

Changes in Catchability in a Bottom-Trawl Fishery for Cape Hake (*Merluccius capensis*)

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Management of the Cape hake (*Merluccius capensis*) stock off the coasts of Angola and Namibia has been based on surplus production modeling, which incorporates an assumption of constant catchability. Results of least-squares catch-at-age analysis and virtual population analysis were used to estimate catchability from 1968 to 1986. Estimated catchability was either relatively constant or gradually increasing from 1968 to 1978, but fluctuated considerably between about 1979 and 1983. The fluctuations may have been due to an inverse relationship between catchability and abundance or to environmental factors affecting fish distribution. The period of highest estimated catchability corresponded to the period of lowest estimated abundance and below-average water temperatures. If management is based on the assumption of constant catchability but catchability is inversely related to abundance, the risk of overfishing will be greatest when the stock is at the lowest levels. Future assessments should place increased reliance on survey data or incorporate an appropriate model of catchability changes.

La gestion du stock de merlu du Cap (*Merluccius capensis*) de la côte de l'Angola et de la Namibie s'est fondée sur la modélisation de la production excédentaire, avec un potentiel de capture supposé constant. Pour estimer le potentiel de capture, de 1968 à 1986, on s'est servi de l'analyse des prises par classes d'âge par la méthode des moindres carrés et de l'analyse de la population virtuelle. Le potentiel de capture estimatif a été, soit relativement constant, soit graduellement croissant, de 1968 à 1978, mais il a considérablement fluctué entre 1979 et 1983. Les fluctuations observées étaient peut-être dues à une relation inverse entre le potentiel de capture et l'abondance ou à l'influence de facteurs du milieu sur la distribution des poissons. La période où le potentiel de capture estimé était le plus élevé correspond à la période où la valeur estimative de l'abondance était la plus faible et les températures de l'eau, sous la moyenne. Lorsque la gestion se base sur un potentiel de capture supposé constant et que ce potentiel est une fonction inverse de l'abondance, le risque de surpêche est maximal lorsque le stock est au plus bas. À l'avenir dans les évaluations, il faudrait se fier davantage aux résultats des relevés ou utiliser le modèle approprié, avec variations de potentiel de capture.

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A substantial fishery for Cape hake (*Merluccius capensis*) has existed off the coasts of Angola and Namibia since 1965. Landings from latitude 15 to 25°S (statistical divisions 1.3 and 1.4 of the International Commission for the Southeast Atlantic Fisheries (ICSEAF)) ranged from 90 500 tonnes (t) in 1980 to 606 100 t in 1972 (Table 1). Catches are made primarily with bottom-trawl gear although some catches are made at night in a midwater-trawl fishery (Crawford et al. 1987) for species such as horse mackerel (*Trachurus* spp.).

Both a surplus production model (Graham 1935) and virtual population analysis (VPA) (Murphy 1965) have been used to assess the status of the hake stock. Effort data used in the surplus production models were obtained from average weighted catch-per-unit-effort (CPUE) data, specifically tonnes per hour fished by Spanish bottom trawlers in tonnage class 7 (1000–1999 GRT). This weighted CPUE index, based on total catch

and effort by fleet, is equivalent to using power factors to adjust for differences in catch rate (Andrew 1986).

A potential limitation of the surplus production model used to manage the hake fishery is the assumption that catchability (q) is constant. That assumption is used to relate observed fishing effort in year y ($f(y)$) to fishing mortality ($F(y)$):

$$F(y) = qf(y).$$

Based on that assumption, CPUE and abundance should be linearly related and management could be based on the CPUE data alone. The assumption that catchability is constant has been shown to be invalid for a number of pelagic species (Abramson and Tomlinson 1972; Fox 1974; MacCall 1976; Peterman and Steer 1981; Shelton and Armstrong 1983; Winters and Wheeler 1985) because of the interaction between fishermen and schooling fishes. Search time is an important component of total effort in many pelagic fisheries whereas the catch per unit of fishing time may simply reflect the within-school density (Paloheimo and Dickie 1964). If within-school density is maintained as abundance decreases, there would be an inverse relationship

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TABLE 1. Catch (thousands of tonnes) and standardized fishing effort (estimated hours fished in ICSEAF divisions 1.3 and 1.4 by Spanish bottom trawlers in tonnage class 7 (1000–1999 GRT)) (Draganik and Sacks 1987).

Year	Catch	Effort
1965	93.5	52 500
1966	212.4	162 500
1967	195.0	214 000
1968	382.7	399 000
1969	320.5	364 000
1970	402.5	447 000
1971	365.6	420 000
1972	606.1	842 000
1973	377.6	662 456
1974	318.8	708 400
1975	309.4	737 000
1976	369.8	880 476
1977	277.5	566 300
1978	258.1	600 200
1979	172.3	430 700
1980	90.5	201 100
1981	92.1	167 500
1982	176.4	332 800
1983	215.8	372 100
1984	228.5	357 000
1985	211.5	320 450
1986	230.9	355 230

between abundance and catchability. An inverse relationship also has been detected for several demersal species (Pope and Garrod 1975; Houghton and Flatman 1980; Angelsen and Olsen 1987; Crecco and Overholtz 1990), and it has been suggested that compensatory fishing mortality at low abundance levels is a general phenomenon among most commercial fisheries (Winters and Wheeler 1985; Crecco and Overholtz 1990).

