

Surplus production, variability, and climate change in the great sardine and anchovy fisheries

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Abstract: We used fishery and survey data to calculate annual surplus production (ASP) and instantaneous surplus production rates (ISPR) for eight anchovy and nine sardine stocks. In addition, we calculated ASP per unit spawning area for six anchovy and six sardine stocks. Median ASP was highest for stocks with highest median biomass (mostly anchovies), and ASP was typically about 16% of stock biomass. ASP was often negative, more frequently for anchovies (36% of years) than for sardines (17% of years). ISPR was less variable for sardines and autocorrelated for longer-lived stocks (mostly sardines). Strong biomass increases tended to be preceded by short, abrupt increases in ISPR, and declines were pronounced when catches exceeded ASP for 5 years or more. The longest “runs” of positive and negative production were 21 and 4 years for sardine off Japan, 10 and 3 years for sardine off California, 8 and 2 years for anchovy off Peru, and 4 and 3 years for anchovy off California. ISPR is more sensitive to environmental changes than catch, biomass, or ASP and appear to be better for identifying environmentally induced regime shifts. Long time series show evidence of density-dependent effects on ASP in anchovies and sardines, but environmentally induced variation appears to dominate.

Résumé : Des statistiques de pêche et des données d’inventaire nous ont servi à calculer la production excédentaire annuelle (ASP) et les taux instantanés de production excédentaire (ISPR) chez huit stocks d’anchois et neuf stocks de sardines. De plus, nous avons calculé l’ASP par unité de surface de frayère chez six stocks d’anchois et six stocks de sardines. L’ASP moyen est maximal chez les stocks qui possèdent la plus grande biomasse médiane (surtout des anchois) et correspond normalement à environ 16% de la biomasse du stock. L’ASP est souvent négative, plus souvent chez les anchois (36% des années) que chez les sardines (17% des années). L’ISPR est moins variable chez les sardines et est autocorrélé chez les stocks à longévité plus grande (surtout des sardines). Les augmentations importantes de biomasse sont normalement précédées d’une croissance abrupte de l’ISPR; lorsque les prises dépassent l’ASP pour

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5 ans ou plus, il y a un déclin prononcé. Les plus longues « séquences » de production positive et négative ont été respectivement de 21 et 4 années pour les sardines au large du Japon, de 10 et 3 années pour les sardines au large de la Californie, de 8 et 2 années pour les anchois au large du Pérou et de 4 et 3 années pour les anchois au large de la Californie. Les ISPR est plus sensible aux changements de l'environnement que ne le sont les captures, la biomasse ou l'ASP et semblent être plus appropriés pour détecter les changements de régime dus à l'environnement. Les longues séries temporelles laissent croire à l'existence d'effets de densité-dépendance sur l'ASP chez les anchois et les sardines, mais la variation attribuable à l'environnement semble dominer.

[Traduit par la Rédaction]

Introduction

Annual surplus production (ASP) is biological production in excess of the amount required, when no fishing occurs, to maintain the same stock biomass level at the beginning of consecutive years (Ricker 1975). ASP is the net result of recruitment, somatic growth, and mortality. It can be expressed as the product of stock biomass and the rate of ASP per unit biomass. The rate may be density independent (constant over time or variable due to environmental factors only), density dependent (variable due to stock biomass), or both.

ASP is a fundamental variable in fishery science and fisheries management. Maximum sustained yield (MSY) is proportional to maximum ASP (i.e., $\delta_{MSY} = ASP_{max}$, see below). In any year, catches larger than $ASP/\bar{\delta}$ reduce stock biomass, while smaller catches increase stock biomass. If ASP is negative, then stock biomass will decline, even with no catch. Thus, ASP is important when managers seek to optimize economic benefits from a fishery, adjust harvest levels to attain biomass targets, prevent overfishing, or rebuild overfished stocks.

According to the theory of density dependence (e.g., Schaefer 1957), and neglecting environmental effects, fishing reduces stock biomass but increases the rate of production per unit biomass because of reduced competition for food and habitat, removal of older, slow-growing individuals, and other factors. If the increased rate of production exceeds the proportional reduction in biomass, then ASP for the stock as a whole increases, and vice versa. ASP is zero at the theoretical extremes when biomass is zero (but the production rate is maximum) and at carrying capacity when stock biomass is high (but the production rate is zero). In theory, maximum ASP occurs at an intermediate biomass level that depends on the shape of the spawner–recruit relationship, density-dependent growth and mortality, fishing mortality rates by age and size, and other factors (Sissenwine and Shepherd 1987). Density-dependent effects on ASP are important because fishing reduces stock biomass and keeps the engine of production “turned on.” Wada and Jacobson (1998) suggested that density-dependent effects on recruitment (an important component of ASP) are typical in sardines but difficult to measure without many years of data and models that accommodate environmental variation.

In contrast with density-dependent effects, environmental effects on ASP by small pelagic fish like sardines and anchovies are often more dramatic, even in short time series (e.g., Barnes et al. 1992), because most small pelagic fish are short-lived and planktivorous (Hunter and Alheit 1995).

Small pelagic fish are major components of large marine ecosystems where they may affect the population dynamics of their planktivorous prey and predators (Cury et al. 2000),

which include marine mammals, birds, and other fish (Hunter and Alheit 1995). Small pelagic species provide a large fraction of the total global catch of marine fish and support some of the largest individual fisheries in the world (Hunter and Alheit 1995). Dramatic changes in ASP and biomass due to recruitment variability, rapid somatic growth, and high mortality rates are characteristic of small pelagic fish, particularly with fishing. Thus, ASP is useful in the study of responses of anchovy and sardine stocks to environmental change, such as regime shifts. We define regimes as periods of high and low surplus production rates (see below) associated with decadal-scale variability in the environment (Trenberth 1990; Lluch-Belda et al. 1992; Schwartzlose et al. 1999).

The main purpose of this paper is to measure and characterize variability in ASP and ASP rates for anchovy (*Engraulis* spp.) and sardine stocks (*Sardinops*, *Sardinella*, and *Sardina* spp.) around the world and to evaluate them as a way to detect regime shifts (Lluch-Belda et al. 1989, 1992). We hypothesize that ASP rates are more sensitive than other population indicators and therefore more effective in identifying regime shifts. Our research was part of a plan coordinated by the Small Pelagic Fish and Climate Change (SPACC) Program of the Global Ocean Ecosystem Dynamics (GLOBEC) Program, with the ultimate objective of understanding and predicting climate-induced changes in the production of small pelagic fish around the world.

Materials and methods

ASP was calculated for annual periods (years, usually calendar years or July–June fishing years) used by managers in assessments for each stock. We restricted analyses to fish ages 1 and older (ages 1+) because anchovies and sardines spawn and recruit throughout the year (Blaxter and Hunter 1982) and recruitment is complete by age 1. Our calculations exclude ASP by age-0 fish (see below). All production calculations and biomass and catch data are in units of body weight.

Catch data used in this analysis were official estimates of total catch in weight (all ages) less an estimate of the catch weight of age-0 fish (Table 1). Age-0 fish (young of the current year) are typically less than 10% of the total catch weight in most anchovy and sardine fisheries (Table 1). It was not always possible to deduct the catch weight of age-0 fish from official catch estimates, however, due to data limitations. The relative error in using catch data that include age-0 fish is a positive bias proportional to catch weight of age-0 fish and inversely proportional to production by older fish (Appendix A).

