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A Review of Variability and Recruitment in Marine Fish

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A REVIEW OF
VARIABILITY AND RECRUITMENT
IN MARINE FISH

By
Nicholas J. Bax

National Oceanic and Atmospheric Administration
National Marine Fisheries Service
Northwest and Alaska Fisheries Center
Resource Ecology and Fisheries Management Division
Resource Ecology and Ecosystem Simulation Task
7600 Sand Point Way N.E.
Building 4, BIN C15700
Seattle, Washington 98115

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ABSTRACT

An assumption in the traditional stock-recruitment relationship is that the history of the stock will repeat itself. The data are rarely sufficient to prove or to disprove this assumption. Published stock and recruit data and/or analyses for 38 marine fish and shellfish stocks are reproduced here together with a cursory statistical analysis of some of these data. Techniques for modelling these data are also reviewed. Long term trends in the relationship between stock abundance and production are apparent in highly smoothed data series, where annual variability has been removed. This trend may not be the same during periods of increasing and decreasing stock biomass. Variability in the stock-recruit relationship has received more emphasis of late and provides a more meaningful description of recruitment than the traditional fitted curve.

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RECRUITMENT FORECASTING

Fisheries science routinely emphasizes trend through time data. The reasons for this derive from the collection of data from commercial fisheries and from the potential for forecasting potential catches in future years. For many years, fisheries scientists have sought the capability to describe a stock-recruitment relationship; that is, to predict how many fish will recruit to a fishery when the parent stock is at a particular level. In this paper I review published data and/or analyses from 38 marine fish and shellfish stocks, and present some of the methods used to describe the relationship between stock and recruits.

Implicit in the search for a stock recruit relationship is the assumption that the history of a stock will repeat itself. This in turn assumes that one can determine the important parameters of a stock accurately enough to know if stock is in fact repeating a previously observed history. The simplest interpretation of the prior assumption implies that the resource will remain constant; that the recruitment observed in the current year will be repeated. Hennemuth et. al.'s (1980) study of eighteen marine fish stocks (Fig. 1) shows a serial correlation between the number of fish recruiting in year i and the number recruiting in year $i + 1$ in only six stocks, while the remaining twelve stocks had no detectable correlation (Table 1).^{1/} Assuming that the stocks' spawning potential in adjacent years would have been similar (an assumption which becomes unreasonable only when very few age-classes comprise the adult stock), these results indicate that in two-thirds of these stocks no stock-recruitment relationship can be expected. The history of each of these twelve stocks may still be repeating itself but the most significant features of those histories do not include adult stock size, nor other features which exhibit little year to year variation.

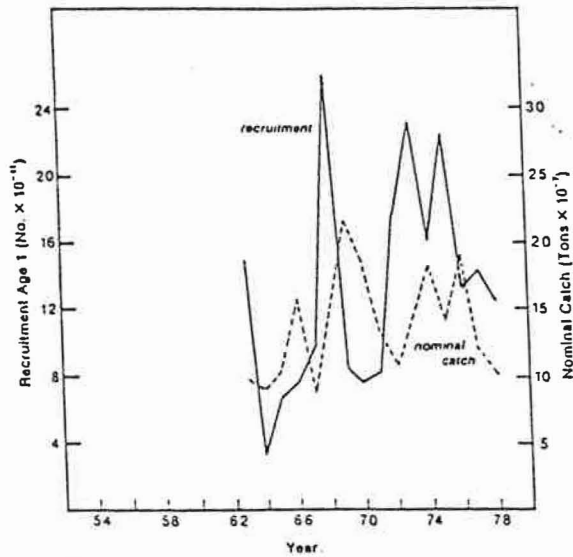
^{1/} Three of the six significant serial correlations are negative to judge from the accompanying plotted data, which would not support the hypothesis of a consistent relationship between stock and recruitment (Fig. 1). Skud (in prep.) hypothesizes a buffering from predation of young of the year by one year old fish of the same stock which would produce negative serial correlations.

Serial correlations for recruitment estimates in 18 selected stocks. (* indicates significance at $\alpha = 0.05$.)

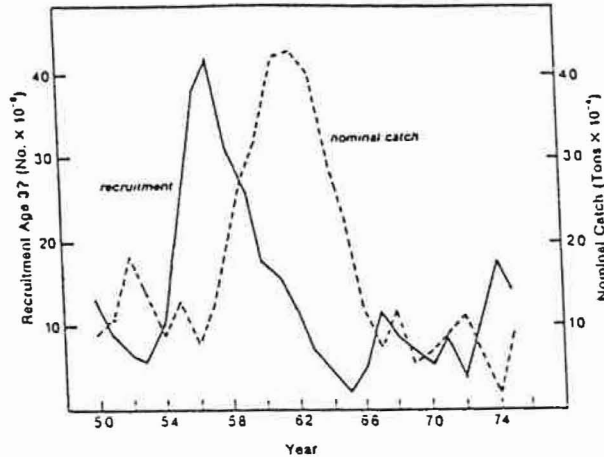
Species	Area	Period	No. of Years	Correlation coefficients		
				1-yr lag	2-yr lag	3-yr lag
Cod	Georges B.	1960-73	14	0.575*	0.359*	0.202
	North Sea	1963-77	15	-0.111	-0.354	—
	NE Arctic	1962-77	16	0.327	-0.274	—
Haddock	Georges B.	1931-73	43	0.201	-0.054	—
	Georges B.	1931-65	35	-0.008	-0.254	—
	Georges B.	1966-73	8	0.207	-0.122	—
	North Sea	1961-78	18	-0.131	-0.342	—
	NE Arctic	1962-78	17	0.058	-0.143	—
Herring	Georges B.	1963-74	12	-0.158	—	—
	North Sea	1957-74	18	-0.224	0.109	—
	Norwegian*	1950-69	20	0.335*	-0.052	—
Mackerel	NW Atlantic	1962-73	12	0.447*	0.134	—
	North Sea	1969-78	10	0.235	0.315	—
Saithe	North Sea	1961-78	18	0.312	-0.013	—
Whiting	North Sea	1963-78	16	0.200	-0.004	—
Pilchard	S Africa	1950-75	26	0.830*	0.510*	0.200
Anchovy	S Africa	1964-76	13	-0.056	0.032	—
Round herring	S Africa	1964-76	13	0.545*	0.124	—
Anchovy	Peru	1961-76	16	0.194	-0.041	—
Silver hake	Georges B.	1955-73	19	0.835*	0.491*	0.101

* Spring spawners.

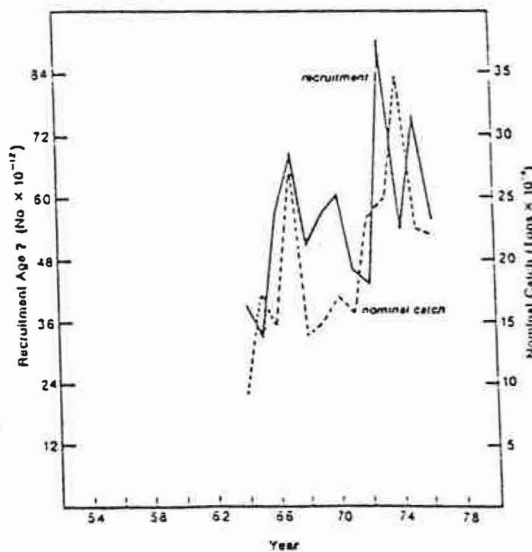
Table 1.--Table 2 of Hennemuth et. al. (1980).



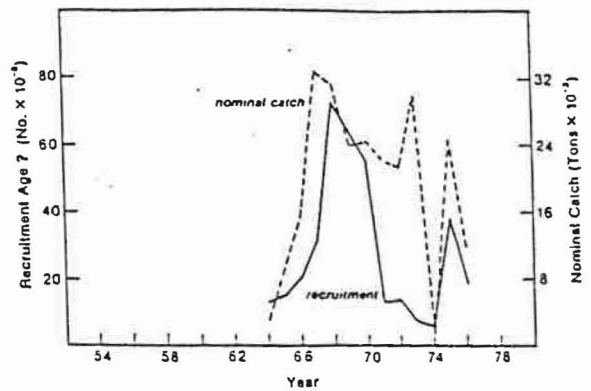
Recruitment and nominal catch for North Sea whiting, 1963-78.



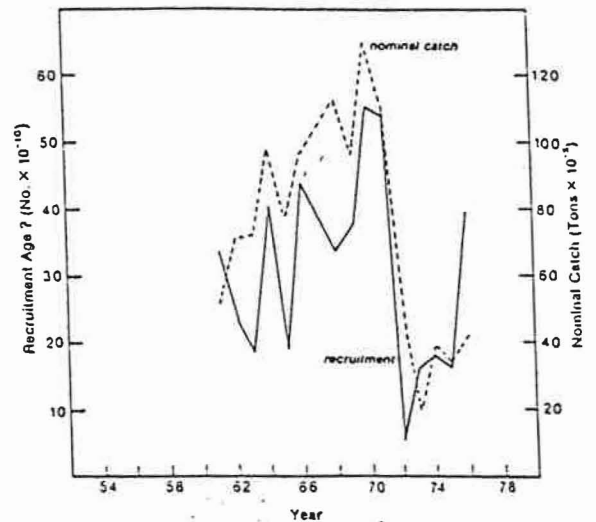
Recruitment and nominal catch for South Africa pilchard, 1950-75.



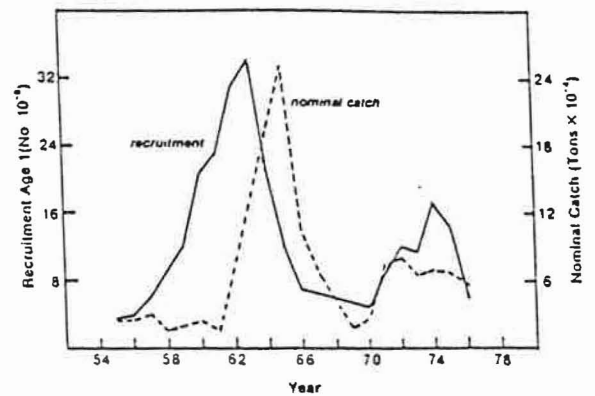
Recruitment and nominal catch for South Africa anchovy, 1964-76.



Recruitment and nominal catch for South Africa round herring, 1964-76.



Recruitment and nominal catch for Peruvian anchovy, 1961-76.



Recruitment and nominal catch for Georges Bank silver hake, 1955-76.

Figure 1.--Figs. 1-18 of Hennemuth et. al. (1980).

