

A HISTORY OF PROPOSALS FOR SUBPOPULATION STRUCTURE IN THE PACIFIC SARDINE (*SARDINOPS SAGAX*) POPULATION OFF WESTERN NORTH AMERICA

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ABSTRACT

Recent work has examined the structure of stocks, races, or subpopulations in the recovering Pacific sardine (*Sardinops sagax*) biomass of the northeast Pacific Ocean. Individual fish characteristics do not clearly indicate the geographic origin of birth, but collections of sardines from different areas show some heterogeneity in growth rate, time of birth and recruitment, blood type, and number of vertebrae. Even when heterogeneity is in question, precautionary management principles, which reduce the risk of overfishing, should support management of stocks of fish in different areas as independent stocks.

The sardines of the northeast Pacific have been estimated to have up to three subpopulations based on tagging, size-at-age, isolated spawning centers, blood groups, vertebral column counts, estimated natural mortality rate, or bimodal seasons of recruitment. Spawning centers are thought to occur off the Gulf of California (GOCAL), Baja California Sur inshore (BSI) and Central California offshore (CCO). cursory genetic examinations of sardines from these areas neither support nor refute these divisions. Genetic analysis of *S. sagax* from four far-flung sardine habitat sectors of the Pacific basin can be described as “shallow,” meaning the separation of all the species in the Pacific is relatively recent. However, on the time scale of fisheries management, decades, the separation of the two stocks on the Pacific coast, BSI and CCO, appears chronic in that the collapse of the northern stock did not stimulate an apparent replacement from the southern stock in decades. Therefore, it would be prudent to institute separate management measures that define the boundary between GOCAL and BSI and the boundary between BSI and CCO regardless of the genetic or habitat basis for stock separation. Three data-rich bases for describing the two stocks’ modern isolation should be used to design careful studies of representative samples of sardines at the boundaries between the stocks for devising the most practical method for allocating catches among the neighboring stocks.

This paper reviews existing data to see which might be applied to a precautionary approach to managing the revived Pacific sardine fisheries. It also examines what advances in our knowledge of these stocks and the meth-

ods used to assess them may be required to ensure an adequate spawning biomass and yield of the sardine fisheries for the northeast Pacific stock(s).

INTRODUCTION

Theories of precautionary management, postulated to reduce the risk of overfishing to a minimum, depend on adequate knowledge of the location and movements of self-sustaining populations and the geographic distribution of landings. At least one stock of Pacific sardines (*Sardinops sagax*) in the northeast Pacific has increased in biomass from low levels in the 1960s and 1970s to a currently managed fishery spanning the Pacific coast from México to Canada (Conser et al. 2004).

The primary purpose of this paper is to review existing data to see which might be applied to a precautionary approach to managing the revived Pacific sardine (*Sardinops sagax*) fisheries. Further, some advancement in our knowledge of these stocks and the methods used to assess them may be required to ensure an appropriate spawning biomass and yield of the sardine fisheries for the northeast Pacific stock(s).

INDICATIONS OF SUBPOPULATION STRUCTURE

Early efforts at describing and monitoring the sardine fishery used only size-frequency and catch location data (Clark 1931). A geographically massive tagging program set a standard for characterizing rapid and extended sardine migrations from northern México to British Columbia. Early attempts at aging the fish were not successful (Thompson 1926), and early meristics studies supported a single stock hypothesis (Hubbs 1925).

Clark (1935) regarded the West Coast stock of sardines as a single population that spawned in the south off California and whose larger fish migrated successively further north up to the Gulf of Alaska. This describes the geography of a single stock (fig. 1a)¹. Tagging soon directly supported this model; tags originating from almost all tagging sites were recovered at northern California fishmeal plants. An exception was noted for sardines tagged and released off southern Baja California.

¹O. E. Sette (deceased). 1935. unpub. ms.