Radovich (1982) noted that catchability will be constant only if (1) fishes are uniformly distributed over the fishing area, (2) effort is distributed randomly over the fishing area, and (3) units of effort are independent. The first assumption is unlikely to be true for Cape hake because schooling behavior has been observed for fish younger than age 2, and older fish form aggregations and migrate to spawning grounds (Shannon and Pillar 1986). The latter two assumptions are almost certainly violated because fishermen work cooperatively to locate and exploit areas of good catches. A preliminary analysis of catch-at-age data from ICSEAF division 1.5 provides evidence that catchability may be an inverse function of biomass (Gordoa and Pertierra 1987). The reliability of those results is unknown, however, because of a limitation in the catch data. Division 1.5 catches contain two hake species (*M. paradoxus* and *M. capensis*) that are quite similar in appearance; unfortunately, the proportion of the two species in historical commercial catches is not known.

The objective of this study was to examine the constant catchability assumption for the Cape hake fishery in divisions 1.3 and 1.4. We used results from VPA and least-squares analysis (Deriso et al. 1985) of the catch-at-age data to estimate fishing mortality rates and catchabilities. Observed trends in catchability were compared with estimates of abundance and information on environmental changes in order to develop hypotheses about the causes of changes in catchability.

Methods

Catch-at-age data for ages 1–10 were available for 1968–86 (Table 2). Catches of fish older than age 10 were negligible.

The age composition estimates were obtained through an at-sea sampling program in which three to four observers measured about 100 000 fish and collected about 5000–6000 otoliths annually. The smallest hake require more time to process and are less valuable; consequently, catches of age 1 hake were underestimated prior to 1973 due to discarding. Discarding is believed to have been negligible in more recent years because of the relatively lower catches of older fishes.

Estimates of fishing mortality rates and catchability coefficients were based on results of VPA and least-squares catch-at-age analysis. The primary advantage of the VPA, which was done by Draganik and Sacks (1987), was that selectivity patterns could vary from year to year. The selectivity pattern for the least-squares analysis was assumed to be constant over selected ranges of years. Because of that simplifying assumption, an advantage of the least-squares analysis was that many fewer parameters had to be estimated. Another advantage was the assumption that catch and effort were measured with error; thus, residuals could be examined for evidence of lack of fit due to violations in the model assumptions (e.g. trends in the effort residuals due to changes in catchability).

The methods used by Draganik and Sacks (1987) in the VPA can be summarized as follows. A linear regression of the average F for ages 1–7 versus standardized fishing effort (from the weighted average CPUE index described above) was fitted using VPA results for 1968–82. The resulting regression equation was used to predict average F 's for 1982–86. The selected starting F for the VPA was the value that minimized the squared difference between the 1982–86 average F 's for ages 1–7 and the values predicted from the regression equation. (The starting F for age 10 fish was assumed to be constant over all years. The starting F 's in 1986 for ages less than the assumed age at full recruitment (age 4) were based on an assumed selectivity pattern.) A natural mortality rate (M) of 0.3 was assumed for all ages and years.

The least-squares model that we used (Deriso et al. 1985) was based on the following assumptions: (1) fishing mortality could be separated into an age-dependent factor (selectivity) and a year-dependent factor (the fishing mortality rate for fully recruited fish, $F(y)$), (2) catchability was constant and predicted fishing effort ($f'(y)$) was obtained as $F(y)/q$, and (3) errors in measuring catch and fishing effort were lognormally distributed. The microcomputer program CAGEAN (Deriso et al. 1985) was used to estimate the model parameters. As in the VPA, we assumed that M was 0.3 for all ages and years (Draganik and Sacks 1987).

Several model parameters were varied to evaluate the model's sensitivity to assumptions about catchability and selectivity. We varied the weighting factor (λ) used to adjust the amount of influence given the auxiliary information on fishing effort (Table 1). A low λ value (1.0) permitted predicted and observed effort to deviate considerably whereas a larger value (10.0) forced relatively close agreement (and adherence to the constant catchability assumption). We were unable to obtain solutions for λ values greater than 10, suggesting an inconsistency between the catch-at-age and effort data.

We evaluated three alternative assumptions about the range of years for which a constant selectivity pattern was assumed to apply: (1) a single selectivity period from 1968 to 1986, (2) two selectivity periods during which trawl mesh size was 70–120 mm (1968–75), or a minimum of 110 mm (1976–86) (Andrew and Butterworth 1988) and (3) selectivity periods 1968–81 and 1982–86 corresponding to the periods before and

TABLE 2. Number of Cape hake caught (in millions) in ICSEAF divisions 1.3 and 1.4 (from Draganik and Sacks 1987).

Year	Age									
	1	2	3	4	5	6	7	8	9	10
1968	2.72	89.83	561.14	193.77	74.17	11.64	2.45	0.00	0.00	0.00
1969	0.00	52.98	231.41	212.35	59.27	17.16	8.33	2.50	1.33	0.00
1970	0.13	128.47	320.82	203.83	110.20	21.97	7.37	1.15	0.67	0.00
1971	0.03	24.84	161.14	264.95	72.17	21.73	11.41	3.64	2.08	0.50
1972	2.91	48.67	549.59	346.37	119.41	38.32	19.59	3.68	1.36	0.63
1973	27.78	53.23	383.21	290.85	48.42	10.52	5.42	6.60	1.25	0.91
1974	32.41	162.77	160.17	60.34	103.79	57.22	15.27	2.62	1.28	0.69
1975	26.78	126.94	362.41	114.99	32.96	18.88	13.88	6.74	3.61	1.89
1976	71.41	345.29	500.98	120.59	14.23	12.90	2.25	1.69	0.80	0.40
1977	51.58	94.33	225.85	181.45	28.39	9.80	7.14	4.65	1.24	1.35
1978	48.49	434.71	307.54	74.92	36.89	11.07	1.69	0.38	0.64	0.11
1979	18.77	113.85	121.15	66.95	23.25	12.85	5.47	3.97	1.62	1.75
1980	44.05	36.19	49.52	40.41	12.89	9.86	4.08	1.35	0.64	0.76
1981	25.15	45.83	45.38	34.39	25.90	11.23	2.24	1.67	0.26	0.06
1982	135.80	312.31	168.97	47.96	13.30	7.34	4.75	2.65	1.01	0.46
1983	872.13	739.33	97.18	42.68	11.61	5.21	2.10	0.80	0.32	0.20
1984	34.76	667.31	295.07	54.26	17.00	5.88	1.63	1.42	0.11	0.76
1985	56.49	127.01	230.17	129.24	31.79	5.45	1.25	0.74	0.15	0.01
1986	25.50	301.40	135.40	114.50	69.10	20.10	10.40	2.50	0.80	0.00