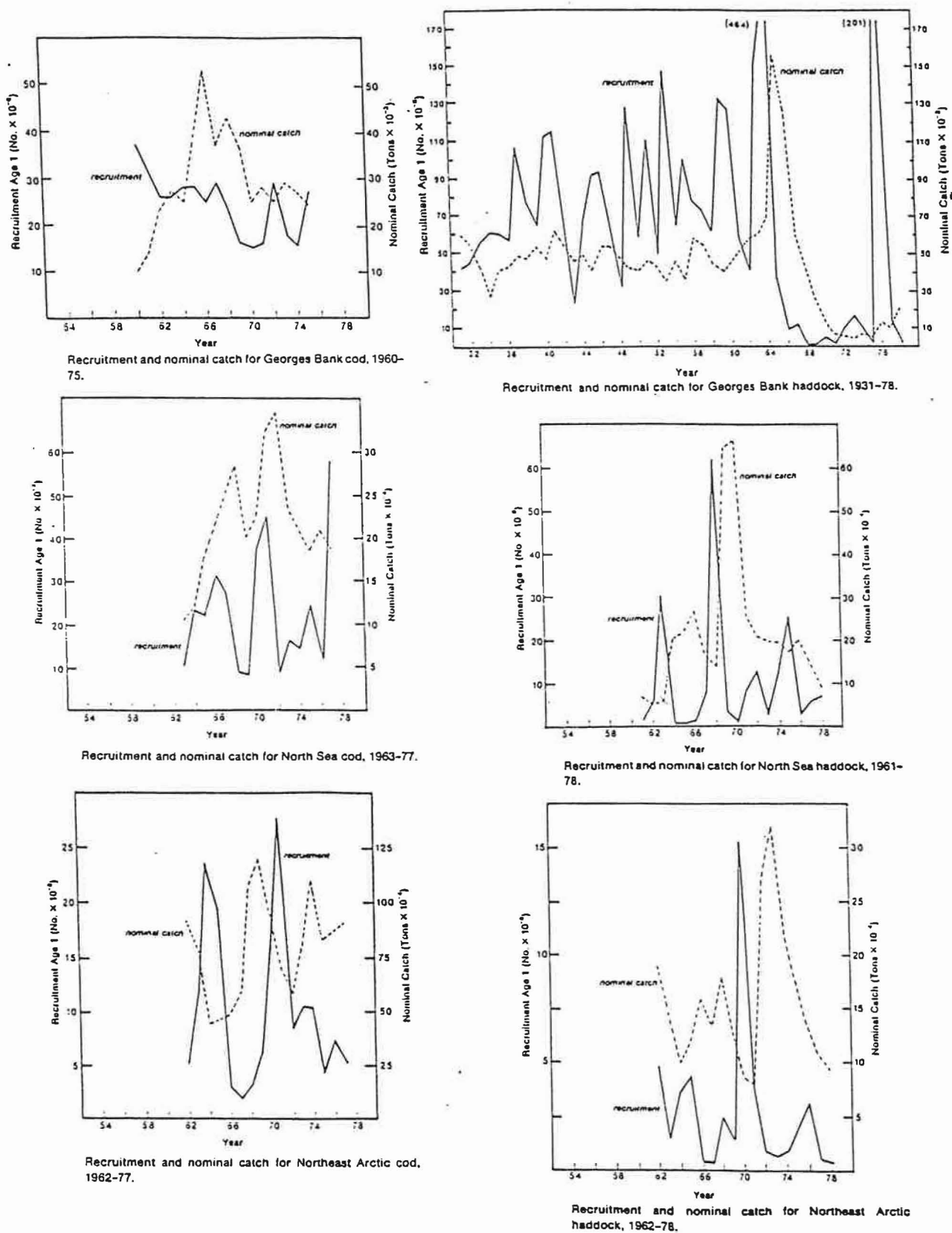
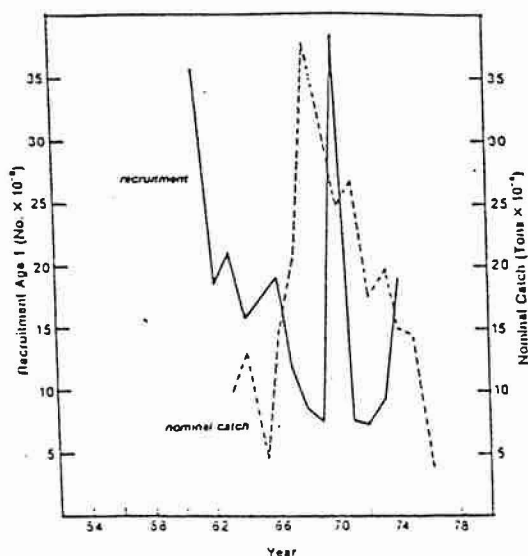
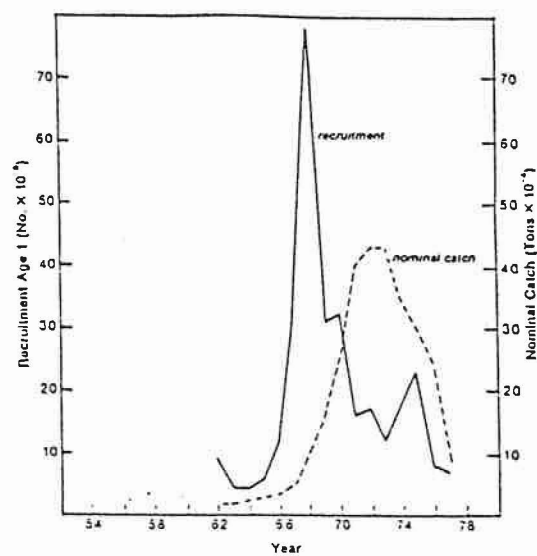


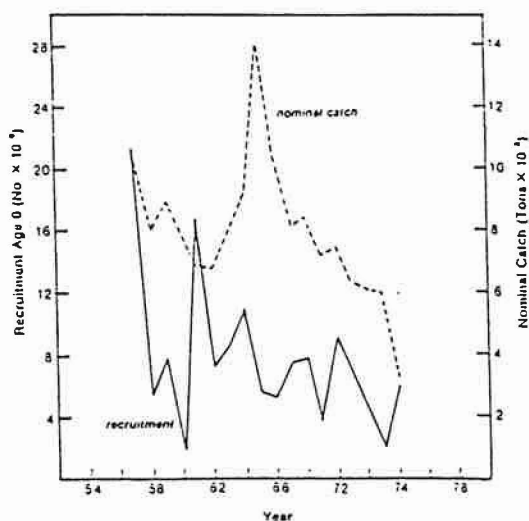
Figure 1 (cont'd).



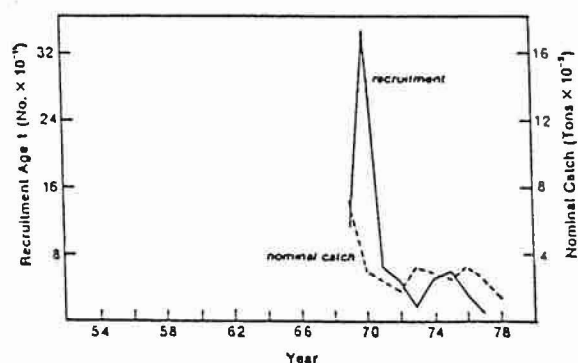
Recruitment and nominal catch for Georges Bank herring, 1961-76.



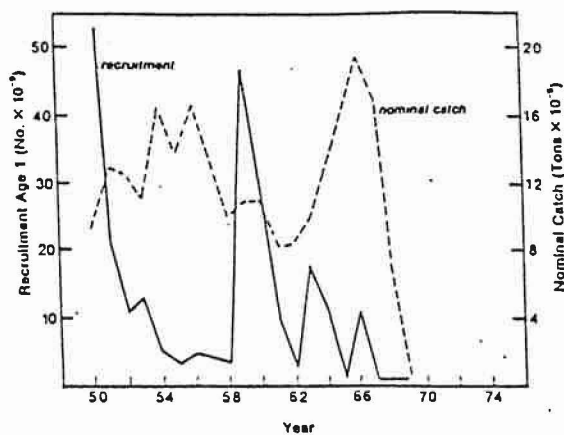
Recruitment and nominal catch for Northwest Atlantic mackerel, 1962-77.



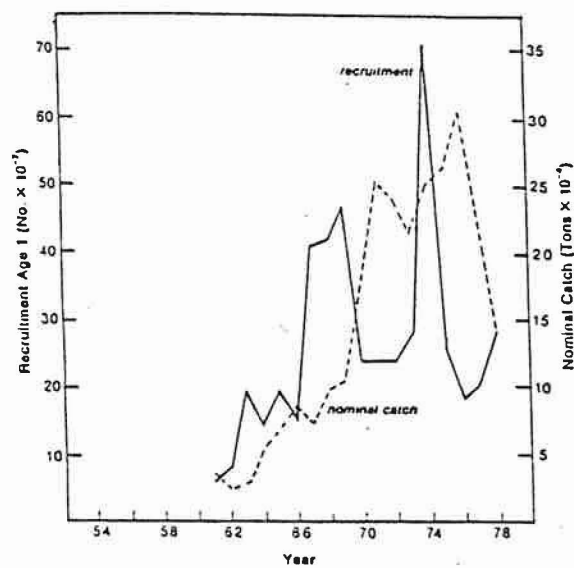
Recruitment and nominal catch for North Sea herring, 1957-74.



Recruitment and nominal catch for North Sea mackerel, 1969-78.



Recruitment and nominal catch for Norwegian spring-spawning herring, 1950-69.



Recruitment and nominal catch for North Sea saithe, 1961-78.

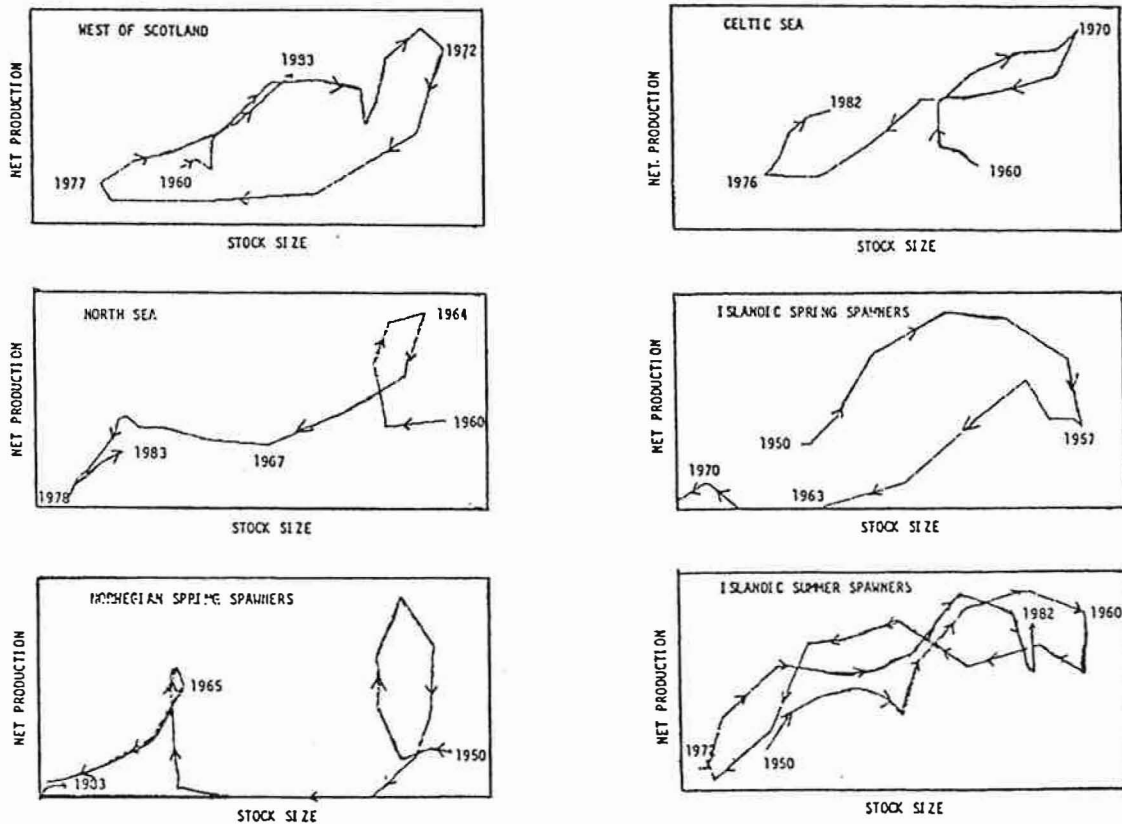
Figure 1 (cont'd.)

A generalization of the assumption that the year-class strength in one year will be repeated the following year is that a pattern of relative year class strengths over several years will repeat itself. Walters (in prep.) estimated net annual production (increase in biomass plus catch) from virtual population analyses (VPA) of six Northeast Atlantic herring stocks, smoothed these data with a cubic spline fit followed by a moving average of three, and compared the resulting smoothed net production values with stock size, also estimated from VPA. His results suggest that for two out of the six stocks the relationship between net production and stock size depends on whether the stock is undergoing a long term increase or decrease; in one stock the relationship between stock and net production was consistent over increasing or decreasing phases; and in the remaining three stocks there were insufficient data to draw any conclusions (Fig. 2).

Different stocks of fish, even if the same species, display different stability characteristics. Caddy and Gulland (1983) suggest that fish stocks would be divided into four classes determined by their natural pattern of variation: steady, cyclical, irregular, and spasmodic (Fig. 3). Skud (1982) indicates the need to include community interactions in the analysis of stock size over time. He suggests that the top, or keystone, predator in a system might have recruitment strongly influenced by environmental features, and that this predator would affect (directly or indirectly) recruitment to the other stocks. A displacement of the top predator might explain apparent reversals of correlations between recruitment in other stocks and environmental variables.^{2/} However, there is no a priori reason to assume that the top predator in the adult stocks is necessarily the top predator during larval and juvenile stages.

^{2/} Skud's and Walter's papers suggest that more is not necessarily better in the analysis of stock and recruitment relationships, if over the longer period of data collection there have been changes in system structure, resulting from predator displacement, or changes in individual stocks resulting from a change to or from an increasing or decreasing trend.

ATLANTIC HERRING STOCKS
(JAKOBSSON DATA)

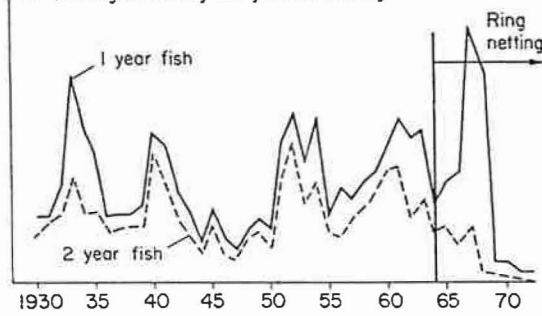


Relationships between surplus production and stock size for Northeast Atlantic herring stocks, estimated from the stock assessments of Jakobsson (1985). Procedure for estimating surplus production described in text.