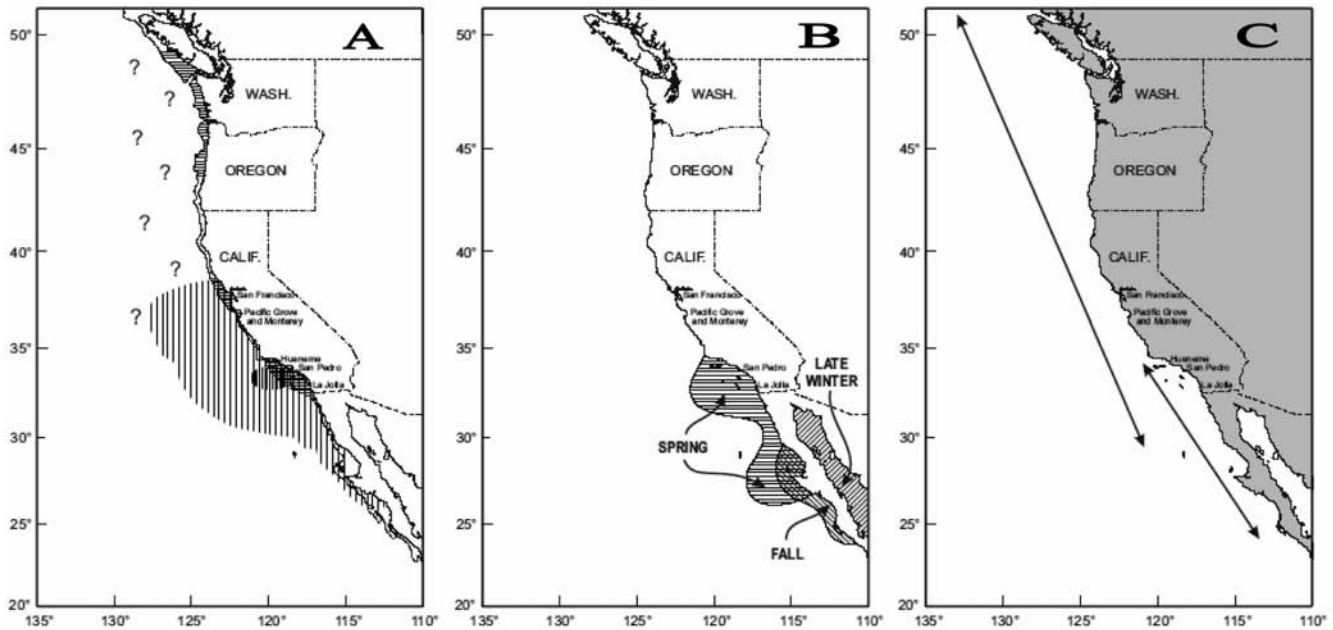


Figure 1. The coastal extent of the major Pacific sardine (*Sardinops sagax*) fisheries, spawning habitat, and migratory range. A) An unpublished diagram of the fisheries (horizontal lines) and spawning areas (vertical lines) showing unmeasured regions (?) for spawning based on knowledge in 1935^a. B) A diagrammatic summary of sardine spawning centers and seasons based on the 1952–1956 CalCOFI surveys (Marr 1960). C) A diagram of the internal boundaries of the migratory range as postulated by Felin (1954), and updated by a geographic review of vertebral counts (Wisner 1960) and blood groups (Sprague and Vrooman 1962; Vrooman 1964) and range northern extent (McFarlane et al. 2002).

None were retrieved in the northerly fishmeal plants (Marr 1957). It was concluded that the fish landings from British Columbia to central and northern Baja California came from a common stock (Clark and Jannson 1945). Godsil's² unpublished paper, however, reported that sardines recruit to San Diego fisheries in April and August.

Once aging from scales and otoliths became available (Walford and Mosher 1943a), two radically different growth patterns were detected (Felin 1954): a stock of small sardines in the south and a stock of larger sardines in the north. At three years, the modal northern sardine length was 219 mm standard length, and the modal southern sardine length was 193 mm. The northern three-year-old sardine was about 50% heavier than the southern. Felin (1954) concluded as follows:

The possibility of heterogeneity in stocks of *Sardinops caerulea* along the Pacific coast of the United States and Canada is examined through evidence from growth and vital statistics of the fished population(s). Growth characteristics of six year-classes sampled in Canada are compared with those from San Pedro. Significant difference in predicted size indicates lack of homogeneity in populations of adults as sampled by the fishery in Canada and in San Pedro. Evidence from qualitative and quantitative differences in individual scale and growth patterns indicates some

independence in the fished stock of the Pacific Northwest and southern California. Bimodality in length composition of certain year classes is evidence that pilchard populations are not homogeneous. Large, long-ranging pilchard may arise from spawning stocks off California while more southern stocks, smaller in size and more short-lived, have limited migration. In view of indications of heterogeneity in growth types of fished stocks of pilchard, whether genotypic or phenotypic in origin, it appears desirable that their population dynamics be studied not only for the coast as a whole but also by geographic areas.

The most comprehensive review of population structure and dynamics was conducted by Marr (1960). Marr assembled and analyzed all of the data from the Pacific sardine fishery, tagging information, and fishery independent surveys of sardine eggs and larvae that were available at the time. Because there were negligible sardine data from the small Mexican fisheries before that time, it was impossible to include data on this southern stock beyond that collected from occasional catches in warm years at San Pedro. The early spawning data collected from off BSI were best described during the "cold" CalCOFI years up to 1956 (Marr 1960).

The early fishery for sardines supported several commercial products, many derived from European prod-

²H. C. Godsil. 1932. Untitled manuscript. Available at: Southwest Fisheries Science Center Library, 8604 La Jolla Shores Drive, La Jolla, CA 92038.

^aO. E. Sette (deceased). 1935. unpub. ms.

ucts: fish meal and oil, bait, fresh and canned fish. There were three sizes of sardine cans. The principal California fisheries provided fish mostly for the one-pound oval can (454 g), lesser quantities for the half-pound oval (227 g), and least of all for the “quarter”-pound square (114 g). The size structure of sardines along the coast determined in what ports each size can was filled. There were two dominant size groups in San Pedro that were canned in the one-pound oval: generally 10 fish per can except during February and March when larger sardines dominated the pack with five fish per one-pound oval (Higgins 1926). In retrospect, this may indicate that an area exists where the different size fish could support an overlap zone that includes San Pedro. “Quarters” were juvenile sardines canned in oil in San Diego in the quarter-pound square can. The sport bait and “quarter oil” cannery drew on two cohorts of juveniles: one appeared in the spring, called the “spring” quarters, and one in the fall, called the “local” quarters³.