after the entry of the apparently strong 1981 and 1982 year classes (i.e. targeting on strong year classes). We also obtained some estimates under the assumption that a range of ages (e.g. 3–5 or 4–6) were equally vulnerable to fishing; the results were similar to those reported here.

We used results from VPA to determine whether there had been obvious changes in selectivity patterns over time. Because the starting F 's would have greatest impact on estimates for the oldest age groups, we calculated VPA selectivity estimates (i.e. age-specific F 's for each year scaled to a maximum of 1.0) using F 's for ages 1–7 only.

By varying the assumptions used in the least-squares analysis, we obtained a wide range of estimated population levels and fishing mortality rates. These solutions appeared to be about equally consistent with the observed catch data; consequently, we rejected some solutions by using the following two alternative sources of recruitment estimates.

(1) Annual trawl survey estimates of absolute abundance have been obtained each August since 1983 using the swept-area method, based on 20 d of trawling with four to five tows per day at randomly selected sites (Macpherson et al. 1985). These surveys were conducted over latitudes 23–30°S, compared with 15–25°S for the commercial catch data. Because of the lack of overlap and difference in coastline length, we used the survey estimates only to rule out extreme solutions.

(2) Based on the convergence property of VPA, we felt that the VPA estimates of recruitment for the 1968–77 year classes should be relatively reliable. For those year classes, the estimated abundance at age 1 was based on a starting F at age 10. The cumulative F for ages 1–9 exceeded 3.5 for each year class, which should be more than sufficient to insure convergence. The VPA estimate of mean recruitment from 1968 to 1977 was 1.67 billion recruits using a starting F of either 0.65 or 0.75 (Draganik and Sacks 1987). Based on those results, we believe that a mean 1968–77 recruitment level substantially different from 1.67 billion is unlikely at the assumed level of natural mortality.

For the catch-at-age analyses, we estimated the approximate overall catchability in year y ($q(y)$) as

$$q(y) = C(y)/(f(y)B_{exp}(y))$$

where $C(y)$ was the catch biomass and $B_{exp}(y)$ was the estimated exploitable biomass in year y . For VPA, we used the estimated selectivity patterns for ages 1–7 (described above) to determine exploitable biomass. Thus, our VPA estimate of catchability applied to ages 1–7 only. Crecco and Overholtz (1990) estimated catchability using total biomass; however, we used exploitable biomass in an attempt to separate selectivity and catchability changes.

Although constant catchability is assumed in the CAGEAN program, estimated catchability will vary among years due to differences between observed and predicted effort unless λ is large. Crecco and Overholtz (1990) used survey estimates of abundance and VPA estimates of catchability to test for a non-linear relationship between abundance and catchability. In our study, both abundance and catchability were estimated using the catch-at-age data; consequently, no significance tests were carried out.

We examined the 23–30°S survey data for evidence of recent (1983–89) changes in the area occupied by *M. capensis*. For each year, we plotted cumulative distributions showing the proportion of total biomass from each survey stratum. A contraction in the area occupied by the stock would cause a larger proportion of the stock to occur in fewer strata.

Results

Estimated Abundance and Selectivity

The least-squares recruitment estimates were most consistent with the survey and VPA estimates and least sensitive to λ for the case where selectivity was assumed to have changed during 1982–86 (relative to 1968–81) in order to target on the apparently strong 1981 and 1982 year classes (Table 3). We estimated that fish ages 1–2 had increased vulnerability to

TABLE 3. Recruitment (billions of age 1 fish) as estimated by VPA (Draganik and Sacks 1987), the swept-area method using trawl survey catches (Macpherson and Roel 1984), and three least-squares analyses using different assumptions about selectivity. λ represents the relative weight given the auxiliary information on fishing effort in the least-squares analyses.

Year	VPA	Survey	Selectivity period					
			1968-86		1968-75, 1976-86		1968-81, 1982-86	
			$\lambda = 1$	$\lambda = 10$	$\lambda = 1$	$\lambda = 10$	$\lambda = 1$	$\lambda = 10$
1968	2.23		2.77	49.43	2.60	25.54	2.85	1.54
1969	2.10		1.21	21.02	1.19	10.54	1.25	0.79
1970	2.61		1.59	26.65	1.85	13.99	1.65	1.24
1971	1.33		0.93	15.68	1.15	8.36	0.94	0.78
1972	0.90		1.08	17.91	1.45	10.23	1.12	0.97
1973	1.60		2.21	36.05	2.86	21.74	2.30	2.11
1974	2.04		2.71	45.05	2.69	26.94	2.73	2.39
1975	1.45		2.53	42.41	2.49	22.39	2.49	2.01
1976	1.20		1.52	25.87	1.06	8.81	1.57	1.18
1977	1.26		1.63	29.21	0.99	9.40	1.77	1.09
1978	0.55		1.46	32.40	0.89	9.75	1.11	0.72
1979	0.44		1.15	29.58	0.65	8.14	0.63	0.52
1980	0.84		2.27	56.00	1.21	14.83	1.18	1.15
1981	1.20		3.37	80.79	1.73	19.45	2.10	1.84
1982	2.82		9.15	213.11	4.24	45.75	3.82	2.64
1983	3.18	3.75	17.74	376.05	6.69	64.70	5.86	3.49
1984	0.84	5.53	5.90	111.52	1.65	13.58	1.23	0.69
1985	1.42	5.38	21.29	343.04	3.48	25.79	2.25	1.21
1986	0.51	4.68	12.82	202.11	0.97	7.34	0.66	0.33
1987		2.51						
1988		1.46						
1989		2.21						