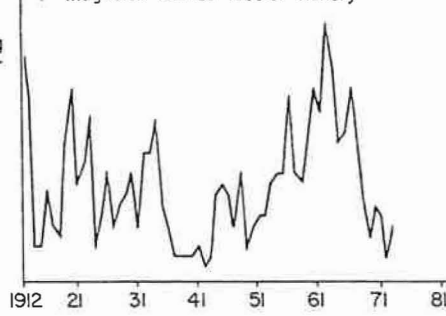
Figure 2.--Fig. 1 from Walters (in prep.).

III Fluctuations with irregular periodicity

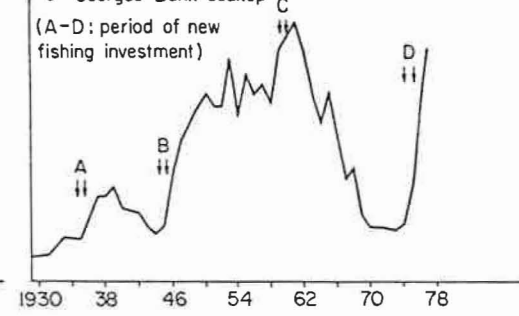
H Norwegian fishery for juvenile herring⁸



I Magdalen Islands lobster fishery⁹

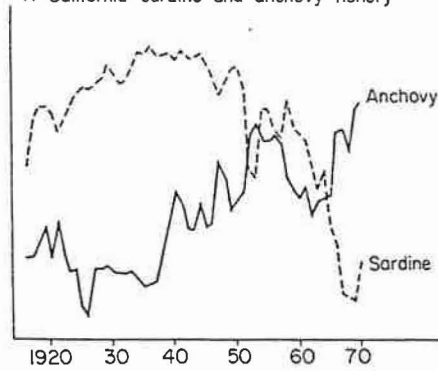


J Georges Bank scallop¹⁰
(A-D: period of new
fishing investment)

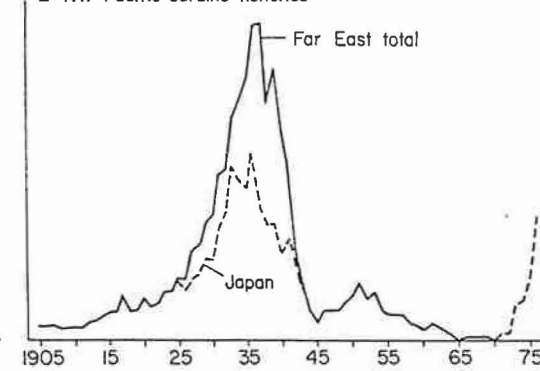


IV Irregular (intermittent) production

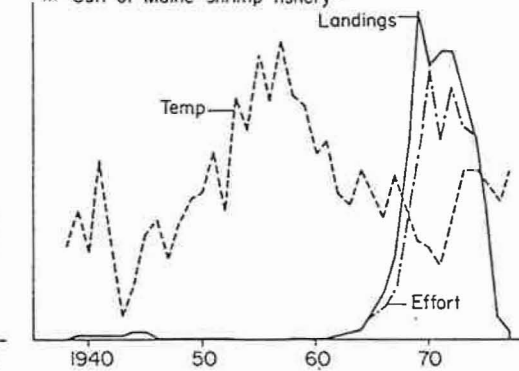
K California sardine and anchovy fishery¹¹



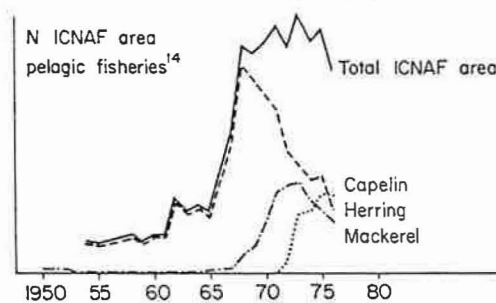
L NW Pacific sardine fisheries¹²



M Gulf of Maine shrimp fishery¹³



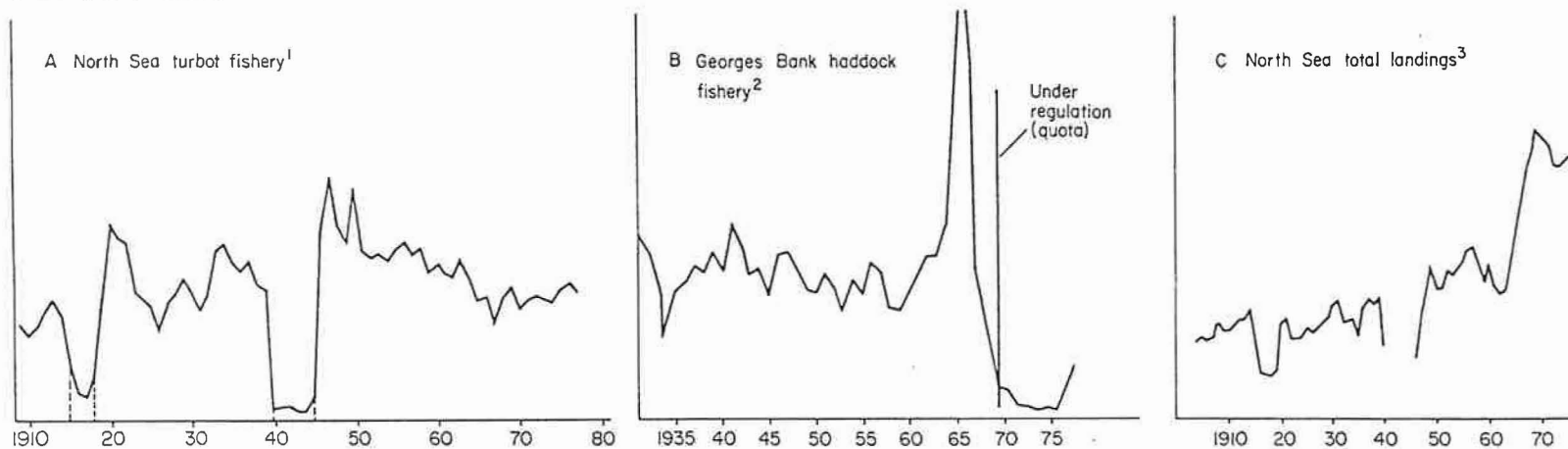
N ICNAF area
pelagic fisheries¹⁴



A tentative classification by long-term landing data of four main types of fishery,

Figure 3.--Fig. 1 from Caddy and Gulland 1983.

I 'Steady state' fisheries



II Regular, periodic fluctuations

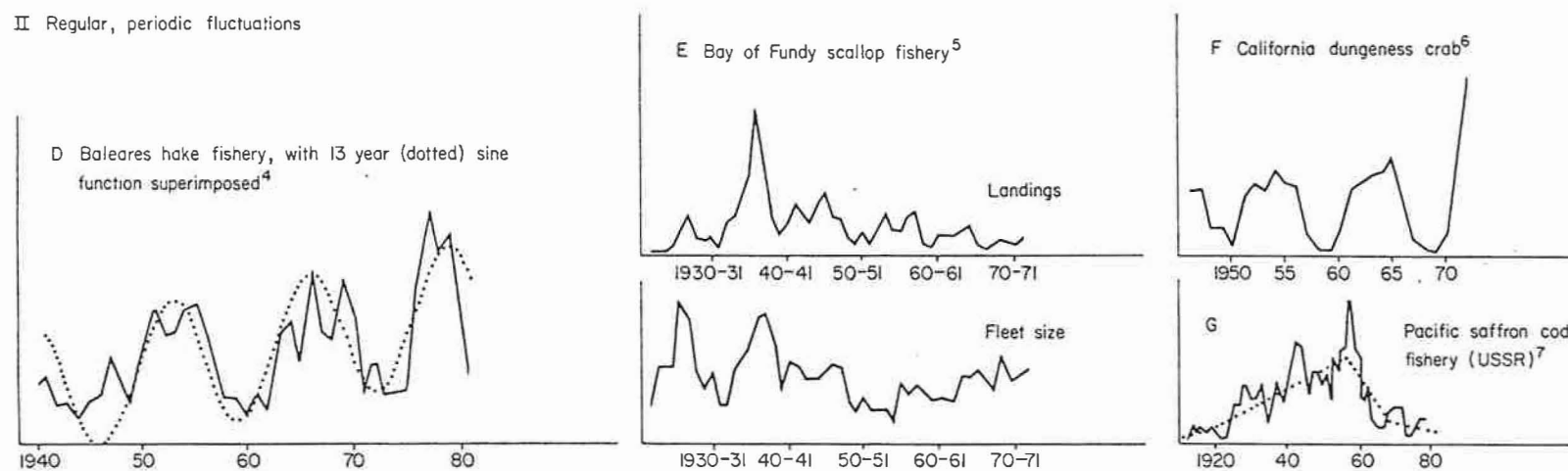


Figure 3 (cont'd).

The search for a simple stock and recruitment relationship for a fish stock is, for most stocks, a hopeless task.^{3/} As Laurence (1981) stated: "The traditional stock-recruitment principle has not been validated and is likely incorrect for most situations." Shepherd and Cushing (1979) extended the traditional stock and recruitment concept in suggesting that a family of stock and recruitment curves was required for each stock, rather than a single curve. Taylor et. al. (in prep.) found recruitment estimates of lake whitefish in northeastern Lake Michigan to be best explained as a synergism between stock size, onset of ice formation, and spring temperatures. They propose different stock and recruitment relationships for years of cold and for years of mild winters. Data requirements for testing this and similarly involuted approaches will often prove prohibitive.

The more recent fisheries literature has emphasized variability in recruitment at different stock levels. Shepherd and Cushing (1979) found that the "most striking feature of recruitment data in fish populations is its variability". Garrod (1983) found no significant indication of a change in recruitment variability over 1 1/2 to 2 orders of magnitude stock size changes in herring, cod, plaice, mackerel, sole, or sardine. However, since he was using logarithmically transformed data he was testing against the null hypothesis that variability was proportional to stock size.

An approach based directly on the historical probabilities of different recruitment levels at different stock sizes that does not require measures of central tendency or a fitted curve is described by Getz and Swartzman (1981). This approach derives a stock-recruitment transition matrix (T), where each

^{3/} The fit of the Shepherd stock-recruit curve to data from twelve fish stocks is discussed in the Appendix.

element ($t_{i,j}$) of the matrix denotes the probability that stock biomass level j will give rise to recruits (at the time of recruitment to the fishery) at recruit level i . Three examples of this matrix taken from Getz and Swartzman are provided in Table 2. Overholtz et. al. (1986) used the same method to forecast the probability of recovery of the Georges Bank haddock stock under different levels of fishing "since it is not subject to problems such as inappropriate model choice, or poor fits to the data". This is overstating the case somewhat as arbitrary decisions must still be made concerning where to make the divisions into the different stock levels and recruit levels; Overholtz et. al. divided the data into three stock levels and four recruit levels (Fig. 4) whereas Getz and Swartzman in this cursory examination of the same haddock stock divided the data into eight stock levels and seven recruit levels (Table 2). Additionally Overholtz et. al. choose to omit the largest recorded recruitment which was more than twice the number of the next largest recruitment recorded. Despite these shortcomings this approach relaxes the assumptions of the more traditional stock-recruit curves and retains the essential variability of the data. Variability can, of course, be retained when applying a stock-recruit curve (e.g., Walters 1985) but this seems to be only rarely included in single-species modelling.