The seasonal and geographic distributions of spawning are the most important data available to describe the geographic separation of the stocks. The most extensive continuous spawning area is currently off Central California in April (Lynn 2003). Spawning also appears to narrowly extend north to the coastlines off Canada and Alaska and south to Cedros Island and Sebastián Vizcaíno Bay off the coastline of northern and central Baja California. The Gulf of California (GOCAL) is also a site of geographically extensive sardine spawning in late fall and winter (Aceves-Medina et al. 2004).

The most enigmatic of the putative stocks is the in-shore spawning population centered near Magdalena Bay, Baja California Sur (BSI) which has a spawning peak in summer. In some years this spawning has extended in a narrow coastal band north to the coast of southern California. The southern limit toward Cape San Lucas is not well known (Ahlstrom 1959; Marr 1960; here fig. 1b). The Marr (1960) spawning diagram is probably the best representation of the spawning centers, but it is drawn from the early cold years of CalCOFI. The contemporary spawning center of the CCO (Central California offshore) sardine is about 500 km (300 nmi) north of the 1939–41 spawning center targeted by Sette and Ahlstrom (1948).

The possible genotypic foundation for geographic limits to the BSI and CCO subpopulations was developed with erythrocyte antigen methods (“blood type”) by 1960 (Sprague and Vrooman 1962). Vrooman (1964) reviewed the outer coastal data and reported additional erythrocyte antigen results from GOCAL. The age structure of the outer coast stocks in the southern California

fishery showed that the CCO sardines were from the 1956 and 1957 year-classes and that the BSI sardines were from the 1958 and 1959 year-classes. A seasonal migration of the two stocks may overlap spatially, but not at the time of spawning. A summary of the blood type data is found in Table 1 with the statistically assigned stock origins.

A summary of geographic data from the 1930s, which supports the idea of a single stock (Clark 1935)⁴, is shown in Figure 1a. The location of the spawning centers of the early 1950s (Marr 1960) is reproduced in Figure 1b. The location of the former spring spawners coincides with the location of the CCO stocks currently monitored in April; the location of the former fall stocks coincides with BSI stocks that spawn in August. Figure 1c illustrates the Pacific coast populations’ migratory paths and limits by combining the migratory data and pattern suggested by Felin (1954). The migration range may be influenced by the size structure of each subpopulation and controlled by ocean temperature (See Parrish and McFarlane papers in this symposium).

ADDRESSING POPULATION STRUCTURE

If subpopulations differ in productivity, the stock with higher productivity could induce overharvest of the other stock if a common quota is used. Even if their productivities are similar, asynchronous recruitment could result in strong recruitment to one stock, leading to overfishing of the other stock. This is especially important in contiguous stocks because markets and fleets can be redeployed causing “domino” collapse. Even shore-side plants can be involved, as was the case following the decline of the Pacific stocks after 1958 when the GOCAL sardine harvest was iced and trucked 500 km overland to idle canneries in Ensenada⁵.

Given the contemporary lack of understanding of the sardine stock, the first priority is to exercise precautionary management to protect the regional stocks near all fishing ports. This policy should be implemented even before knowledge is gained of the essential details of the current geographic structure and seasonal migrations of the stock.

The second priority is to study the contemporary intermixture, if any, of sardines among the fishing areas around major ports. As a starting point, the boundary between the CCO and BSI stocks should be documented relative to the harbors of Ensenada and San Pedro. These efforts should be model driven (see Parrish this symposium) and prioritized by the level of fishing relative to the existing fishery management plan of the U.S. and the developing fishery management plan of Mexico.

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⁴O. E. Sette (deceased). 1935. unpub. ms.

⁵R. S. Wolf (retired), pers. comm.