As described above, ASP is defined as the change in stock biomass from one year to the next with no fishing. ASP by a single cohort (age group) in an unfished stock is

$$(1) \quad P_{t,a} = B_{t+1,a+1}^* - B_{t,a}$$

where $B_{t,a}$ is the biomass of the cohort at age a and at the beginning of year t . The asterisk is for the special case of no fishing during year t . ASP by a cohort in a fished stock depends on catch as well as biomass:

$$(2) \quad P_{t,a} = B_{t+1,a+1} - B_{t,a} + \delta_{t,a} C_{t,a}$$

where $C_{t,a}$ is catch weight and $\delta_{t,a}$ converts catches to units of equivalent population biomass at the beginning of the next year (MacCall 1978; Opsomer and Conrad 1994) to account for losses and gains due to natural mortality and growth that would have occurred if the catch had not been taken. For simplicity, it is assumed that the fishery operates continuously throughout the year (MacCall 1978), although most anchovy and sardine fisheries are seasonal.

In some cases, age-specific estimates of abundance and catch were not available (e.g., Jacobson et al. 1994). We therefore modified eq. 2 to approximate ASP for ages 1+:

$$(3) \quad P_t = B_{t+1} - B_t + \bar{\delta} C_t$$

where $\bar{\delta}$ was an average (see below) adjustment factor, assumed constant over time. We considered using time-dependent catch adjustment factors but found too much variability in annual growth data and mortality estimates. In our calculations, recruitment at the beginning of year $t + 1$ (part of B_{t+1}) was counted as production during year t .

The adjustment factor $\bar{\delta}$ was an approximate weighted average:

$$(4) \quad \bar{\delta} = \frac{\sum_{a=1}^A \tilde{C}_a \delta_a}{\sum_{a=1}^A \tilde{C}_a}$$

where \tilde{C}_a was proportional to age-specific catch weight per recruit at average fishing mortality rates (see below). Based on a quadratic regression model for the results in table 1 of MacCall (1978) (with $F = 0.5 \cdot \text{year}^{-1}$), age-specific adjustment factors were, $\delta_a = 0.999 - 0.529k_a + 0.0899k_a^2$ where $K_a = M - G_a$ was the difference between instantaneous rates for natural mortality (M) and growth (G_a) (see below).

Average instantaneous growth rates were $\bar{G}_a = \ln(w_{a+1}/w_a)$ with weights at age (w_a) from a von Bertalanffy curve (Ricker 1975). We used a single von Bertalanffy growth curve to smooth the data and obtain approximate average growth rates.

The term used to compute $\bar{\delta}$ in eq. 4 was

$$(5) \quad \tilde{C}_a = \frac{\bar{F}_a}{\bar{Z}_a} \left(1 - e^{-\bar{Z}_a}\right) \beta_a$$

where $\bar{Z}_a = \bar{F}_a + M - \bar{G}_a$ and \bar{F}_a was the average fishing mortality rate for age a from stock assessment work (constant for all ages when age-specific estimates were not available). In our calculations, \tilde{C}_a was approximately proportional to age-specific catch weight per recruit at average fishing mortality rates because

$$\beta_a = e^{\sum_{t=0}^{a-1} -\bar{Z}_t} \quad (\text{with } \bar{Z}_0 = 0)$$

was proportional to age-specific biomass per recruit.

Summary statistics

To make comparisons among stocks and species, we calculated ASP (in kilotonnes per year), as described above, as well as the instantaneous surplus production rate (ISPR):

$$(6) \quad \rho_t = \ln \left[\frac{P_t + B_t}{B_t} \right]$$

with units per year. ISPR measures the net rate of somatic growth, recruitment, and natural mortality. With no fishing in year t , $B_{t+1}^* = B_t e^{\rho_t}$; with fishing, $B_{t+1} = B_t e^{\rho_t - F_t}$ where F_t is the instantaneous fishing mortality rate (Appendix B summarizes the relationships among ρ_t , F_t , and C_t). In either case, ASP is $P_t = B_t(e^{\rho_t} - 1)$.

ISPR calculations for anchovies and sardines are useful because they help distinguish between effects on ASP due to changes in stock biomass B_t and changes in the rate of production per unit biomass (measured by ρ_t). That is, ISPR calculations convert estimates of gross ASP (which vary among stocks due to overall stock size) to instantaneous “per capita” measures that can, like instantaneous fishing mortality rates, be compared for stocks of different size. The logarithm in eq. 6 makes distributions of annual instantaneous rates more symmetrical and easier to compare. Other measures, such as production per unit biomass (P_t/B_t), are similar to ISPR. We also calculated production per unit spawning area $\phi_t = P_t/A_t$ when estimates of spawning area (A_t) were available.

To minimize the effects of measurement and estimation errors in biomass estimates (often considerable, e.g., Jacobson et al. 1994; Deriso et al. 1996), we used medians ($Q_{50\%}$) to measure the central tendency of estimates. We used 10% and 90% quantiles ($Q_{10\%}$ and $Q_{90\%}$) to measure range and the difference between the median and 84% quantile $\sigma_r = (Q_{84\%} - Q_{50\%})$ as a “robust” measure of standard deviation. The robust statistic was analogous to traditional standard deviation values because, for the normal distribution, $Q_{84\%}$ is 1 SD to the right of the mean.

Data

Biomass estimates were available for eight anchovy stocks (*Engraulis* spp.) (Table 1). Catch data were available for all anchovy stocks with the exception of two almost unexploited stocks off Northern Patagonia and Uruguay – Buenos Aires (Table 1). Biomass and catch data were available for nine exploited sardine stocks (*Sardinops* spp., *Sardinella brasiliensis*, and *Sardinella pilchardus*) (Table 1).

We used the best available information for each stock in surplus production calculations. Depending on advice from the responsible scientists, the type of biomass estimate, and situation, we omitted up to five of the most recent biomass estimates because recent estimates are often the least reliable (Pope 1972). When necessary, official biomass statistics for ages 0+ were adjusted by subtracting the biomass of age-0 fish. Biomass estimates for *S. sagax* off northern Chile and southern Peru began at age 2, and we back-calculated biomass of younger age groups assuming natural mortality with no fishing. As described above, catch weights of age-0 fish were deducted from official catch records where possible (Table 1).

Results

Natural mortality rates (M) assumed in stock assessment work for stocks in our study ranged from 0.8 to 1.2·year⁻¹ (median 1.1·year⁻¹) for anchovies and from 0.3 to 0.96·year⁻¹ (median 0.51·year⁻¹) for sardines (Table 1). For most stocks, average adjustment factors for catch ($\bar{\delta}$) were large enough to affect production calculations. They ranged from 0.61 to 0.78 (median 0.67) for anchovies and from 0.76 to 1.03 (median 0.85) for sardines (Table 1).

Natural mortality rates and average adjustment factors for catch data were highly correlated (Fig. 1). This could be ex-

Table 1. Anchovy and sardine stocks and stock areas, years with biomass estimates (at the time of the analysis), years with production estimates used in this study, natural mortality rates (M) from stock assessments, average catch adjustment factors ($\bar{\delta}$), and average percentage (by weight) of age-0 fish in catches.