Both the stock and recruit curves and the probability transition matrix neglect temporal information contained in the stock and recruitment time series. Hennemuth et. al. (1980) show that information contained in these time series indicates serial correlations in a few stocks. Rothschild and Mullen (1985) constructed a schematic of the temporal connections in stock and recruitment

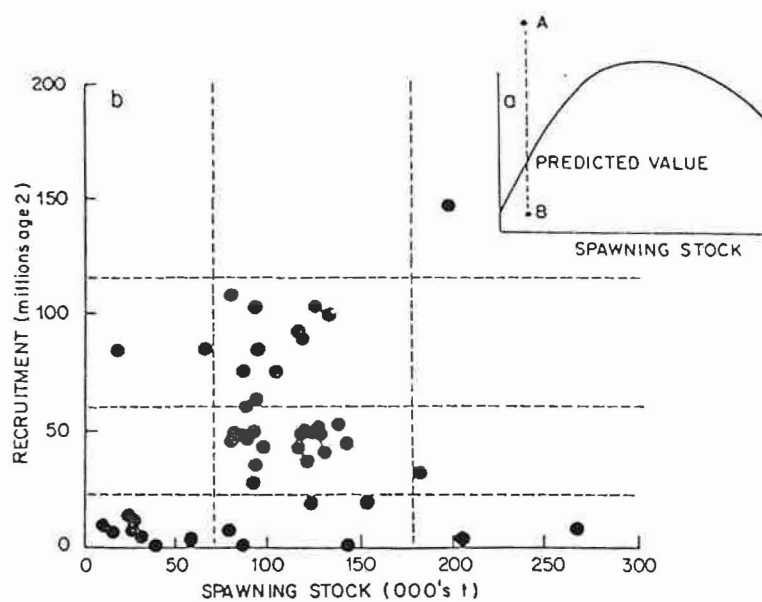
Stock-recruitment probability transition matrices. The transition matrix elements t_{ij} represent the probability that a stock biomass in subdivision j ($j \leq m_j$) will result in the number of recruits being in subdivision i ($i < m_i$). Note that each column of elements represents a probability distribution of recruitment frequencies corresponding to the indicated stock level (j).

Anchovy										
Recruitment levels (<i>i</i>)	High	7(= <i>m</i>)	0.00	0.05	0.05	0.05	0.05	0.05	0.05	0.05
		6	0.00	0.05	0.10	0.10	0.15	0.20	0.25	0.25
		5	0.05	0.10	0.15	0.25	0.30	0.35	0.35	0.35
		4	0.15	0.20	0.35	0.30	0.25	0.20	0.20	0.20
		3	0.15	0.40	0.25	0.25	0.20	0.15	0.10	0.10
		2	0.45	0.15	0.10	0.05	0.05	0.05	0.05	0.05
	Low	1	0.20	0.05	0.00	0.00	0.00	0.00	0.00	0.00
<i>i</i> \ <i>j</i>		1	2	3	4	5	6	7	8 (= <i>m_j</i>)	
Low ← Stock levels (= <i>j</i>) → High										

Flounder										
Recruitment levels (<i>i</i>)	High	6(= <i>m</i>)	0.00	0.00	0.10	0.05	0.20	0.00	0.00	0.00
		5	0.00	0.00	0.05	0.26	0.20	0.10	0.05	0.00
		4	0.00	0.00	0.05	0.25	0.20	0.10	0.15	0.00
		3	0.00	0.15	0.15	0.15	0.20	0.15	0.40	0.20
		2	0.50	0.40	0.30	0.15	0.20	0.40	0.20	0.40
	Low	1	0.50	0.45	0.35	0.15	0.00	0.25	0.20	0.40
<i>i</i> \ <i>j</i>		1	2	3	4	5	6	7	8 (= <i>m_j</i>)	
Low ← Stock levels (<i>j</i>) → High										

Haddock										
Recruitment levels (<i>i</i>)	High	7(= <i>m</i>)	0.10	0.10	0.05	0.12	0.00	0.00		
		6	0.10	0.10	0.05	0.12	0.00	0.00		
		5	0.10	0.05	0.25	0.12	0.10	0.00		
		4	0.10	0.10	0.05	0.12	0.20	0.00		
		3	0.10	0.25	0.50	0.12	0.30	0.30		
		2	0.20	0.25	0.05	0.40	0.30	0.30		
	Low	1	0.30	0.15	0.05	0.12	0.10	0.40		
<i>i</i> \ <i>j</i>		1	2	3	4	5	6 (= <i>m_j</i>)			
Low ← Stock levels (<i>j</i>) → High										

Table 2.--Table 2 of Getz and Swartzman (1981).



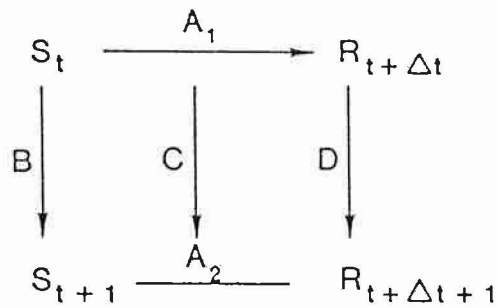
(a) Hypothetical stock-recruitment curve with predicted value and possible observed values for a particular stock size. (b) Spawning stock biomass (age 3 and older) and subsequent recruitment (age 2) for Georges Bank haddock, 1931-79. The 1963 point (194 700 t and 368.8 million recruits) has been omitted.

Figure 4.--Fig. 2 of Overholtz et. al. (1986).

data (Fig. 5). They concluded that traditionally only relationships A_1 and A_2 , the stock-recruit relationships, are considered and typically A_1 and A_2 are assumed equal; that is, the relationship C, which describes any changes in the stock-recruit relationship over time, is considered to be an identity. Hennemuth et. al. (1980) considered relationship D, temporal trends in recruitment alone. Time series analyses of stock size are also conducted, relationship B. Skud (in prep.) studies relationship C by analyzing whether the level of recruits R_t can affect the stock-recruit relationship A_2 at time $t + 1$.

Rothschild and Mullen (1985) examined stock and recruit data from 5 stocks, dividing both stock and recruitment into two levels, high and low, where the division was made on the median of the respective data (Fig. 6). This is similar to the probability transition matrix method (note, however, a third classification scheme for the Georges Bank haddock). However, instead of just tabulating the historical probability of occurrence of high or low recruitment given a particular stock level (Table 3), they computed the number of transitions from one state to another (Table 4a) and from these the probability of transitions between the different states (Table 4b). Further analyses of these data, under the assumption that transitions are Markovian (primarily that the transition probabilities are constant and depend only on the previous state) enabled the authors to estimate the expected time of passage from one state to another (Table 5). The authors concluded:

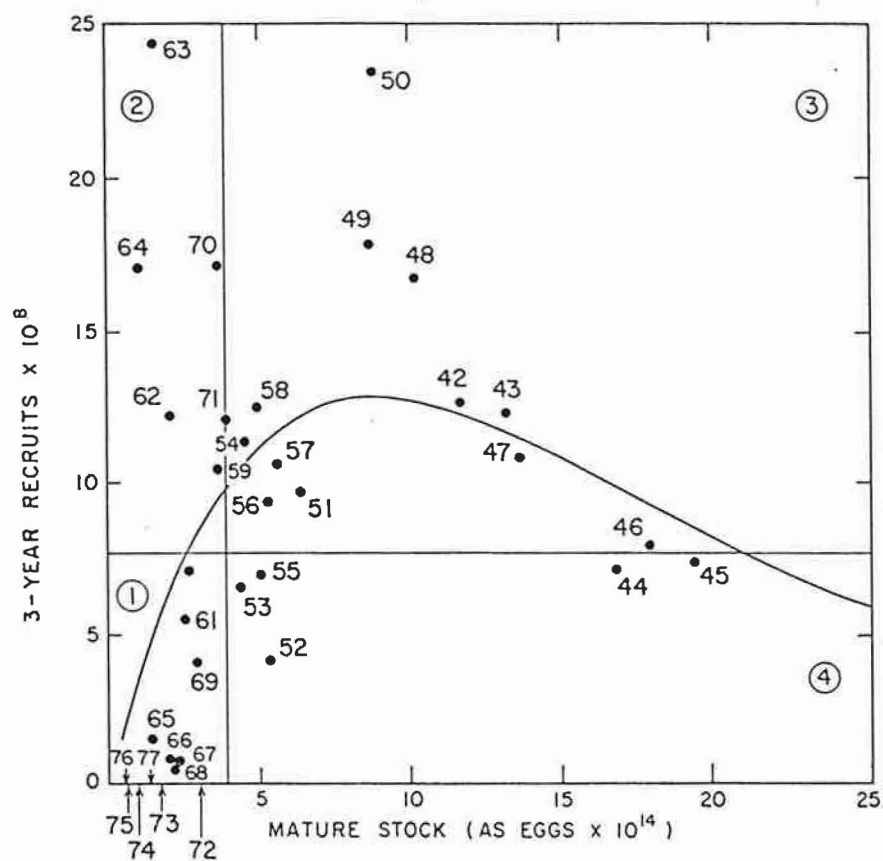
"...relating recruitment to a stock is neither a problem of classical regression analysis, nor a univariate time-series analysis. Stock and recruitment are two time series which may not be independent of each other. Instead of simply attempting to predict recruitment from stock, the relationship between both the stock and recruitment time series needs to be considered. This, of course, increases the demand for information, or to put it differently, reduces what can be said on the basis of, at best, a very limited series of data."



Relation between stock (S) and recruitment (R), where (t) refers to a particular year and (Δt) refers to the time elapsed between spawning and recruitment. The letters A, B, C, and D refer to relationships among the various entities in the diagram. See text for further description.

Figure 5.--Fig. 1 of Rothschild and Mullen (1985) ,

where A_1 is the stock-recruit relationship at time t, A_2 the stock-recruit relationship at time t + 1, and C describes the relationship between the two. B represents the temporal trend in stock and D the temporal trend in recruitment.



Recruitment versus stock size for Arcto-Norwegian cod (after Cushing (1981): Fig. 74g). Median lines are drawn for recruitment and stock.

Figure 6, Fig. 2 of Rothschild and Mullen (1985).

Observed stock-recruitment points classified by the four states identified in the text.

Stock	S_1	S_2	S_3	S_4	Total no. of points
	low stock/ low recruitment	low stock/ high recruitment	high stock/ high recruitment	high stock/ low recruitment	
a. North Sea haddock	11	9	11	9	40
b. Georges Bank haddock.....	9	9	8	9	35
c. Arcto-Norwegian cod	13	5	13	5	36
d. Pacific halibut	6	10	6	10	32
(southern grounds)					
e. Pacific halibut	7	7	6	7	27
(western grounds)					

Table 3.--Table 1 of Rothschild and Mullen (1985).

Number of transitions among states for each species. Also included for each species is the total number of transitions per cell if the number of transitions was distributed uniformly among the cells, the calculated value of chi-square, and an indication of significance at the 5 % level with 15 degrees of freedom.

a. North Sea haddock

State	1	2	3	4
1	4	2	2	2
2	2	5	2	0
3	4	1	3	3
4	0	1	4	3

Transitions, 38. Expected for each cell, 2.4. $\chi^2 = 13.4$. Degrees of freedom, 15, not significant.

b. Georges Bank haddock

State	1	2	3	4
1	3	2	2	1
2	1	3	2	2
3	2	3	1	1
4	3	0	3	3

Transitions, 32. Expected for each cell, 2.0. $\chi^2 = 6.5$. Degrees of freedom, 15, not significant.

c. Arcto-Norwegian cod

State	1	2	3	4
1	10	2	0	0
2	2	2	1	0
3	1	1	8	3
4	0	0	3	2

Transitions, 35. Expected for each cell, 2.2. $\chi^2 = 56.9$. Degrees of freedom, 15, significant.

d. Pacific halibut
(southern grounds, Area 2)

State	1	2	3	4
1	2	4	0	0
2	3	5	2	1
3	2	2	6	0
4	0	1	1	8

Transitions, 37. Expected for each cell, 2.3. $\chi^2 = 36.1$. Degrees of freedom, 15, significant.

e. Pacific halibut
(western grounds, Area 3)

State	1	2	3	4
1	3	3	1	0
2	3	4	0	0
3	0	0	3	5
4	1	0	4	1

Transitions, 28. Expected for each cell, 1.8. $\chi^2 = 26.9$. Degrees of freedom, 15, significant.

Table 4a.--Table 2 of Rothschild and Mullen (1985).

Transition probabilities among states. Elements in the probability matrices refer to the probability of transition between the i-th row and the j-th column. For example, the estimated probability of transition between State 3 and State 2 for North Sea haddock is equal to 0.09.

a. North Sea haddock

State	1	2	3	4
1	0.40	0.20	0.20	0.20
2	0.22	0.56	0.22	0.0
3	0.36	0.09	0.27	0.27
4	0.0	0.12	0.50	0.37

b. Georges Bank haddock

State	1	2	3	4
1	0.37	0.25	0.25	0.12
2	0.12	0.37	0.25	0.25
3	0.29	0.43	0.14	0.14
4	0.33	0.0	0.33	0.33

c. Arcto-Norwegian cod

State	1	2	3	4
1	0.83	0.17	0.0	0.0
2	0.40	0.40	0.20	0.0
3	0.08	0.08	0.62	0.23
4	0.0	0.0	0.60	0.40

d. Pacific halibut
(southern grounds, Area 2)

State	1	2	3	4
1	0.33	0.67	0.0	0.0
2	0.27	0.45	0.18	0.09
3	0.20	0.20	0.60	0.0
4	0.0	0.10	0.10	0.80

e. Pacific halibut
(western grounds, Area 3)

State	1	2	3	4
1	0.43	0.43	0.14	0.0
2	0.43	0.57	0.0	0.0
3	0.0	0.0	0.37	0.62
4	0.17	0.0	0.67	0.17

Table 4b.--Table 3 of Rothschild and Mullen (1985).

