

EASTERN CENTRAL PACIFIC - PACIFIC CENTRO-ORIENTAL

VARIABILITY OF PELAGIC FISH STOCKS OFF CALIFORNIA

by

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Resumen

Los stocks de peces pelágicos costeros de California muestran una variedad de patrones de fluctuación. Los stocks de sardinas del Pacífico se redujeron drásticamente por la excesiva presión de pesca, y su recuperación ha sido lenta. Algún tiempo después de la reducción de la sardina, la anchoveta aumentó, alcanzando aparentemente una abundancia de equilibrio a mediados de los años 1960. Tanto California como México han desarrollado pesquerías de reducción de anchoveta, y el stock está ahora plenamente explotado. El stock de caballa fue reducido a mediados de los años 1960. Pero ahora se ha ido rehabilitando debido a un reclutamiento favorable y a una explotación estrictamente controlada, y en estos momentos sostienen una pesquería saludable. El jurel es un recurso grande y prácticamente no explotado a excepción de una pequeña pesquería en las áreas de cría frente a la parte sur de California. El bonito del Pacífico es una población marginal que recientemente se ha establecido en las aguas al sur de California y su permanencia es cuestionable. El recurso de barracuda de California también está reducido, pero la composición por edades está respondiéndole favorablemente a una limitación del tamaño mínimo de pesca. El estado del robalo blanco de mar es poco claro, pero el recurso está posiblemente sobreexplotado.

La variabilidad de los recursos de peces pueden generarse por muchas causas. Las fluctuaciones del reclutamiento son particularmente importantes para especies de vida corta. El reemplazamiento de especies parece ocurrir, pero es favorecido o ocurre a través de cambios ambientales. Contrario a las asunciones estándar, los cambios en la tasa de mortalidad natural pueden ser una causa importante de las fluctuaciones en abundancia.

INTRODUCTION

This paper is divided into two sections: the first reviews historical fluctuations in abundance of several pelagic fishes and larger predatory fishes off California. The second section examines assorted pieces of evidence relating to mechanisms causing those fluctuations.

HISTORICAL REVIEWS

Pelagic fishes

California Sardine *Sardinops sagax caerulea*

Population analyses by Murphy (1966) and MacCall (1979) document the history of the Pacific sardine stock (here termed the California sardine to avoid confusion). When plotted on a logarithmic scale (Figure 1), the decline in abundance appears as a coherent trend extending over the entire thirty years of the historical fishery. There are no discontinuities which could be interpreted as adverse environmental changes. Rather, the sustained rate of decline (average instantaneous rate of increase is approximately $-0.2/\text{yr}$) suggests that the fishery consistently exceeded sustainable yields by about 18 percent.

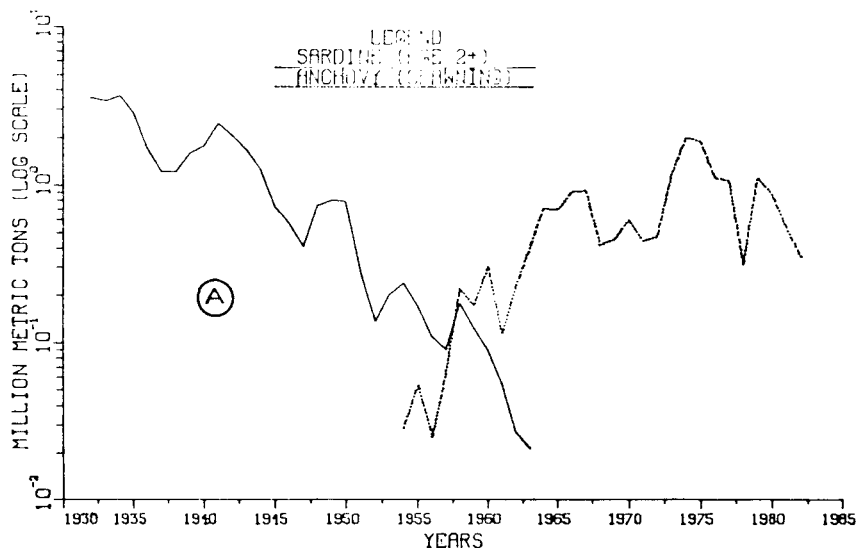


Figure 1. Time series of sardine (age 2+) and anchovy spawning biomass (log scale) off California and northern Baja California. "A" denotes approximate anchovy spawning biomass in 1940-41 (interpreted from Smith 1972).