TABLE 1
Sardinops blood type frequency 1958–1962

Site	L ^a	D ^b	N ^c	N C+ ^d	%C+	Subpop.	Reference
Monterey, CA	36	–222	150	18	12.0	North	Sprague & Vrooman 1962
Morro Bay	35	–111	147	22	15.0	North	Sprague & Vrooman 1962
San Pedro	34	0	145	16	11.0	North	Sprague & Vrooman 1962
San Pedro	34	0	98	15	15.3	North	Sprague & Vrooman 1962
Santa Cruz Island	34	0	88	10	11.4	North	Vrooman 1964
Catalina	34	0	98	18	18.4	North	Vrooman 1964
Catalina	34	0	99	14	14.1	North	Vrooman 1964
San Pedro	34	0	100	6	6.0	South	Vrooman 1964
San Diego	33	111	110	12	10.9	North	Sprague & Vrooman 1962
San Diego	33	111	96	14	14.6	North	Sprague & Vrooman 1962
San Diego	33	111	184	7	3.8	South	Sprague & Vrooman 1962
San Diego	33	111	197	10	5.1	South	Sprague & Vrooman 1962
San Diego	33	111	100	15	15.0	North	Vrooman 1964
San Diego	33	111	56	7	12.5	North	Vrooman 1964
San Diego	33	111	247	34	13.8	North	Vrooman 1964
San Diego	33	111	140	18	12.9	North	Vrooman 1964
Del Mar	33	111	99	14	14.1	North	Vrooman 1964
San Diego	33	111	80	13	16.3	North	Vrooman 1964
San Diego	33	111	99	12	12.1	North	Vrooman 1964
San Diego	33	111	100	11	11.0	North	Vrooman 1964
San Diego	33	111	98	12	12.2	North	Vrooman 1964
San Diego	33	111	86	11	12.8	North	Vrooman 1964
San Diego	33	111	98	13	13.3	North	Vrooman 1964
San Diego	33	111	98	13	13.3	North	Vrooman 1964
San Diego	33	111	94	5	5.3	South	Vrooman 1964
San Diego	33	111	100	8	8.0	South	Vrooman 1964
San Diego	33	111	292	21	7.2	South	Vrooman 1964
Ensenada	32	222	100	12	12.0	North	Sprague & Vrooman 1962
San Quintin Bay	30	444	41	8	19.5	North	Sprague & Vrooman 1962
San Quintin	30	444	100	5	5.0	South	Vrooman 1964
Blanca Bay	29	556	74	6	8.1	South	Vrooman 1964
Vizcaíno Bay	28	667	100	5	5.0	South	Sprague & Vrooman 1962
Vizcaíno Bay	28	667	99	6	6.1	South	Sprague & Vrooman 1962
Vizcaíno Bay	28	667	105	7	6.7	South	Sprague & Vrooman 1962
Vizcaíno Bay	28	667	100	5	5.0	South	Vrooman 1964
Magdalena Bay	25	1000	151	7	4.6	South	Sprague & Vrooman 1962
Magdalena Bay	25	1000	100	6	6.0	South	Sprague & Vrooman 1962
Magdalena Bay	25	1000	100	7	7.0	South	Vrooman 1964
Magdalena Bay	25	1000	99	7	7.1	South	Vrooman 1964
Cresciento Island	24	1111	199	13	6.5	South	Vrooman 1964
Agua Verde Bay	25	1667	101	14	13.9	Gulf	Vrooman 1964
Mangles Point	26	1778	95	16	16.8	Gulf	Vrooman 1964
Carmen Island	26	1778	100	16	16.0	Gulf	Vrooman 1964
Carmen Island	26	1778	98	12	12.2	Gulf	Vrooman 1964
San Pedro Bay	28	2000	95	18	18.9	Gulf	Vrooman 1964
Los Animas Bay	28	2000	97	16	16.5	Gulf	Vrooman 1964
San Francis. Bay	28	2000	53	10	18.9	Gulf	Vrooman 1964
Puertecitos	31	2334	99	21	21.2	Gulf	Vrooman 1964

^adegrees north latitude

^bnominal km from San Pedro, CA by sea into Gulf of California

^cnumbers of fish processed

^dnumbers of fish with C+ reaction

Finally, harvest guideline (HG) models with separate biomass estimates should be implemented as in Conser et al. (2004) each year for each putative stock. Their parameters need to be based on new geographic boundary simulations, possibly with SIO (Scripps Institution of Oceanography) pier temperatures augmented, or replaced, by temperatures chosen from different locations.

A separate management model is required for each stock (in the notation used by the Coastal Pelagic Species plan⁶ for sardine):

$$HG_a = (BIOMASS_a - CUTOFF_a) \cdot \text{FRACTION}_a \cdot \text{USA DISTRIBUTION}_a \quad (1)$$

$$HG_b = (BIOMASS_b - CUTOFF_b) \cdot \text{FRACTION}_b \cdot \text{USA DISTRIBUTION}_b \quad (2)$$

⁶PFMC (Pacific Fishery Management Council). 1998. Amendment 8 to the Northern Anchovy Fishery Management Plan incorporating a name change to: The Coastal Pelagic Species Fisheries Management Plan. Pacific Fishery Management Council, Portland, OR 97220.

where HG is the harvest guideline; BIOMASS is the annual estimate of spawning biomass in tons; CUTOFF is the threshold biomass below which no fishing occurs; FRACTION is a value between 0.05 and 0.15 based on temperature at Scripps Pier; and USA DISTRIBUTION is the proportion allocated to U.S. fishermen.

The current harvest guideline is derived from studies of early (1930–90) catches and estimated biomass (Jacobson and MacCall 1995). Jacobson and MacCall (1995) performed simulations assuming a single stock north of Punta Baja, Baja California Norte. The criterion for CUTOFF was that the stock should be able to recover rapidly from a series of recruitment failures. FRACTION was a value that would minimize the frequency of collapses during cold and warm phases of the California Current region. The USA DISTRIBUTION value is arbitrary. To successfully implement the pair of models, the seasonal geographic location and biomass estimates of all subpopulations must be approximated with respect to the fishery from each port. The criteria, productivity, and variability used for simulation would have to be established with new parameters and latitudinal ranges for each of the proposed stocks.

DATA FOR MANAGING SARDINE STOCKS

The geographic location and extent of the stocks' seasonal spawning areas should be monitored frequently. The fishery only exists in the coastal region of the sardines' total distribution. There may be insufficient data on fisheries landing catches at Cedros Island or directly at tuna-rearing pens along this stretch of coastline. Historical information on length-at-age, vertebral count, temperature, and season-of-capture may suffice for allocating catches for current management purposes.

