

Seabird-fishery trophic interactions in eastern Pacific boundary currents: California and Peru

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1. Abstract

The nature of seabird-fishery trophic interactions is investigated by comparative and simulation studies. Peru and California have very similar fish communities, but the seabird communities are less similar. The relationship between seabirds and fisheries cannot be considered outside the context of natural patterns of forage availability. The forage base is characterized by extreme variability, serial correlation over years, geographic expansion and contraction with changes in abundance, and species replacement events. El Niño presents special reproductive and survival problems to Peruvian seabirds. Seabird impact on fish abundance may have been significant in Peru, but is probably small in California. Fisheries may reduce food availability to seabirds with subsequent decrease in reproductive success. A simulation model suggests that a variable food supply results in variable seabird abundance. Fisheries may reduce food to levels below those necessary to sustain seabird populations, but patterns of decline may easily be misinterpreted due to long trends of population increase and decrease.

2. Résumé

L'auteur examine la nature des interactions trophiques existant entre les oiseaux de mer et la pêche par des études comparatives et simulées. Le Pérou et la Californie comptent des communautés de poissons très voisines, ce qui n'est pas le cas pour celles des oiseaux de mer. Il est impossible d'étudier le rapport entre les oiseaux de mer et la pêche sans tenir compte des modes de distribution naturels et de la disponibilité de la nourriture. La source de nourriture se caractérise par une extrême variabilité, une corrélation périodique au fil des ans, une expansion et une contraction géographiques selon les fluctuations d'abondance et certains cas de remplacement d'espèces. Le courant El Niño pose des problèmes de reproduction et de survie spécialement chez les oiseaux de mer péruviens. La prédation des oiseaux de mer peut avoir eu un effet important sur l'abondance du poisson au Pérou, mais cet effet est probablement modeste en Californie. En revanche, la pêche peut réduire la disponibilité de nourriture pour les oiseaux de mer suivie d'une baisse de la réussite de la reproduction. L'application d'un modèle de simulation révèle qu'un approvisionnement de nourriture variable entraîne des fluctuations d'abondance chez les oiseaux de mer. La pêche peut réduire la disponibilité de nourriture à des niveaux inférieurs à ceux nécessaires pour soutenir les populations

d'oiseaux de mer, mais les courbes de déclin des populations peuvent être facilement mal interprétées à cause des tendances à long terme d'augmentation et de baisse des populations.

3. Introduction

Fisheries can perturb trophic relationships in an ecosystem to an extent far exceeding the scope of conventional ecological experiments. However, interpretation of fishery effects is very difficult due to lack of replication or experimental control. Two methods of confronting these problems are comparative studies and simulation modelling. Comparison of fisheries and components of ecosystems may aid our understanding of those entities to the extent that they are similar, but the consequences of their differences must also be recognized. Simulation modelling is a complementary tool of great potential, especially if supported by a sound empirical basis of natural history. The model may grossly simplify fishery and ecosystem components, but the range of possibilities within that model can be fully explored by means of perfectly replicated and controlled "experiments." These two approaches are used here to examine seabird-fishery relationships in southern California and Peru.

3.1. Eastern boundary currents

Southern California is strongly influenced by the California Current, which is one of four similar ocean currents in the world. The other three of these "eastern boundary currents" are the Peru Current, the Canary Current, and the Benguela Current off southwest Africa. These currents are similar in many respects, both physical and biological. They represent the eastern limbs of major oceanic gyres, and are characterized by a wide and moderately slow equatorward flow. Characteristically, the near-shore regions of these currents are sites of coastal upwelling, whereby wind patterns combine with the effects of the earth's rotation to cause deep, cold, nutrient-rich water to be brought to the surface as large plumes. The upwelled water often supports high primary production of phytoplankton, with subsequent secondary production of zooplankton. These in turn support an abundance of higher predators such as fish and squid, and finally larger fishes, marine mammals, and seabirds. Useful reviews of eastern boundary current characteristics are given by Bakun and Parrish (1980), and Wooster and Reid (1963). The California Current has been the most thoroughly studied example.

and is reviewed by Hickey (1979) and by Reid *et al.* (1958). Upwelling itself is the subject of a recent symposium edited by Richards (1981).

3.2. Species assemblages

Eastern boundary currents are characterized by remarkably consistent assemblages of pelagic fishes (Table 1). As pointed out by Bakun and Parrish (1980), this similarity suggests that the environmental processes which determine the reproductive success of these fishes are similar as well. Except for the hake (*Merluccius* spp.) and in some cases the larger jack mackerel (*Trachurus* spp.), all of the fishes in Table 1 tend to be the object of surface fisheries utilizing purse-seine technology. The collapse of the fishery for each of these surface fishes has occurred in at least one of the four current systems (see Clark 1977, Murphy 1977, Newman and Crawford 1980, Troadec *et al.* 1980, Radovich 1981). The reason for these collapses has tended to be excessive growth of fishing capacity combined with extreme natural variability of the resource. The latter subject will be discussed in the following section.