Exploitation continued until 1970, when a moratorium on sardine landings was enacted by the State of California. During the following decade the resource remained at nearly undetectable levels, and showed no signs of recovery until 1980, when sardines became increasingly frequent as incidental catches in landings of other pelagic fishes. Abundance has increased noticeably as of 1982. A 1982 pelagic fish survey captured sardines in 14 midwater trawl tows, whereas sardines had occurred in only three other tows in the entire previous 20 years of surveys (Mais 1982). A small fishery will be allowed when the stock reaches a biomass of 20,000 tons, which is a possibility in the near future.

Northern Anchovy *Engraulis mordax*

Understanding of northern anchovy population fluctuations has been revolutionized by recent development of an "egg production method" of biomass estimation (see Parker 1980, Picquelle and Hewitt 1983 in press). Previous population estimates based on larva

abundance have been insensitive to changes in true population abundance because egg and larval mortality rates are positively correlated with initial egg production (Hewitt 1982), and hence adult abundance. Since 1980 anchovy abundance estimated (over the range of the stock by an ichthyoplankton survey) by the daily fecundity per gram of adult fish (estimated by histological examination of ovaries from adult fish, see Hunter and Goldberg 1980). The resulting egg production biomass estimates have been lower than simultaneous estimates of larva census biomass. The difference is due probably to an erroneous prior assumption concerning relative spawning frequencies of anchovies and sardines. Whereas the two species off California were assumed to spawn with equal frequency (Smith 1972), recent egg production method surveys in Peru indicate that the anchoveta *Engraulis ringens* spawns more frequently than does the sardine, *Sardinops sagax* (J. Alheit, PROCOPA, c/o IMARPE, Callao, Peru, personal communication).

By extrapolating egg and larva abundance-at-age back to the time of spawning, Lo (Southwest Fisheries Center, La Jolla, California, manuscript in preparation) has calculated an index of historic egg production. This index was analyzed by MacCall (1982) and Methot (1982) to produce a time series of estimated anchovy spawning biomasses from 1954 to 1982 (Figure 1). From very low abundance in the early 1950's, anchovy abundance increased, reaching an erratic equilibrium beginning about 1964. The increase in anchovy abundance lagged the sardine decline, and did not occur until sardine abundance dropped to one-tenth of its peak value. Whereas previous analyses indicated a peak anchovy abundance of four to five million mtons in 1964-66 (MacCall 1980), the new time series shows peak biomasses of about two million mtons to have occurred a decade later. Tentative biomass estimates for 1940-41 have been added to the time series, based on Smith's (1972) larva census estimates which are very similar to larva censuses for 1957-58 (Figure 1).

A reduction fishery was initiated in California in 1966, and a Mexican fishery expanded in the mid-1970's. Total annual harvests in 1980 and 1981 were about 300,000 mtons, very near the estimated MSY. Thus, the northern anchovy is "fully utilized" by common fishery standards. Recruitment has been highly variable since 1974, and has been declining since 1978. Unless recruitment improves, the anchovy resource is likely to continue to decline in abundance, given the current rate of exploitation.

Pacific Mackerel *Scomber japonicus*

Historical abundance of Pacific mackerel has been calculated by Parrish and MacCall (1978). Due to a string of very strong year classes, abundance in the 1930's probably exceeded average virgin stock levels (Figure 2; the fishery began about 1928). Over the following years spawning success (recruits per spawner) varied with a distinct six- to seven-year cycle which ended with collapse of the resource about 1965. A moratorium on Pacific mackerel catches was enacted by the State of California in 1970, and in 1972 the moratorium was supplemented by a formula for future harvests based on estimated stock abundance.

