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BIOLOGICAL EFFECTS OF OCEAN VARIABILITY: TIME AND SPACE SCALES OF BIOLOGICAL RESPONSE

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Present biological sampling activities are heavily biassed toward time and space scales of convenience to man, ships and existing equipment rather than to the time and space scales of important events and the biological response to them. Fish populations are observed to undergo sustained increases and decreases for several decades without a commercial fishery. In the first year of life, a California coastal fish may depend on food concentrations less than a metre in extent and be fed upon appreciably by an immature migratory predator (the albacore) spawned 10000 km away. Two multi-million ton fish populations which co-existed in 1940 simultaneously declined in that decade and the unfished anchovy recovered while the sardine did not. The apparently niche-mediated replacement took approximately 10 years, or more than twice the generation time of either species. Since both species are pelagic schooling fish, "competition" is likely to be based on events at the level of the school rather than the individual. These observations, while haphazard in time and space scales, lead to the conclusion that the causes of "unexpected" changes in commercial fish populations should be sought systematically in time and space.

INTRODUCTION

To become more precise, fishery management will require what is not now generally available to it: a suite of carefully timed and spaced measurements of the biological properties contributing to the success or failure of the reproductive process in the open ocean. Vast savings and new insight may be possible by merging physical and chemical oceanography and meteorology with biological oceanography so that critical fishery predictions can be formulated and tested. The main constraint to such a multi-disciplinary approach appears to be the difficulty of obtaining properly timed and spaced data series of sufficient length. It is the purpose of this paper to relate some examples of time and space scales of biological response to ocean variability which are only yet dimly perceived.

THE DECLINE OF THE NORTHERN SUB-POPULATION OF THE PACIFIC SARDINE

After the development of a fishery which peaked at 700000 tons in the 1936–1937 season (Fig. 98), it appears that the spawning biomass of the northern sub-population of the Pacific sardine declined from 4 million metric tons in the early 1930's to less than 10 thousand metric tons by 1965. This 400-fold drop in 30 years was undoubtedly influenced in its later stages by a continued intensive fishery on the small remaining fraction of the stock. It appears that the direct effects of the fishery were augmented by two indirect population effects and their environmental root causes.

The first indirect effect of the fishery was to reduce the number of effective spawning year classes from ten to two. It now appears that two successive failures in reproductive success dramatically lowered the population and this was followed by increased fishing mortality rates. The smaller number of reproducing year classes had sensitized the population to shorter and more frequent survival anomalies (Murphy, 1966). The second indirect effect of the fishery was that the reproductive portion of the stock, being smaller than in the virgin stock, progressively ranged over far smaller areas. This spatial equivalent of the temporal sensitivity induced by the fishery may have made the sardine stock sensitive to reproduction failures over a much smaller geographic region.

In what stage did these survival anomalies take place? If the years 1952 to 1956 are representative, survival variation increased rather steadily from the short embryonic and larval stages through the period when the fish entered the fishery at two years of age. The winter productivity minimum may have accelerated the process somewhat (Fig. 99).

In what area did these survival anomalies take

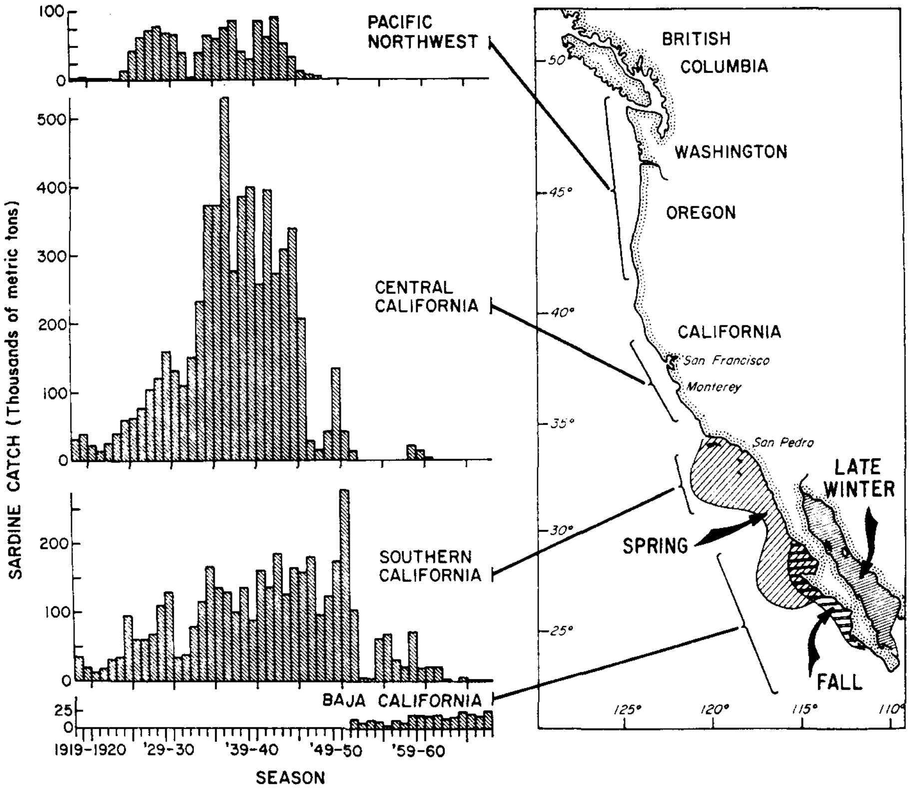

Figure 98. Time series of seasonal catch of Pacific sardine by region (Table 1, p. 184–185, Ahlstrom and Radovich, 1970) of catch compared with the spawning regions and seasons (Marr, 1960).