Stock and stock area	Years with biomass estimates (first year–last year)	Years with production estimates (first year–last year (N))	M (year ⁻¹)	$\bar{\delta}$	Age-0 fish in catch
Anchovies					
<i>Engraulis anchoita</i> (N. Patagonia) ^a	1993–1995	1993–1994 (2)	1.1	na	na
<i>E. anchoita</i> (Uruguay – Buenos Aires) ^a	1993–1995	1993–1994 (2)	1.1	na	na
<i>E. capensis</i> (South Africa) ^b	1985–1995	1985–1994 (10)	1.2	0.62	Substantial; no adjustments
<i>E. encrasicolus</i> (Bay of Biscay) ^c	1987–1995	1987–1993 (7)	1.2	0.61	Range 1–22%; mean 7%; adjusted
<i>E. japonica</i> (Japan) ^{d,f}	1978–1997	1978–1996 (19)	Mean 1.1	0.77	Range 2–40%; mean 15%; adjusted
<i>E. mordax</i> (California) ^e	1953–1995	1953–1990 (38)	0.8	0.71	Mean probably <10%; no adjustments
<i>E. ringens</i> (N. Chile – S. Peru) ^f	1984–1993	1984–1990 (7)	1.0	0.61	range 0–12%; mean 4%; adjusted
<i>E. ringens</i> (Peru) ^f	1962–1993	1962–1989 (28)	Mean 0.92	0.78	Range 0–33%; mean 8%; adjusted
Sardines					
<i>Sardinops melanostictus</i> (Japan) ^g	1951–1995	1951–1991 (41)	0.4	0.92	Range 0–20%; mean 5% during 1978–1999; pre-1978 unknown; no adjustments
<i>S. melanostictus</i> (South Korea) ^f	1971–1996	1971–1992 (22)	0.51	0.85	Range 0–22%; mean 3%; adjusted
<i>S. sagax</i> (South Africa) ^f	1988–1996	1988–1993 (6)	0.6	0.85	Substantial; no adjustments
<i>S. sagax</i> (N. Chile – S. Peru) ^f	1974–1993	1974–1988 (15)	0.3	0.94	Zero; no adjustments
<i>S. sagax</i> (California) ^h	1932–1996	1932–1961, 1983–1992 (40)	0.4	0.83	Mean probably <10%; no adjustments
<i>S. sagax</i> (Gulf of California) ⁱ	1972–1989	1972–1984 (13)	0.7	0.86	Range 0–3%; mean 1%; no adjustments
<i>S. sagax</i> (Magdalena Bay) ^j	1981–1996	1981–1992 (12)	0.7	0.76	Range 0–28%; mean 5%; adjusted
<i>Sardina pilchardus</i> (Iberian Peninsula) ^f	1976–1996	1976–1994 (19)	0.33	1.03	Zero; no adjustments
<i>Sardinella brasiliensis</i> (Brazil) ^k	1977–1992	1977–1988 (12)	0.96	0.71	<1%; no adjustments

Note: na, not applicable.

^aSánchez et al. (1996).

^bButterworth et al. (1993).

^cInternational Council for the Exploration of the Sea (1996).

^dHayashi (1961).

^eJacobson et al. (1994), Jacobson et al. (1995), and Methot (1989).

^fUnpublished estimates (Japanese data from T. Wada, NRIFS, Japan; Chile and Peru data from R. Serra, IFOP, Chile; Korea data from J.Y. Kim, NFRDI, South Korea; South Africa data from J. De Oliveira, MCM, South Africa; Iberian Peninsula data from A. Uriarte, AZTI, Spain).

^gWada and Jacobson (1998).

^hBarnes et al. (1997) and Deriso et al. (1996).

ⁱCisneros-Mata et al. (1995).

^jFélix-Uraga et al. (1996).

^kCergole (1995).

Fig. 1. Average catch adjustment factors ($\bar{\delta}$) used in production calculations and natural mortality rates used in stock assessments for sardines (open squares) and anchovies (solid circles).

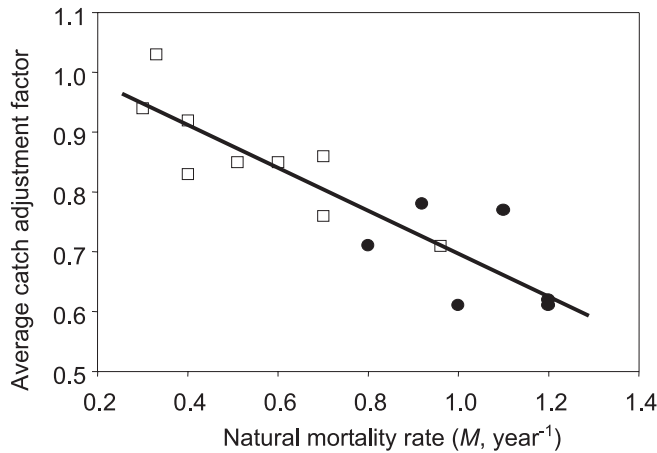


Fig. 2. Median ASP and median stock biomass for anchovy (solid circles) and sardine (open squares) stocks. Median production values near 2000 kt are for *E. encrasicolus* (northern Patagonia stock) and *E. capensis* off South Africa.

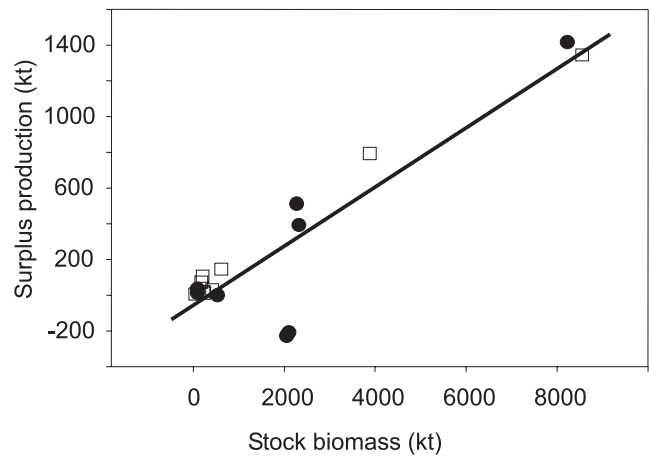


Table 2. Median biomass and median production estimates for anchovy and sardine stocks.

Stock and stock area	Median biomass (kt)	Median production (kt)
Anchovies		
<i>Engraulis anchoita</i> (N. Patagonia)	2105	-211
<i>E. anchoita</i> (Uruguay – Buenos Aires)	2339	390
<i>E. capensis</i> (South Africa)	2050	-230
<i>E. encrasicolus</i> (Bay of Biscay)	94	9
<i>E. japonica</i> (Japan)	91	34
<i>E. mordax</i> (California)	547	-1
<i>E. ringens</i> (N. Chile – S. Peru)	2274	507
<i>E. ringens</i> (Peru)	8238	1412
Sardines		
<i>Sardinops melanostictus</i> (Japan)	237	12
<i>S. melanostictus</i> (South Korea)	3880	794
<i>S. sagax</i> (South Africa)	172	74
<i>S. sagax</i> (N. Chile – S. Peru)	8549	1346
<i>S. sagax</i> (California)	224	21
<i>S. sagax</i> (Gulf of California)	202	106
<i>S. sagax</i> (Magdalena Bay)	41	7
<i>Sardina pilchardus</i> (Iberian Peninsula)	617	146
<i>Sardinella brasiliensis</i> (Brazil)	412	31

pected because age-specific adjustment factors (δ_a in eq. 4) were computed as a function of natural mortality rate (see above). However, based on our results, the linear regression model $\bar{\delta} = 1.05 - 0.353M$ ($R^2 = 78\%$, $n = 15$) would suffice to approximate average correction factors $\bar{\delta}$ for any sardine or anchovy stock.

Median ASP was highest for stocks with high median biomass, although South African and northern Patagonian anchovy stocks had relatively low median ASP levels (Table 2; Fig. 2). The correlation between median ASP and median biomass was 0.91. A linear regression equation $P_{\text{median}} = 0.16B_{\text{median}}$ (forced through the origin) suggests that ASP is typically about 16% of biomass in exploited anchovy and sardine stocks. Stocks with the highest biomass were mostly anchovies. The relatively low median ASP for South African anchovy was due to a declining biomass trend during 1985–1994, and the median ASP for the northern Patagonian an-

chovy stock was based on only 3 years of biomass estimates (Table 1). Larger sample sizes would likely give higher estimates of median ASP for both stocks.