Subsequent recovery of the resource is documented by a series of annual reports to the California legislature (Richard Klingbeil, California Department of Fish and Game, Long Beach, California, unpublished reports). During the 1970's relatively strong recruitments occurred in even years (1972, 1974, 1976, 1978), showing a very different pattern of spawning successes than had occurred previously. The 1976 year class was sufficient to allow opening of a small fishery in 1977-78. The subsequent 1978 year class is probably the largest in the documented history of the fishery, and has supported increased harvests. The fishery and resource are now at historically high levels (Figure 2), and prospects are good that the fishery will continue indefinitely (at varying levels) under the present program of management.

Jack Mackerel *Trachurus symmetricus*

No substantial fishery has developed for jack mackerel in California or Mexico. A small fishery for young fish (less than age six) off southern California has existed since 1950, but the industry has had difficulty marketing the product. Much of the biomass consists of large adults in oceanic waters ranging from southern Baja California to the Aleutian Islands, and as much as 1500 km offshore. These fish may exceed 30 years of age (Fitch 1956), and stock size may be around two million mtons (MacCall and Stauffer 1983 in press).

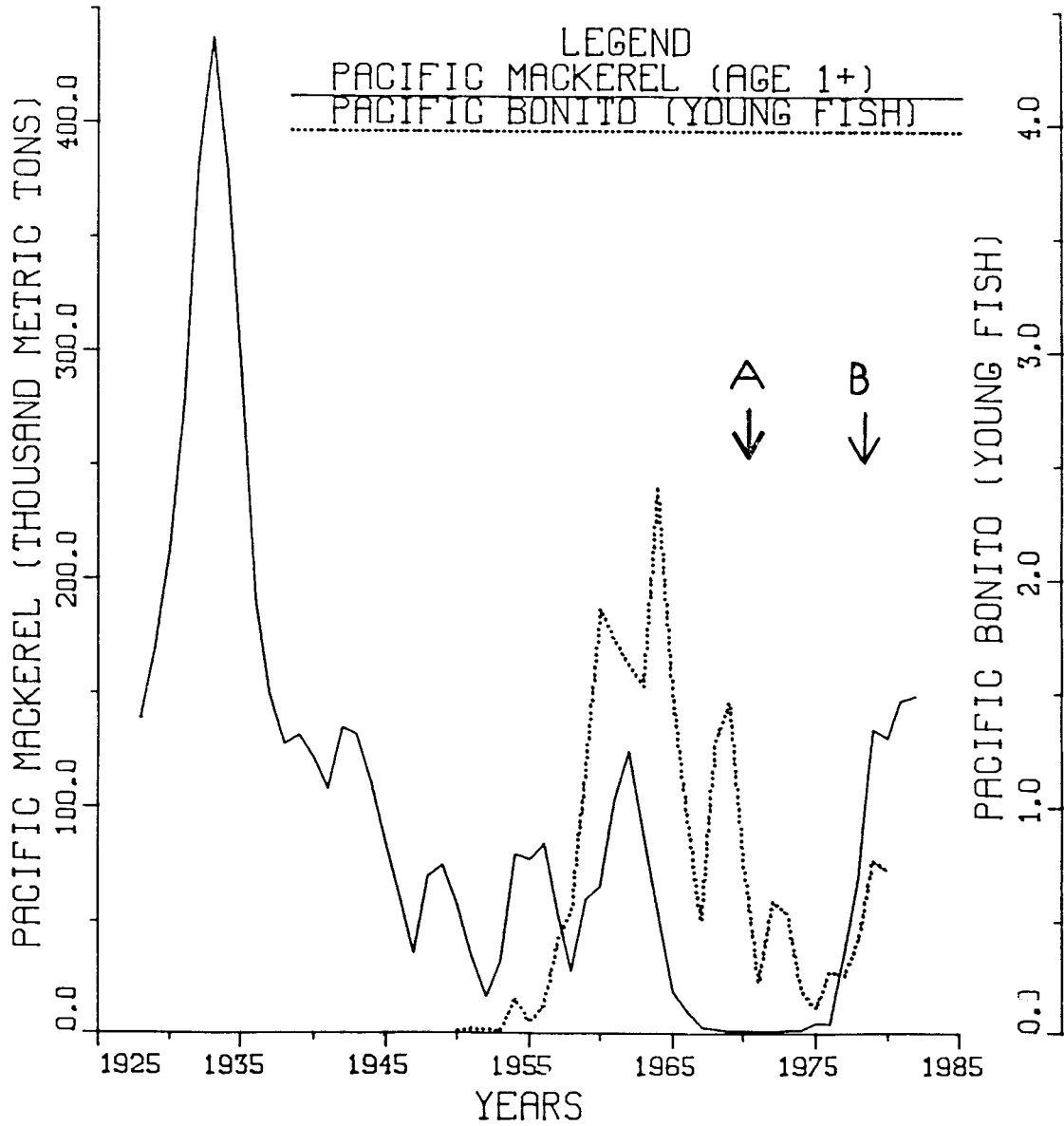


Figure 2. Time series of Pacific mackerel total biomass (age 1+) and Pacific bonito catch-per-effort. "A" denotes beginning Pacific mackerel fishing moratorium, and "B" denotes re-opening of the fishery.