place? (Fig. 100). In the virgin stock, it would appear that following spawning, the adults would migrate northward to the productive upwelling areas off northern California, Oregon, Washington and British Columbia. Following the autumnal decline in the zooplankton standing stock (Fig. 101), the adults returned to the spawning grounds in the south off Mexico and the southern half of California. Fat stored as a result of feeding along the entire 1500 miles of upwelling coastline was used by the fish to elaborate egg yolk in the southern 500 miles. It appears from subsequent time series of zooplankton volume and temperature distribution that the boundary of low plankton volume in the south and the boundary of low temperature in the north shifted north and south along the coast. These boundaries may also have approached each other, restricting the geographic range of the sardine spawning, or separated broadening the geographic range of the sardine. The virgin stock spawned over the entire area and the annual position of an optimum survival area would be occupied by the population each year. With the reduction of the adult population by the fishery, the stock was unable to occupy the whole area and the optimum site for survival might not coincide with the location of the reduced population.

Beyond these unsatisfying generalizations, little information can now be assembled in retrospect. It may be that as the results of overfishing progress from inconvenience to economic failure, to possible human disaster, we will need to expend more resources on exploratory research systematically along time scales and space scales specifically designed to determine the causes of "unexpected changes" in reproductive success of fish populations.

TIME SCALES

On the short time scale of days–weeks, upwelling, advection and mixing may be observed to be unfavourable for clupeid brood areas (Lasker, 1975). Indeed, the spawning of sardine and anchovy appears

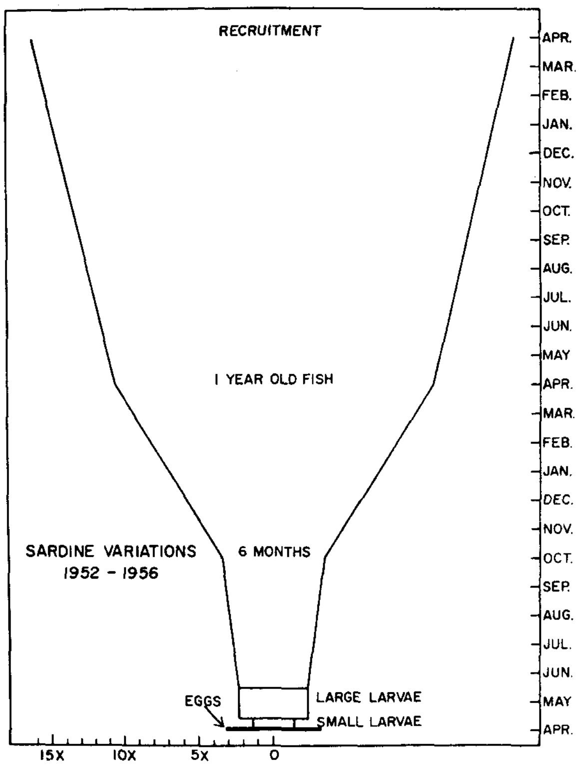

Figure 99. Time course and amplitude of annual variation in the numbers of sardine eggs, larvae, juveniles and pre-recruits from 1952 through 1956.

to occur principally in the stable periods and areas of the western coast of North America rather than the areas of maximum upwelling, mixing and advection, though such areas may be optimal later on for the juvenile states. It is likely that the analysis of these short-term events, in the context of the spring bloom and the spawning and survival of the commercial fishes will require observation each two weeks for several months at the beginning of each year off California. Analysis of survival in other areas may require similar intense and precisely timed observations.

On an annual time scale, juvenile Pacific sardine and northern anchovy must compete with the standing stock of the adults of its own species and to varying degrees with the adults of other species having similar requirements. It appears likely that food, and particularly the location of the remaining food, becomes critical in the winter when primary and secondary production are apparently relatively low and the standing crop of net zooplankton is decreasing. Furthermore, the juveniles contain little fat, and are usually located not far from the spawning grounds during the winter period when the adults return from feeding migrations of the preceding few months. While the individual juveniles are lighter in weight, their tremendous numbers make their total weight, and therefore their food requirements, often larger than the next most abundant, and one year older year class. The winter confrontation between the 0-group juveniles and older fishes is a period which requires special study.

The decadal time scale offers one of the great puzzles of fishery population work. One would expect from theory and from examination of the annual controls on survival that there would be a simple alternation of successful and unsuccessful year classes since the most important direct competitor of the 0-group is the immediately preceding year class, the I-group. Instead, one observes that successful year classes of Pacific sardine and mackerel arrive in series of years. The sardine has significant runs of 2, 3, 4 and 5 years and the Pacific mackerel has runs of about the same length and with a somewhat greater intensity (Fig. 102). As yet, the causes of these successful sets of year classes have not been identified, but population recruitment can be satisfactorily duplicated by simple auto-correlation simulation (Lenarz, 1971) (Fig. 103).