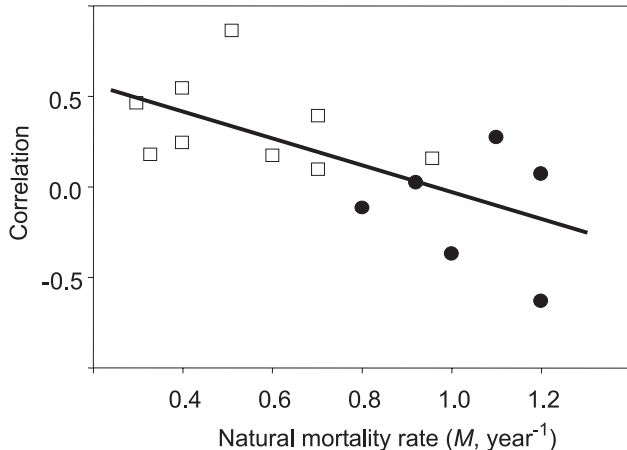
Years of negative ISPR and ASP were common, particularly for anchovies, reflecting the possibility of declines in biomass, even in the absence of fishing. ISPR (and ASP) were negative in 36% of years ($n = 113$ for all years and all stocks) for anchovies and 17% of years ($n = 180$) for sardines (Table 3). For individual anchovy and sardine stocks, the percentage of years with negative ASP and ISPR ranged from 14 to 60% for anchovies and from 0 to 33% for sardines.

For anchovies, median ISPR (all years and all stocks) was 0.14 and the robust measure of standard deviation was $\sigma_r = 0.52$ (Table 3). For sardines, median ISPR was 0.18 and $\sigma_r = 0.28$. Production rates in consecutive years (Table 3; Fig. 3) were positively correlated for long-lived stocks with low nat-

Table 3. ISPR (year⁻¹) summary statistics.

Stock and stock area	$Q_{10\%}$	Median	$Q_{90\%}$	$Q_{90\%} - Q_{10\%}$	σ_r	% negative years	Lag 1 auto correlation
Anchovies							
<i>Engraulis anchoita</i> (N. Patagonia)	na	-0.11	na	na	na	50	na
<i>E. anchoita</i> (Uruguay – Buenos Aires)	na	0.20	na	na	na	50	na
<i>E. capensis</i> (South Africa)	-0.45	-0.07	0.64	1.09	0.42	60	0.07
<i>E. encrasicolus</i> (Bay of Biscay)	-0.20	0.16	0.88	1.09	0.67	43	-0.63
<i>E. japonica</i> (Japan)	-0.01	0.41	0.80	0.81	0.74	16	0.27
<i>E. mordax</i> (California)	-0.41	0.01	0.76	1.17	0.68	50	-0.12
<i>E. ringens</i> (N. Chile – S. Peru)	0.06	0.27	0.67	0.60	0.66	14	-0.37
<i>E. ringens</i> (Peru)	-0.24	0.17	0.66	0.90	0.48	25	0.02
All anchovies	-0.37	0.14	0.75	1.12	0.52	36	na
Sardines							
<i>Sardinops melanostictus</i> (Japan)	-0.30	0.10	0.49	0.79	0.48	27	0.54
<i>S. melanostictus</i> (South Korea)	0.09	0.21	0.42	0.34	0.41	0	0.85
<i>S. sagax</i> (South Africa)	0.11	0.43	0.66	0.55	0.58	0	0.17
<i>S. sagax</i> (N. Chile – S. Peru)	0.07	0.16	0.24	0.17	0.24	0	0.46
<i>S. sagax</i> (California)	-0.15	0.18	0.59	0.74	0.46	33	0.23
<i>S. sagax</i> (Gulf of California)	0.12	0.45	0.80	0.68	0.66	0	0.38
<i>S. sagax</i> (Magdalena Bay)	-0.09	0.12	0.63	0.72	0.50	25	0.09
<i>Sardina pilchardus</i> (Iberian Peninsula)	0.12	0.22	0.30	0.18	0.29	0	0.17
<i>Sardinella brasiliensis</i> (Brazil)	-0.06	0.08	0.37	0.43	0.28	33	0.16
All sardines	-0.08	0.18	0.51	0.59	0.28	17	na

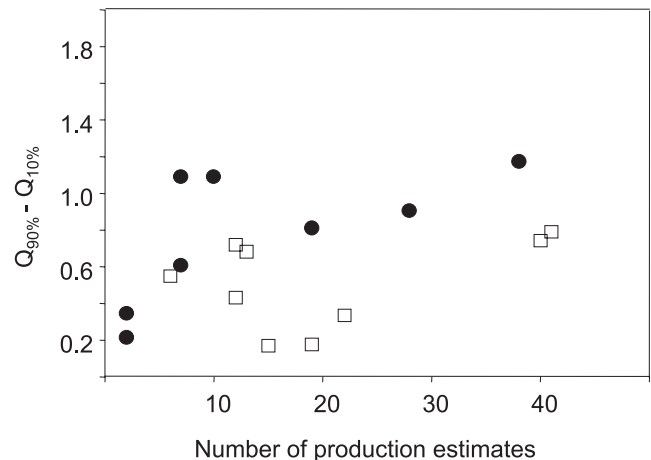
Note: $Q_{10\%}$ and $Q_{90\%}$ are the 10 and 90% quantiles and σ_r is a robust measure of standard deviation. na, not applicable.

Fig. 3. Autocorrelation (lag 1 year) in ISPR for anchovies (solid circles) and sardines (open squares).

ural mortality rates (mostly sardines) and uncorrelated or negatively correlated for shorter-lived stocks with high natural mortality rates (mostly anchovies).

Long time series

About 30 years of data may be required to measure the full range in ISPR for anchovy and sardine stocks. The $Q_{90\%} - Q_{10\%}$ values (a measure of range, see above) for two sardine stocks (*S. melanostictus* off Japan and *S. sagax* off California) and two anchovy stocks (*E. ringens* off Peru and *E. mordax* off California) with at least 28 years of production data were generally higher than $Q_{90\%} - Q_{10\%}$ values for stocks with fewer years of production data (Tables 1 and 3; Fig. 4). However, this generalization did not hold true for

Fig. 4. $Q_{90\%} - Q_{10\%}$ (a measure of range) for ISPR and number of years of production data for sardines (open squares) and anchovies (solid circles). The two points with high $Q_{90\%} - Q_{10\%}$ values at 8 and 10 years of data are for *E. encrasicolus* (Bay of Biscay) and *E. capensis* (South Africa). Data for two *E. anchoita* stocks with only 2 years of production data are excluded.

two anchovy stocks (*E. encrasicolus* in the Bay of Biscay with 8 years of production data and *E. capensis* off South Africa with 10 years of production data). In the exceptions, high values of $Q_{90\%} - Q_{10\%}$ were observed despite relatively low numbers of years with production estimates.

Stocks with at least 28 years of ASP estimates included two anchovy stocks and two sardine stocks. There were 38 years of ASP estimates for *E. mordax* off California, 28 years for *E. ringens* off Peru, 41 years for *S. melanostictus* off Japan, and 40 years for *S. sagax* off California. We ana-

Fig. 5. Left panels: catch data (open circles), biomass (solid circles), and ASP (solid triangles) estimates. Right panels: ISPR estimates for (a and b) Japanese sardine *S. melanostictus*, (c and d) Californian sardine *S. sagax*, (e and f) Peruvian anchovy *E. ringens*, and (g and h) Californian anchovy *E. mordax*.



