Science (Hunter and Alheit, 1995) and Implementation (Hunter and Alheit, 1997) plans of SPACC were developed at three international meetings in La Paz, Mexico (1994), Swakopmund, Namibia (1995), and Mexico City (1996). SPACC's objective is to clarify the effect of climate variability on the population dynamics of pelagic fish by comparing the ecosystems that support such populations (Hunter and Alheit, 1995). The goals are (i) to describe the characteristics and variability of the physical environment and of zooplankton population dynamics and their impact on small pelagic fish populations in each key ecosystem and (ii) to improve understanding of the nature and causes of long-term changes in these ecosystems. SPACC uses two general approaches to meet these goals:

(1) Retrospective studies, wherein ecosystem histories are reconstructed by means of fishery data and zooplankton and other time series and paleoecological data. This initiative was started in 1994 when SPACC researchers analyzed long-term data from ecosystems rich in small

pelagics, together with SCOR Working Group 98 on "World-wide Large-Scale Fluctuations of Sardine and Anchovy Populations" (Schwartzlose *et al*., 1999).

(2) Process studies in which cause-and-effect linkages between zooplankton, fish population dynamics and ocean forcing are inferred from comparisons of standard measurements made in different ecosystems.

The long-range goal is to develop predictive scenarios for the fate of small pelagic fish populations. Results of the SPACC project are presented in the following chapters.

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NOTES

1 Intergovernmental Oceanographic Commission.
2 Food and Agriculture Organization.
3 Scientific Committee on Oceanic Research.
4 Advisory Committee of Experts on Marine Resources Research.
5 Peruvian–German Cooperative Program for Fisheries Investigations.
6 Instituto del Mar del Perú.
7 European Sardine–Anchovy Recruitment Program.
8 Global Ocean Ecosystem Dynamics.
9 US National Oceanic and Atmospheric Administration/ National Marine Fisheries Service.
10 Office de la Recherche Scientifique et Technique Outre Mer.
11 International Center for Living Aquatic Resources Management.

REFERENCES

Alheit, J. (1993). Use of the daily egg production method for estimating biomass of clupeoid fishes: a review and evaluation. *Bull. Mar. Sci.* **53**: 750–767.

Alheit, J. and Bakun, A. (1991). Reproductive success of sprat (*S. sprattus*) in German Bight during 1987. *ICES C.M.* 1991/L:44.

Alheit, J. and Bernal, P. (1993). Effects of physical and biological changes on the biomass yield of the Humboldt Current ecosystem. In K. Sherman, L.M. Alexander, and B.D. Gold (eds.), *Large Marine Ecosystems – Stress, Mitigation and Sustainability*, pp. 53–68. Washington, DC: American Association for the Advancement of Science, 376 pp.

Alheit, J. and Niquen, M. (2004). Regime shifts in the Humboldt Current ecosystem. *Prog. Oceanogr.* **60**: 201–222.

Alheit, J., Ciechomski, J., Djurfeldt, L. *et al.* (1991). SARP studies on the Southwest Atlantic anchovy, *Engraulis anchoita*, off Argentina, Urugay and Brazil. *ICES C.M./L*: 46, 32 pp.

Bakun, A. (1996). *Patterns in the Ocean: Ocean Processes and Marine Population Dynamics.* University of California, La Jolla: California Sea Grant College System, 323 pp.

Bakun, A. and Parrish, R.H. (1981). Environmental inputs to fishery population models for eastern boundary current regions. In *Workshop on the Effects of Environmental Variation on Survival of Larval Pelagic Fishes, Lima, 20 April – 5 May 1980,* Sharp, G.D., ed. Intergovernmental Oceanographic Commission, **Unesco**, Paris, Workshop Rep. 28, p. 67–104.

Bakun, A., Beyer, J., Pauly, D., Pope, J.G., and Sharp, G.D. (1982). Ocean sciences in relation to living resources. *Can. J. Fish. Aquat. Sci.* **39**: 1059–1070.