Techniques for obtaining environmental parameters from research ships and space (Lynn 2003), and obtaining egg samples and surface salinity from ships underway at full speed, should be given priority for development, because the current sardine fleet would not be useful for the long-range requirements of establishing boundaries of spawning grounds. The boundaries of spawning biomass can be monitored in the peak spawning seasons using egg-pump surveys. When the stocks overlap, spawning biomass can be estimated from Punta Eugenia to Alaska in April for the CCO stock and from Point Conception south to the tip of Cape Lucas in August for the BSI stock. If the GOCAL stock is to be managed at the same time as the BSI and CCO stocks, the initial spawning area surveys should be from Cape San Lucas to the northern margin of the GOCAL in November–January (Moser et al. 1993; Aceves-Medina et al. 2004). While index methods may suffice for management, these biomass values should be validated periodically by daily egg production methods (Lasker 1985)

using adult and area egg production methods. Adult sampling conducted to determine egg production should include analysis of vertebral counts, otolith determinations of trace metals, growth, and season of birth.

Blood type analysis is probably not feasible for monitoring racial boundaries, and current genetic approaches can barely distinguish between sardines in the far-flung reaches of the Pacific and Indian Oceans (Hedgecock et al. 1989; Parrish et al. 1989; Grant and Leslie 1996; Bowen and Grant 1997; Grant and Bowen 1998; Lecomte et al. 2004). Thus, the development of genetic techniques is a necessity.

At the time of egg production assessment, scientific sampling for genetic analyses should be instituted. Current genetic studies are hampered by a number of factors; many have used specimens collected haphazardly by volunteers, and these are geographically biased because volunteer collectors do most of their collecting near the coast. Compared with the definitive vertebral count studies and erythrocyte antigen studies (Vrooman 1964; Wisner 1980), existing genetic studies may have used insufficient numbers of fish to define within-region stock boundaries.

Representative genetic samples should be allocated by use of the seasonal and spatial distribution of egg-pump samples. As a matter of priority, fisheries in the area where stock migrations overlap—San Pedro to Ensenada—could be studied more intensely in April and August. Existing data (tab. 1) on blood types (Sprague and Vrooman 1962; Vrooman 1964) and vertebral counts (tab. 2; fig. 2) (Wisner 1960) should serve to design the quantitative genetics work (Sprague and Vrooman 1962; Vrooman 1964) rather than the small number of specimens used by Hedgecock et al. (1989) and Lecomte et al. (2004).

STANDARDS FOR DEFINING FISHERY STOCK GENETICS

In his classic review of fishery biochemical genetics, Utter (1991) restated the logical principle that “absence of proof is not proof of absence.”

. . . it is important to note that differences in frequencies between collections of individuals sampled from distinct locations or at different times are usually reliable evidence for genetic differentiation between the sampled populations . . . the absence of such differences is not in itself positive evidence that the samples were drawn from a single panmictic population.

The works of Rodriguez-Sanchez et al. (2002) and Lecomte et al. (2004) support a major alternative to the established three-stock idea. For example, it is possible that the immuno-genetic approach to stock definition

TABLE 2
Pre- and Post-Sardine Collapse Vertebral Count

Precollapse (Clark 1947)							
Collection Area	Sea km from San Pedro	Number of Fish	Number of Fish >51	Proportion Fish >51	Std Error	Lower 95% Limit	Upper 95% Limit
Gulf of California	1713	735	121	0.165	0.027	0.138	0.191
Magdalena Bay	1296	795	250	0.314	0.032	0.282	0.347
Pta. Eugenia-CSLaz	963	710	261	0.368	0.035	0.332	0.403
Sebastian Vizcaino Bay	741	1093	651	0.596	0.029	0.567	0.625
San Diego	148	6553	4380	0.668	0.011	0.657	0.680
San Pedro	0	9652	6490	0.672	0.009	0.663	0.682

Postcollapse (Wisner 1960)							
Collection Area	Sea km from San Pedro	Number of Fish	Number of Fish >51	Proportion Fish >51	Std Error	Lower 95% Limit	Upper 95% Limit
Gulf of California	1713	611	122	0.200	0.032	0.168	0.231
Magdalena Bay	1296	679	209	0.308	0.035	0.273	0.343
Santa Maria Bay	1204	842	314	0.373	0.033	0.340	0.406
Pta. Eugenia-CSLaz	963	1967	849	0.432	0.022	0.410	0.454
Sebastian Vizcaino Bay	741	559	234	0.419	0.041	0.378	0.460
Cedros San Benito	685	783	417	0.533	0.035	0.498	0.568
Ensenada	269	10670	5325	0.499	0.009	0.490	0.509
San Diego	148	666	343	0.515	0.038	0.477	0.553
San Pedro	0	1864	940	0.504	0.023	0.482	0.527