Fig. 6. Probability distributions of annual ISPR for (a) *E. mordax* (California), (b) *E. ringens* (Peru), (c) *S. melanostictus* (Japan), and (d) *S. sagax* (California). Bar plots are histograms rescaled so that frequencies sum to 1. Smooth lines are nonparametric density estimates (Venables and Ripley 1999) based on the same data.

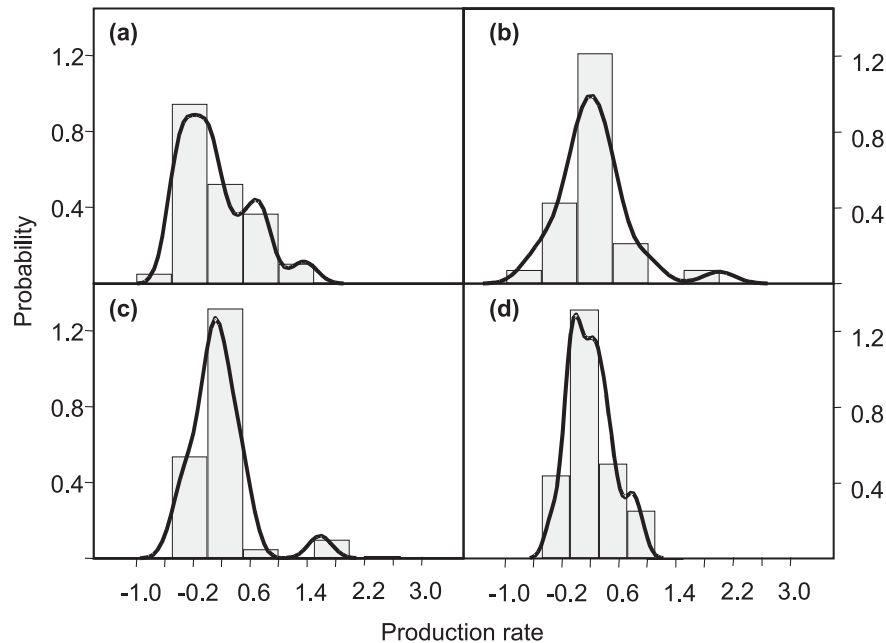


Table 4. Schaefer surplus production models $P_t = \alpha B_t + \beta B_t^2$ fit to biomass (B_t) and ASP (P_t) estimates by simple linear regression forced through the origin.

Stock and stock area	Residual df	α	P for α	β	P for β	Multiple R^2 (%)
<i>Sardinops melanostictus</i> (Japan)	39	0.29	0.041	-1.5×10^{-5}	0.10	16
<i>S. sagax</i> (California)	38	0.28	0.011	-9.2×10^{-5}	0.014	16
<i>Engraulis ringens</i> (Peru)	26	0.46	0.046	-1.4×10^{-5}	0.25	32
<i>E. mordax</i> (California)	36	0.31	0.11	-2.3×10^{-4}	0.052	11

Note: P values test the hypothesis that a parameter was zero.

lyzed the time series of catch data, ASP, ISPR, and biomass estimates for these stocks in detail.

Results for stocks with long time series show that declines in biomass tend to be pronounced whenever catch exceeds ASP for 5 or more years (Fig. 5). Strong biomass increases and highly productive regimes appear to be preceded by abrupt increases in ISPR. Statistical distributions for ISPR were skewed with relatively long tails over positive values and with modes around zero (Fig. 6).

Periods with positive ASP and ISPR were longer than periods with negative values (Fig. 5). Consistent with the autocorrelation results (see above), long-term time series plots (Fig. 5) of ISPR for sardine stocks (*S. melanostictus* off Japan and *S. sagax* off California) were smoother and less variable than for anchovy stocks (*E. ringens* off Peru and *E. mordax* off California). The longest "runs" of positive ASP and ISPR were 21 years for *S. melanostictus* off Japan, 10 years for *S. sagax* off California, 8 years for *E. ringens* off Peru, and 4 years for *E. mordax* off California (Fig. 5). The longest runs of negative ASP and ISPR were 4, 3, 2, and 3 years (Fig. 5). ASP and ISPR were positive in all years for five other sardine stocks, but the time series were shorter (≤ 22 years) (Tables 1 and 2). Duration of runs is

likely to be underestimated in some cases because time series began or ended in the middle of a run.

Density-dependent relationships between ASP and biomass were explored by fitting crude Schaefer (1957) surplus production models $P_t = \alpha B_t + \beta B_t^2$ to annual production and biomass estimates by linear regression forced through the origin (Table 4; Fig. 7). Residuals from regression models for sardines were autocorrelated, with runs of years with ASP higher or lower than predicted by the model (Fig. 7).

Production per unit spawning area

ASP per unit spawning area was higher for sardines than for anchovies. Median ASP per unit of spawning area was $0.66 \text{ t} \cdot \text{km}^{-2} \cdot \text{year}^{-1}$ for anchovies (all years and all stocks) and $5.3 \text{ t} \cdot \text{km}^{-2} \cdot \text{year}^{-1}$ for sardines (Table 5). Median ASP per unit spawning area for individual stocks ranged from -2.3 to $8.7 \text{ t} \cdot \text{km}^{-2} \cdot \text{year}^{-1}$ for anchovies and from 1.4 to $16 \text{ t} \cdot \text{km}^{-2} \cdot \text{year}^{-1}$ for sardines. Median ASP values per unit spawning area for *E. ringens* and *S. sagax* off northern Chile and southern Peru were relatively high but calculated using spawning area estimates based on general knowledge about spatial distribution during the spawning season rather than annual ichthyoplankton or acoustic surveys (Table 5).

Fig. 7. ASP and stock biomass for (a) *E. mordax* (California), (b) *E. ringens* (Peru), (c) *S. melanostictus* (Japan), and (d) *S. sagax* (California). Solid lines are Schaefer surplus production models fit by quadratic linear regression forced through the origin. Broken lines connect ASP and biomass estimates for consecutive years and the earliest year is identified in each plot. Data for *S. sagax* off California are missing for the years 1962–1982. Some points are obscured due to overlap.

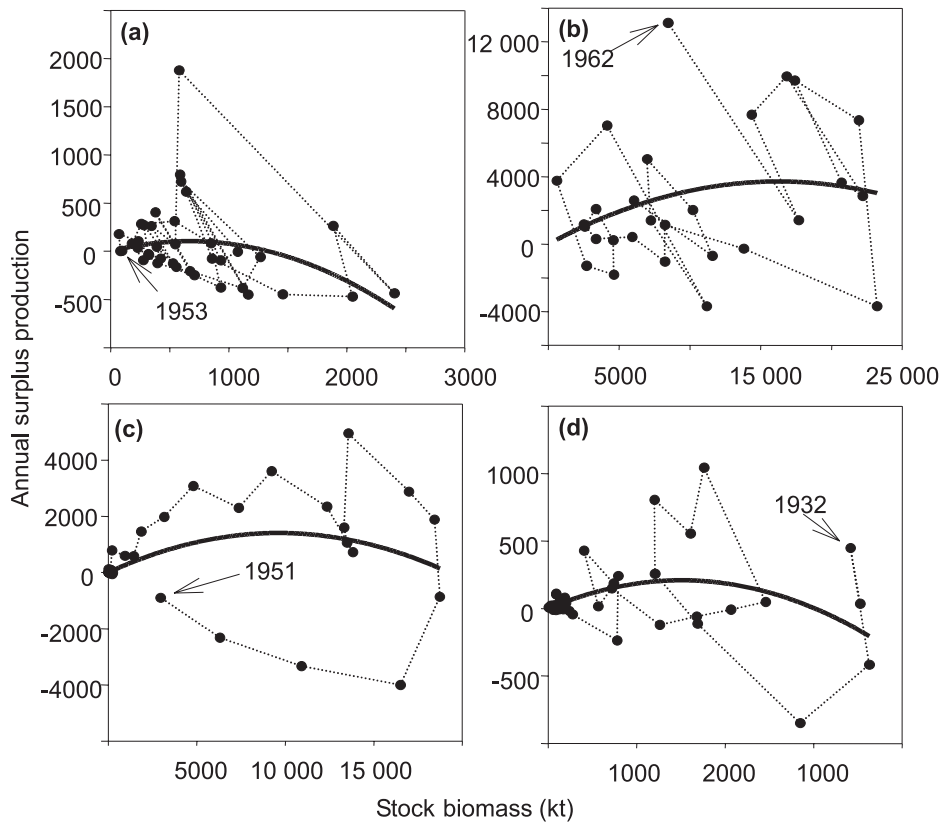


Table 5. ASP per unit spawning area (1000 kt-year⁻¹ km⁻²) for anchovy and sardine stocks.