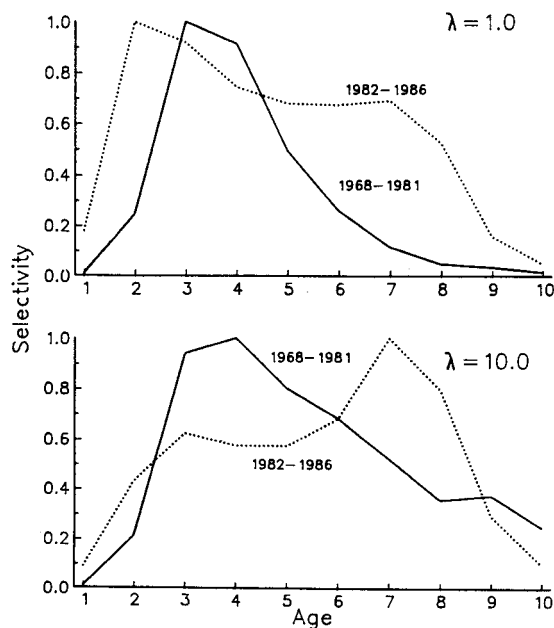


FIG. 1. Least-squares estimates of the selectivity patterns for periods 1968-81 and 1982-86. λ represents the relative weight given the auxiliary information on fishing effort.

fishing during 1982-86 relative to 1968-81 (Fig. 1); thus, the large recent catches were attributed both to strong recruitment and selectivity changes. The increased vulnerability of fish ages 1-2 also was evident in the 1982-85 selectivity patterns based on the VPA results (Fig. 2). There were no apparent trends in the least-squares catch residuals for this case, except that the predicted catches of age 1 fish were much larger than the observed catches during 1969-71 (i.e. years in which discarding was thought to occur).

When a single selectivity period (1968-86) was assumed, the large catches during 1982-86 were attributed solely to strong incoming year classes. The estimates of 1982-86 recruitment were considerably higher than either the survey or VPA estimates (Table 3). When selectivity periods 1968-75 and 1976-86 were assumed (before and after the minimum mesh regulation was implemented), recruitment estimates for $\lambda = 1.0$ were similar in magnitude to the survey and VPA estimates whereas the results for $\lambda = 10.0$ were substantially higher (Table 3). As in the previous case, recruitment estimates generally were highest during 1982-86. We did not find evidence in our VPA selectivity estimates (Fig. 2) of a consistent change in selectivity due to the minimum mesh regulation. Based on these results, we limit subsequent discussion of the least-squares analysis to the case where selectivity periods 1968-81 and 1982-86 were assumed.

The 1968 number-at-age vectors and resultant biomass estimates differed considerably for the two λ values (Fig. 3), although the biomass estimates converged somewhat by 1982 due to the similar estimates of recruitment during the 1970's (Fig. 4). The larger change in biomass from 1968 to 1982 corresponded to the larger change in predicted fishing effort, which was associated with the smaller λ value (Fig. 5). The

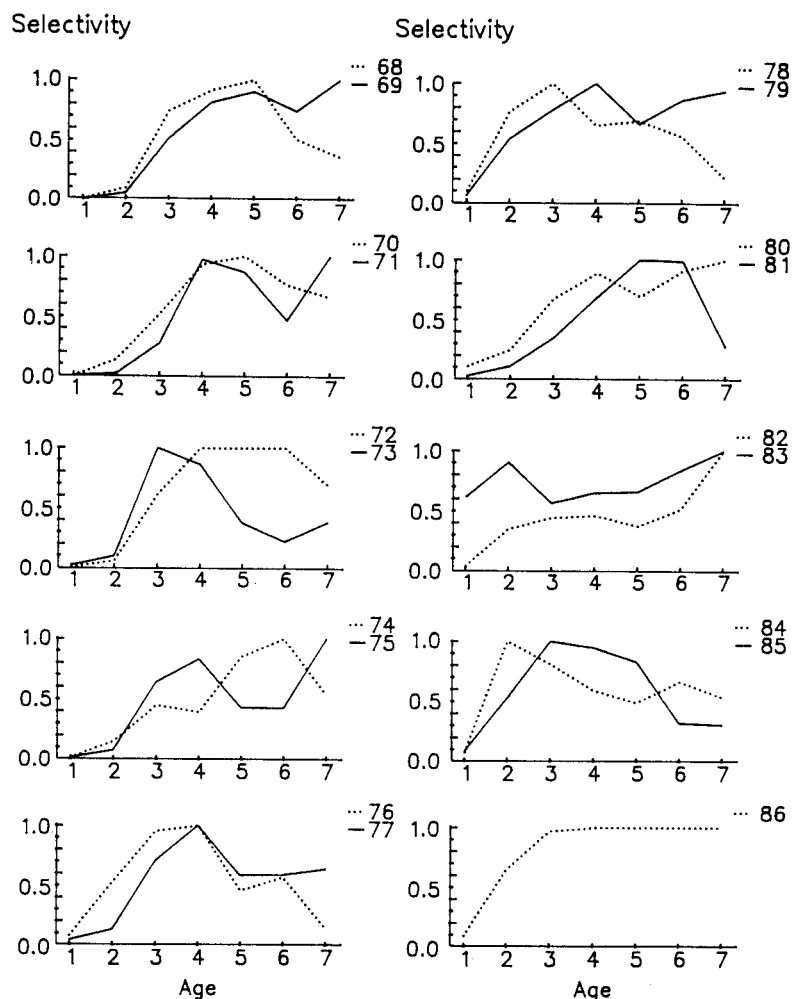


FIG. 2. Estimated annual selectivity patterns for fish ages 1–7, based on VPA results obtained by Draganik and Sacks (1987). Fishing mortality rates (F) for age 10 fish were assumed values. For that reason, F 's for fish ages 8–10 were not used to calculate selectivities to reduce their impact on the estimated selectivity patterns.

change in biomass was much smaller when predicted and observed effort were forced to agree more closely.