In the time-series data on scale deposition in the Santa Barbara and Soledad basins (Soutar and Isaacs, 1974) there is no evidence of significant runs of 5-year averages over a 200-year time period (Fig. 104). In addition, there are no correlations between the successes and failures of the total estimated epipelagic fishes and the Pacific hake which dwells below the mixed layer (Fig. 105). The total biomass of these fishes is subject to far less variation than the biomass of the individual species (Table 10).

SPACE SCALES

Rather than the usual spatial scales, I choose to recognize four scales related to the species: the behavioural, the hydrographic, the physiological and the external. By *behavioural*, I mean the scale of aggregation induced by the individual behaviour of the organism. In the clupeids this is the fish school. By *hydrographic*, I mean the scale which attracts and holds fish in a small geographic area like an upwelled water mass, or a rich zooplankton bloom area. By *physiolological*, I mean the distribution of a species, constrained by physiological limits such as temperature tolerance. By *external*, I mean the scale of event by which food or predators enter the environment of a species from outside its distribution area.

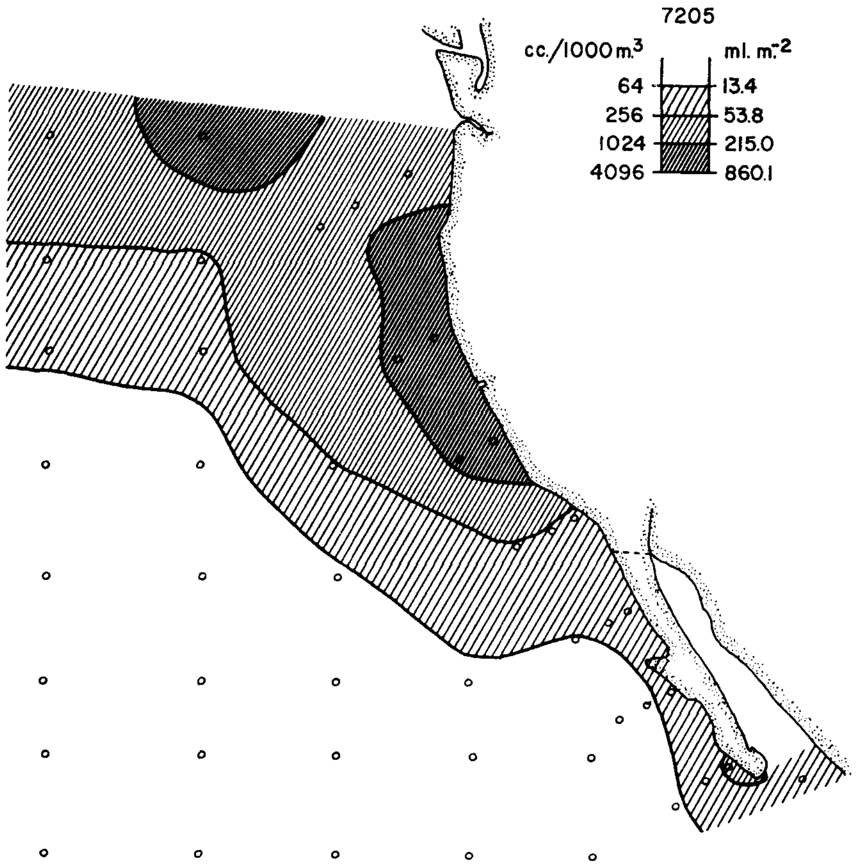

Figure 100. Zooplankton volume off the west coast of North America in April, May and June of 1972. Regions occupied indicated by clear circle. Stations per region were from 3 to 20.

BEHAVIOUR SPACE SCALE

The schooling habit of the major populations of schooling fishes presents a paradox in competition for food among individual, intraspecific competition and limitation of population size. During the decline of the sardine, the schooling habit at spawning time apparently remained, even as the population declined to less than 10 000 tons from a population of 4 million tons.

A schooling fish ultimately depends on the primary productivity in the immediate area of the school whether it feeds on the phytoplankton directly, the herbivores, or the carnivorous and omnivorous species and growth stages of species. The northern anchovy (*Engraulis mordax*) is an omnivore. Anchovy schools frequently contain 15 000 g of fish under each metre of sea surface. The food requirement for a school of this compaction is of the order of 16 g of carbon per square metre of fish school per day. Since this is about 16 times the average primary production under each square metre of sea surface off southern California, the school must move several times its own area each day. While this would require only a trivial amount of swimming by an individual, a large school may be forced to maintain a high steady rate of swimming. I find that fish schools are most common in the 20 to 30 m diameter range, but half of the fish are in schools of 90 m diameter up to an observed maximum of 400 m.