Bakun, A., Alheit, J., and Kullenberg, G. (1991). The Sardine-Anchovy Recruitment Project (SARP): rationale, design and development. *ICES C.M. 1991/L: 43.*

Barber, R.T., Csirke, J., Jones, R., Lasker, R., Parrish, R., and Tomczak., M. (1982). *Report of SCOR/ACMRR Working Group 67, Oceanography, Marine Ecology and Living Resources.* SCOR/WG-67, 21pp.

Cury, P. and Roy, C. (1989). Optimal environmental window and pelagic fish recruitment success in upwelling areas. *Can. J. Fish. Aquat. Sci.* **46**: 670–680.

Durand, M.-H., Cury, P., Mendelssohn, R., Roy, C., Bakun, A., and Pauly, D. (eds.) 1998. *Global Versus Local Changes in Upwelling Systems.* Paris: ORSTOM editions, 594 pp.

FAO (1983). Proceedings of the Expert Consultation to Examine Changes in Abundance and Species Composition of Neritic Fish Resources. *FAO Fish. Rep.* **291**, 1224 pp.

Hunter, J.R. and Alheit, J. (1995). *International GLOBEC Small Pelagic Fishes and Climate Change Program*. GLOBEC Report No. 8, 72 pp.

Hunter, J.R. and Alheit, J. (1997). *International GLOBEC Small Pelagic Fishes and Climate Change Program. Implementation Plan*. GLOBEC Report No. 11, 36 pp.

Hunter, J.R. and Goldberg, S.R. (1980). Spawning incidence and batch fecundity in northern anchovy, *Engraulis mordax. Fish. Bull. (US)* **77**: 641–652.

IOC (1981). *Workshop on the Effects of Environmental Variation on Survival of Larval Pelagic Fishes, Lima, 20 April– 5 May 1980.* G.D. Sharp (ed.). Intergovernmental Oceanographic Commission, **Unesco**, Paris, Workshop Rep. 28, 323 pp.

IOC (1983). *Workshop on the IREP Component of the IOC Programme on Ocean Science in relation to Living Resources (OSLR).* Intergovernmental Oceanographic Commission, **Unesco**, Paris, Workshop Rep. 33, 17 pp.

Kawasaki, T. (1983). Why do some pelagic fishes have wide fluctuations in their numbers? – Biological basis of fluctuations from the viewpoint of evolutionary ecology. In *Proceedings of the Expert Consultation to Examine Changes in Abundance and Species Composition of Neritic Fish Resources*, Sharp, G. and Csirke, J., eds. *FAO Fish. Rep.* **291**: 1065–1080.

Lasker, R. (1975). Field criteria for survival of anchovy larvae: the relation between inshore chlorophyll maximum layers and successful first feeding. *Fish. Bull. (US)* **73**: 453–462.

Lasker, R. (1978). The relation between oceanographic conditions and larval anchovy food in the California Current: identification of factors contributing to recruitment failure. *Rapp. P.-v. Réun. Cons. Int. Explor. Mer.* **173**: 212–230.

Lasker, R. (ed.) (1981). *Marine Fish Larvae: Morphology, Ecology and Relation to Fisheries*. Seattle: University of Washington Press, 131 pp.

Lasker, R. (ed.) (1985). *An egg production method for estimating spawning biomass of pelagic fish: application to the northern anchovy (Engraulis mordax).* NOAA Techn. Rep. NMFS 36, 99 pp.

Lluch-Belda, D., Schwartzlose, R.A., Serra, R. *et al.* (1992). Sardine and anchovy regime fluctuations of abundance in four regions of the world oceans: a workshop report. *Fish. Oceanogr.* **1**: 339–347.

López-Jamar, E. and Garcia, A. (1992). Foreword. *Boletín Instituto Espanol de Oceanografía* **8**: 3–4.

MacCall, A.D. (1980). The consequences of cannibalism in the stock-recruitment relationship of planktivorous pelagic fishes such as *Engraulis*. In *Workshop on the Effects of Environmental Variation on the Survival of Larval Pelagic Fishes*, G. Sharp, ed. Intergovernmental Oceanographic Commission, **Unesco**, Paris, Workshop Report 28, pp. 201–220.

MacCall, A.D. (1990). *Dynamic Geography of Marine Fish Populations*. Seattle: University of Washington Press, 153 pp.