The assemblages of guano-producing seabirds breeding in eastern boundary current areas also tend to be similar, although not as similar as assemblages of fishes. Seabirds are particularly influenced by the quality of breeding sites, which may explain the paucity of species breeding in the Canary Current. The assemblages in the two areas in the southern hemisphere bear the greatest similarity, in that they share penguins and sulids (boobies and gannets). The California Current lacks these two groups, but features a large assemblage of alcids (auks, puffins, murre, guillemots) which closely parallel the penguins in many respects (Storer 1960). Pelicans are abundant off California and Peru, but the species residing off South Africa seems to have affinity for freshwater fishes rather than for coastal pelagic fishes (Burger and Cooper, this volume). Cormorants are perhaps the quintessential guano bird, the name itself being associated with the Guanay Cormorant (*Phalacrocorax bougainvillei*) of Peru. Although the dominant cormorants off Peru and South Africa feed mainly on pelagic fishes, those off California feed more on fishes associated with the bottom (Ainley *et al.* 1981). In addition to the species listed in Table 1, gulls and terns (Laridae), shearwaters (Procellariidae), and storm petrels (Hydrobatidae) commonly are associated with eastern boundary currents, as well as many other coastal habitats. Although seabirds would seem to be more geographically mobile than fishes, the fish assemblages are more consistent among the eastern boundary current systems.

The preceding discussion has purposefully excluded offshore archipelagoes. The Canary Islands and the Galapagos Islands are similarly situated at offshore and equatorward ends of their respective currents. Both are rich in

tropical and open-ocean seabirds, but are not likely to be impacted by coastal pelagic fisheries due to their relative isolation from the mainland.

4. The forage base

The remainder of this paper will focus on Peru and southern California. In these systems only the anchovy is small enough to be a universal forage item for seabirds. However, younger individuals of the other surface species appear in seabird diets, and of course larger seabirds can consume larger prey. Clupeoids (anchovy and sardine) are the dominant forage items, and the following discussion will treat the variability of these species as well as their inter-relationships.

4.1. Temporal variability

The northern anchovy (*Engraulis mordax*) off California has been monitored closely since 1950 by the California Cooperative Oceanic Fisheries Investigations (CalCOFI) even though a substantial commercial fishery for it did not develop until the mid 1960s. The dynamics of the stock have been sufficiently studied so that satisfactory population models have been developed (Huppert *et al.* 1980, MacCall 1980a). The anchovy stock has shown large fluctuations in the 30 years it has been monitored by CalCOFI, but the nature of its probable variability is better demonstrated by a time segment from a long-term simulation model (Fig. 1).

The anchovy simulation model is described by Huppert *et al.* (1980). Simulated "actual" abundances are generated by random variability about the historical stock-stock relationship of CalCOFI anchovy abundance estimates. Simulated "observed" abundances include another random variable representing relative measurement error. The simulation includes effects of fishery harvest, which is governed by a quota of one-third of the excess over one million metric tons "observed" biomass.

Two properties of this time-series are especially important. The first property is extreme variability in abundance: simulated biomass varies over a 30-fold range from smallest to largest values in this segment of the simulation. Actual estimates of anchovy abundance off California increased 30-fold from 1952 to 1965 (MacCall 1980a), suggesting that the simulation model may even be conservative in its variability. MacCall showed the long-term variability of anchovy abundance by means of probability distributions (Fig. 2), which suggest that abundance is approximately log-normally distributed over time.

The second property of anchovy abundance is its year-to-year serial correlation. Huppert *et al.* (1980) examined the serial-correlation properties of the simulation model, and found sequential biomasses to have a correlation coefficient (r) of about 0.6. Abundant years tend to be followed by abundant years and scarce years tend to be followed by scarce years. Approximately 40% (r^2) of the variance in abundance can be explained by the previous year's abundance, and indeed this is very near the annual survival rate of anchovy biomass, which is about 45% (MacCall 1980a).

The Peruvian anchoveta (*Engraulis ringens*) also appears to be quite variable in abundance, but the extent of that variability is not clear. The anchoveta sustained adult biomasses of 10–25 million metric tons despite intense harvesting during the 1960s. However, after the collapse of

Table 1
Comparison of pelagic fish species in three major eastern boundary currents (from Bakun and Parrish 1980)

	California	Peru	South Africa
Anchovy	<i>Engraulis mordax</i>	<i>E. ringens</i>	<i>E. capensis</i>
Sardine	<i>Sardinops sagax</i>	<i>S. sagax</i>	<i>S. ocellatus</i>
Jack mackerel	<i>Trachurus symmetricus</i>	<i>T. symmetricus</i>	<i>T. trachurus</i>
True mackerel	<i>Scomber japonicus</i>	<i>S. japonicus</i>	<i>S. japonicus</i>
Bonito	<i>Sarda chiliensis</i>	<i>S. chiliensis</i>	<i>S. sarda</i>
Hake	<i>Merluccius productus</i>	<i>M. gayi</i>	<i>M. capensis</i>

the resource in the early 1970s, biomasses have fluctuated between 2.5 and 6 million metric tons under greatly reduced fishing pressure (Tsukayama and Alvarez 1980, 1981).

Sardine (*Sardinops sagax*) stocks in Peru and California also appear to be volatile. MacCall (1979) showed recruitment in the California sardine to be highly variable, serially correlated, and to show little compensatory *per capita* increase at depressed stock sizes. Sardines in Peru increased from negligible abundances during the decade of the anchoveta fishery to a large fishery in the early 1980s.