Stock and stock area	<i>n</i>	<i>Q</i> _{10%}	Median	<i>Q</i> _{90%}	Type of spawning area estimate
Anchovies					
<i>Engraulis anchoita</i> (N. Patagonia) ^a	2	-3.4	-1.8	-0.060	AIS
<i>E. anchoita</i> (Uruguay – Buenos Aires) ^a	2	0.62	4.9	9.2	AIS
<i>E. capensis</i> (South Africa) ^b	10	-16.0	-2.3	24.0	AAS, AIS
<i>E. encrasicolus</i> (Bay of Biscay) ^c	6	-0.28	0.66	3.8	AIS
<i>E. mordax</i> (California) ^d	5	-3.0	-0.030	11.0	AIS
<i>E. ringens</i> (N. Chile – S. Peru) ^c	7	2.1	8.7	35.0	AD
All anchovies	32	-4.7	0.66	20.0	
Sardines					
<i>Sardinops melanostictus</i> (Japan) ^c	14	-11.0	6.0	18.0	AIS
<i>S. sagax</i> (South Africa) ^b	6	0.76	3.6	9.1	AAS, AIS
<i>S. sagax</i> (N. Chile – S. Peru) ^c	15	5.0	11.0	21.0	AD
<i>S. sagax</i> (California) ^e	7	1.6	2.0	4.0	AIS
<i>Sardina pilchardus</i> (Iberian Peninsula) ^c	2	15.0	16.0	16.0	AIS
<i>Sardinella brasiliensis</i> (Brazil) ^c	5	-1.3	1.4	5.3	AIS
All sardines	49	-1.9	5.3	17.0	

Note: Spawning areas were estimated either by annual ichthyoplankton surveys (AIS) or annual acoustic surveys (AAS) or from average distributions during the spawning season (AD).

^aSánchez et al. (1996).

^bBarange et al. (1999).

^cUnpublished data (Chile and Peru data from R. Serra, IFOP, Chile; Bay of Biscay and Iberian Peninsula data from A. Uriarte, AZTI, Spain, and C. Porteiro, Instituto Español de Oceanografía, Spain; Japan data from T. Wada, NRIFS, Japan; Brazil data from Y. Matsuura, Universidade de Sao Paulo, Brazil).

^dFiedler et al. (1986).

^eBarnes et al. (1997).

Table 6. ASP at age over the life span of a hypothetical cohort of *S. sagax* off California based on data from Butler et al. (1993).

Age (years)	Annual natural mortality rate (year ⁻¹)	Individual body weight (g)	Cohort number	Cohort weight (g)	ASP (g·year ⁻¹)
0	13.4	0	1.000	0.0000	0.0810
1	0.4	53	0.00154	0.0810	0.0148
2	0.4	93	0.00103	0.0958	-0.0109
3	0.4	123	0.00069	0.0850	-0.0146
4	0.4	152	0.00046	0.0704	-0.0176
5	0.4	170	0.00031	0.0528	-0.0126
6	0.4	193	0.00021	0.0402	-0.0120
7	0.4	202	0.00014	0.0282	-0.0090
8	0.4	205	0.00009	0.0192	-0.0063
9	0.4	205	0.00006	0.0128	-0.0042
10	0.4	205	0.00004	0.0086	-0.0028
11	0.4	205	0.00003	0.0058	-0.0019
12	0.4	205	0.00002	0.0039	-0.0013
13	0.4	205	0.00001	0.0026	

Discussion

A total of eight anchovy and nine sardine stocks were studied, including populations from the southeast, southwest, and northeast Atlantic Ocean and the southeast, northeast, and northwest Pacific Ocean. Results provide a comprehensive overview of the interannual and interdecadal variability in ASP and ISPR for anchovies and sardines around the world.

Medians of annual ASP/B ratios were 0.15 for anchovies and 0.20 for sardines. As described above, $\bar{\delta}$ values were 0.67 for anchovies and 0.85 for sardines. These results suggest that median ASP harvest rates of about 10% for anchovies and 17% for sardines would give increased and decreased stock biomass levels in the next year with equal probability. However, these calculations ignore differences among individual stocks. The relative benefits of median ASP harvest rate policies are unknown and should be a topic for future research through simulation.

Median average adjustment factors $\bar{\delta}$ for catch in ASP calculations (Table 1) were 0.67 for anchovies and 0.85 for sardines. This suggests that 1 t of foregone catch under prevailing conditions in anchovy and sardine fisheries would result in 0.67 t of additional anchovy biomass or 0.85 t of additional sardine biomass after 1 year. Increases in biomass due to foregone catch would be in addition to gains from recruitment.

In the absence of better information, estimates of ASP per unit spawning area for anchovy and sardine stocks may be useful in setting management quotas based on annual estimates of spawning area or in estimating the potential yield of unfished sardine and anchovy stocks based on estimates of spawning area. However, it is important to remember that the spawning area and ASP estimates used in our analysis were 1 year out of phase because spawning in year t results in recruitment of age-1 fish at the beginning of season $t + 2$ that was recorded as production in season $t + 1$. Also, spawning area estimates were usually for periods near the peak spawning season that did not coincide in any fixed way to annual seasons used for productivity calculations. For *S. sagax* off California, for example, spawning area data for February–March 1994 were used to estimate productivity per

unit of spawning area during the 1993 season, which extended from the beginning of July 1993 to the end of June 1994.

Higher variability in anchovies may be due to shorter life span and higher natural mortality rates that reduce the number of age-classes in anchovy relative to sardine stocks (e.g., Barange et al. 1999), differences in geographic distribution, or other differences in life history. Higher variability in anchovies has important practical and scientific ramifications. Based on available data, fishery managers should recognize that years with negative ASP occur in both anchovies and sardines but more commonly in anchovies. In addition, managers should expect periods with positive ASP to last longer in sardines than in anchovies. Scientists should recognize that differences in life history may make sardine and anchovy stocks in the same general area respond differently to the same climatic signal. For example, trends in ISPR for *E. mordax* and *S. sagax* off California are not similar. In general, ISPR rates are less variable for sardines than for anchovies, and sardines appear better able to buffer short-term environmental variability.

Instantaneous production rates for stocks with long time series were skewed to the right with a few relatively large values. Skewed distributions for ISPR with more positive values than negative values would be expected in exploited stocks due to density dependence. In addition, distributions of ISPR should resemble distributions for recruitment, which are usually skewed to the right (Hilborn and Walters 1992). In the worst-case scenario of no recruitment, distributions of ISPR are bounded below by the sum of instantaneous rates for (negative) natural mortality and (positive) somatic growth (i.e., in an unfished stock, $\rho \geq -M + G$ because $\rho = -M + G + R$ and the recruitment rate $R \geq 0$). The hard lower bound at $-M + G$ and the absence of a hard upper bound likely contribute to skewed distributions in ISPR.