Nearly all the spawning occurs in oceanic waters far from shore; however, subsequent young-of-the-year appear inshore, mainly off southern California. Recruitment strength is highly variable (Figure 3). Virtual recruitment strength was calculated by summing the percentage contributions of each year class to the fishery over the duration of the cohort. Strong year classes tend to be isolated by several weak year classes, with a suggestion of periodicity. Age compositions for more recent catches are unavailable, but the 1976 and 1982 year classes seem to be relatively prominent.

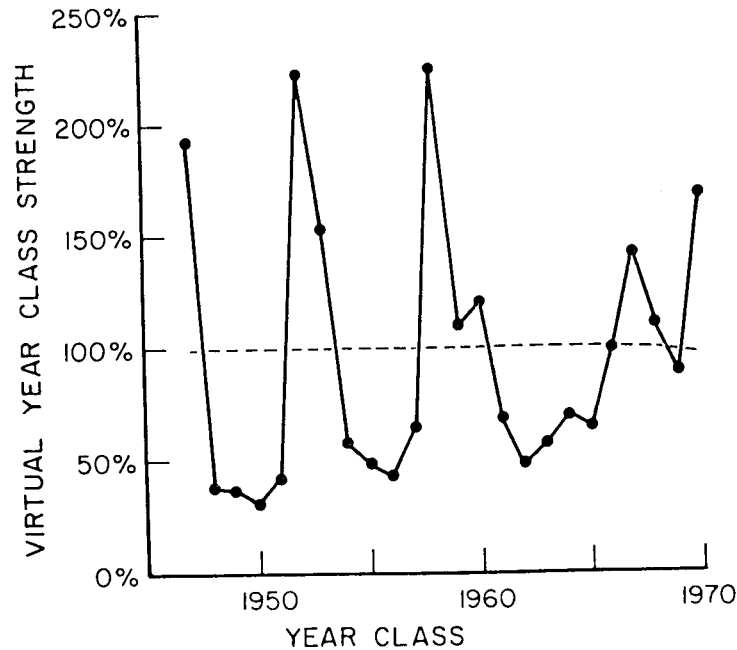


Figure 3. Virtual year class strengths of jack mackerel off California (from MacCall and Stauffer 1983).

LARGER COASTAL PREDATORY FISHES

Information on many of these fishes tends to be limited to catch histories and scattered biological observations with little continuity. Many of these fishes are migratory, with the bulk of the populations residing in Mexican waters. Migration strength is strongly associated with large scale ocean temperature anomalies (Radovich 1961), and the resulting environmental noise may conceal trends in stock abundance. These species are popular targets of both recreational fisheries and commercial fisheries, with catches of roughly equal magnitude.

Pacific Bonito *Sarda chiliensis*

Pacific bonito have long been visitors to California waters, with large adults appearing off southern California in the late summer and fall. However, an apparently self-sustaining younger population seems to have established residence in southern California waters only since the mid-1950's (see Collins et al. 1980 for a complete review). Recreational anglers catch mostly young fish, and catch-per-angler-trip is the best available index of the non-migrant stock (Figure 2).