4.2. Geographic variability

As Murphy (1977) points out, clupeoid fish stocks typically expand and contract with changes in abundance. For example, the range of the northern anchovy off California, as indicated by the occurrence of larvae, expanded from 1952 to 1965 (Fig. 3). As a result of this expansion, the density of anchovies spawning in the nearshore region of southern California changed relatively little with respect to overall abundance. Similar patterns have been observed in Peru, where the anchoveta has contracted into local pockets along the coast, and sardines have expanded offshore (Santander 1980, 1981).

In view of the tendency of the forage base to expand and contract, location may be an important factor in productivity and stability of seabird colonies. Colonies located near the centre of the fish stock will tend to have a more constant food supply than will colonies located toward the

periphery. Examples of this geographic aspect of seabird-fishery interactions are provided by the California sardine fishery, which contracted southward into southern California during the mid 1940s (Murphy 1966). Ainley and Lewis (1974) have speculated that the larger seabirds breeding at the Farallon Islands near San Francisco were severely impacted by the disappearance of sardines. Unfortunately, seabird activity at the Farallon Islands was not consistently

Figure 2

Long-term probability distributions for observed northern anchovy abundance under two levels of exploitation (from MacCall 1980a): I) Unfished; II) Quota of one-third of the observed adult biomass in excess of one million metric tons (cf. Fig. 1)

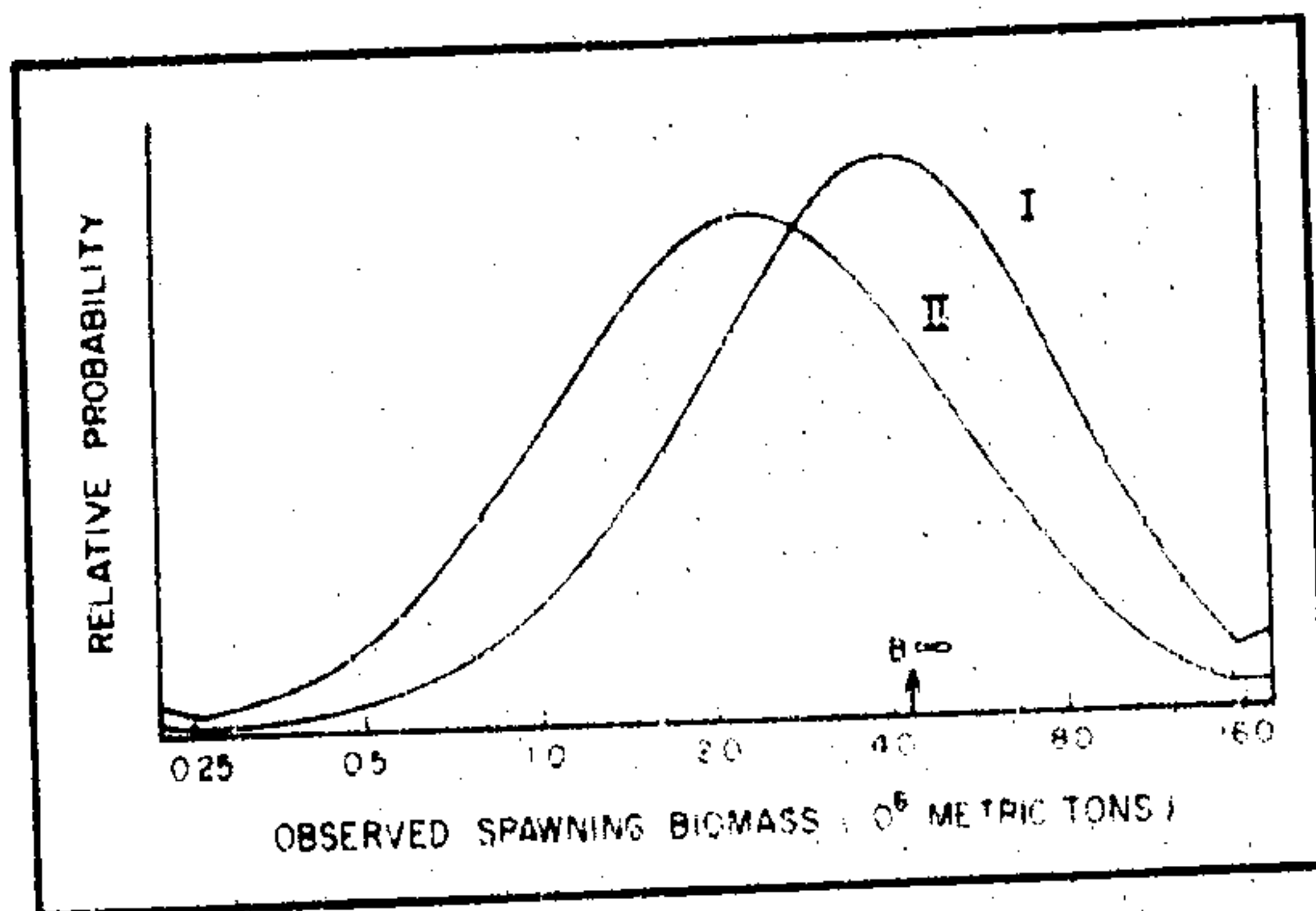


Figure 1

Simulated time series of "actual" and "observed" northern anchovy abundance (from Huppert *et al.* 1980). Dashed line is "observed" abundance below which fishery quota is zero. See text for details