Estimated Catchability Changes

The relative weight given the auxiliary information on fishing effort strongly affected the estimated F 's, or equivalently, the predicted fishing effort levels (Fig. 5). When λ was low, predicted effort increased at a much faster rate from 1968 to 1979 than did observed effort. Observed and predicted effort levels were generally similar from 1983 to 1986.

Estimated catchability was relatively constant prior to about 1979 but fluctuated considerably between about 1979 and 1983 (Fig. 6). The decrease in catchability after 1981 corresponded

to a period of increasing numerical abundance due to strong recent recruitment (Fig. 3). These changes resulted in an apparent inverse relationship between estimated abundance and catchability, particularly for the least-squares analysis with $\lambda = 1.0$ (Fig. 7). This relationship is highly tentative, however, because estimated total biomass appears as a variable on both axes of the catchability plot.

Changes in Spatial Distribution

The differences we observed in area occupied by *M. capensis* from 1983 to 1989 (Fig. 8) were not consistent with the changes in estimated biomass (Fig. 2). The apparent contraction in 1986 and 1987 did not persist in 1988 and 1989, despite further decreases in estimated biomass.

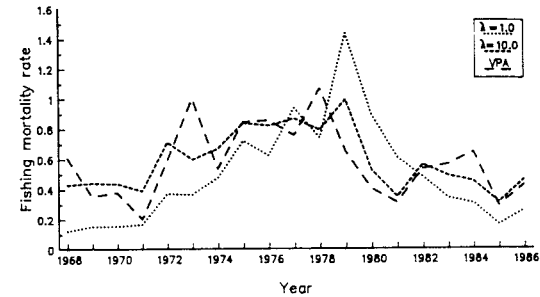
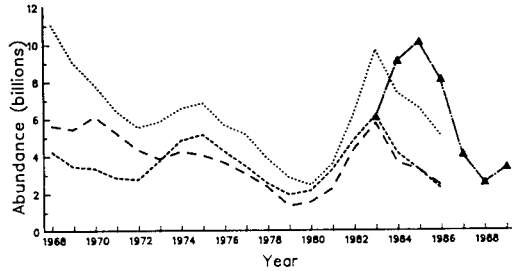
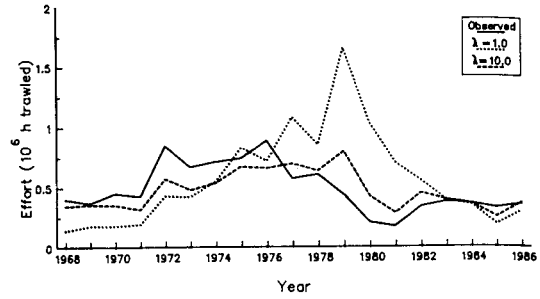
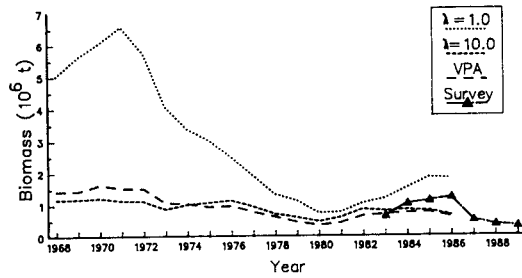


FIG. 3. Estimated levels of biomass and numerical abundance from 1968 to 1986, based on a least-squares catch-at-age analysis. λ represents the relative weight given the auxiliary information on fishing effort.

FIG. 5. Upper panel: observed fishing effort (Draganik and Sacks 1987) and predicted levels based on least-squares catch-at-age analysis. Lower panel: fishing mortality rates obtained from least-squares catch-at-age analysis and from VPA (Draganik and Sacks 1987). λ represents the relative weight given the auxiliary information on fishing effort in the catch-at-age analyses.

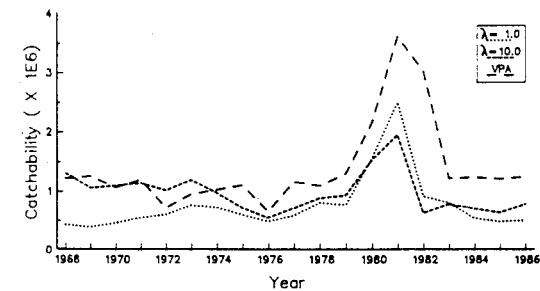
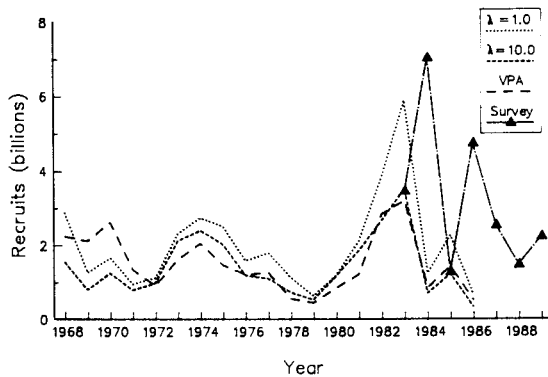


FIG. 4. Estimates of annual recruitment (billions of age 1 fish), based on a least-squares catch-at-age analysis (where λ represents the relative weight given the auxiliary information on fishing effort), VPA (Draganik and Sacks 1987), and swept-area estimates from 1983 to 1989 trawl surveys at latitudes 23–30°S (Macpherson and Roel 1984).