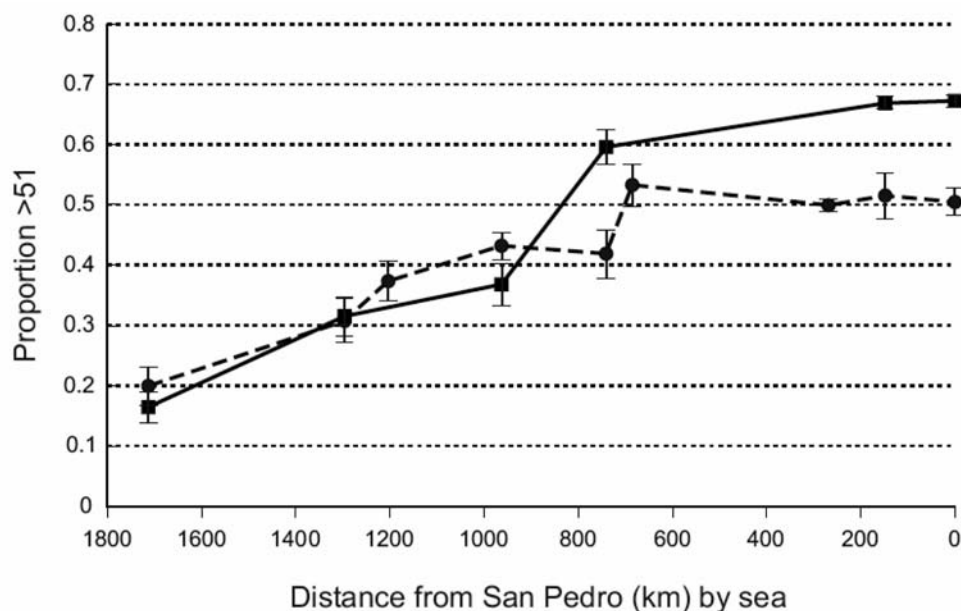


Figure 2. Geographic position of a postulated internal range boundary derived from a comparison of the latitudinal gradient of vertebral fractions ($p > 51$) from before the Pacific sardine (*Sardinops sagax*) fishery collapse (solid line) and after the fishery collapse (dashed line).

is not able to isolate the genetic/environmental balance of controls⁷. It is possible that the CCO stock was so reduced that it has now been replaced from a migrant BSI stock. Hedgecock et al. (1989), however, discounted the idea that the recent decline of sardines was evidence of an evolutionary bottleneck.

Simulations of the CCO stock (Gaggiotti and Vetter

1999) also indicate that it is unlikely that the genetics of the putative CCO stock were reduced in biomass enough to have become a genetic "bottleneck."

The use of vertebral counts appears to be a robust, if tedious, method for distinguishing the BCS and CCO stocks. Data on vertebral counts are available for the 1900s. Wisner (1960) plotted the results from two periods: before the collapse of 1921–41 and after the collapse of 1951–59 (fig. 2). From the comparison of collection

⁷W. S. Grant. 2004. pers. comm. P.O.Box 240104, Anchorage, AK 99524.

sites, the two lines appear to diverge north of Sebastián Vizcaíno Bay; this latitudinal cline was expected based on analysis of temperature data. This suggests that the underlying rate of increase of vertebral count distribution is a function of temperature at birth, and the two lines may result from genotypic differences as in the case of the coincident blood types. The genetic origin of vertebral count distribution has been illustrated by experiments on Atlantic silverside (*Menidia menidia* (L.))⁸.

The few contemporary vertebral counts off Southern California (61.5%) and Oregon (Survey 76.5%; Fishery 69.2%)⁹ estimate the percentage of vertebral counts at or above 52. If the South Baja inshore stock had invaded the coast from Central California to Alaska, one would expect fewer vertebrae than those found in the 1950s. Birth date determination by daily otolith ring counting indicates that as many sardines were born in August as in April in San Diego waters in 1982–83 (Butler 1987). The putative northern stock declined to less than 10,000 tons for the period between 1964 and 1980 (fishing moratorium 1967–84). The southern stock near Magdalena Bay was not diminished in this period according to juvenile bait fish estimates of population size and geographic distribution analyzed by Rodriguez et al. (2002). The failure of the southern stock to fill in for decades after the virtual disappearance of the northern stock militates against the deregulation of fisheries based on hope that a stock decline can be rectified by migration from adjacent habitats (Taylor and Dizon 1999). Lastly, in a comprehensive study of sardine and anchovy fisheries (Jacobson et al. 2001), it was found that the instantaneous natural mortality rates ranged from 0.7 for GOCAL and BSI stocks to 0.4 for the CCO stock; this difference alone would require separate management models irrespective of whether the stocks are separated on habitat or genetic bases.

SUMMARY

The sardines (*Sardinops sagax*) of the northeast Pacific have been referred to as three subpopulations based on tagging (Clark 1947), size-at-age (Felin 1954), isolated spawning centers (Marr 1960), blood groups (Vrooman 1964), vertebral column count (Wisner 1960), estimated natural mortality rate (Murphy 1966; MacCall 1979; Jacobson et al. 2002), or bimodal seasons of recruitment

(Butler 1982)¹⁰. Spawning centers are in the Gulf of California (GOCAL), Baja California Sur inshore (BSI) and Central California Offshore (CCO). cursory genetic examination of sardines from these areas neither supports nor refutes these divisions (Hedgecock et al. 1989; Lecomte 2004). Studies to date are considered cursory because the sardine geographic areas and boundaries have not been contemporarily, systematically, and representatively sampled. Genetic analysis of *S. sagax* from four far-flung sardine habitat sectors of the Pacific basin can be described as “shallow,” (Parrish et al 1989; Grant and Bowen 1998) meaning that the separation of all the species in the Pacific is relatively recent. However, on the time scale of fisheries management, decades, the separation of the stocks appears chronic in that the virtual collapse of the northern stock, 1940–79, did not stimulate an apparent replacement from the southern stock in decades. Therefore, it would be prudent to institute separate management measures defining the boundary between GOCAL and BSI and the boundary between BSI and CCO regardless of the genetic or habitat basis for stock separation. Three data-rich bases for describing stocks’ modern isolation should be used to design careful studies of representative samples of sardines at the boundaries between the stocks for devising the most practical method for allocating catches among the neighboring stocks.