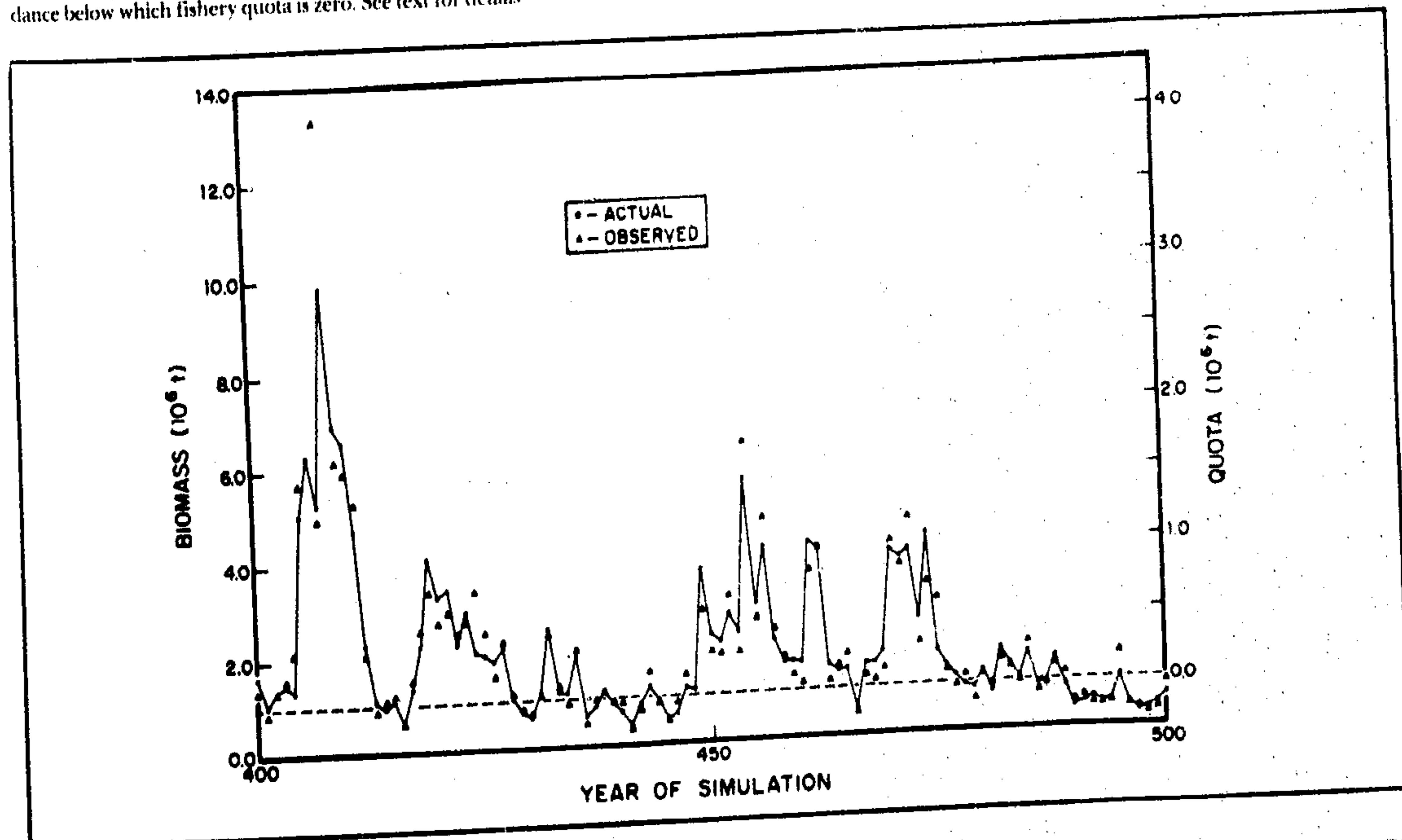
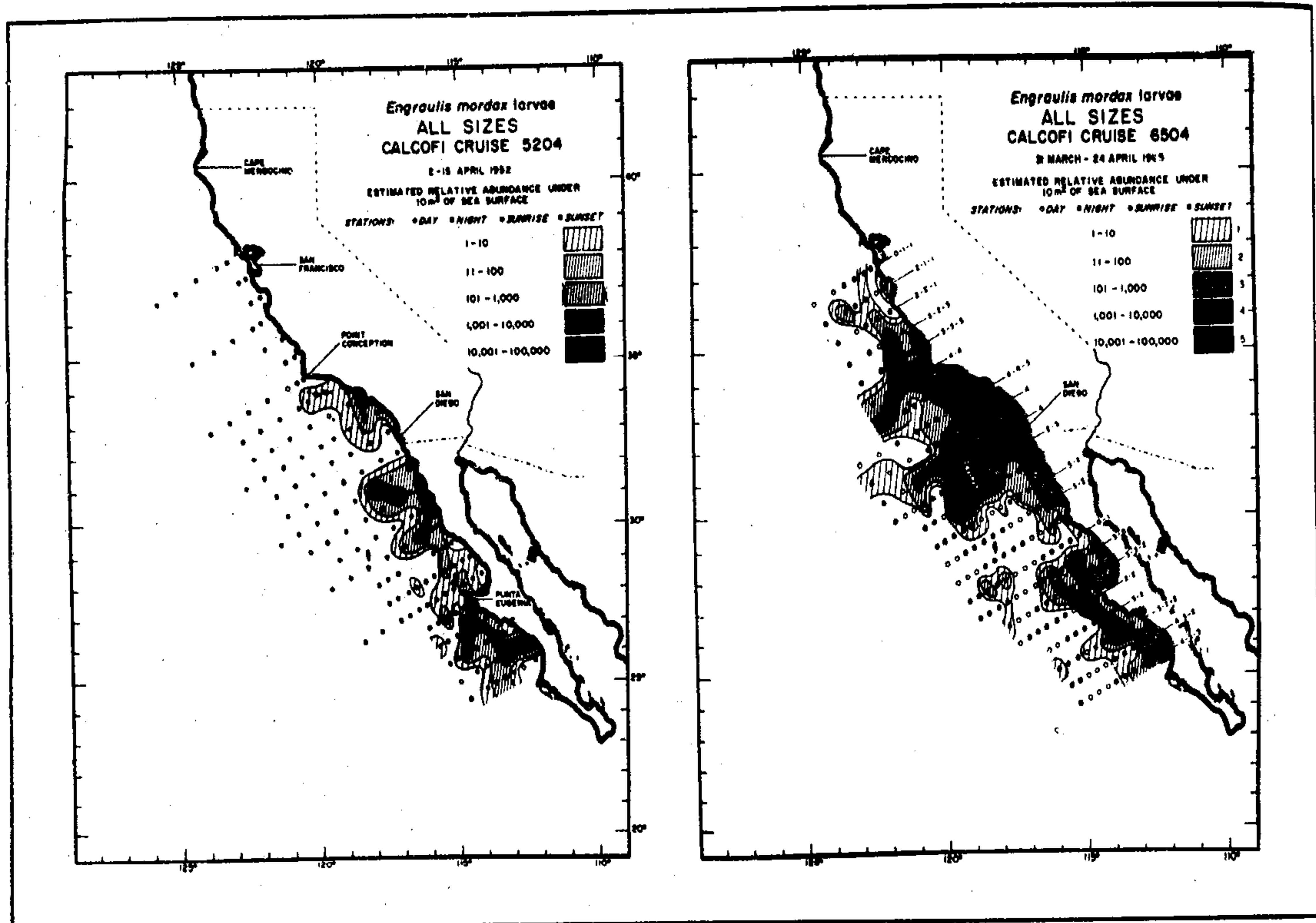