Methot, R.D. (1983). Seasonal variation in survival of larval anchovy, *Engraulis mordax*, estimated from the age distribution of juveniles. *Fish. Bull. (US)* **81**: 741–750.

Pauly, D. (1989). An eponym for Reuben Lasker. *Fish. Bull. (US)* **87**: 383–384.

Pauly, D. and Tsukayama, I. (eds.) (1987). *The Peruvian anchoveta and its upwelling ecosystem: Three decades of change*. ICLARM Studies and Reviews **15**, 351 pp.

Pauly, D., Muck, P., Mendo, J., and Tsukayama, I. (eds.) (1989). *The Peruvian upwelling ecosystem: Dynamics and interactions*. ICLARM Conference Proceedings **18**, 438 pp.

Peterman, R.M. and Bradford, M.J. (1987). Wind speed and mortality rate of a marine fish, the northern anchovy *(Engraulis mordax*). *Science* **235**: 354–356.

Rothschild, B.J. and Rooth, C. (eds.) (1982). *Fish Ecology III. A Foundation for REX, A Recruitment Experiment*. University of Miami Tech. Rep. 82008; Miami, Florida, USA, 389 pp.

Santander, H., Alheit, J., and Smith, P.E. (1984). Estimación de la biomasa de la población desovante de anchoveta peruana, *Engraulis ringens*, en 1981 por aplicacion del "Método de Producción de Huevos". *Boletin Instituto del Mar del Perú-Callao* **8**: 208–250.

Schwartzlose, R.A., Alheit, J., Bakun, A. *et al.* (1999). Worldwide large-scale fluctuations of sardine and anchovy populations. *S. Afr. J. Mar. Sci.* **21**: 289–347.

Stratoudakis, Y., Bernal, M., Ganias, K., and Uriarte, A. (2006). The daily egg production method: recent advances, current applications and future challenges. *Fish Fish.* **7**: 35–57.

Valenzuela, G.J., Alheit, J., Coombs, S., and Knust, R. (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.*

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# 2 A short scientific history of the fisheries

*Alec D. MacCall*

CONTENTS



## Summary

This chapter briefly summarizes the history of scientific understanding of the fluctuations of small pelagic fishes and fisheries. The classical quantitative models underlying modern fishery analysis and management were developed in the 1950s and 1960s. Although California and Japan had previously experienced collapses of major fisheries for small pelagics in the 1940s and 1950s, it was the collapse of the "scientifically managed" Peruvian anchoveta fishery in the early 1970s that drew worldwide attention to the problem of collapsing small pelagic fisheries. The inability of the anchoveta to regain its former levels of productivity cast doubt on the classical equilibrium fishery models. In the late twentieth century, substantial progress was made toward understanding the environmental influences on these fishes. Some of the major environmental influences (which often may not be specifically identified) fluctuate at interdecadal time scales, giving rise to prolonged periods of high and low fish productivity, abrupt transitions including collapses, global teleconnections and phase relationships. These so-called "regimes" have recently become a major topic of research in fishery science. Despite scientific progress in understanding many facets of these fisheries and their fluctuations, there still is no accepted theory of the fishery–oceanographic dynamics of small pelagic fishes that links their commonly shared properties and that provides the predictive capability needed for ecosystem-based management.

## Introduction

This history of small pelagic fisheries focuses specifically on the development of a scientific understanding of their dynamics, especially regarding their problematic fluctuations in abundance. Fréon *et al*. (2005) describe several distinct historical periods in the study of pelagic fish stocks, a system that is adopted for this review. During the pre-1900 "mother nature period", oceanic fish stocks tended to be regarded as inexhaustible, and little attention was given to the patterns and dynamics of their fluctuations. Fréon *et al*. do not give a name to the first half of the twentieth century, but it could be called the "developmental period." They describe the period 1900–1950 as being a time of industrial development, the beginnings of scientific studies, and growing awareness of environmental influences. The third quarter of the twentieth century, which could be called "the classical period" saw the development of the classical models of fish population dynamics, and is where this brief review begins.