Expected first-passage times for the number of years on average that a stock-and-recruitment system in a particular state will take to return to a particular state. (For example, it would take 7.7 years for North Sea haddock in State 3 to "return" to State 2.)

a. North Sea haddock				
State	1	2	3	4
1	3.8	6.8	3.9	6.2
2	4.3	4.2	4.2	8.1
3	4.0	7.7	3.5	5.5
4	5.7	7.8	2.4	4.8
b. Georges Bank haddock				
State	1	2	3	4
1	3.6	4.0	3.8	5.9
2	4.6	3.6	3.7	5.0
3	4.1	3.4	4.1	5.6
4	3.5	5.2	3.4	4.8
c. Arcto-Norwegian cod				
State	1	2	3	4
1	1.9	6.0	23.0	40.7
2	5.6	5.8	17.0	34.7
3	11.8	12.0	4.5	17.7
4	13.5	13.7	1.7	11.6
d. Pacific halibut (southern grounds, Area 2)				
State	1	2	3	4
1	4.5	1.5	9.7	5.2
2	5.2	2.6	8.2	7.3
3	5.1	3.3	4.6	8.7
4	10.1	6.6	9.1	10.1
e. Pacific halibut (western grounds, Area 3)				
State	1	2	3	4
1	4.0	7.0	14.0	16.7
2	2.3	4.0	16.3	19.0
3	14.0	21.0	3.5	2.7
4	12.4	19.4	4.0	4.7

Table 5.--Table 5 of Rothschild and Mullen (1985).

Rothschild and Mullen were unable to achieve high precision with their methods, because they did not consider a finer division than high or low recruitment from high or low stock to be practical, but as they note, "... precision when accompanied by very high variance is illusory". In instances where the data have less associated error parametric methods might be more appropriate.

ERRORS IN STOCK AND RECRUITMENT DATA

Variability in stock and recruitment data is high, yet this variability is often overlooked in the description of the "underlying" stock-recruit relationship. If errors in the estimates of stock size and recruit numbers were considered then there would be little information in many stock-recruit scatterplots, except for the requirement that a fitted line pass through the origin.

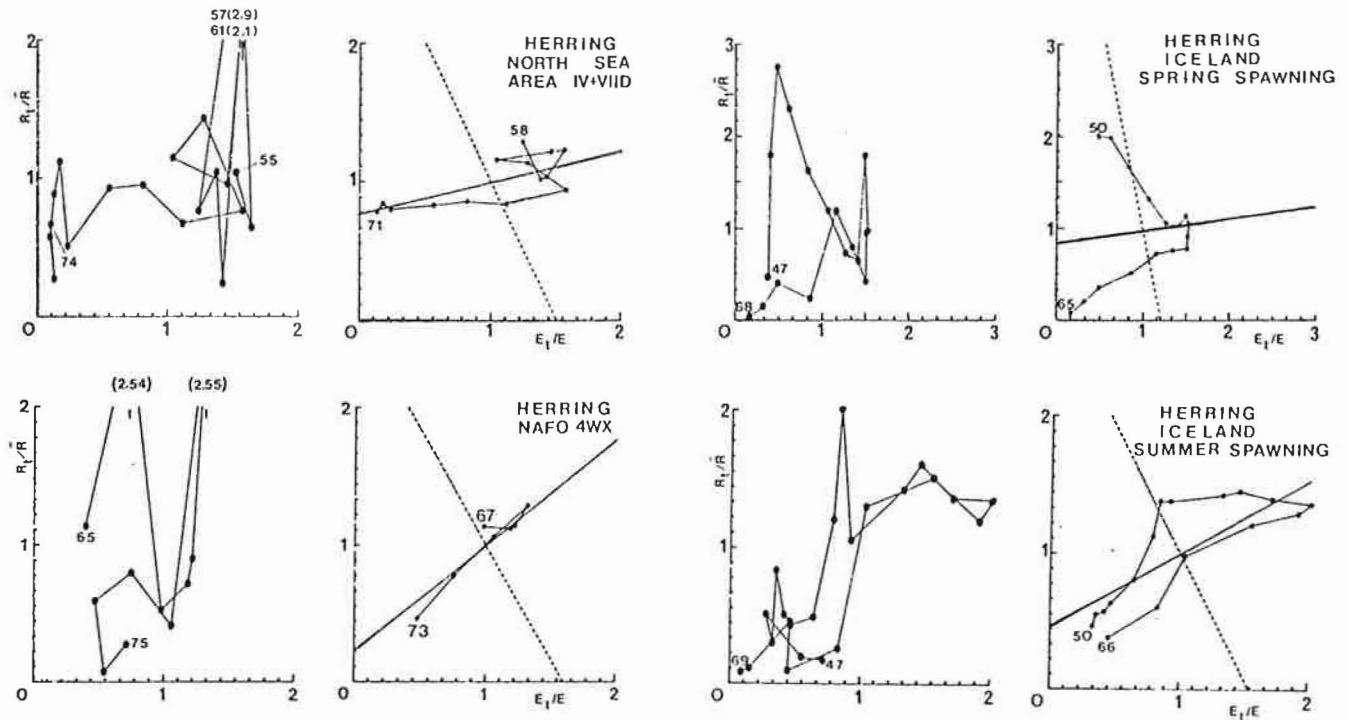
Welch (1986) assumed recruitment variability to consist of two components, a stochastic environmental noise and a density dependent prerecruit survival. He noted that "if the influence of stochastic noise in recruitment is large, there is a systematic tendency to overestimate the degree of density dependence in populations whose stock-recruitment relationship is only weakly density dependent (Goodyear and Christensen 1984)". Welch applied time invariant linear filters to reduce the total standard error of recruitment to 1/2 or 1/3 that of the unfiltered data, based on the observation that variability in individual year class strengths tends to cancel out when several years are averaged. Welch's assumption that density dependent survival is solely a function of the 0 group strength and that no other density dependent effects (cannibalism or juvenile buffering against predation, Skud (in prep.)) impact recruitment, is not valid for many stocks. However, his method does reduce irregular variability

(Fig. 7). The approach is similar to the smoothing techniques used by Walters (in prep., c.f. Fig. 2), and produces similar long term trends.

Unexplained variability in recruitment or around a stock-recruit relationship is often assumed to be caused by environmental variability. Multiple regression techniques are then applied to find a variable which matches some of the unexplained variability. Walters and Ludwig (1981) emphasize the importance of accounting for measurement error. Using a simple simulation model (linear stock-recruit relationship with environmental noise) these authors demonstrate that when spawning stocks are estimated with a coefficient of variation of 50% (lognormal error - 95% of values fall within 0.37 to 2.66 of the mean) recruitment appears to be independent of spawning stock (Fig. 8)^{4/}. As Walters and Ludwig conclude, "...it is obvious that the fishery manager should not trust models based on the assumption that recruitment is independent of spawning stocks, at least until he can clearly demonstrate that spawning stocks have been measured "accurately" (i.e. error less than $\pm 30\%$ or so). Such demonstrations are rare in the fisheries literature".

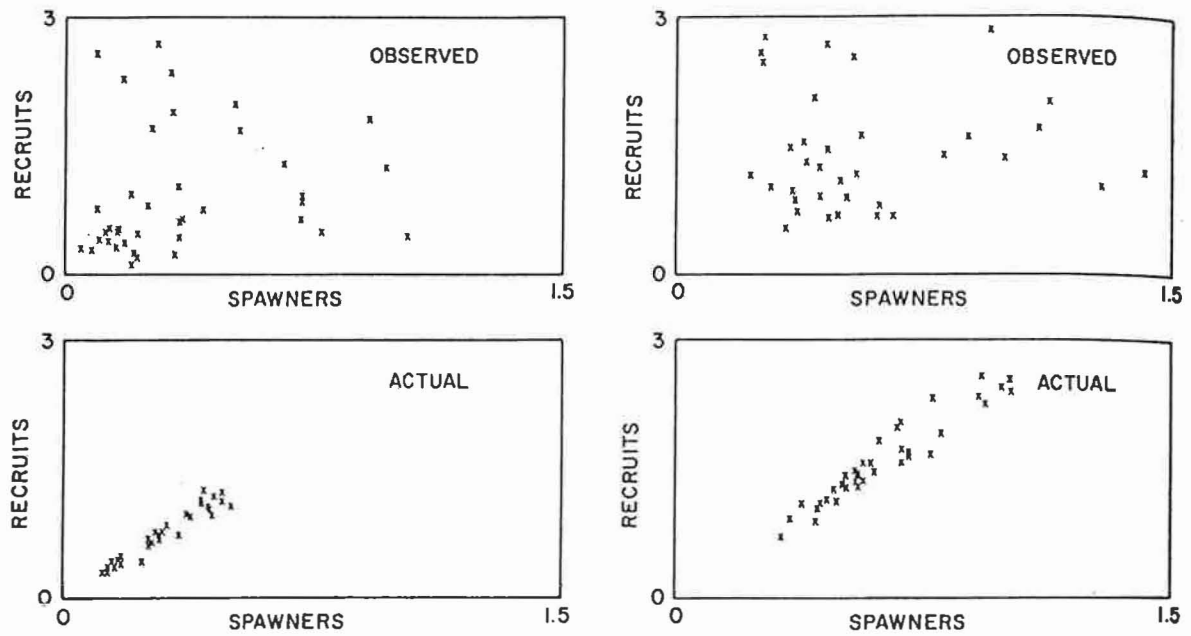
A second effect of measurement error on stock-recruit relationships is the occurrence of patterns in the data which are unrelated to the underlying relationship. Thus in Walters and Ludwig's (1981) model when the coefficient of variation in measurement of spawning stock size was greater than 32% there was a tendency for an inverse relationship between spawning stock size and recruitment. Eberhardt (1970) found that on average plots of R_{t+1} vs R_t , where R_t is a time series of completely independent observations, show a correlation coefficient of -0.707. An extreme example of such spurious relationships is that

^{4/} Measurement errors in the estimation of recruit numbers were not included in this model.



Stock-recruitment analyses for herring populations. The left- and right-hand panels show, in this and subsequent figures, the relationship between stock and recruitment before (left) and after (right) filtering the recruitment data. Straight lines indicating the proportional recruitment response are indicated by a solid line. A broken line indicates the threshold value for the critical stock-recruitment slope R'_m . Permanent limit cycles in population size will occur for stock-recruitment slopes steeper than R'_m , while at less negative slopes long-wavelength cycles in population size will occur that are driven by the environmental noise.

Figure 7, --Figure 12 of Welch (1986).



"Actual" and observed stock-recruit relationships for two simulated populations that are severely overexploited. The actual data were generated with recruitment proportional to spawning stock; the observed data were generated by applying observation errors to the actual data.

Figure 8.--Fig. 1 of Walters and Ludwig (1981).

plots of two independent series of random number can be as convincingly fitted with a Ricker stock-recruit curve as many published data series from the fisheries literature (Fig. 9). Correlation coefficients were close to zero for these fits to random numbers but this has not prevented publication of stock-recruit curves (Appendix 1).

APPLICATION OF STOCK-RECRUITMENT RELATIONSHIPS TO MODELLING

Larkin in his 1977 paper opines that the only thing as bad as a biologist who doesn't realize the limitation of his data is a modeller-mathematician who doesn't have data. If as biologists we accept the limitations of most stock-recruit relationships, we cannot as modellers realistically construct models dependent on these relationships. Unfortunately examples abound in forecasting, management, and fisheries economics models where these relationships are used.

The first requirement in the analysis of stock-recruit data must be to account for variability due to measurement error around the hypothesized relationship. Averaging and filtering techniques may be of use here when a long time series of data is available, and when long term trends are the data of interest. However, Skud (1981) and Walters (in prep.) caution against emphasizing long term trends, questioning whether they will be replicated in the future. Averaging techniques will also tend to pool measurement error with density independent changes in recruitment (i.e. environmental variability; species interactions).