Figure 3
Geographic distribution and abundance of northern anchovy larvae at two levels of stock abundance (from Kramer and Ahlstrom 1968)



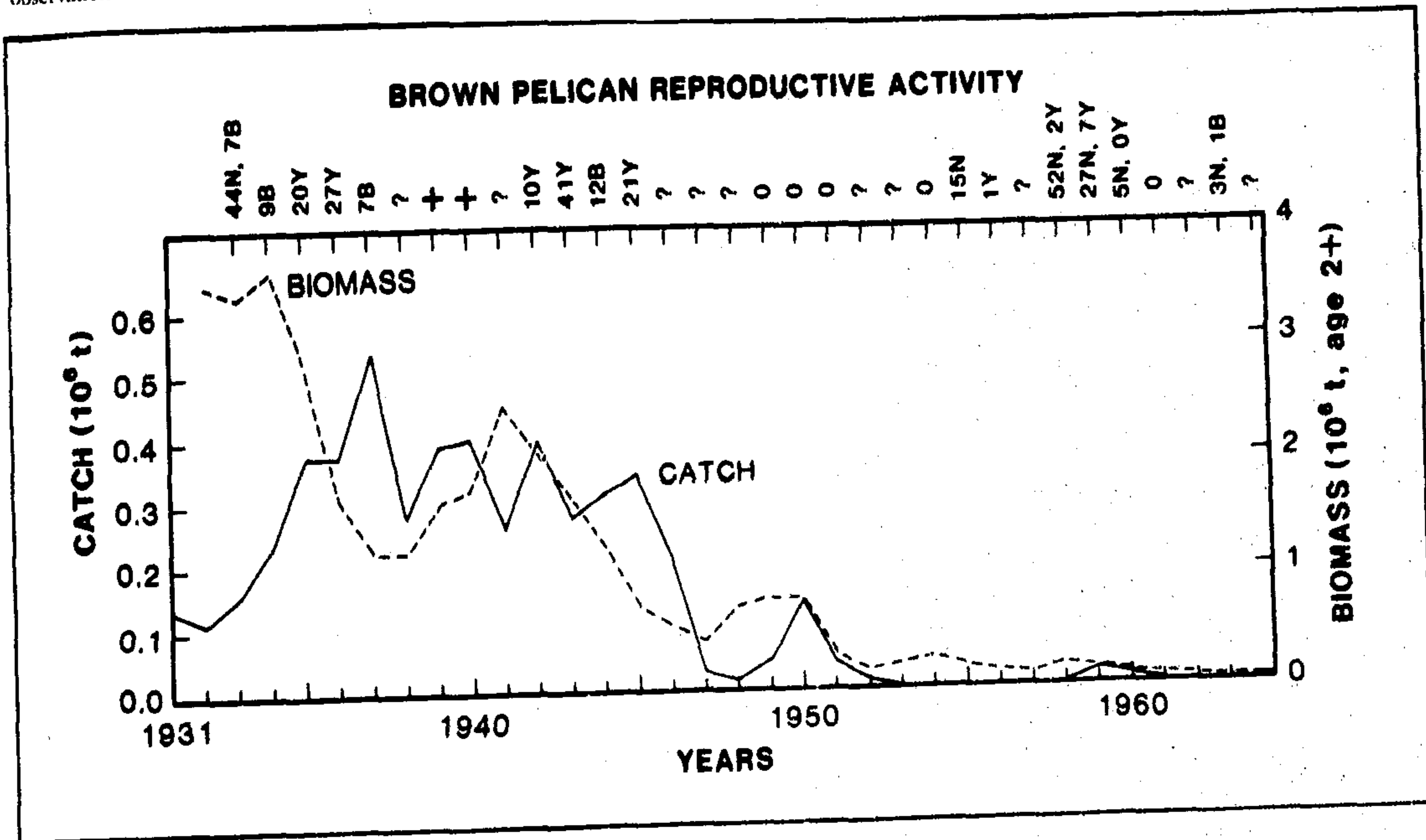
monitored until recently. A somewhat better case can be made for the Brown Pelican, (*Pelecanus occidentalis californicus*) which has sporadically nested at Point Lobos, near Monterey (Fig. 4). Baldrige (1973) has compiled a fairly continuous history of pelican breeding activity at that location since 1933. Pelican nesting activity, reproductive effort, and success roughly coincide with local sardine abundance as indicated by central California sardine fishery harvests. Although the sardine fishery continued for several years in southern California, the 1944-45 season was the last prosperous year for both the Monterey sardine fishery and the Point Lobos pelican colony. Notably, an extreme warming of the waters off California occurred during 1957-60, the so-called "warm water" period. The southern California sardine fishery briefly improved during these years, and many marine organisms extended their ranges northward (Radovich 1960, 1961). The pelican breeding attempts at Point Lobos during the late 1950s were probably associated with this warm period. The very poor success of the nesting activity was most likely due to the combination of DDT pesticide contamination (Anderson *et al.* 1975) and insufficient forage. Keith (1978) has shown that these two factors combine synergistically to severely reduce reproductive success.