Abundance has declined since the early 1960's. Some of that decline must be attributed to the commercial fishery which began harvesting bonito in 1966, but sustainability cannot necessarily be expected from a resource which has only recently come into existence. The bonito stock off California is a marginal population which hovers near the edge of viability--one hypothesis is that warm-water discharges from power generating stations have provided overwintering refuges for fish that would normally migrate south (Robson Collins, California Department of Fish and Game, Long Beach, California, personal

communication). Faced with increasingly intense exploitation of pre-spawning fish, a minimum size regulation was implemented in 1982 in order to protect fish through their first spawning season. This management measure should help to maintain a southern California bonito stock during those periods when conditions are favorable.

California Barracuda *Sphyraena argentea*

Catch rates and size composition declined severely in the 1960s, leading to imposition of a strict size limit in 1972. This regulation caused a severe drop in U.S. recreational landings, but size composition has improved steadily over the past decade. Numerical abundance has shown little increase, but the improved spawning capacity of the stock has improved the prospects for recovery (Schultze 1983).

White Seabass *Atractoseion nobilis*

Recreational catch per effort has declined severely over the last 25 years, but commercial catch rates have remained relatively constant. Once abundant as far north as San Francisco, the range has steadily contracted southwards under exploitation (Collins 1982, Vojkovich and Reed 1983), indicating that population size may have declined more than local density would suggest. Mortality rate estimates calculated for the period 1958-60 (Thomas 1968) indicate that the fishing mortality rate (F) considerably exceeded the natural mortality rate (M). Perhaps due to the strong immigration of white seabass during the anomalously warm period of Thomas' study, he advocated increased fishing intensity. However, in light of more recent "rules-of-thumb" (e.g. Alverson and Pereyra 1969, Gulland 1970), which suggest that F is near M at MSY, the above relationship gives reason to suspect overfishing.

CAUSES OF FLUCTUATIONS

Fluctuations in fish stocks are caused by complex interactions of fishery, biological, and environmental factors. The social and economic tragedy that accompanies fishery collapses calls for "explanations," whereby people are eager to lay blame on the environment, the fishermen, or the government. There has been an unfortunate tendency toward simplistic single-factor explanations, and available data often are insufficient to explore more complicated hypotheses. In addition, scientists may interpret and "filter" data in favor of rationalizations and preconceived assumptions (Gould 1978). I suspect that analyses of stock fluctuations are especially prone to this problem. With hindsight, we can usually prescribe a management policy which would have averted the tragedy; such wisdom is much more difficult to apply with foresight. However, now with the cumulative experience of scores of similar fisheries and resources around the world, observed over decades of variability, fishery management is emerging from unexplored territory into a realm where experience provides a reliable guide. There will always be risk associated with these fluctuations; some of that risk can be reduced by appropriate resource management, and the remainder must be recognized as an unavoidable characteristic of the resource.

The fisheries and oceanography of the California Current are among the most thoroughly studied in the world. The California Cooperative Oceanic Fisheries Investigations (CalCOFI) Program, established over thirty years ago as a response to the collapsing sardine fishery, has provided a remarkable fishery-independent data base of physical and biological observations. This local knowledge is supplemented by experience in several analogous eastern boundary currents including those of Peru and South Africa (e.g. Bakun and Parrish 1980, 1982). This accumulation provides evidence for several mechanisms causing variability in coastal pelagic fish stocks, some of which will be reviewed briefly here (also see Lasker and MacCall 1983 in press).

Variability of Recruitment

Causes of recruitment variability is a popular area of fishery research, especially for coastal pelagic fishes (see Lasker 1981, and Sharp 1980 for reviews). As a source of stock fluctuations, recruitment variability is important in three cases: short-lived fishes, age class-specific fisheries, and high serial correlation of reproductive success. Population size behaves as an exponential moving average of recruitment strengths; variability of population size is therefore a function of the variability of recruitment itself and of the exponential decay coefficient or mortality rate. Fishes may be short-

lived due to high natural mortality rates (e.g, anchovies) or due to high total (natural plus fishing) mortality rates (e.g, sardines). In the latter case, reduction of fishing intensity may help stabilize population fluctuations by averaging recruitment over longer periods. Age class-specific fisheries occur often as nursery ground fisheries such as the southern California jack mackerel fishery. Empirical probability distributions of reproductive variability can be developed in both of these cases. However the third case of high serial correlation is more insidious. The long-term probability distribution may be an inadequate description of near-term behavior, as near-term probabilities are conditional on current environmental or stock status. During long periods of good recruitment, the fishery may become overcapitalized. This tends to delay appropriate reductions in fishing intensity during the inevitable succeeding period of poor recruitment.