The fourth quarter of the twentieth century was aptly termed "the doubt period" by Fréon *et al*. (2005). Whereas the mathematical models developed during the preceding period had engendered a confidence that good science would lead to high and sustainable yields, a growing worldwide list of fishery collapses (Mullon *et al*., 2005) steadily eroded that confidence. Because ideas and events after 1980 are extensively covered by several other chapters, recent developments are treated more briefly in this chapter.

## The classical period

By the mid twentieth century, there was a widespread perception that fisheries for small pelagics tend to be more prone to collapse than are those for other types of marine fishes. Large fisheries for sardines off Japan (*Sardinops melanosticta*) and California (*S. sagax caerulea*) collapsed during the 1940s. After a long decline, the Hokkaido herring (*Clupea harengus pallasi*) fishery finally collapsed in the mid 1950s, shortly followed by a much more sudden

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collapse of Norwegian herring (*C. harengus harengus*). In the mid 1960s yet another sardine (*S. sagax ocellata*) fishery collapsed, this time off South Africa. All of these stocks appeared to withstand intense exploitation for an extended length of time, but suddenly failed to exhibit the vigorous productivity that characterized their pre-collapse fisheries. There was intense debate (e.g. Clark and Marr, 1955) whether these collapses were due to the effects of fishing, or whether they were unavoidable consequences of environmental fluctuations.

Development of now-classical quantitative theories of fishery dynamics during the 1950s and 1960s provided convincing evidence that marine fish stocks can be depleted by intense fishing even in the absence of environmental perturbations. The monumental treatise by Beverton and Holt (1957) was especially influential, as it demonstrated the analytical power and insights that could be gained from rigorous mathematical modeling of fish populations. Quantitative fishery scientists developed nearly all of the elements of modern fishery analysis between the mid 1950s and mid 1960s. Some landmark contributions during this period include Ricker's (1954) examination of the stock-recruitment relationship, Schaefer's (1954) development of the stock production model, and development of Virtual Population Analysis (VPA) independently by Murphy (1965) and by John Gulland (1965). One of the first modern stock assessments based on VPA was Murphy's (1966) analysis of the California sardine fishery.

In contrast to the problem of "growth overfishing" seen in the North Sea where individual fish were being harvested at too small a size, other ecosystems faced the problem of "recruitment overfishing" whereby intense fisheries remove individuals faster than they could be generated by the parental reproduction (e.g. Cushing, 1973). The notable small pelagic fishery collapses cited above were generally considered to be examples of recruitment overfishing.

A Peruvian fishery for anchoveta (*Engraulis ringens*) developed rapidly during the late 1950s and early 1960s, accelerated by the transfer of existing equipment and expertise from the collapsed sardine industry in California (Radovich, 1981; Ueber and MacCall, 1992). The Peruvian fishery, which quickly became the largest in the world, was also notable as being managed "scientifically" under advice from the United Nations Food and Agriculture Organization (FAO) and a panel of the world's leading fishery scientists using the newly developed kit of mathematical tools. It came as a shock to both the scientific world and the global economy when the anchoveta fishery collapsed in 1972. As had been prophesied by Paulik (1971), the collapse appeared to be the result of intense fishing on a resource made vulnerable by the El Niño conditions in 1972 that concentrated the fish in the nearshore region. The initial sense of shock slowly evolved into a sense of numbness, as following years saw no substantial recovery of the anchoveta resource, despite major reductions in fishing pressure. The problem could no longer be associated simply with the El Niño of 1972. Something had mysteriously changed in the ecosystem. In the early 1970s, sardines (*S. sagax sagax*) unexpectedly appeared in abundances sufficient to support an alternative fishery (see below).