4.3. Anchovy-sardine relationship

The decline of the California sardine population was followed by a large increase in anchovy abundance in southern California and to a lesser extent in central California. Murphy (1966) interpreted these trends as competitive replacement, and on the basis of goodness-of-fit, Silliman (1969) claimed to have used these data to substantiate the Lotka-Volterra competition theory. On the other hand, evidence of sardines and anchovy abundance from scale deposition rates in anaerobic sediments of a southern California basin indicated that the two species have varied similarly, rather than inversely, over the past 150 years (Soutar and Isaacs 1974). Reviews of the anchovy-sardine replacement hypothesis are given by Daan (1980) and MacCall (1980a).

The recent decline of anchoveta and increase of sardine in Peru has tended to strengthen the idea of replacement as a characteristic phenomenon among clupeoid fishes. Still, the mechanisms causing these changes have not been determined. Both anchovies and sardines are filter feeders, and cannibalism of their own eggs and larvae is probably the main density-dependent mechanism regulating their abundance (MacCall 1980b). If these two fishes

Figure 4
Brown Pelican reproductive activity at Point Lobos (Baldridge 1973) in relation to central California sardine catch (Murphy 1966) and total adult sardine biomass (Murphy 1966, MacCall 1979). Symbols: N = nests, B = broods, Y = young, + = some activity, 0 = no activity, ? = no observations made



inhabit the same area, they are certain to also be predators on each other's spawning products. Given the relatively low degree of compensation in the stock-recruitment relationships of these fishes, interspecific predation rather than competition is probably the mechanism governing their interaction. Such a mechanism would be expected to result in a relatively unstable relationship between the two fishes. Differential responses to exogenous influences such as environmental variability and selective fisheries may further destabilize the relationship.

Given the slow response time characteristic of anchovy-sardine replacement events, seabirds and other predators may not benefit from the relative stability usually attributed to a diverse forage base. However, the sedimentary scale record of Soutar and Isaacs (1974) suggests that maintenance of sardine-anchovy diversity may be a viable management objective. Sardine scales were present in all but one 5-year time segments in the 140 years up to 1950, but in only one segment in the 20 years following 1950. By reducing fishing pressure on either species when its abundance is low, fishery management should be able to maintain both species in at least moderate abundances, and by doing so, reduce the response time for replacement when conditions are favourable.

Anchovy-sardine replacement events have now occurred in both California and Peru. In both cases, the sardine-dominated system apparently has been centered poleward of the anchovy-dominated system. In California, the sardine fishery was largest in central California, and

extended as far north as British Columbia (Murphy 1966), whereas the anchovy stocks have been most abundant in southern and Baja California (Fig. 3). In the Peruvian case, the anchoveta fishery was largest in northern and central Peru, but the recent sardine fishery has extended to southern Peru and northern Chile (G. Sharp, FAO, Rome, pers. comm.). A similar poleward shift in Peruvian fish production, although of unknown species composition, has been indicated for early historic times (Hutchinson 1950, p. 48).