The northern anchovy, an omnivore, achieves its growth and ultimate stock size by succeeding in harvesting a portion of the primary production of its local area by eating phytoplankton, herbivores and other omnivores. Anchovy school size determines the rate at which each anchovy must swim to secure energy for respiration, growth, and reproduction

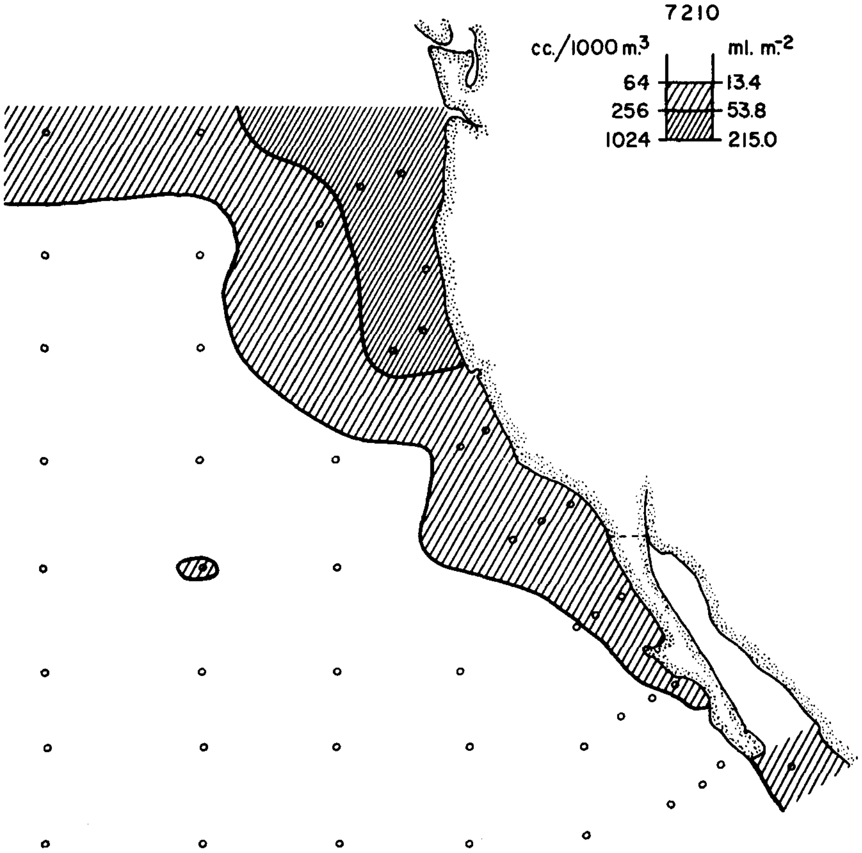

Figure 101. Zooplankton volume off the west coast of North America in September and October of 1972. Regions and stations indicated, the same as in Figure 100.

within the combined constraints of local primary and secondary production and the production of other consumers of that production. For a numerical example, a 200 m diameter school of anchovies with a food chain conversion efficiency of 0·12, in an area with a local primary production rate of 1 g C $m^{-2}day^{-1}$, and having a compaction of 15 000 g per square metre would have to move 21 km per day (or two body lengths per second for the 12 cm anchovy) to maintain parity with the local primary production. This consideration of a single school does not include passing into areas where other schools have just fed, nor repeated entry of the area grazed. While the two body lengths per second seems plausible for individual swimming, feeding activities would slow the mean rate of progress of the school.

I interpret this to mean that the severe food competition imposed by membership in a large fish school

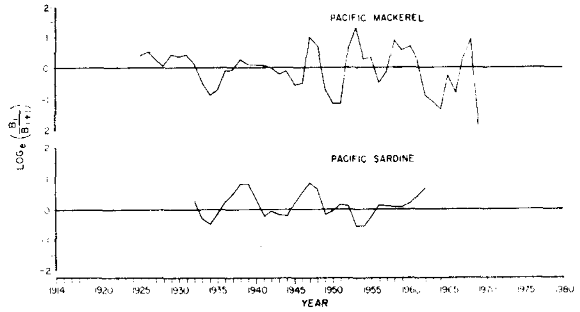

Figure 102. Time series of reproductive success as inferred from annual estimates of age specific biomass (Murphy, 1966; MacCall, in prep.; and MacCall, pers. comm.). The time series indicates significant coherence as estimated from the non-parametric runs test within each species, but no correlation in the reproductive success between species.

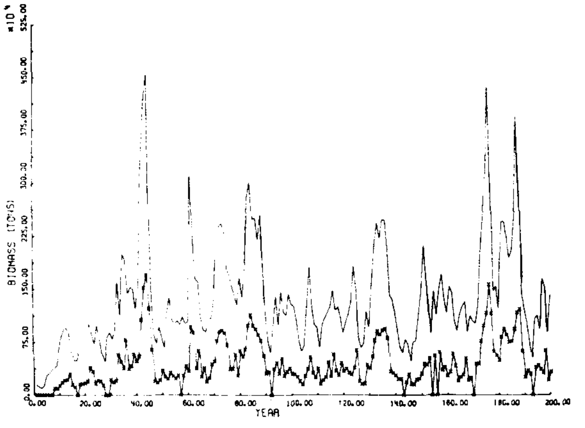

Figure 103. A simulation of the Pacific sardine population for 200 years using the observed random variation and autocorrelation parameters of the Pacific sardine recruitment (Lenarz, 1971) derived from the age specific biomass estimates published by Murphy (1966). Fishing mortality was varied from 0·4 to 0·8 depending on stock sizes in excess of 300000 tons. Fishing on the simulated stock was stopped if the biomass was below 300000 tons. Beginning biomass was estimated to be that at 1966 (Smith, 1972) and no fishery was conducted for 8 years.