Through the 1970s the conventional viewpoint was strongly based on equilibrium fishing assumptions: If fishing pressure could be reduced sufficiently, it should be possible to rehabilitate these collapsed fisheries. In view of a sustained increase in abundance of California's anchovies (*E. mordax*) in the 1950s following the decline of the sardine, simple ecological competition models allowed the equilibrium fishing view to be extended to a multispecies equivalent whereby competition from anchovies was thought to be the reason for low sardine productivity. In California, fishery managers were being urged to "intentionally overfish" anchovies to assist recovery of the sardine resource (Sette, 1969; McEvoy, 1986). A nearly identical rise in anchovies (*E. capensis*) off South Africa during the 1960s generated similar claims of dynamics driven by inter-species competition (Stander and Le Roux, 1968). Immediately following the anchoveta collapse in South America, sardine abundance increased rapidly in the 1970s, leading to widespread acceptance of some form of sardine–anchovy alternation, usually described as "species replacement." Indeed, the South American fishery on sardines was quickly developing toward levels rivaling those of the previous anchoveta fishery. Sardines formerly had been relatively scarce in Peru and Chile, but coincident with the 1970s' increase in apparent abundance, their range also expanded nearly 1000 km southward to Talcahuano, Chile, where they had never before been seen (Serra, 1983).

A decade after the Peruvian anchoveta collapse, Gulland (1983) still viewed the problem in equilibrium terms, although recognition of the increasing abundance of Peruvian sardines extended his concern to interactions in a multispecies system. Gulland (1983, p. 1019) observed that these pelagic species have been especially susceptible to collapse as the result of recruitment overfishing, but also that the collapse of one species frequently coincided with the rise of another. Notably, he says "The collapses have too often followed a period of very heavy fishing to be due solely to chance or environmental effects, and also the rise of a competing species has now occurred too often to be based on chance alone …"

## The doubt period

Fréon *et al.* (2005) insightfully called the last quarter of the twentieth century "the doubt period." Ushered in by the catastrophic collapse of the Peruvian anchoveta fishery, which had been the largest fishery in the world, this period saw a growing worldwide list of fishery collapses. It seemed that small pelagic fish were especially prone to collapse. However, it should be noted that in hindsight, Mullon *et al.* (2005) recently found that collapses of small pelagics were no more frequent than in other fisheries. More disturbing than the collapses themselves was the frequent lack of recovery relative to the former productivity of those fisheries. Both "the classical period" and "the doubt period" produced significant advances in understanding many of the underlying patterns and mechanisms of pelagic fish fluctuations, but remarkably little progress was made toward integrating those components into a complete theory of small pelagic fish dynamics that had useful predictive power. By the end of the twentieth century it was apparent that small pelagic fish fluctuations presented a scientific puzzle that was far more difficult than anyone had imagined (e.g. Chavez *et al*., 2003).

In contrast to the classical equilibrium fishery models, an alternative, non-equilibrium view was beginning to emerge during the 1970s. Soutar and Isaacs (1969, 1974) developed a remarkable time series of prehistoric sardine and anchovy abundances based on fish scales preserved in laminated anerobic sediments found in a nearshore basin in southern California. The 2000-year paleosedimentary record indicated that unfished sardine abundances have always been highly variable off California, with some virtual disappearances (however, at the coarse resolution of ca. 0.5 million tons) even in the absence of fishing. It was not possible to explain those prehistoric fluctuations in terms of equilibrium models, and the new paleosedimentary evidence was eagerly taken to absolve the fishery of responsibility for the disappearance of the resource: "Nor can the virtual absence of the sardine from the waters off Alta California be considered an unnatural circumstance" (Soutar and Isaacs 1974), Another of Soutar and Isaacs' surprising findings was that there was no indication of anchovy–sardine alternations of abundance in the paleosedimentary time series, despite scientific consensus that the two species were competitors (e.g. Sette, 1969). Probably due to the strong circumstantial pattern of anchovy–sardine alternations recently experienced in fisheries off California, South Africa and South America, the lack of paleosedimentary evidence for sardine–anchovy alternation received little attention.

The pattern of sardine fluctuations implied by the paleosedimentary record could not be reconciled with the conventional equilibrium view of an approximately constant "reference" state of the resource corresponding to an unfished condition (i.e. carrying capacity, in ecological terms). Isaacs (1976), expressed this concern clearly, and coined the term "regime" to describe the tendency of ecosystems to fall into prolonged states and patterns that would suddenly change to a new and different pattern (Box 2.1). The terms "regime" and "regime shift" have become common key words in recent climate-related fisheries and oceanographic publications (Fig. 2.1).