It is also noteworthy that the rather unproductive region south of Pisco Bay, as far south as Iquique [i.e. southern Peru], seems from the 16th to the early 19th centuries to have been regarded as a more important source of guano than the central Peruvian coast. . . . The only reasonable, though admittedly speculative, explanation of the decline of importance of the southern islands . . . is that minor changes in the dominant hydrographic pattern have occurred, tending to alter the distribution of the centers of abundant fish.

Evidence of sardine abundance during a period consistent with Hutchinson's speculations could be looked for in Peruvian anaerobic sediments. DeVries and Pearcey (1982; Fig. 9) found isolated sardine scales in central Peruvian coastal sediments at depths indicative of the above period.

Further investigation of Peruvian and Chilean coastal dry lakes by the methods of Goodman (1972), might elucidate the nature of these biogeographic shifts.

4.4. El Niño

El Niño is an oceanic condition which reaches a unique extreme in Peru. During El Niño the Peru Current episodically weakens, upwelling weakens, and the coast is flooded with warm, nutrient-poor water. A similar but less intense phenomenon occurs in other eastern boundary currents. Mechanisms and physical oceanography of El Niño are discussed by Quinn *et al.* (1978), and biological effects are discussed by Idyll (1973), Valdivia (1978), and Cushing (1981). Biological effects can be severe: reduced primary productivity may lead to fish die-offs, and ultimately to extensive mortality of seabirds, a characteristic sign of El Niño. Ashmole (1971) observes that compared to that of land birds, the life table for seabirds is characterized by low reproductive rate and high survivorship. Duffy (1980) speculates that the high food availability punctuated by severe shortages during El Niño give Peruvian seabirds an unusual life table with high reproductive rate and low survivorship.

El Niño events can be seen in the history of Peruvian guano production and/or guano-bird abundance (Fig. 5). As Idyll (1973), Duffy (1980), and others have observed, El Niño-related population declines have been more severe since the initiation of the anchoveta fishery, and population recoveries have been weak. This decrease in the resilience of the Peruvian guano birds appears to be the result of the fishery having reduced the availability of forage, both through a general reduction in anchoveta abundance, and through direct competition for available surface schools.

Hutchinson (1950:373) and Murphy (1954) have suggested that a nutrient gradient may exist in waters around guano islands, fertilizing the area, and eventually enhancing local fish abundance. This speculation takes on greater potential when El Niño conditions are considered. The Peruvian coast is normally lacking in rainfall, but during El Niño the coast may become subject to tropical downpours which have been termed "disastrous" to the

guano industry (Murphy 1954), due to large amounts of guano washed into the sea. This local nutrient enrichment could be substantial under the nutrient-poor conditions of El Niño, and any attraction of fish would undoubtedly improve the foraging prospects of the seabirds inhabiting the islands, and might improve survival conditions for the fish as well. Both Hutchinson (1950) and Murphy (1954) remark that guano birds tend to retain their feces until they return to their island (although no actual evidence was given). This has usually been interpreted as contributing to improved nesting substrate, but it might also contribute to long-term forage stability and increased survivorship through the forage enhancing mechanism hypothesized above. Although this hypothesis is admittedly speculative, it could be experimentally tested by maintaining a specified minimum guano thickness on selected islands, such that the full effect of local enrichment could be observed during El Niño events (of course, fishing activity in the area would have to be restricted). Geochemical analysis, combined with past rainfall patterns could produce an estimate of optimal guano thickness, so that harvest of the excess could continue. It would indeed be ironic if overharvesting by the guano industry contributed to the collapse of the Peruvian anchoveta fishery!