Variability around any stock-recruit relationship should be included in the modelling process if variability due to measurement error has been accounted for. For example, in Laevastu and Larkins' (1981) multispecies simulation such variability is partly accounted for by the predator-prey

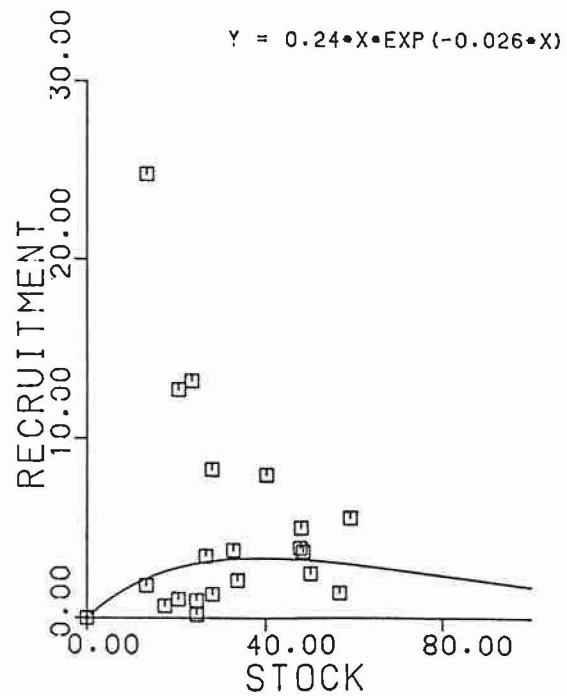
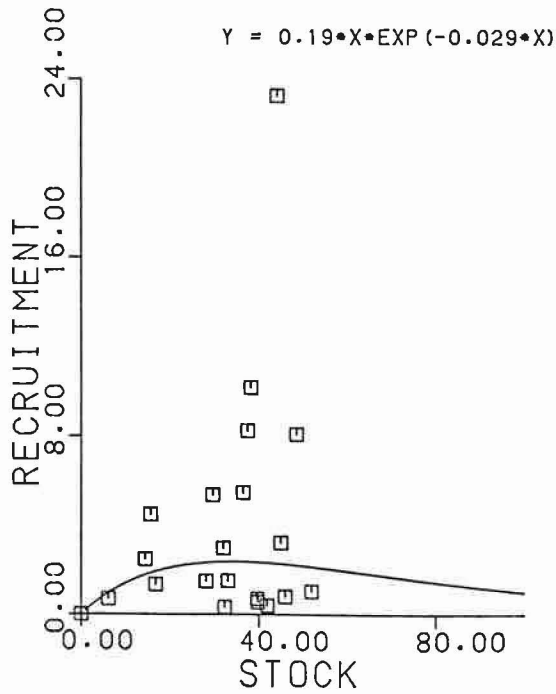
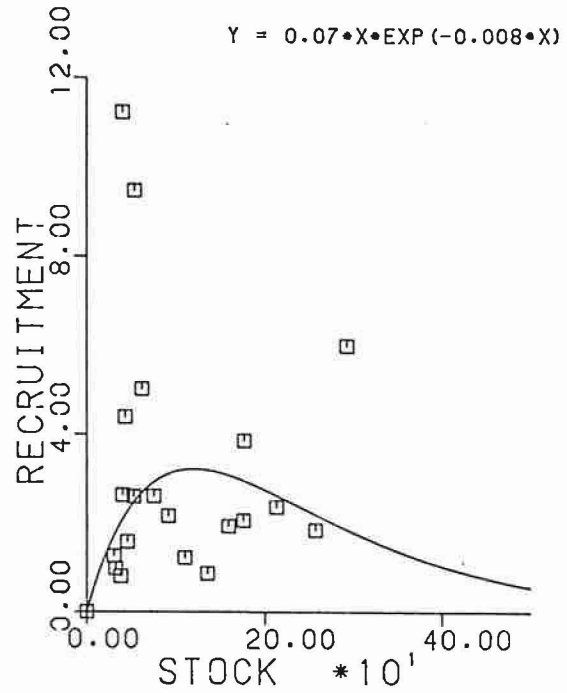
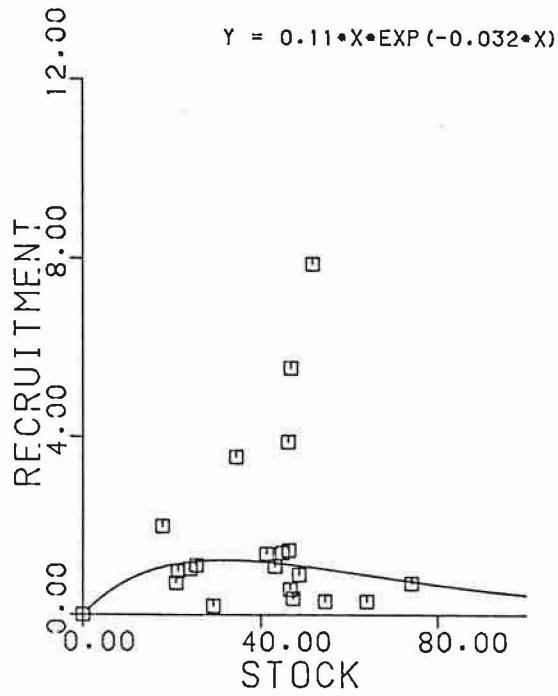


Figure 9.--Ricker stock-recruitment curves fitted to independent time series of random numbers. Moving average of 5 applied to "stock" time series.

interactions. However, the simulations may omit variability induced in the first six months of the fishes life because life processes are so dynamic (extremely high growth and mortality) in these first months that simulation is problematical. One method to crudely simulate variability in these first months is to introduce some form of random error. This may successfully model the general form of biomass dynamics but cannot predict actual events, for example, the time and size of the, often rare, good year classes which exert a long term influence in many fisheries. In fisheries dominated by the occurrence of these occasional super abundant year classes, research is needed to determine the factors related to their development - timing, environmental conditions, predator concentrations, food availability, and egg production potential. This is likely to be more rewarding than forcing a stock-recruit curve to data sets plagued with large, but unknown, errors, with (sometimes) the exclusion of those very "outliers" which have contributed most to the historic productivity of the fishery.

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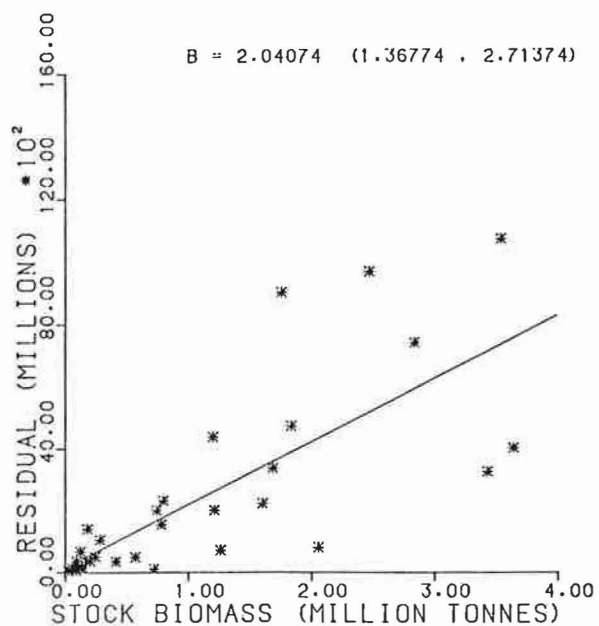
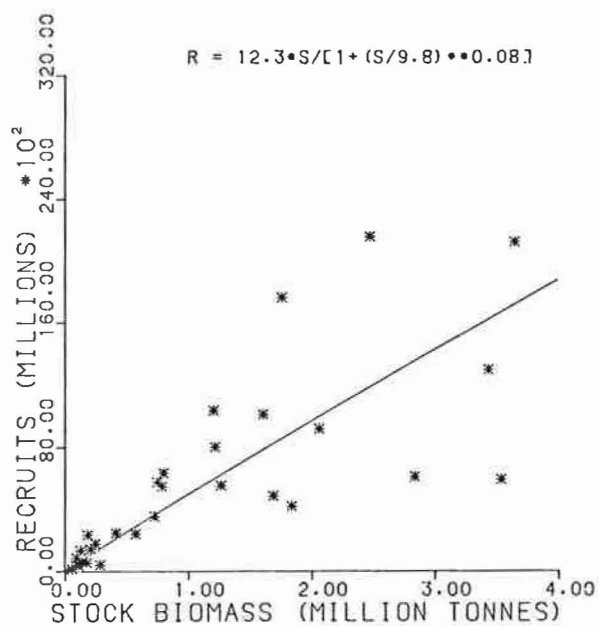
APPENDIX

Garrod (1982) provides data on adult biomass and recruitment numbers for 12 fish stocks. These time series range in length from 10 to 48 years. Garrod also provides least square fits of the 3 parameter Shepherd stock-recruit curve to these data. Appendix Fig. 1 reproduces the data provided by Garrod (1982) and derived plots of residuals. Correlation coefficients of the fits of the Shepherd curve were computed using the means adjusted correlation coefficient (R_1^2) of Kvalseth (1983), together with serial correlation coefficients of the recruitment data with a one-year time lag (Appendix Table 1). Significance tests are not appropriate for these statistics because of non-independence of the variables. Only two of the twelve stocks consistently had positive correlation coefficients. One of these, the St. Lawrence mackerel, had a stock-recruit relationship which departs from the customary conception of a stock-recruit relationship (Appendix Fig. 1).

Appendix Table 1.--Correlations between a) recruitment and estimated recruitment from a 3 parameter Shepherd stock and recruit curve, and b) serial correlation in recruitment indices with a one year time lag. Data from Garrod (1982).

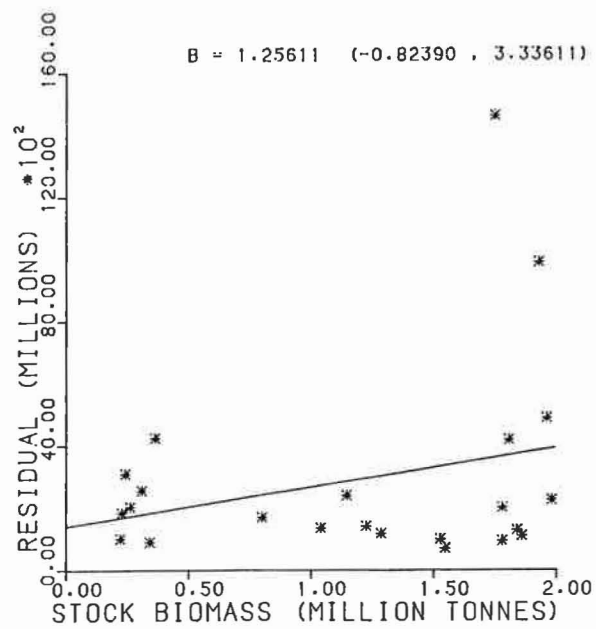
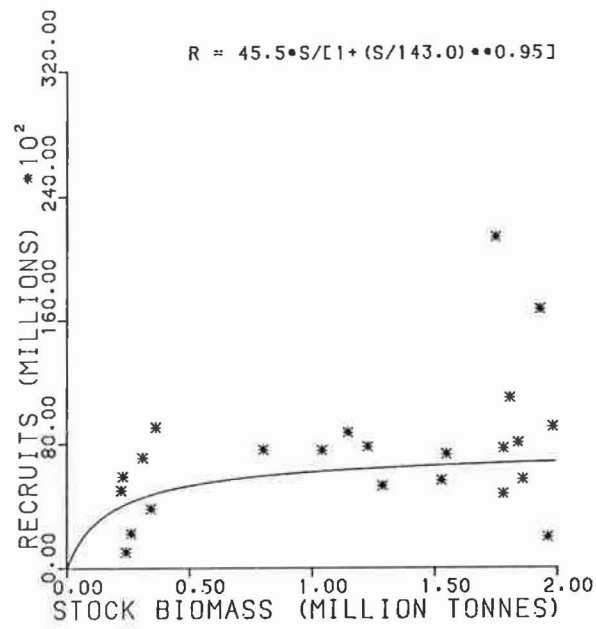
Stock	Time period	Years of data	Raw Data		Logarithms	
			Stock and recruit curve	Serial correlation	Stock and recruit curve	Serial correlation
California sardine	1932-62	31	0.57	0.37	0.85	0.69
Norwegian spring herring	1950-69	20	-0.12	-1.71	0.17	-0.33
North Sea herring	1952-74	23	0.03	-1.33	0.19	-0.95
St. Lawrence mackerel	1966-75	10	0.31	-0.87	0.40	-0.60
North Sea haddock	1920-67	48	-0.17	-1.32	-0.08	-0.85
Georges Bank haddock	1936-63	28	-0.07	-0.14	0.00	-0.68
NE Arctic haddock	1950-76	27	-0.13	-1.11	0.49	-0.71
Arcto-Norwegian cod	1950-75	26	-0.09	-0.50	-0.06	-0.06
Greenland cod	1958-77	20	-0.10	0.05	0.26	0.23
St. Lawrence cod	1950-74	25	0.13	-0.02	0.10	-0.22
North Sea plaice	1947-76	30	-0.06	-0.86	-0.02	-0.62
North Sea sole	1957-76	20	-0.08	-1.18	0.01	-1.22