ISPR may be better for identifying the onset of unfavorable and, particularly, favorable regimes (Luch-Belda et al. 1989, 1992; and defined above) than many other measures. Estimates of stock biomass are slower in reflecting regime shifts to unfavorable conditions because stock biomass in-

cludes age-classes that may persist for several years. Similarly, stock biomass may take time to build after the onset of favorable conditions. ASP estimates respond slowly to favorable regime shifts when biomass is low because even high ISPR gives little ASP under low biomass conditions. Catch data are the least sensitive indicator of regime shifts because economic factors, policy, and fishery management procedures affect catches. For example, catches may remain high after regime shifts from favorable to unfavorable conditions, even after biomass falls, because of market demand or lack of fishery management or because policies for setting total allowable catch limits aim to maintain stable catches from year to year.

ISPR values are more sensitive than other measures, but sensitivity comes at the cost of more variability. ISPR in any particular year during an unfavorable regime may be as high as typical values during favorable periods, and vice versa. For example, compare ISPR for *S. melanostictus* off Japan during 1958 when conditions were generally not favorable with ISPR during 1974–1980 when conditions were generally favorable. ISPR is more sensitive and better for identifying the timing of regime shifts retrospectively, but several years of high or low ISPR might be required to determine whether a regime shift has just taken place.

For example, a shift to favorable regime conditions is evident in ISPR for *S. melanostictus* off Japan by 1970 but not reflected in biomass and ASP estimates until at least 1972 and not evident in catch data until at least 1976. A shift to unfavorable conditions in the same stock was evident in the ISPR and ASP by 1986 but not evident in biomass estimates until at least 1990 and never clearly evident in the catch data. For *S. sagax* off California, a favorable regime during the 1980s and 1990s is clearly evident in the ISPR estimates but not evident in biomass, ASP estimates, or catch data. For *E. ringens* off Peru, a period of unfavorable conditions is evident in ISPR and ASP estimates for 1970, while catches and biomass were at maximum levels. ISPR increased to near normal levels by 1975, long before stock biomass, catches, and ASP showed substantial increases. Finally, the period of high biomass and apparently productive conditions for *E. mordax* off California during the 1973–1977 was due to a single year of high production and production rates in 1972 followed by several years of mostly negative production and production rates.

As described above, our analysis focused on environmental effects on ASP and ISPR, and we did not partition variability into density-dependent and density-independent (i.e., environmental) components. However, preliminary production model results in this paper indicate that environmental effects likely contribute more variance to ASP and ISPR than density-dependent effects for anchovy and sardine stocks in our study. Production models fit to long time series of production estimates for *S. melanostictus* off Japan, *S. sagax* off California, *E. ringens* off Peru, and *E. mordax* off California explained relatively low to moderate proportions (average 19%) of the total variance in production. Parameter estimates for the production models were usually statistically significant but were misleading in at least two cases. The production models for Japanese and California sardine imply that B_{MSY} is in the vicinity of 1×10^7 and $1 \times$

10^6 t, respectively. In contrast, Wada and Jacobson (1998) determined that carrying capacity (and B_{MSY}) changed by a factor of about 75 following regime shifts in Japanese sardine. Similarly, Jacobson and MacCall (1995) found that B_{MSY} for California sardine changed from about 270 000 to 1800 t when 3-year average temperatures changed by 0.8°C.

Based on recruitment success in Japanese sardine and California sardine, Wada and Jacobson (1998) hypothesized that density-dependent effects on recruitment (an important component of production) “typically exist for *Sardinops* spp. but can only be measured using long time series of data with large (thousand fold) changes in abundance.” By analogy with recruitment, we hypothesize that density-dependent effects on ASP and ISPR are best measured, even in long time series, using relatively complex models that accommodate environmental variability.

There are difficulties in using fisheries data to track environmental changes that are difficult to circumvent and not to be ignored. Most time series of production estimates are shorter than required (about 30 years) to completely appreciate variability. Catch data are often available for longer periods of time but, as shown above, are relatively insensitive to climate change.

Another disadvantage is that fishery data provide little information about ages younger than taken in the fishery (e.g., eggs, larvae, and juveniles). A quick calculation (Table 6) based on “best” estimates of natural mortality rates and stage durations for age-0 fish and weight at age data (all from tables 2 and 3 in Butler et al. 1993) with $M = 0.4 \cdot \text{year}^{-1}$ for ages 1+ (assumed in stock assessment work) shows that ASP is negative for an unexploited cohort of *S. sagax* off California after age 2 and that the bulk of positive production occurs at age 0 (as individuals grow from eggs to stage-III juveniles at age 1). Thus, ASP in our study due to a strong or weak recruitment of age-1 fish might have resulted from environmental factors during the previous year (while the cohort was age 0) or 2 years previous (during gametogenesis). The same calculation shows that the effect of a large persistent year-class on ASP is negative after age 2.

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References

- Barange, M., Hampton, I., and Roel, B.A. 1999. Trends in the abundance and distribution of anchovy and sardine on the South