FIG. 6. Estimates of annual catchabilities obtained from least-squares catch-at-age analysis (where λ represents the relative weight given the auxiliary information on fishing effort) and from VPA (Draganik and Sacks 1987). Catchability estimates for VPA represent ages 1–7 only.

Discussion

Our recruitment estimates were highly sensitive to the assumption that the selectivity pattern was constant over time, and we obtained unreliable estimates for two of the three cases we examined. Our results supported earlier studies indicating that a model with more than one selectivity period was required (Butterworth et al. 1986a) and that the mesh regulation did not change overall catchability significantly (Andrew and Butter-

worth 1988). Butterworth et al. (1986a) examined the hypothesis that selectivity for young fish increased gradually from 1968 to 1983, due perhaps to changes in the spatial distribution of fishing effort. They concluded that the changes in catch-at-age data appeared more complex than could be accounted for by the selectivity submodel that they assumed. The results obtained in our study (based on three additional years of catch data) appear to support selectivity changes in response to fluctuations in year-class strength (i.e. targeting on strong year classes).

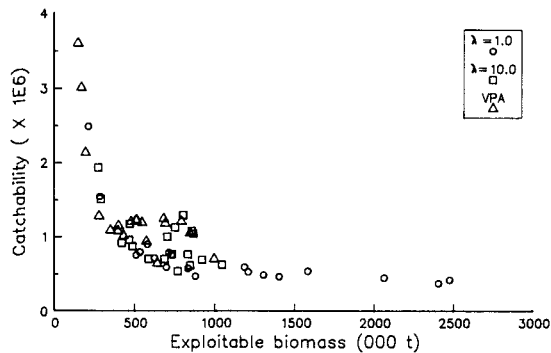


FIG. 7. Estimates of catchability versus exploitable biomass obtained from least-squares catch-at-age analysis (where λ represents the relative weight given the auxiliary information on fishing effort) and from VPA (Draganik and Sacks 1987). Catchability and exploitable biomass estimates for VPA represent ages 1–7 only.

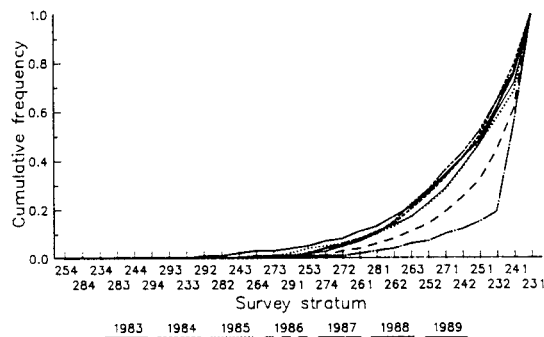


FIG. 8. Cumulative proportion of total biomass accounted for annually by each sampling stratum, based on trawl survey estimates of abundance for the area 23–30°S. Sampling strata are ordered from lowest to highest 1983–89 average catch rate.

The selectivity patterns from the least-squares analysis were sensitive to λ for 1982–86. Estimates for the latter selectivity period should stabilize over time as additional years of data are included in the analysis. For three of the four selectivity patterns, vulnerability to fishing decreased at older ages (Fig. 1). A similar trend was apparent in some of the VPA selectivity patterns, although those patterns varied substantially from year to year (Fig. 2). Decreased vulnerability for older fish may be reasonable because (1) vulnerability to trawl gear decreases at older ages for some species (e.g. Pacific whiting (*M. productus*), Hollowed et al. 1988; sablefish (*Anoplopoma fimbria*), Methot and Hightower 1988) and (2) Cape hake older than age 10 occur rarely in trawl catches but have been caught in exploratory fishing with hook-and-line gear.

An advantage of this and earlier catch-at-age analyses was the ability to identify alternative population trends that could account for the observed catch and effort patterns. In a traditional surplus production model, the recent increases in CPUE would be attributed to large increases in recruitment. In the catch-at-age analyses, the CPUE increases would be attributed

either to strong recruitment or to moderate recruitment and changing selectivity and catchability. Because of discrepancies between results from surplus production and age-structured models, Butterworth et al. (1986a) hypothesized that the CPUE increases may have been due partly to a change in the spatial distribution of fishing effort. They suggested that the increased catches of young fish may have been due to increased fishing in inshore areas inhabited by younger hake. Our results suggest that the CPUE increases were due to a combination of changes in selectivity, catchability, and the strength of incoming year classes.

Estimated catchability generally increased from 1968 to 1981 in the catch-at-age analysis for the lower λ value (Fig. 6) because catchability changes could occur as a trend in the effort residuals. Those changes in estimated catchability would be consistent with increasing fishing power, due perhaps to increased knowledge of the fishing grounds or improvements in gear. For the least-squares analysis using the higher λ value, catchability was more constrained to fluctuate about a constant level.

If catchability increased gradually over time, then recent quotas derived from surplus production modeling would be overestimated (Butterworth and Andrew 1987). However, the fluctuations in catchability observed in all cases from about 1979 to 1983 suggested that factors other than changes in fishing power contributed to the observed trends. The temporal changes in estimated biomass and numerical abundance (Fig. 3) resulted in an apparent inverse relationship between estimated catchability and abundance (Fig. 7). Crecco and Overholtz (1990) noted a similar relationship for Georges Bank haddock (*Melanogrammus aeglefinus*), which they attributed to changes in the area occupied by the stock.