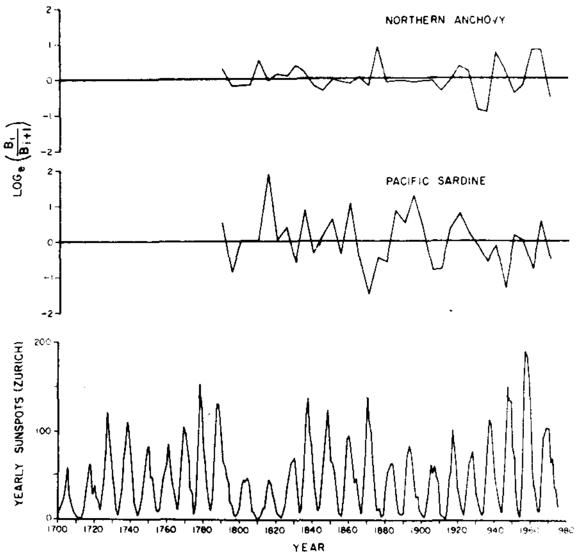

Figure 104. Reproductive success of the northern anchovy and Pacific sardine since 1790 as calculated comparison of biomass (Soutar and Isaacs, 1974) in one 5-year period with biomass in the next 5-year period (Table 9). There is no significant coherence in the series for either species nor is there evidence for correlation either positive (limited productivity) or negative (species competition). Neither do the 11- or 90-year cycles in the sunspot number appear to show agreement with reproductive success on cursory examination.

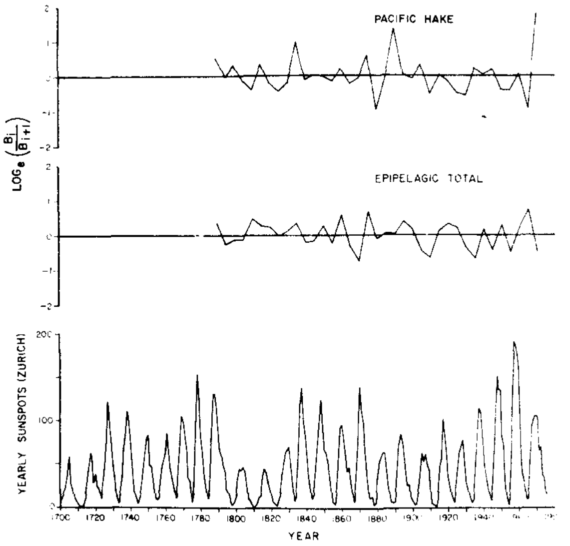

Figure 105. Reproductive success of the Pacific hake below the thermocline with the total 5-year average reproductive success of the epipelagic fishes. Reproductive success estimated from adjacent biomass estimates (Table 9) (Soutar and Isaacs, 1974) as in Figure 104. There is no agreement of the reproductive success of the total epipelagic fish and the Pacific hake, nor are the time series of reproductive success significantly coherent. Agreement of the sunspot cycle maxima in the last four 10-year cycles and the epipelagic total reproductive success minima of the same period does not obtain in the earlier data.

is outweighed by the diminution of predation and the facilitation of reproduction conferred by the schooling habit. The relatively short distances between fish within schools and the long distances between schools raise the possibility that population size limits are imposed by the competition for food between schools rather than the competition for food within schools.

THE HYDROGRAPHIC SPACE SCALE

The school paradox is further heightened by the apparent aggregation of schools into school groups. These school groups (Smith, 1975) are not well defined yet because of our lack of tools to observe underwater phenomena at the 10 km scale. The glimpse afforded by sonar indicates groups of 3500 schools or so in a 10 km diameter area. Such an aggregation of anchovy might contain 1 % of the estimated biomass of the total anchovy stock. The prime characteristic of the school group is that it contains a mixture of fish sizes and ages far broader than that of a school. The hydrographic features which control this scale have not been identified, though features like those