Climatic Change and Species Replacement

There is some dispute as to whether climatic regimes are distinguishable from the patterns of variability arising simply from an autoregressive mechanism. As in any correlation study, empirical serial correlation spectra cannot be used to infer mechanisms, and existing time series of physical observations tend to be too short to test more sophisticated hypotheses. Recently Shuntov and Vasil'kov (1982) have suggested that sardine and anchovy variability may be driven by solar periodicity. Whichever the physical cause, biological systems tend to respond with regimes--protracted periods of similar behavior with abrupt transitions to a different mode of behavior.

The supposed "competitive replacement" of the sardine by the anchovy in California has now become a textbook case; the simulation study by Silliman (1969) was cited in Odum's (1971) ecology text as substantiation of the Volterra competition equations (Radovich 1981). This conclusion is very attractive to theoretical ecologists, whose mathematical models often have found little support in the real world. However, closer inspection (Daan 1980), and the following geographic argument severely weaken the case for simple competitive replacement.

The most important argument against competitive replacement is that the anchovy and sardine stocks have not occupied the same habitats. Typically, sardine stocks are distributed polewards of the respective anchovy stocks: The California sardine was abundant from Baja California to British Columbia, with a large portion of the population north of Pt. Conception, whereas the northern anchovy resides mostly south of Pt. Conception. Similarly, the Peruvian sardine is now abundant in northern Chile, whereas the previous anchoveta stock was scarce south of Pisco. There is evidence that the anchoveta resource has recently shifted southwards as well (Figure 4). A similar poleward shift in Peruvian fish production, although of unknown species composition, has been suspected for early historic times (Hutchinson 1950: p48), "It is also noteworthy that the rather unproductive region south of Pisco Bay, as far south as Iquique, seems from the 16th to the early 19th centuries to have been regarded as a more important source of guano than the central Peruvian coast...the only reasonable, though admittedly speculative, explanation of the decline of importance of the southern islands...is that minor changes in the dominant hydrographic pattern have occurred, tending to alter the distribution of the centers of abundant fish". Under the competitive replacement hypothesis, the replacing species should occupy the habitat of the former competitor. This does not seem to be the case for anchovies and sardines. Rather, geographic shifts of stock distribution indicate large scale environmental influences.

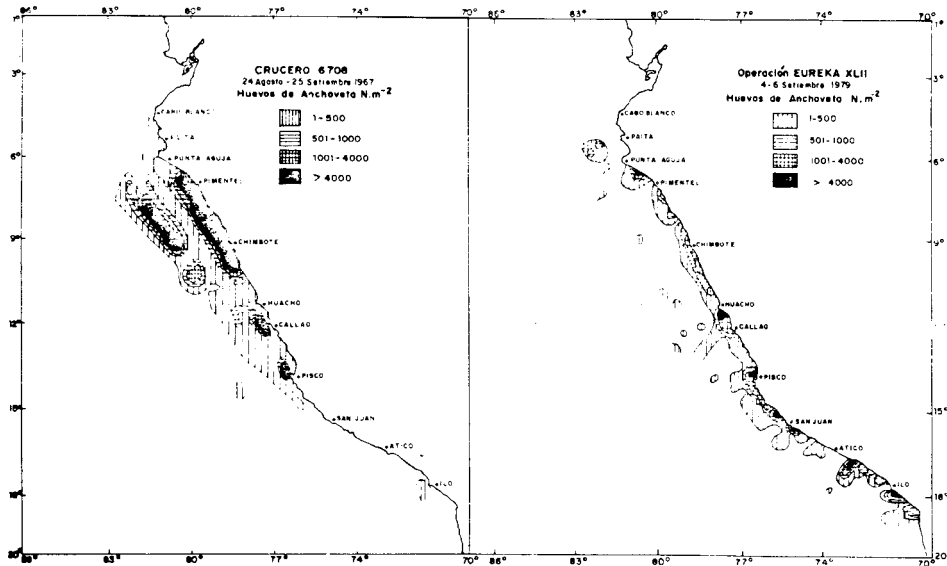


Figure 4. Sampling area and geographic distribution of anchoveta egg samples before and after 1971 (from Santander et al, 1982).