CALIFORNIA SARDINE



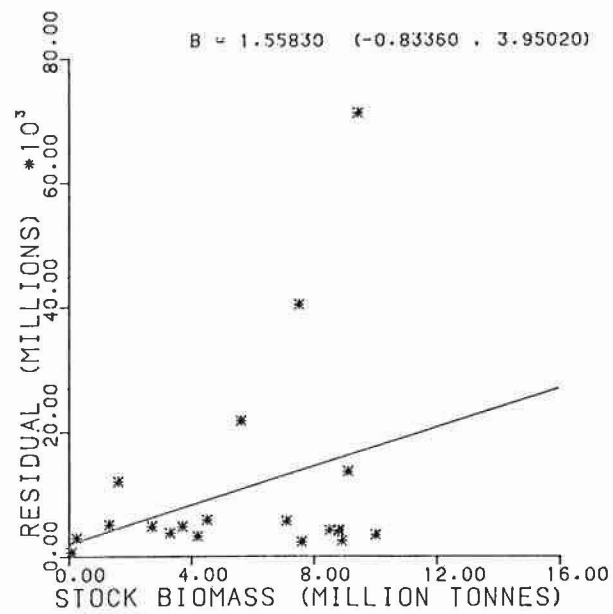
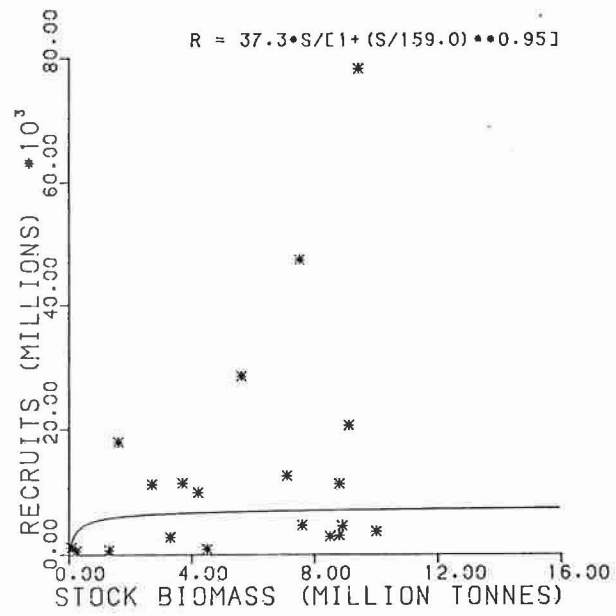
Appendix Figure 1.--Stock and recruitment data with fitted Shepherd curve as derived by Garrod (1982). Residuals from this fit are plotted in the lower graph.

NORTH SEA HERRING



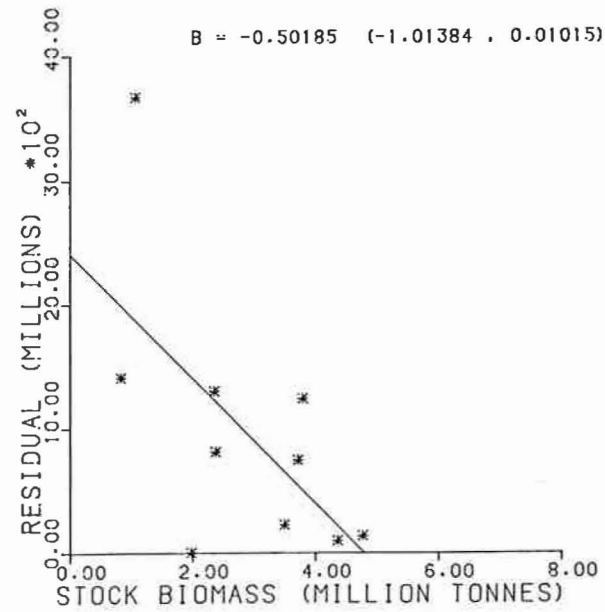
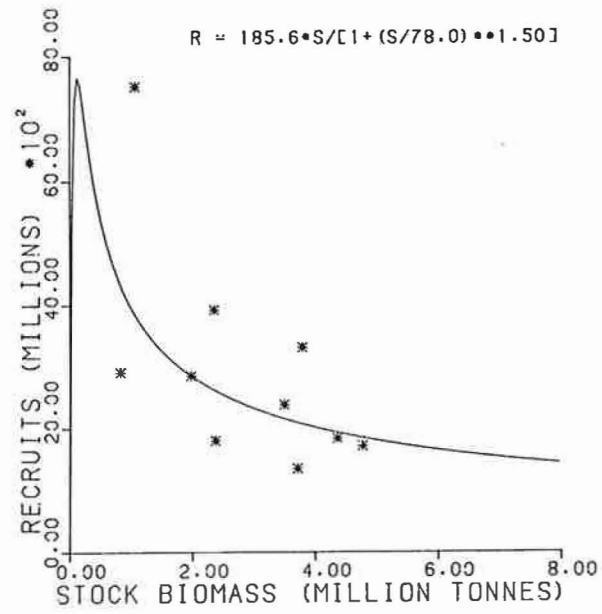
Appendix Fig. 1 (cont'd).

NORWEGIAN HERRING



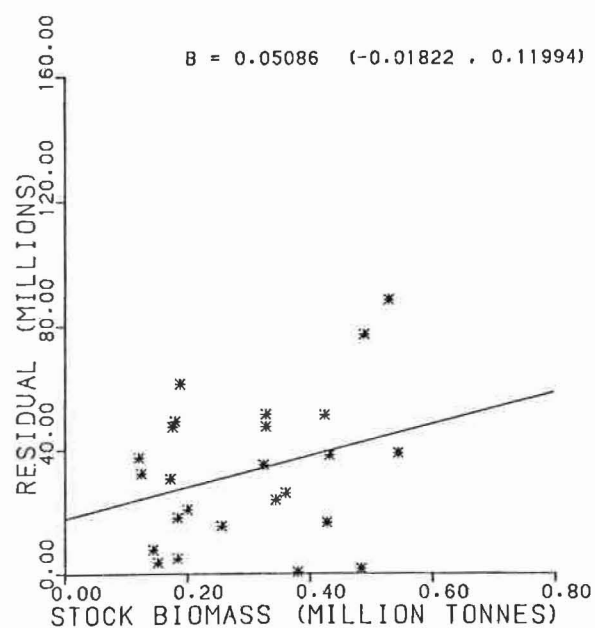
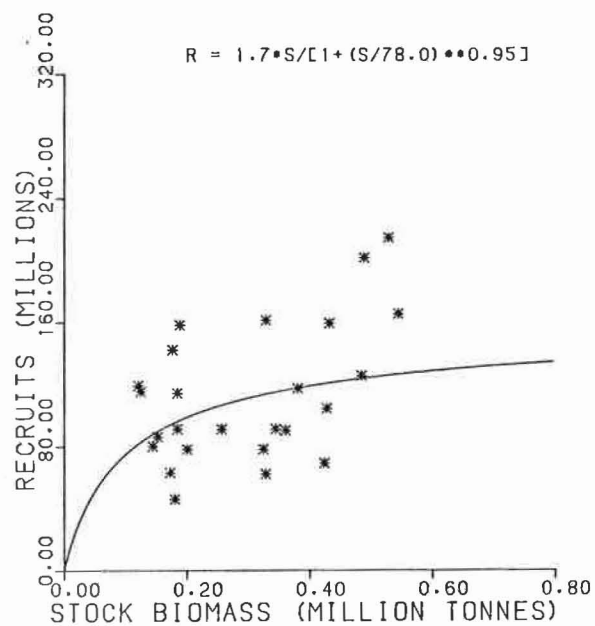
Appendix Fig. 1 (cont'd.)

ST. LAWRENCE MACKEREL



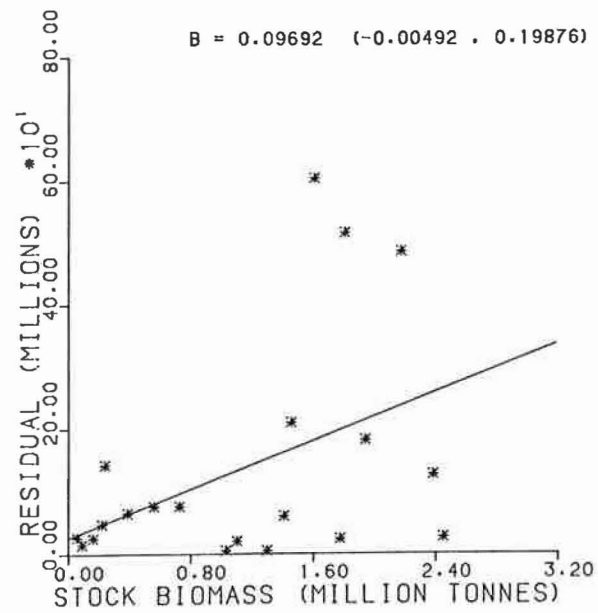
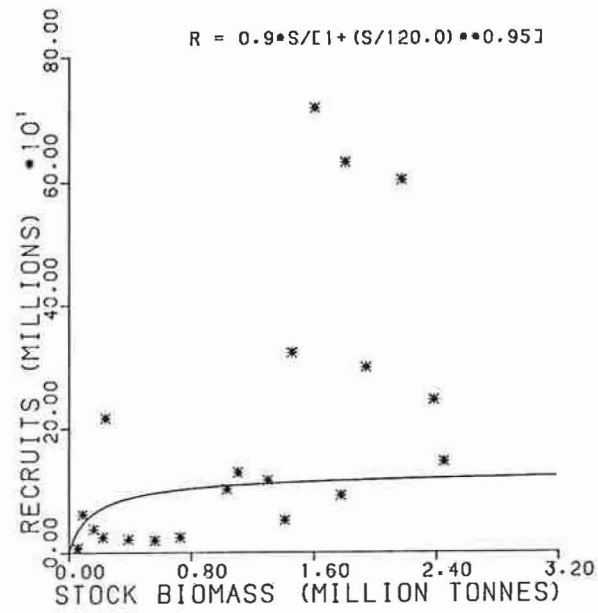
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ST. LAWRENCE COD



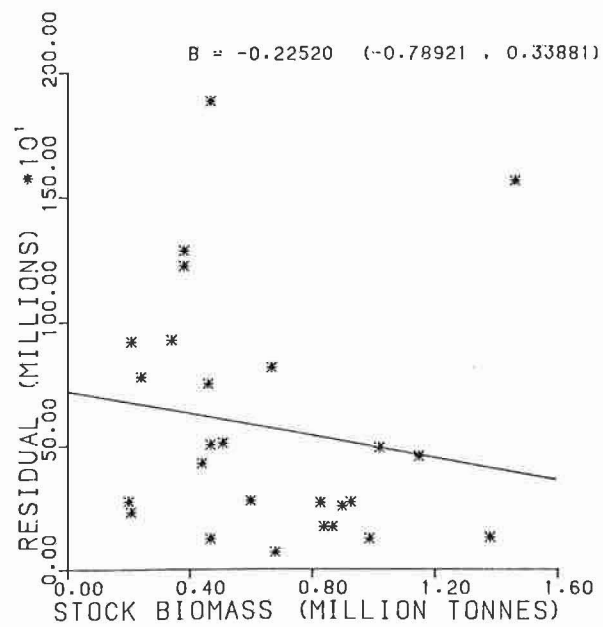
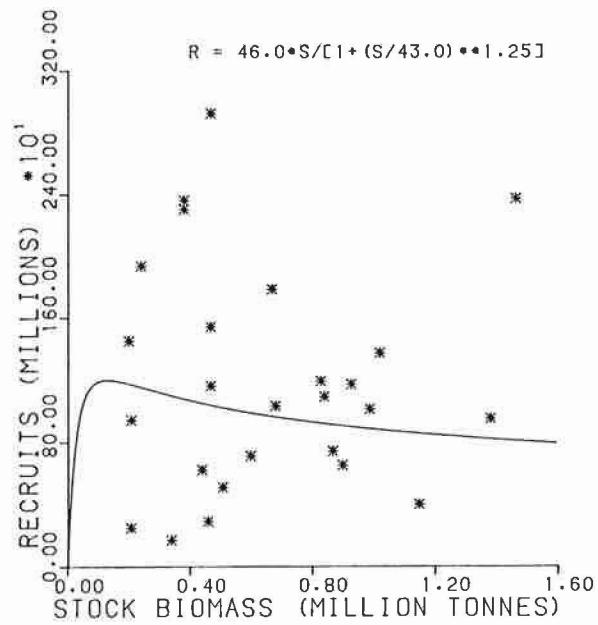
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GREENLAND COD