A review of the literature characterizing sardine catch and fishery independent samples of eggs and adults lends support for the continued existence, at important times, of isolated subpopulations of sardines in the northeast Pacific. That panmixia existed, on the other hand, has been concluded from cursory examination of regional genetic characteristics and is likely based on flawed logic; absence of evidence is not evidence of absence of subpopulation structure. It appears that historical data on blood types, vertebral counts, and spawning areas would serve to design practical approaches to determining the contemporary distribution of sardine stocks in this region.

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⁸Methodological Note: The original analyses of vertebral count used analysis of variance on a distribution composed of six integer values (49–54 vertebrae) with leptokurtic deviations from normal distribution. While these analyses and frequencies are published, I have chosen to treat the vertebral counts as two categories: greater than 51 and less than or equal to 51 vertebrae expressed as a fraction. This separation near the median allows precise binomial descriptions of the proportions and a normal approximation of confidence limits (fig. 2; tab. 2). It is easier to envision differences in proportions r than differences in averages which differ by only hundredths of a vertebra.

⁹D. Ambrose. 2004. pers. comm. NOAA/NMFS/SWFSC, 8604 La Jolla Shores Dr., La Jolla, CA 92037.

¹⁰H. C. Godsil. 1932. Untitled manuscript. Available at: Southwest Fisheries Science Center Library, 8604 La Jolla Shores Drive, La Jolla, CA 92038.