Variability of Natural Mortality Rates

Fishery models invariably assume a constant rate of natural mortality. Whether or not this is valid, fishery modelers have taken comfort in a long tradition of making this assumption. The quantity of fishery-independent information on California's anchovy stock has allowed Methot (1982) to attempt to reconcile age compositions with independent estimates of stock abundance. He concluded that the high anchovy biomass in the mid-1970s was not simply the product of strong recruitment, but rather was due to a substantial decrease in the natural mortality rate. If variability in natural mortality rate is a major factor in variability of pelagic fish stocks, methods such as cohort analysis are unreliable, and fishery-independent estimates of abundance are necessary. On the other hand, patterns of known variation in M may lead to development of meaningful multispecies fishery management models.

CONCLUSIONS

California coastal pelagic fish stocks show a variety of patterns of fluctuations. Pacific sardines have been depleted by excessive fishing pressure, and have been slow to recover. With some delay following the decline of the sardine, anchovies increased, reaching apparent equilibrium abundance in the mid-1960's. Both California and Mexico have developed reduction fisheries on anchovy, and the stock is now fully exploited. Pacific mackerel were depleted by the mid-1960's, but now have been rehabilitated due to favourable recruitment and strictly controlled harvest, and support a healthy fishery. Jack mackerel is a large resource, unfished except for a small fishery on the nursery grounds off southern California. Pacific bonito is a marginal population having recently established itself in southern California waters, and sustainability is questionable. The California barracuda resource is depressed, but age composition is responding favourably to a minimum size limit. The status of white seabass is somewhat unclear, but the resource is probably overexploited.

Variability in fish stocks can arise from many causes. Recruitment fluctuations are particularly important for short-lived fish. Species replacement seems to occur, but is environmentally mediated. Contrary to standard assumptions, changes in the rate of natural mortality of adults may be an important cause of fluctuations in abundance.

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REFERENCES

- Alverson, D. and W. Pereyra. 1969. Demersal fish exploration in the northeastern Pacific Ocean - an evaluation of exploratory fishing methods and analytical approaches to stock size and field forecasts. J.Fish.Res.Bd.Canada. 26:1985-2001.
- Bakun, A. and R. Parrish. 1980. Environmental inputs to fishery population models for eastern boundary current regions. pp. 67-104. In Intergovernmental Oceanographic Commission Workshop Rep.No. 28 Rep. (G.D.Sharp, ed.) IOC/UNESCO, Paris.
- _____. 1982. Turbulence, transport and pelagic fish in the California and Peru Current systems. Calif.Coop.Oceanic Fish.Invest.Rep. 23:99-112.
- Collins, R., D. Huppert, A. MacCall, J. Radovich and G. Stauffer. 1980. Pacific bonito management information document. Calif.Dep.Fish and Game. Mar.Res.Tech.Rep. 44:94 p.
- Daan, N. 1980. A review of replacement of depleted stocks by other species and the mechanisms underlying such replacement. Rapp. P.-v.Réun.Cons.int.Explor.Mer. 177:405-421.
- Fitch, J. 1956. Jack mackerel. Calif.Coop.Oceanic Fish.Invest.Progr.Rep. 1 April 1955 to 30 June 1956. pp. 27-28.
- Gould, S. 1978. Morton's ranking of races by cranial capacity. Science. 200:503-509.
- Gulland, J. 1970. The fish resources of the ocean. Food.Agric. FAO Fish.Tech.Pap. 97:1-425.
- Hewitt, R. 1982. Spatial pattern and survival of anchovy larvae: implications of adult reproductive strategy. Ph.D. Dissertation, Univ.of California at San Diego. 187 p.
- Hunter J. and S. Goldberg. 1980. Spawning incidence and batch fecundity in northern anchovy, Engraulis mordax. Fish.Bull.(U.S.) 77:641-652.
- Hutchinson, G. 1950. Survey of existing knowledge of biogeochemistry. 3. The biogeochemistry of vertebrate excretion. Bull.Amer.Mus.Nat.Hist. 96:1-554.
- Lasker, R. (ed.). 1981. Marine fish larvae: morphology, ecology and relation to fisheries. Univ. of Washington Press, Seattle. 131 p.
- Lasker, R. and A. MacCall. 1983. (in press). New ideas on the fluctuations of the clupeoid stocks off California. Can.J.Fish.Aquat.Sci. 40:
- MacCall, A. 1979. Population estimates for the waning years of the Pacific sardine fishery. Calif.Coop.Oceanic Fish.Invest.Rep. 20:72-82.
- _____. 1980. Population models for the northern anchovy (Engraulis mordax) Rapp.P.-v.Reun.Cons.int.Explor.Mer. 177:292-306.
- _____. 1982. Complete northern anchovy biomass time series for 1951-1982 based on the egg production method and other indices. Southwest Fisheries Center Admin.Rep. LJ:82-26.
- MacCall, A. and G. Stauffer. 1983. (in press). Biology and fishery potential of jack mackerel (Trachurus symmetricus). Calif.Coop.Oceanic Fish.Invest.Rep. 24:
- Mais, K. 1982. Cruise Report 82-X-6. Assessment of commercial fisheries resources. California Dept.Fish and Game. Marine Resources Region, Long Beach, California.
- Method, R. 1982. Age-specific abundance and mortality of northern anchovy. Southwest Fisheries Center Admin.Rep. LJ:82-31.
- Murphy, G. 1966. Population biology of the Pacific sardine (Sardinops caerulea). Proc.Calif.Acad. Sci.4th Ser. 34(1):1-84.
- Odum, E. 1971. Fundamentals of ecology. 3rd ed. W.B. Saunders, Philadelphia. 226 p.
-