One explanation for an inverse relationship between catchability and abundance is that fish populations tend to contract toward the most favorable habitat as they are fished down (MacCall 1990). We did observe a substantial apparent contraction using the approach proposed by Crecco and Overholtz (1990) (for each year, summing the area of strata for which the catch rate exceeded the long-term median). However, based on the cumulative distribution plots (Fig. 8), we inferred that the decreases in stratum catch rates represented overall decreases in abundance. The apparent changes in spatial distribution for the area surveyed (23–30°S) (Fig. 8) were not consistent with changes in abundance in areas 1.3 and 1.4, but could be due to changes in other factors such as temperature or food availability. We are unable to determine whether the stock contracted during the period of highest estimated catchability because of the absence of survey data prior to 1983.

Changes in water temperature could have affected catchability. The period from 1979 to 1983 was one of below-average sea-surface temperatures (SST) for the Benguela system (McLain et al. 1985). Based on monthly mean SST for 3° blocks, anomalies of less than -0.5°C were observed during most of 1979–83, with greatest negative anomalies (less than -1°C) during November 1981 to May 1982 (McLain et al. 1985). Using SST data through 1984 in a modified catch-effort model, Butterworth (1988) reported a significant temperature effect on catchability assuming a 1-yr lag but none if a 0-yr lag was assumed.

If catchability is inversely related to abundance, management problems would be greatest when the stock declined to low levels: (1) biomass and catch quotas obtained from traditional surplus production models would tend to be overestimated

(because catchability would be higher than the historical mean) and (2) further management errors would be likely when setting either effort or catch quotas because of the rapidly changing relationship between effort and fishing mortality (Gulland 1977; Winters and Wheeler 1985).

We agree with Butterworth (1988) that conservative management is warranted until the factors affecting catchability can be reliably determined. Our results suggest that catchability and selectivity have changed over time; however, the apparent changes in catchability would also bias our estimates of it. Less biased estimates of catchability (and abundance) could presumably be obtained by using survey estimates of abundance to constrain the catch-at-age analysis (Winters and Wheeler 1985; Butterworth 1988). In our study, survey abundance estimates from an overlapping area were compared with the results of catch-at-age analysis and VPA. The survey estimates were useful for rejecting highly implausible solutions, but temporal changes in survey abundance were at odds with the VPA and catch-at-age analysis results (Fig. 3 and 4). A precise survey of areas 1.3 and 1.4, preferably measuring absolute abundance (Kimura 1989), would eliminate the need for potentially biased estimates of fishing effort. An additional advantage of survey data would be the opportunity to test for a relationship between catchability and abundance (Crecco and Overholtz 1990).

An alternative approach for dealing with catchability changes over time would be to use both survey estimates of abundance and commercial fishing effort data, but to vary the weighting factors to determine the sensitivity of population trends to the two sources of auxiliary data. Another alternative, for either a surplus production or catch-at-age model, would be to define catchability as a function of stock size or age structure or a constant that differed among periods (Fox 1974; Butterworth et al. 1986b; Deriso et al. 1989). Given the difficulty of exactly modeling catchability changes over time, that approach might be more effective if survey data were available to help constrain the catch-at-age analysis. Other approaches include analyzing catch and effort data on a finer spatial scale to separate changes in abundance from changed fishing distribution patterns and conducting a detailed reexamination of vessel power factors used to combine effort among fleets (Butterworth 1988).

In summary, our results suggest that catchability has varied over time, due perhaps to changes in fishing power, resource abundance, or oceanographic factors. Improved estimates of abundance and short-term yield can be obtained by incorporating precise survey data or an appropriate submodel of catchability changes into either a surplus production or age-structured model. Conservative management is warranted until factors affecting catchability can be identified.