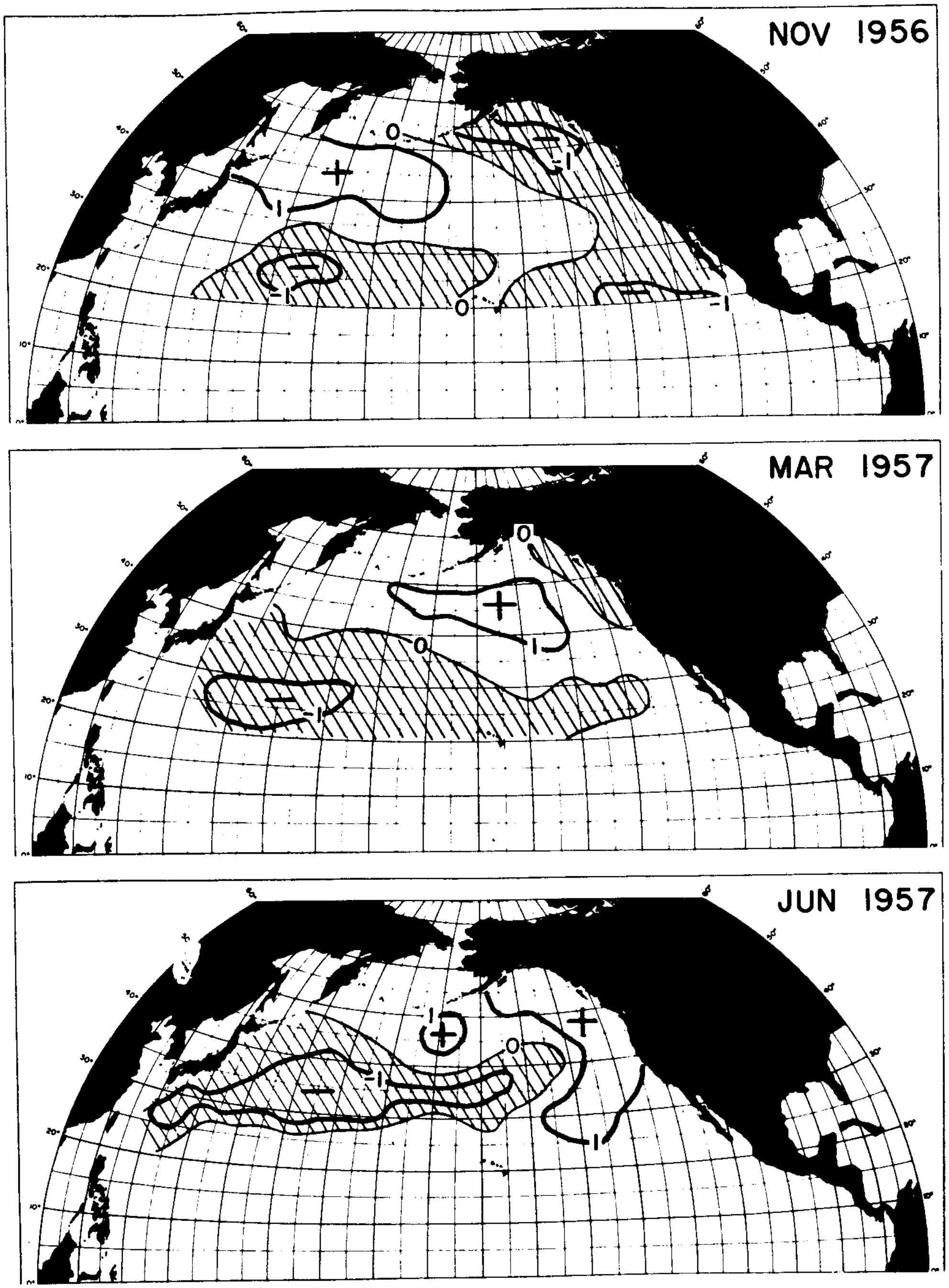

Figure 106. Surface temperature anomalies (Eber, 1971) in the period preceding the notable warming of the eastern temperate Pacific (Sette and Isaacs, 1960).

Table 9. Standing crops of major fish stocks of the California Current as inferred from present day stock sizes and scale deposition rates in the 19th and 20th centuries (thousands of metric tons). Slope and intercept used to convert scale deposition rate to biomass

Year	Pacific sardine	Northern anchovy	Pacific mackerel	Pacific saury	Epipelagic total	Pacific hake	Total
1785	475	3 917	24	105	4 521	4 534	9 055
90	791	5 218	24	328	6 361	7 545	13 906
95	326	4 315	96		4 737	7 447	12 184
1800	326	3 598	96		4 020	10 299	14 319
05	326	3 034	96		3 456	8 824	12 280
10	326	5 068	24		5 418	5 971	11 389
15	2 054	4 909	│		6 963	8 275	15 238
20	2 151	5 666	│	751	8 568	6 760	15 328
25	3 082	5 197	│	110	8 389	4 283	12 672
30	1 704	7 574	↓	55	9 333	3 496	12 829
35	3 975	8 993	60		13 028	8 952	21 980
40	2 823	7 471	60		10 354	8 193	18 547
45	3 264	5 406	24		8 694	8 345	17 039
50	5 798	5 234	24		11 056	8 226	19 282
55	3 944	4 741	42		8 727	7 079	15 806
60	11 093	4 119	24	40	15 276	8 718	23 994
65	6 502	4 213	│		10 715	7 016	17 731
70	1 464	3 426	↓		4 890	6 549	11 439
75	909	8 428	60		9 397	11 432	20 829
80	500	7 714	24	51	8 289	4 274	12 563
85	1 148	7 205	33	132	8 518	4 168	12 686
90	1 850	6 668	24	40	8 582	15 686	24 268
95	6 504	5 873	51	40	12 468	16 015	28 483
1900	9 177	5 475	33		14 685	14 800	29 485
05	3 882	5 044	33	40	8 999	19 818	28 817
10	1 738	2 770	42		4 550	11 725	16 275
15	2 444	2 598	60		5 102	12 075	17 177
20	5 055	3 690	24	51	8 820	10 264	19 084
25	6 226	4 378	60	51	10 715	6 314	17 029
30	5 300	1 803	150	120	7 373	3 562	10 935
35	2 900	705	132	0	3 737	4 376	8 113
40	2 532	1 477	105	152	4 266	4 482	8 748
45	679	1 862	114	773	2 732	5 375	8 107
50	765	1 208	51	1 535	3 559	3 675	7 234
55	732	986	69	353	2 140	2 447	4 587
60	326	2 168	33	140	2 667	2 535	5 202
65	553	4 755	24	40	5 372	977	6 349
70	326	2 797	24	133	3 280	5 927	9 207
Slope *b*	1 417·37	459·45	90	250		499·39	
Intercept *a*	325·93	96·59	24	0		0	