- Parker, K. 1980. A direct method for estimating northern anchovy, Engraulis mordax, spawning biomass. Fish.Bull.U.S. 78:541-544.
- Parrish, R. and A. MacCall. 1978. Climatic variation and exploitation in the Pacific mackerel fishery. Calif.Dep.Fish and Game. Fish.Bull. 167:110 p.
- Picquelle, S. and R. Hewitt. 1983 (in press). The northern anchovy spawning biomass for the 1982-83 California fishing season. Calif.Coop.Oceanic Fish.Invest.Rep. 24:
- Radovich, J. 1961. Relationships of some marine organisms of the northeast Pacific to water temperatures particularly during 1957 through 1959. Calif.Dep.Fish and Game.Fish.Bull. 112:62 p.
- _____. 1981. The collapse of the California sardine fishery: What have we learned? pp. 107-136. In Resource management and environmental uncertainty: lessons from coastal upwelling fisheries. (M. Glantz and J. Thompson, eds.) John Wiley and Sons, New York.
- Santander, H., P. Smith and J. Alheit. 1982. Determination of sampling effort required for estimating egg production of anchoveta, Engraulis ringens, off Peru.Insto.del Mar del Peru. Bol. 7(1): 18 p.
- Schultze, D. 1983 (in press). California barracuda life history, fisheries and management. Calif.Coop.Oceanic Fish.Invest.Rep. 24:
- Sharp, G. (ed.) 1980. Workshop on the effects of environmental variation on the survival of larval pelagic fishes. Intergov.Ocean.Comm.Workshop Rep. 28:323 p.
- Shuntov, G. and V. Vasil'kov. 1982. Long-term population fluctuations of North Pacific sardines. II. Epochs of atmospheric circulation and cyclic nature of the population dynamics of the Pacific and California sardines. J.Ichth. (USSR) 22(2):10-23.
- Silliman, R. 1969. Population models and test populations as research tools. Bioscience. 19:524-528.
- Smith, P. 1972. The increase in spawning biomass of northern anchovy, Engraulis mordax. Fish.Bull.U.S. 70:849-874.
- Thomas, J. 1968. Management of the white seabass (Cynoscion nobilis) in California waters. Calif.Dep.Fish and Game. Fish.Bull. 142:34 p.
- Vojkovich, M. and R. Reed. 1983 (in press). White seabass, Atractoscion nobilis, in California-Mexican waters: Status of the fishery. Calif.Coop.Oceanic Fish.Invest. Rep. 24:
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