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References

- ABRAMSON, N. J., AND P. K. TOMLINSON. 1972. An application of yield models to a California shrimp population. U.S. Fish. Bull. 70: 1021-1041.
- ANDREW, P. A. 1986. Dynamic catch-effort models for the southern African hake populations. Ph.D. thesis. University of Cape Town. 248 p.
- ANDREW, P. A., AND D. S. BUTTERWORTH. 1988. An examination of the effect of changes in mesh size on the catchability coefficient (q) and sustainable yield of the Southern African hake stocks. Collect. Sci. Pap. Int. Comm. SE Atl. Fish. 15(1): 23-45.
- ANGELSEN, K. K., AND S. OLSEN. 1987. Impact of fish density and effort level on catching efficiency of fishing gear. Fish. Res. 5: 271-278.
- BUTTERWORTH, D. S. 1988. Some recommendations regarding the assessment methodologies used by ICSEAF. Collect. Sci. Pap. Int. Comm. SE Atl. Fish. 15(1): 107-155.
- BUTTERWORTH, D. S., AND P. A. ANDREW. 1987. Further results from the application of dynamic catch-effort models to the hake stocks in the ICSEAF convention area. Collect. Sci. Pap. Int. Comm. SE Atl. Fish. 14(1): 109-160.
- BUTTERWORTH, D. S., M. O. BERGH, AND P. A. ANDREW. 1986a. A comparison of dynamic catch-effort model and VPA assessments for the hake stocks in ICSEAF divisions 1.3-1.6. Collect. Sci. Pap. Int. Comm. SE Atl. Fish. 13(1): 131-165.
- BUTTERWORTH, D. S., M. O. BERGH, P. A. ANDREW, AND A. E. PUNT. 1986b. Some aspects of management strategies for and the assessment of the hake stocks off southern Africa. Collect. Sci. Pap. Int. Comm. SE Atl. Fish. 13(1): 167-193.
- CRAWFORD, R. J. M., L. V. SHANNON, AND D. E. POLLOCK. 1987. The Benguela Ecosystem. Part IV. The major fish and invertebrate resources. Oceanogr. Mar. Biol. Annu. Rev. 25: 353-505.
- CRECCO, V., AND W. J. OVERHOLTZ. 1990. Causes of density-dependent catchability for Georges Bank haddock *Melanogrammus aeglefinus*. Can. J. Fish. Aquat. Sci. 47: 385-394.
- DERISO, R. B., P. R. NEAL, AND T. J. QUINN. 1989. Further aspects of catch-age analysis with auxiliary information. p. 127-135. In R. J. Beamish and G. A. McFarlane [ed.] Effects of ocean variability on recruitment and an evaluation of parameters used in stock assessment models. Can. Spec. Publ. Fish. Aquat. Sci. 108.
- DERISO, R. B., T. J. QUINN II, AND P. R. NEAL. 1985. Catch-age analysis with auxiliary information. Can. J. Fish. Aquat. Sci. 42: 815-824.
- DRAGANIK, B., AND R. SACKS. 1987. Stock assessment of Cape hakes (*Merluccius capensis* and *M. paradoxus*) in the convention area. Divisions 1.3 + 1.4 Collect. Doc. Pap. Int. Comm. SE. Atl. Fish. Doc. 18b.
- FOX, W. W. 1974. An overview of production modelling. p. 142-156. In Proceedings of the ICCAT workshop on tuna population dynamics, Nantes, France, Sept. 1974.
- GORDOA, A., AND J. P. PERTERRA. 1987. Catch fluctuations observed in the Cape hake fishery in division 1.5. Collect. Sci. Pap. Int. Comm. SE Atl. Fish. 14(1): 207-218.
- GRAHAM, M. 1935. Modern theory of exploiting a fishery and application to North Sea trawling. J. Cons. Int. Explor. Mer. 10: 264-274.
- GULLAND, J. A. 1977. The stability of fish stocks. J. Cons. Int. Explor. Mer. 37: 199-204.
- HOLLOWED, A. B., R. METHOT, AND M. DORN. 1988. Status of the Pacific whiting resource in 1988 and recommendations to management in 1989. Appendix A in Status of the Pacific Coast groundfish fishery through 1988 and recommended acceptable biological catches for 1989. Pacific Fishery Management Council, Portland, OR.
- HOUGHTON, R. G., AND S. FLATMAN. 1980. The exploitation pattern, density-dependent catchability, and growth of cod, *Gadus morhua*, in the west-central North Sea. J. Cons. Int. Explor. Mer. 39: 271-287.
- KIMURA, D. K. 1989. Variability, tuning, and simulation for the Doubleday-Deriso catch-at-age model. Can. J. Fish. Aquat. Sci. 46: 941-949.
- MACCALL, A. D. 1976. Density-dependence of catchability coefficient in the California Pacific sardine, *Sardinops sagax caerulea*, purse-seine fishery. CalCOFI Rep. 18: 136-148.
1990. Dynamic geography of marine fish populations. University of Washington Press, Seattle, WA.
- MACPHERSON, E., AND B. ROEL. 1984. Estudio del reclutamiento de la merluza en la divisiones 1.4 y 1.5. Collect. Sci. Pap. Int. Comm. SE Atl. Fish. 11(1): 159-165.
- MACPHERSON, E., B. ROEL, AND B. MORALES. 1985. Reclutamiento de la merluza y abundancia y distribución de diferentes especies comerciales en las divisiones 1.4 y 1.5 durante 1983-1984. Collect. Sci. Pap. Int. Comm. SE Atl. Fish. 12: 1-61.
- MCLAIN, D. R., R. E. BRAINARD, AND J. G. NORTON. 1985. Anomalous warm events in eastern boundary current systems. CalCOFI Rep. 26: 51-64.
- METHOT, R., AND J. HIGHTOWER. 1988. Status of the Washington-Oregon-California sablefish stock in 1988. Appendix B in Status of the Pacific Coast groundfish fishery through 1988 and recommended acceptable biological catches for 1989. Pacific Fishery Management Council, Portland, OR.

- MURPHY, G. 1965. A solution to the catch equation. *J. Fish. Res. Board Can.* 22: 191-202.
- PALOHEIMO, J. E., AND L. M. DICKIE. 1964. Abundance and fishing success. *Rapp. P.-V. Réun. Cons. Int. Explor. Mer* 155: 152-163.
- PETERMAN, R. M., AND G. STEER. 1981. Relation between sport-fishing catchability coefficients and salmon abundance. *Trans. Am. Fish. Soc.* 110: 585-593.
- POPE, J. G., AND D. J. GARROD. 1975. Sources of error in catch and effort quota regulations with particular reference to variation in the catchability coefficient. *Int. Comm. Northwest Atl. Fish. Res. Bull.* 11: 17-30.
- RADOVICH, J. 1982. Catch-per-unit-of-effort: fact, fiction, or dogma. *CalCOFI Rep.* 18: 31-34.
- SHANNON, L. V., AND S. C. PILLAR. 1986. The Benguela ecosystem. Part III. Plankton. *Oceanogr. Mar. Biol. Annu. Rev.* 24: 65-170.
- SHELTON, P. A., AND M. J. ARMSTRONG. 1983. Variations in parent stock and recruitment of pilchard and anchovy populations in the southern Benguela system. *In* G. D. Sharp and J. Csirke [ed.] *Proceedings of the Expert Consultation to Examine Changes in Abundance and Species Composition of Neritic Fish Resources*, San Jose, Costa Rica, April 1983. *FAO Fish. Rep.* 291(3): 1113-1132.
- WINTERS, G. H., AND J. P. WHEELER. 1985. Interaction between stock area, stock abundance, and catchability coefficient. *Can. J. Fish. Aquat. Sci.* 42: 989-998.