- African continental shelf in the 1990s, deduced from acoustic surveys. *S. Afr. J. Mar. Sci.* **21**: 367–392.
- Barnes, J.T., Jacobson, L.D., MacCall, A.D., and Wolf, P. 1992. Recent population trends and abundance estimates for the Pacific sardine (*Sardinops sagax*). *Calif. Coop. Oceanic Fish. Invest. Rep.* **33**: 60–75.
- Barnes, J.T., Yaremko, M., Jacobson, L.D., Lo, N.C.H., and Stehly, J. 1997. Status of the Pacific sardine (*Sardinops sagax*) resource in 1996. NOAA Tech. Memo. NMFS, **237**: 1–17.
- Blaxter, J.H.S., and Hunter, J.H. 1982. The biology of clupeoid fishes. *Adv. Mar. Biol.* **20**: 1–223.
- Butler, J.L., Smith, P.E., and Lo, N.C.H. 1993. The effect of natural variability of life-history parameters on anchovy and sardine population growth. *Calif. Coop. Oceanic Fish. Invest. Rep.* **34**: 104–111.
- Butterworth, D.S., De Oliveira, J.A.A., and Cochrane, K.L. 1993. Current initiatives in refining the management procedure for the South African anchovy resource. In *Proceedings of the International Symposium on Management Strategies for Exploited Fish Populations*. Edited by G. Kruse, D.M. Eggers, R.J. Marasco, C. Pautzke, and T.J. Quinn II. Alaska Sea Grant College Program Rep. No. 93-02. University of Alaska Fairbanks, Fairbanks, Alaska. pp. 439–474.
- Cergole, M.C. 1995. Stock assessment of Brazilian sardine, *Sardinella brasiliensis*, of the south-eastern coast of Brazil. *Sci. Mar.* **59**: 597–610.
- Cisneros-Mata, M.A., Nevárez-Martínez, M.O., and Hammann, M.G. 1995. The rise and fall of the Pacific sardine, *Sardinops sagax caeruleus* Girard, in the Gulf of California, Mexico. *Calif. Coop. Oceanic Fish. Invest. Rep.* **36**: 136–143.
- Cury, P., Bakun, A., Crawford, R.J.M., Jarre, A., Quiñones, R.A., Shannon, L.J., and Verheye, H.M. 2000. Small pelagics in upwelling systems: patterns of interaction and structural changes in “wasp-waist” ecosystems. *ICES J. Mar. Sci.* **57**: 603–618.
- Deriso, R.B., Barnes, J.T., Jacobson, L.D., and Arenas, P.R. 1996. Catch-at-age analysis for Pacific sardine (*Sardinops sagax*). *Calif. Coop. Oceanic Fish. Invest. Rep.* **37**: 175–187.
- Felix-Uraga, R., Alvarado-Castillo, R.M., and Carmona-Piña, R. 1996. The sardine fishery along the western coast of Baja California, 1981–1994. *Calif. Coop. Oceanic Fish. Invest. Rep.* **37**: 188–192.
- Fiedler, P.C., Methot, R.D., and Hewitt, R.P. 1986. Effects of California El Niño 1982–1984 on the northern anchovy. *J. Mar. Res.* **44**: 317–338.
- Hayashi, S. 1961. Fishery biology of the Japanese anchovy, *Engraulis japonica*. *Bull. Tokai Reg. Fish. Res. Lab.* **31**: 145–268.
- Hilborn, R., and Walters, C.J. 1992. *Quantitative fisheries stock assessment: choice, dynamics and uncertainty*. Routledge, Chapman and Hall, Inc., New York.
- Hunter, J.R., and Alheit, J. (Editors). 1995. *International GLOBEC Small Pelagic Fishes and Climate Change Program*. Report of the First Planning Meeting, La Paz, Mexico, June 20–24, 1994. GLOBEC Rep. No. 8.
- International Council for the Exploration of the Sea. 1996. Report of the working group on the assessment of mackerel, horse mackerel, sardine and anchovy. ICES CM1997/Assess:3. pp. 279–320.
- Jacobson, L.D., and MacCall, A.D. 1995. Stock–recruitment models for Pacific sardine (*Sardinops sagax*). *Can. J. Fish. Aquat. Sci.* **52**: 566–577.
- Jacobson, L.D., Lo, N.C.H., and Barnes, J.T. 1994. A biomass-based assessment model for northern anchovy, *Engraulis mordax*. *Fish. Bull. U.S.* **92**: 711–724.
- Jacobson, L.D., Lo, N.C.H., Herrick, S.F., Jr., and Bishop, T. 1995. Spawning biomass of the northern anchovy in 1995 and status of the coastal pelagic fishery during 1994. *Southwest Fish. Sci. Cent. Admin. Rep.* LJ-95-11.
- Lluch-Belda, D., Crawford, R.J.M., Kawasaki, T., MacCall, A.D., Parrish, R.H., Schwartzlose, R.A., and Smith, P.E. 1989. Worldwide fluctuations of sardine and anchovy stocks: the regime problem. *S. Afr. J. Mar. Sci.* **8**: 195–205.
- Lluch-Belda, D., Schwartzlose, R.A., Serra, R., Parrish, R.H., Kawasaki, T., Hedgecock, D., and Crawford, R.J.M. 1992. Sardine and anchovy regime fluctuations of abundance in four regions of the worlds oceans: a workshop report. *Fish. Oceanogr.* **1**: 339–347.
- MacCall, A.D. 1978. A note on production modeling of populations with discontinuous reproduction. *Calif. Fish Game*, **64**: 225–227.
- Methot, R.D. 1989. Synthetic estimates of historical abundance and mortality for northern anchovy. *Am. Fish. Soc. Symp.* **6**: 66–82.
- Opsomer, J.D., and Conrad, J.M. 1994. An open-access analysis of the northern anchovy fishery. *J. Environ. Econ. Manage.* **27**: 21–37.
- Pope, J.G. 1972. An investigation of the accuracy of virtual population analysis using cohort analysis. *Int. Comm. Northwest Atl. Fish. Res. Bull.* **9**: 65–74.
- Ricker, W.E. 1975. Computation and interpretation of biological statistics of fish populations. *Bull. Fish. Res. Board Can.* No. 191.
- Sánchez, R.P., Pájaro, M., and Maachi, G.G. 1996. The application of the daily egg production method to the assessment of SW Atlantic anchovy (*Engraulis choitita*), spawning biomass off Argentina. *ICES CM 1996/H:29*.
- Schaefer, M.B. 1957. A study of the dynamics of the fishery for yellowfin tuna in the eastern tropical Pacific Ocean. *Inter-Am. Trop. Tuna Comm. Bull.* **2**: 245–285.
- Schwartzlose, R.A., Alheit, J., Bakun, A., Baumgartner, T.R., Cloete, R., Crawford, R.J.M., Fletcher, W.J., Green-Ruiz, Y., Hagen, E., Kawasaki, T., Lluch-Belda, D., Lluch-Cota, S.E., MacCall, A.D., Matsuura, Y., Nevarez-Martinez, M.O., Parrish, R.H., Roy, C., Serra, R., Shust, K.V., Ward, M.N., and Zuzunaga, J.A. 1999. Worldwide large-scale fluctuations of sardine and anchovy populations. *S. Afr. J. Mar. Sci.* **21**: 289–347.
- Sissenwine, M.P., and Shepherd, J.G. 1987. An alternate perspective on recruitment overfishing and biological reference points. *Can. J. Fish. Aquat. Sci.* **44**: 913–918.
- Trenberth, K.E. 1990. Recent observed interdecadal climate changes in the Northern Hemisphere. *Bull. Am. Meteorol. Soc.* **71**: 988–993.
- Venables, W.N., and Ripley, B.D. 1999. *Modern applied statistics with S-PLUS*. Springer-Verlag, New York.
- Wada, T., and Jacobson, L.D. 1998. Regimes and stock–recruitment relationships in Japanese sardine (*Sardinops melanostictus*), 1951–1995. *Can. J. Fish. Aquat. Sci.* **55**: 2455–2463.

Appendix A

We want to measure annual surplus production (ASP) for ages 1+ using eq. 3, but official catch records may include catch of fish age 0 so that $C_t = C_{t,0} + C_{t,1+}$. With catch of age 0 fish, the calculation in eq. 3 becomes

$$(A1) \quad P_t^* = B_{t+1} - B_t + \bar{\delta}(C_{t,0} + C_{t,1+}) = P_t + \bar{\delta}C_{t,0}$$

and the relative error in calculation of ASP due to catch of age-0 fish is

$$(A2) \quad \frac{(P_t^* - P_t)}{P_t} = \frac{\bar{\delta}C_{t,0}}{P_t}$$

Appendix B

The instantaneous annual surplus production rate (ISPR) is the sum of rates for recruitment (R_t), somatic growth (G_t), and natural mortality (M). Following MacCall (1978):

$$(B1) \quad B_{t+1} = B_t e^{R_t + G_t - M - F_t}$$

where F_t is the fishing mortality rate. MacCall (1978) assumed that recruitment was a seasonal "pulse." We assume that recruitment is a continuous process (because most sardines and anchovies recruit throughout the year), but the difference in convention is not important. With no fishing during year t :

$$(B2) \quad B_{t+1}^* = B_t e^{R_t + G_t - M}$$

As shown above, $B_{t+1}^* = B_t e^{\rho_t}$, where ρ_t is the ISPR. Substi-

tuting terms for B_{t+1}^* gives $\rho_t = R_t + G_t - M$ and $B_{t+1} = B_t^* e^{-F_t}$.

The relationship between ISPR, F_t , and catch is given by Baranov's catch equation (Ricker 1975):

$$(B3) \quad C_t = \frac{F_t}{Z_t} (1 - e^{-Z_t}) B_t$$

where $Z_t = F_t + \rho_t$. The adjustment factor $\bar{\delta}$ converts units of catch to units of ASP (see above) so that $B_{t+1}^* - B_t = \bar{\delta} C$.

Appendix B references

MacCall, A.D. 1978. A note on production modeling of populations with discontinuous reproduction. *Calif. Fish Game*, **64**: 225-227.

Ricker, W.E. 1975. Computation and interpretation of biological statistics of fish populations. *Bull. Fish. Res. Board Can.* No. 191.