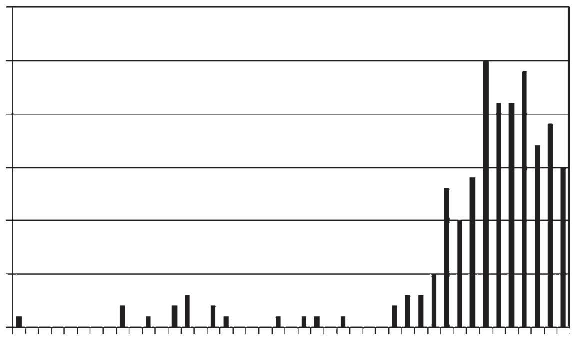

Fig. 2.1. Number of publications containing the keyword "regime" together with "climate" and "fish" or "fisheries" in the *Aquatic Sciences and Fisheries Abstracts* database. Recent years are incomplete.

**Box 2.1. The origin of the "regime" concept**

At the 1973 Symposium of the California Cooperative Oceanic Fisheries Investigations (CalCOFI), John Isaacs (1976) formalized his concern that sardine–anchovy systems may be far less predictable than our simplistic models would suggest. Not only was this was the first use of the term "regime" in its modern fishery meaning but the explanation of what he meant by the term was extraordinarily clear:

"…there are probably a great number of possible regimes and abrupt discontinuities connecting them, flip–flops from one regime to another… Sardines, for example, are either here or not here… There are internal, interactive episodes locked into persistence, and one is entirely fooled if one takes one of these short intervals of a decade or so and decides there is some sort of simple probability associated with it… organisms must respond to more than just fluctuations around some optimum condition…. Fluctuations of populations must be related to these very large alternations of conditions."

An early development in the field of dynamical systems that gained popularity in the 1970s was "catastrophe theory" (Thom, 1993), which provided a useful explanation of the dynamics of fishery collapses. A number of studies had shown that searching behavior by fishermen, especially for surface-schooling fishes, could result in a tendency for catch-per-unit-effort (CPUE) to be insensitive to declines in underlying fish abundance (Paloheimo and Dickie, 1964; Pope and Garrod, 1975; MacCall,

**Box 2.2. Catastrophe theory and fishery collapse**

The classical Schaefer model assumes that abundance (as measured by catch-per-unit-effort, CPUE) declines linearly as fishing effort increases (Fig. 2.2, thin lines). However, experience has shown that the fishing mortality rate generated per fishing effort may increase rapidly when abundance is low. Thus at low abundances, fishermen are able to locate and catch the few remaining fish, so that a small amount of fishing effort can catch a very large fraction of the population. Although the underlying relationship between abundance and fishing mortality rate may still be described by a Schaefer model, the relationship between apparent abundance (CPUE) and nominal fishing effort (e.g., vessel–days) is severely distorted (Fig. 2.2, thick lines). There is now a stable upper equilibrium, and an unstable lower equilibrium. As nominal fishing effort increases, the relationship initially behaves like a Schaefer model, but at some intermediate fishing rate sustainability is no longer possible, resulting in sudden collapse. Rebuilding requires severely reducing fishing effort to where it falls on the left side of the equilibrium line (Fig. 2, upper), where abundance can increase. The associated rebuilding catch is very low.