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LITERATURE CITED

- Aceves-Medina, G., S. P. A. Jimez-Rosenberg, A. Hinojosa-Medina, R. Funes-Rodriguez, R. J. Saldierna-Martinez, and P. E. Smith. 2004. Fish larvae assemblages in the Gulf of California. *J. Fish Biol.* 65:832–847.
- Ahlstrom, E. H. 1959. Distribution and abundance of the eggs of the Pacific sardine, 1952–1956. *Fish. Bull., U.S.* 60:185–213.
- Billerbeck, J. M., G. Orti, and D. O. Conover. 1997. Latitudinal variation in the vertebral number has a genetic basis in the Atlantic silverside, *Menidia menidia*. *Can. J. Fish. Aquat. Sci.* 54:1796–1801.
- Bowen, B. W. and W. S. Grant. 1997. Phylogeography of the sardines (*Sardinops* spp.): assessing biogeographic models and population histories in temperature upwelling zones. *Evolution* 51:1601–1610.
- Butler, J. L. 1987. Comparisons of the early life history parameters of Pacific sardine and northern anchovy and implications for species interactions. Ph.D. Dissertation. University of California, San Diego. 242 pp.
- Clark, F. N. 1931. Dominant size groups and their influence in the fishery for the California sardine (*Sardine caerulea*). *Calif. Div. Fish Game Bull* 31:1–43.
- Clark, F. N. 1935. A summary of the life-history of the California sardine and its influence on the fishery. *Calif. Fish. Game*, 21:1–9.
- Clark, F. N. and J. F. Janssen. 1945. Movements and abundance of the sardine as measured by tag returns. *Calif. Fish. Game Bull.* 61:1–42.
- Clark, F. N. 1947. Analysis of populations of the Pacific sardine on the basis of vertebral counts. *Calif. Dep. Fish Game Fish. Bull.* 65, 26pp.
- Conser, R., K. Hill, P. Crone, N. Lo, and R. Felix-Uraga. 2004. Assessment of the Pacific sardine stock for U.S. management in 2005. Briefing document of Pacific Fishery Management Council, Portland, OR. November 2004. pp. 1–139.
- Felin, F. E. 1954. Population heterogeneity in the Pacific pilchard. *Fish. Bull., U.S.* 54:201–225.
- Gaggiotti, O. E., and R. D. Vetter. 1999. Effect of life history strategy, environmental variability, and overexploitation on the genetic diversity of pelagic fish populations. *Can. J. Fish. Aquat. Sci.* 56:1–13.
- Grant, W. S. and B. W. Bowen. 1998. Shallow population histories in deep evolutionary lineages of marine fishes: insights from sardines and anchovies and lessons for conservation. *J. Hered.* 89:415–426.
- Grant, W. S. and R. W. Leslie. 1996. Late Pleistocene dispersal of Indian-Pacific sardine populations in an ancient lineage of the genus *Sardinops*. *Mar. Biol.* 126:133–142.
- Hedgecock, D., E. S. Hutchinson, G. Li, F. L. Sly, and K. Nelson. 1989. Genetic and morphometric variations in the Pacific sardine *Sardinops sagax caerulea*: comparisons and contrasts with historical data and with variability in northern anchovy *Engraulis mordax*. *Fish. Bull., U.S.* 87:653–671.
- Higgins, E. 1926. A study of fluctuations in the sardine fishery of San Pedro. California Fish and Game Commission. *Calif. Fish. Bull.* 11:125–158.
- Hubbs, C. L. 1925. Racial and seasonal variation in the Pacific herring, California sardine, and California anchovy. California Fish and Game Commission. *Calif. Fish. Bull.* 8:1–23.
- Jacobson, L. D. and A. D. MacCall. 1995. Stock-recruitment models for Pacific sardine (*Sardinops sagax*). *Can. J. Fish. Aquat. Sci.* 53:566–577.
- Jacobson, L. D., J. A. A. De Oliveira, M. Barange, M. A. Cisneros-Mata, R. Felix-Uraga, J. R. Hunter, J. Y. Kim, Y. Matsuura, M. Niquen, C. Portreiro, B. Rothschild, R. P. Sanchez, R. Serra, A. Uriarte, and T. Wada. 2001. Surplus production, variability, and climate change in the great sardine and anchovy fisheries. *Can. J. Fish. Aquat. Sci.* 58:1891–1903.
- Lasker, R. 1985. ed. 1985. An egg production method for estimating spawning biomass of pelagic fish: application to the northern anchovy (*Engraulis mordax*). U.S. Dep. Commer. NOAA Tech. Rep. NMFS 36, 99 pp.
- Lecomte, F., W. S. Grant, J. J. Dodson, R. Rodriguez-Sanchez, and B. W. Bowen. 2004. Living with uncertainty; genetic imprints of climate shifts in east Pacific anchovy (*Engraulis mordax*) and sardine (*Sardinops sagax*). *Mol. Ecol.* 13(8):2169–2182.
- Lynn, R. J. 2003. Variability in the spawning habitat of Pacific sardine (*Sardinops sagax*) off southern and central California. *Fish. Oceanogr.* 12:3:1–13.
- Marr, J. C. 1957. The subpopulation problem in the Pacific Sardine *Sardinops caerulea*. In Contributions to the study of subpopulations of fishes, U.S. Dept. Interior Fish. Wildl. Svc. Special Scientific Report. Fisheries No. 208, Washington, DC, pp. 108–125.
- Marr, J. C. 1960. The causes of major variations in the catch of the Pacific sardine, *Sardinops caerulea* (Girard). In Proceedings of the World Scientific meeting on the Biology of Sardines and Related Species. Rosa, H. and G. I. Murphy, eds. Food and Agriculture Organization of the United Nations III:667–791.
- McFarlane, G. A., P. E. Smith, T. R. Baumgartner, and J. R. Hunter. 2002. Climate variability and Pacific Sardine Populations and Fisheries. American Fisheries Society Symposium 32:195–214.
- Moser, H. G., R. L. Charter, P.E. Smith, D. A. Ambrose, S. R. Charter, C. A. Meyer, E. M. Sandknop, and W. Watson. 1993. Distributional atlas of fish larvae and eggs in the California Current Region: Taxa with 1000 or more total larvae, 1951–1984. *CalCOFI Atlas* 31, 231pp.
- Parrish, R. H., R. Serra, and W. S. Grant. 1989. The monotypic sardines, *Sardina* and *Sardinops*: their taxonomy, distribution, stock structure and zoogeography. *Can. J. Fish. Aquat. Sci.* 46:2019–2036.
- Rodriguez-Sanchez, R., D. Lluch-Belda, H. Villalobos, and S. Ortega-Garcia. 2002. Dynamic geography of small pelagic fish populations in the California Current System on the regime time scale (1931–1997). *Can. J. Fish. Aquat. Sci.* 59:1980–1988.
- Sprague, L. M. and A. M. Vrooman. 1962. A racial analysis of the Pacific sardine *Sardinops caeruleus* based on studies of erythrocyte antigens. *Ann. N. Y. Acad. Sci.* 97:131–138.
- Taylor, B. L. and A. E. Dizon. 1999. First policy then science: why a management unit based solely on genetic criteria cannot work. *Mol. Ecol.* 8:S11–S16.
- Thompson, W. F., 1926. Errors in the method used in the study of the California sardine. *Calif. Fish Bulletin* 11:159–189.
- Utter, F. M. 1991. Biochemical genetics and fishery management: an historical perspective. *J. Fish Biol.* 39: Supplement A, 1–20.
- Vrooman, A. M. 1964. Serologically differentiated subpopulations of the Pacific sardine, *Sardinops caerulea*. *J. Fish. Res. Bd. Canada* 21:691–701.
- Wahlford, L. A. and K. E. Mosher. 1943a. Determination of the age of (sardine) juveniles by scales and otoliths. U.S. Dept. Int. Fish Wildl. Svc. Special Scientific Report; Fisheries No. 15:31–95*. Washington, DC.
- Wahlford, L. A. and K. E. Mosher. 1943b. Determination of the age of (sardine) adults by scales, and effect of environment on first year's growth as it bears on age determination. U.S. Dept. Int. Fish Wildl. Svc. Special Scientific Report; Fisheries No. 15:96–131*. Washington, DC.
- Wisner, R. L. 1960. Evidence of a northward movement of stocks of the Pacific sardine based on the number of vertebrae. *Calif. Coop. Oceanic Fish. Invest. Rep.* 8:75–82.

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