described in Walsh (1976) do occur at this scale. Small, (pers. comm.) describes diel winds which can generate "newly" upwelled blebs of water. These may foster the aggregation of vertically migratory herbivorous zooplankton which could slow the mean progress of schools. This would cause local aggregations of schools with fish of diverse sizes as observed in school groups thus far.

PHYSIOLOGICAL SPACE SCALE

An important feature of the physiological scale is that physiological limits vary during the life cycle. An example is the Pacific sardine, all of whose viable eggs were spawned in temperatures above 13°C: the adults commonly migrated to areas far colder to the north of the spawning area to feed in the highly productive subarctic and transition waters 1200 miles away. The Pacific hake undergoes a similar migration through the same area, but at ~100 m depth.

EXTERNAL SPACE SCALE

It is still undetermined what the nature and magnitude of influences external to the fishes' own physiological scale might be, but one does not have to look far for interesting examples. The albacore is spawned in the western equatorial Pacific and some proportion

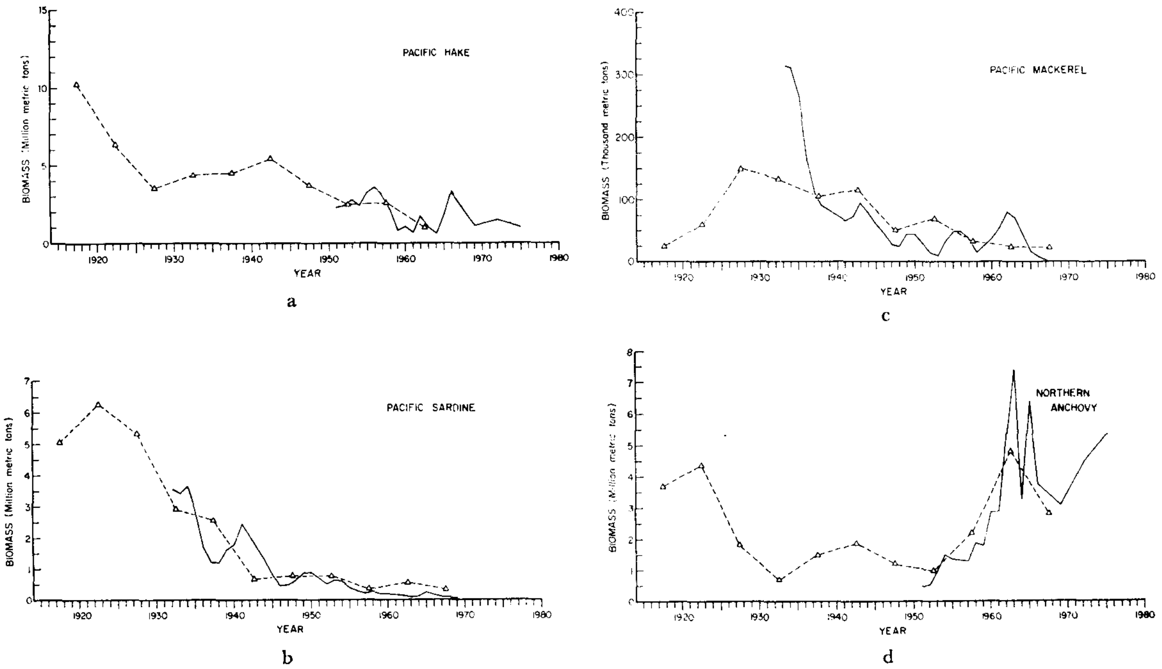

Figure 107a, b, c, d. Time series of biomass of some major species (a, Pacific hake; b, Pacific sardine; c, Pacific mackerel; d, northern anchovy) off the west coast of North America. Dashed lines and triangles at 5-year intervals are from Soutar and Isaacs (1974). Solid line is from annual biomass estimates by fishery analysis or annual (1951–1966) and triannual (1966–1975) estimates from spawning surveys.

of the young migrate through the transition waters to the subarctic, transition and upwelled waters off the North American coast. The predation of these fish on anchovies may approach 15% of the production of the northern anchovy population (Brownell et al, 1976). The north-south shift of albacore (Laurs et al, 1976) catch and the offshore-onshore distribution of anchovy appear to interact broadly. This interaction has sufficient magnitude that the albacore may be an external spatial source of the multi-year cohort changes in reproductive success noted above. Other predators come from outside the anchovy distribution as well. For instance, the northern fur seal predatory capacity has been estimated as 7% of the anchovy production capacity (Brownell et al, 1976).