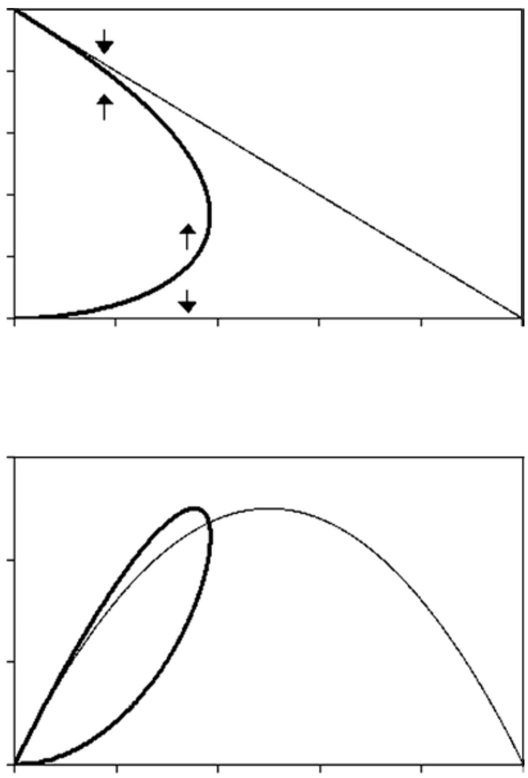

Fig. 2.2. Effect of a population-dependent catchability coefficient on fishery production curves. Thin line: CPUE is proportional to true abundance. Thick line: CPUE varies as the square root of abundance, which is typical in fisheries for small pelagic fish.

1976; Ulltang, 1976). Equivalently, a unit of nominal fishing effort, such as a vessel–day, could generate an ever-increasing fishing mortality rate as stock size becomes small. The role of this mechanism in fishery collapses and its critical importance in management of fisheries for small pelagics was recognized at a 1978 ICES Symposium (Ulltang, 1980). The phenomenon has more recently found to be widespread also in demersal fisheries (Harley, 2002), and is largely due to the effectiveness of modern fish-finding technology. Fox (1974, also reported by Gulland, 1977) incorporated this non-linearity in a production model, and obtained a model akin to a "fold catastrophe" that helped explain fishery collapses and quantified the extreme reductions in fishing pressure needed to rebuild stocks even under equilibrium biological dynamics (Box 2.2).

By the end of the 1970s, fisheries on small pelagics were showing alarming fluctuations around the world. Following the 1960s' collapse of the southern Benguela fishery for sardines, a large fishery developed on the northern Benguela sardine stock off Walvis Bay, but that too collapsed shortly afterward. Anchovies were becoming the dominant small pelagic fish in both subregions of the Benguela system. By the late 1970s, large sardine fisheries had developed in South America and Japan, while at long last there were signs of improvement in sardines off California. The Peruvian anchoveta remained at a low level. In California the anchovy population reached peak abundances earlier in the decade, but decades too late to be explained by competitive release due to lack of sardines (Methot, 1989). A large number of herring stocks in the North Atlantic were in various stages of collapse, with unprecedented fishing bans being imposed on some of them (Jakobsson, 1980; Schumacher, 1980). Fluctuations of small pelagics had become a serious problem in world fisheries. The mechanisms were more puzzling than ever. The good news, especially from the Japanese sardine (Kondo, 1980), was that small pelagic fishery collapses might not be permanent.

The optimism that the puzzle would soon be solved generated a flurry of workshops and symposia in the 1980s. At a workshop in Lima, Peru, Bakun and Parrish (1980) presented an outline of the essential elements of fishery–oceanography associated with small pelagic fishes, and greatly expanded that treatment in a presentation to a 1983

FAO Expert Consultation in San Jose, Costa Rica (Parrish *et al*., 1983). Fréon (1983) produced one of the first regime-like environmentally driven pelagic fish population models. Also at this meeting, an apparent worldwide synchrony of sardine fluctuations was captured vividly by Kawasaki (1983). Although the synchrony now appears less clear than Kawasaki portrayed it, in 1983 the strength and contrast of the worldwide pattern suggested that the underlying mechanism should be easily discovered. Shortly afterward, Pauly and Tsukayama edited a comprehensive analysis of the Peruvian ecosystem, and in his concluding chapter, Pauly (1987) clearly departed from the classical equilibrium paradigm in favor of a regime-like model of ecosystem behavior. Combined with the oceanographic mechanisms elucidated by Parrish, Bakun, and others, it appeared that all of the pieces of the puzzle were now in hand. A breakthrough seemed to be imminent, generating major pelagic fish symposia in Capetown, South Africa, and Vigo, Spain in 1986 and in Sendai, Japan in 1989. Lluch-Belda *et al*. (1989) captured the essence of "the regime problem" as being fundamentally different from "the recruitment problem" that had dominated fishery science for decades. Yet the answer remained elusive.