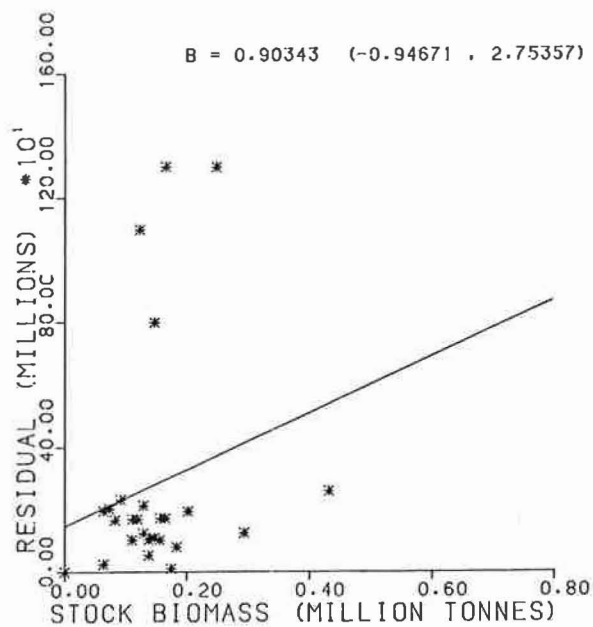
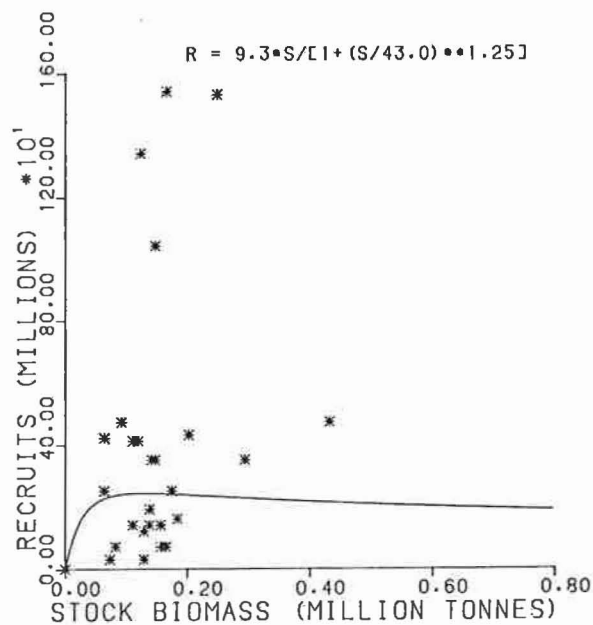
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NORWEGIAN COD



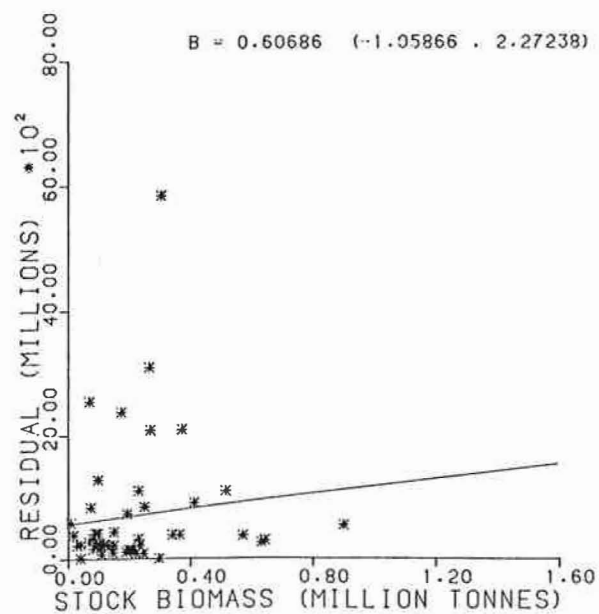
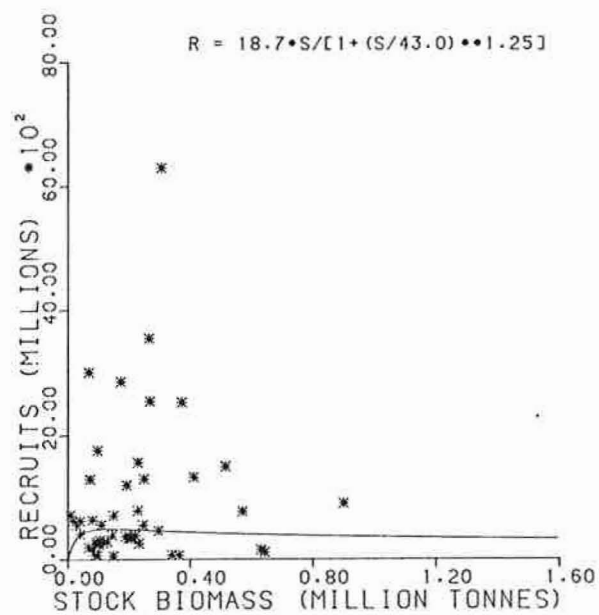
Appendix Fig. 1 (cont'd.)

N.E. ARCTIC HADDOCK



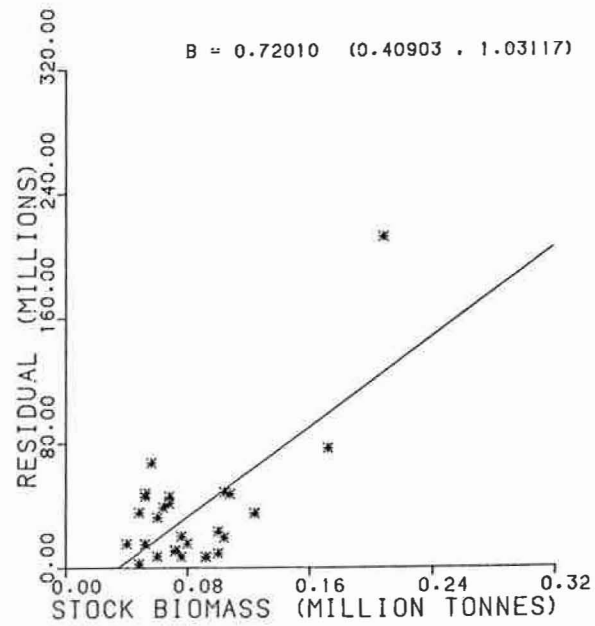
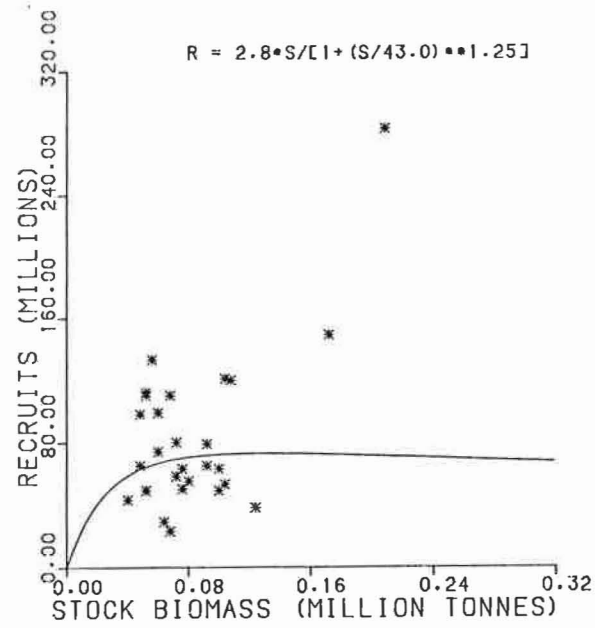
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NORTH SEA HADDOCK



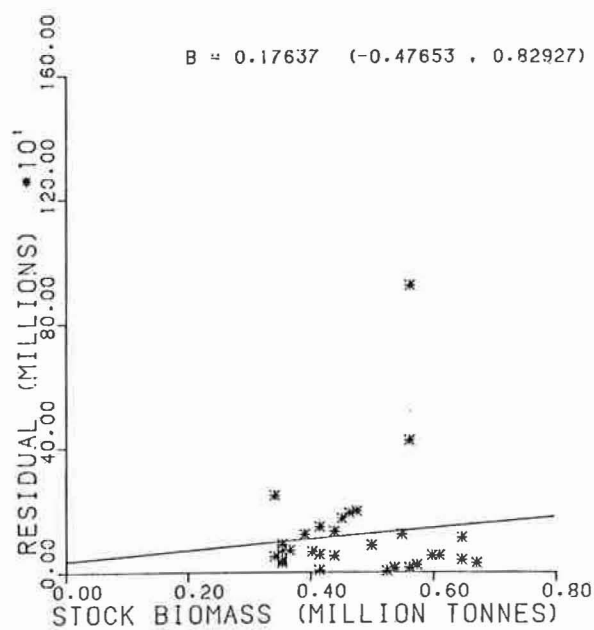
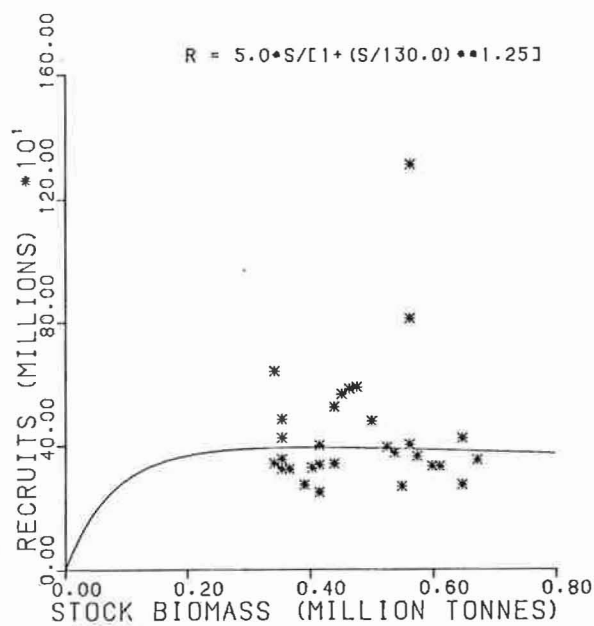
Appendix Fig. 1 (cont'd.)

GEORGES BANK HADDOCK



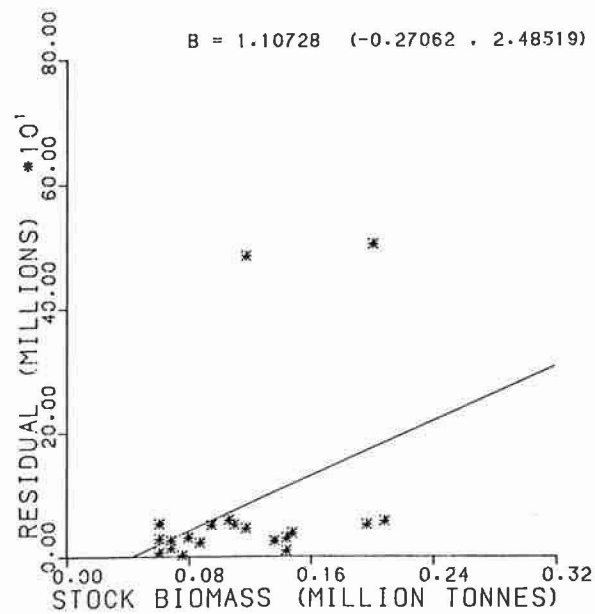
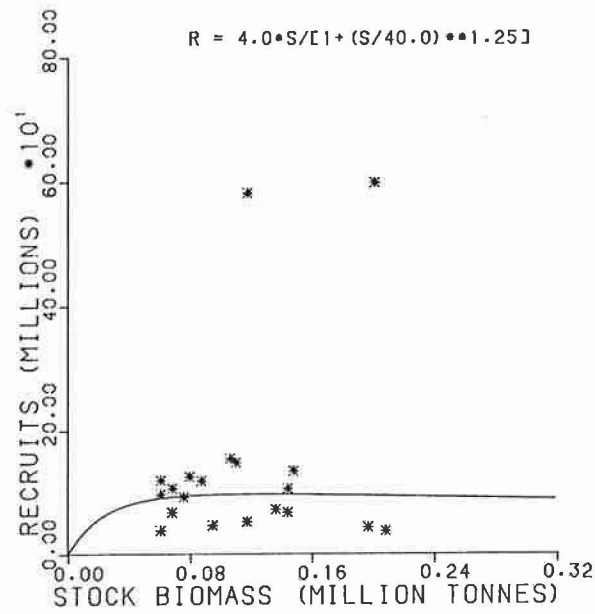
Appendix Fig. 1 (cont'd.)

NORTH SEA PLAICE



Appendix Fig. 1 (cont'd.)

NORTH SEA SOLE



Appendix Fig. 1 (cont'd.)