To estimate the impact of the transpacific migration of albacore from the western tropical Pacific and the migration of fur seals from the Bering Sea, studies of the blocking or guiding effects of the transition zone would be necessary. How dynamic the zone might be at this scale is illustrated by a major warm anomaly of surface temperature (Eber et al, 1968) which moved across the Pacific about 6000 miles and replaced the cold anomaly off the California coast in November 1956 (Fig. 106) and endured there for three years. Eber's (1971) interpretation of this anomaly motion is that a standing wave in the transition zone which alternately causes slight northward and southward displacements of the horizontal thermal gradient of the subarctic to central water mass transition, underwent a gradual phase change. This resulted in the partitioning of the west wind drift water at the coastline so that the water was predominantly transported to the Alaskan gyre rather than the California Current. It is necessary to acquire the ability to translate these major oceanic events to the scale of interest of fish population managers.

ULTIMATE COMMUNITY CARRYING CAPACITY

The fish communities which inhabit the eastern boundary current upwelling zones of the Pacific and of the south Atlantic have strikingly similar species composition. Recent estimates of fish production (MacCall et al, 1976) in the California region indicate that the potential here is somewhat less than the eastern south Atlantic and much less than the Peru–Chile coastline. It also appears (Table 9) that the

Table 10. Crude spawning success ratios in 5-year intervals for pelagic fish off the temperate section of the Pacific coast of North America as estimated from sediment records of fish scales

ln (*R*/*S*)	Proportionate change	Pacific sardine	Northern anchovy	Pacific mackerel	Pacific saury	Epipelagic total	Pacific hake	Total biomass
– 2·0	*X* 0·14	–	–	–	1	–	–	–
– 1·5	*X* 0·22	2	–	1	2	–	–	–
– 1·0	*X* 0·37	4	2	4	2	1	2	–
– 0·5	*X* 0·61	8	4	5	1	9	7	7
0	*X* 1·00	10	23	17	2	17	20	23
0·5	*X* 1·65	8	5	4	1	10	5	7
1·0	*X* 2·71	3	3	5	4	–	1	–
1·5	*X* 4·48	1	–	1	1	–	1	–
2·0	*X* 7·39	1	–	–	–	–	1	–
Number.............		37	37	37	14	37	37	37
Mean...............		– 0·01	0·04	0·01	– 0·11	– 0·01	0·04	0·00
Standard deviation ...		0·778	0·447	0·661	1·147	0·399	0·582	0·312

California Current area is in a relatively low biomass era for the fish stocks of interest. It is interesting to examine together the biomass time series from scale deposition rates (Soutar and Isaacs, 1974), spawning surveys (Smith, 1972) and fishery analysis (Murphy, 1966; MacCall, in prep.). The scale deposition series is very important because it allows us to use existing brief relationships between biomass estimates to see time series over two centuries. This permits the perspective of natural fluctuations so that possible chronic effects of fishing or environmental change by man can be viewed in the context of natural variation (Longhurst et al, 1972).

Examination of the long-term record does not reveal any substantive effects which can be attributed to the major El Niño years, sunspots, or the volcanic activities in the late 19th century. Of the highest interest in the context of ultimate community carrying capacity, the Pacific hake (Fig. 107a), Pacific sardine (Fig. 107b) and Pacific mackerel (Fig. 107c), are all presently low with respect to their levels early in this century. The sardine and mackerel were subjected to intensive fisheries in the 1930's and the Pacific hake was unfished until the mid-1960's. The northern anchovy now appears to be as high in population as the 1920's scale index (Fig. 107d). Classical ecological theory would indicate that the replacement of stocks of low reproductive capacity by stocks of high reproductive capacity may be one indicator of environmental disturbance.

One can see from the 200-year frequency of proportionate changes in the population in Table 10 that the anchovy is the least variable of the fish stocks at 5-year intervals. If ecological theory concerning high reproductive rate holds, this means that the California Current area is one of almost continual environmental disturbance favouring the anchovy. Occasionally, one can observe an outbreak of stability which favours the longer lived stocks with moderate reproductive rates.

The overall minimum in standing stocks is in the 1955 (1949–1954) 5-year period. It is reasonable to ascribe the depth of this nadir, a factor of 2·5 below the previous total biomass minima in 1870 and 1810, to the combined presence of heavy fisheries and low overall productivity. It seems plausible that the decline beginning in 1930–1935 might have been arrested by the high reproductive success observed in the late 1930's had not a massive fishery intervened (Table 9).

The major objective of the CalCOFI (California Cooperative Oceanic Fisheries Investigations) has been to determine the causes of the large fluctuations in fish populations off the west coast of North America. The decline of the Pacific sardine has been observed with scales in varved sediments and fishery analysis. The increase in the northern anchovy has also been observed with scales from varved sediments and spawning surveys. Other massive populations, the jack mackerel and the Pacific hake, have been discovered. It still remains to resolve these features, described at haphazard scales of space and time, in terms of the requirements for wise management of resources in the face of environmental change.

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