There was growing awareness that environmental shifts were associated in some way with changes in pelagic fish productivity in such places as South Africa, Peru and Japan. The "new" sardine fisheries off Japan and Peru–Chile collapsed by the early 1990s, while South Africa experienced a long-awaited resurgence of sardines. An environmentally explicit management policy was adopted for sardines in the US portion of the California Current, based on Jacobson and MacCall's (1995) use of sea surface temperature as a proxy for the admittedly unknown causal mechanism in the stock–recruitment relationship. International research efforts continued, such as the Scientific Committee on Oceanic Resources Working Group 98, titled, "Worldwide Large-Scale Fluctuations of Sardine and Anchovy Populations" (Schwartzlose *et al*., 1999), and GLOBEC's "Small Pelagics and Climate Change" (reported in the present volume). However, the twentieth century ended without a generally accepted theory of small pelagic fish dynamics capable of explaining the nature and causes of their fluctuations (e.g. Chavez *et al*., 2003).

## A new millennium

Of course, history only becomes clear with the passage of time, and it is perhaps too soon to say whether we have yet emerged from "the doubt period." Fréon *et al*. (2005) optimistically assert that we are now in "the era of ecosystem-based management," and there is certainly widespread interest in moving beyond single-species approaches. Fisheries for small pelagics seem to offer an excellent opportunity for development of an ecosystem approach to management. An open question is whether this can be done without a predictive theory of the dynamics of small pelagic fishes on which to base management decisions. Notwithstanding the repeated disappointments of the past few decades, the science of fisheries–oceanography again seems to be close to achieving this breakthrough.

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REFERENCES

Bakun, A. and Parrish. R. (1980). Environmental inputs to fishery population models for eastern boundary current regions. In *Workshop on the Effects of Environmental Variation on the Survival of Larval Pelagic Fishes*. IOC Workshop Rep. 28, IOC/UNESCO, Paris, pp. 67–104.

Beverton, R. J. H. and Holt, S. J. (1957). *On the dynamics of exploited fish populations*. HM Stationary Off., London, *Fish. Invest*., Ser. 2, Vol. **19**, 533 pp.

Chavez, F. P., Ryan, J. Lluch-Cota, S. E., and Ñiquen M. C. (2003). From anchovies to sardines and back: multidecadal change in the Pacific Ocean. *Science* **299**: 217–221.

Clark, F. N. and Marr, J. C. (1955). Population dynamics of the Pacific sardine. *Calif. Coop. Oceanic Fish. Invest. Prog. Rep*., 1 July 1953 to 31 March 1955: 11–48.

Cushing, D. H. (1973). Dependence of recruitment on parent stock. *J. Fish. Res. Board Can*. **30**: 1965–1976.

Fox, W. W. (1974). An overview of production modeling. pp. 142–156. In *Workshop on Population Dynamics of Tuna. ICCAT Collective Volume of Scientific Papers*, Vol. **3**.

Fréon, P. (1983). Production models as applied to sub-stocks depending on upwelling fluctuations. pp. 1047–1064 In *Proceedings of The Expert Consultation to Examine Changes in Abundance and Species Composition of Neritic Fish Resources*. San Jose, Costa Rica, 18–29 April 1983. FAO Fish. Rep. 291.

Fréon, P., Cury, P., Shannon, L., and Roy, C. (2005). Sustainable exploitation of small pelagic fish stocks challenged by environmental and ecosystem changes. *Bull. Mar. Sci*. **76**: 385–462.

Gulland, J. A. (1965). Estimation of mortality rates. Annex Northeast Arctic Working Group. Council Meeting. G 3. 9pp. Mimeo.

Gulland, J. A. (1977). The stability of fish stocks. *J. Cons. Int. Explor. Mer*. **37**:199–204.

Gulland, J. A. (1983). World resources of fisheries and their management. pp. 839–1061. In *Marine Ecology*, Vol. **5**, part 2. Chichester, UK: John Wiley and Sons.

Harley, S. J. (2002). *Meta-Analytical Approaches to the Study of Fish Population Dynamics*. PhD dissertation, Dalhousie University, Halifax, Canada. 221pp.

Isaacs, J. D. (1976). Some ideas and frustrations about fishery science. *Calif. Coop. Oceanic Fish. Invest. Rep*. **18**: 34–43.