5. Fishery-seabird dynamics

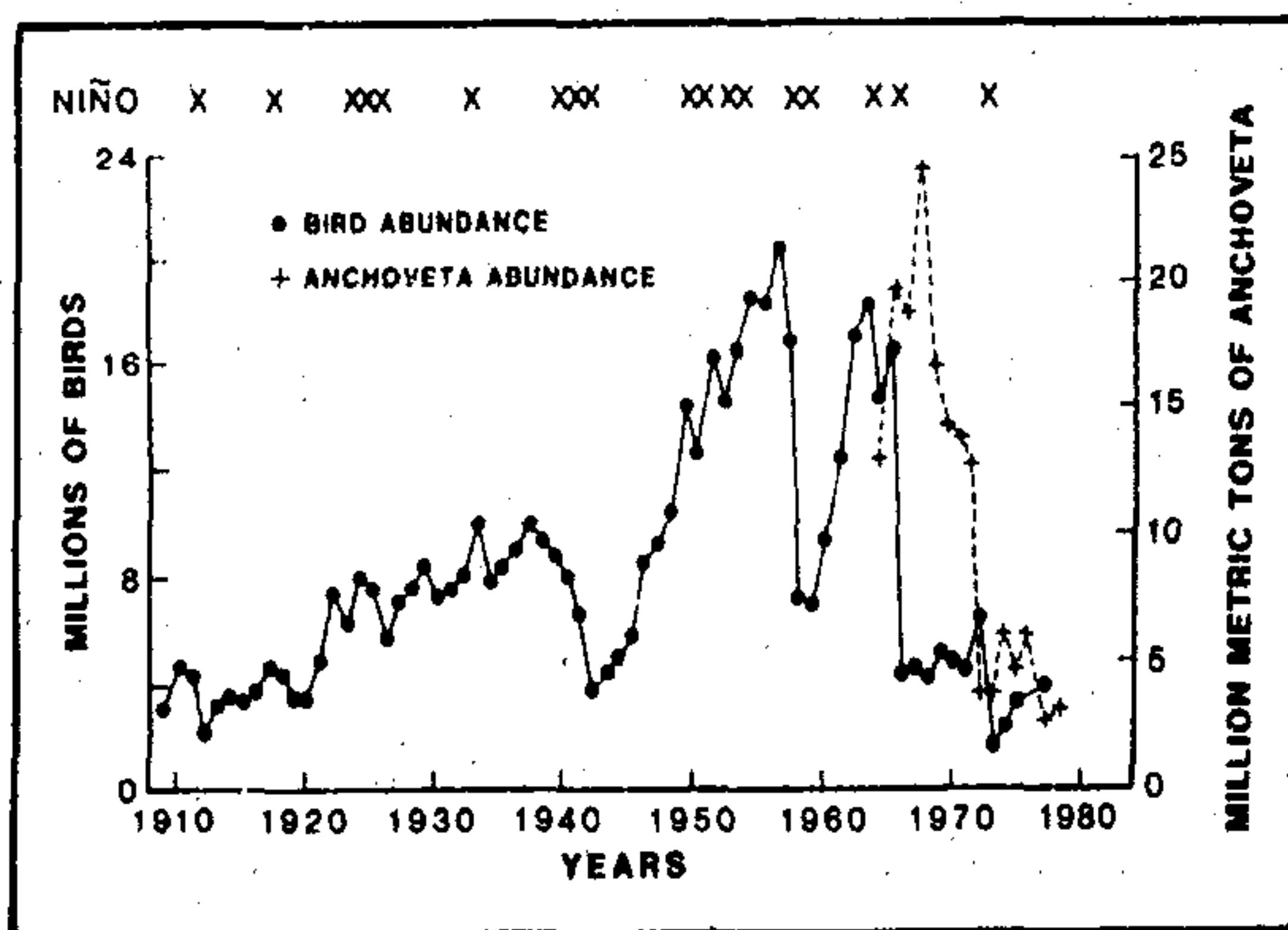
The topic of fishery-seabird dynamics includes two fairly distinct topics: the influence of seabirds on the fishery, and the influence of the fishery on seabirds. Some aspects of these relationships have been qualitatively touched upon in the preceding discussion. The remainder of this paper will attempt to examine these relationships quantitatively.

5.1. Impact on the fishery

Furness (this volume) has reported that seabirds in several ecosystems may consume 20 to 30% of local annual pelagic fish production. This represents a potentially large increased fishery catch if numbers of birds were to be reduced. Calculations of this sort have been made for the Peruvian anchoveta fishery by Schaefer (1970), who treated the guano birds as a competing fishing fleet. Schaefer estimated that the early-fishery (i.e. 1960-63) bird population of 16 million may have consumed about 2.5 million metric tons of anchoveta per year, or about one-third the amount of the fishery. Jordan (1967) also estimated the early-fishery anchovy consumption by birds to have been between 1.8 and 2.8 million metric tons annually. This consumption rate corresponds to 28% of the initial abundance of anchoveta. This level of fish consumption is likely to have had an effect on forage abundance, and may have been a contributing factor regulating pre-fishery bird abundance. As the anchoveta fishery expanded and the bird populations declined, anchoveta harvest shifted directly from the birds and associated guano industry to the fishery.

Cushing (1981) has performed similar calculations for the quantity of anchoveta in the incoming or "recruiting" age group consumed by the seabirds. Again, the fishery catch effectively replaced anchoveta consumption by the declining seabird population. Cushing assumes the birds to have eaten mainly smaller anchoveta in the recruiting age group. This assumption is consistent with Jordan (1967) who notes that the birds consumed somewhat smaller fish than were taken by the fishery. Cushing (1981) concludes

Figure 5
Peruvian guano bird abundance estimated from guano production, anchoveta abundance, and occurrence of El Niño in Peru (modified from Duffy 1980, anchoveta abundance from Tsukayama and Alvarez 1980, 1981)



that the change in seabird consumption of recruits distorted the apparent anchoveta stock-recruitment relationship, giving a false appearance of being dome-shaped.

Consumption of fish by seabirds inhabiting the California Current has not been fully calculated. Wiens and Scott (1975) modelled the seabird-forage relationships off Oregon, and concluded that the birds may consume as much as 22% of the local annual production of pelagic fishes. A large fraction of the total consumption was attributed to the numerous Sooty Shearwaters (*Puffinus griseus*) that pass along the Oregon coast during their migrations. A more ambitious attempt at calculating overall seabird consumption of forage in the California Current was made by Green (1978). Lacking precise estimates of seabird abundance or forage requirements, Green arrived at a tentative total seabird forage consumption of 230 000 – 630 000 t per year, with 140 000 – 380 000 t of that being small pelagic schooling fishes such as anchovy. This "educated guess" corresponds to less than 10% of recent anchovy biomass, leading to the conclusion that seabirds probably are not a major source of anchovy mortality in the California Current. Seabirds also consume large amounts of juvenile rockfish (*Sebastes* spp.) but impact on that resource has not been quantified (Ainley *et al.* 1981).

5.2. Impact on the seabirds

Fishery impacts on seabird populations, presumably through trophic interactions rather than direct mortality, have been inferred for Peru (Schaefer 1970, Anon. 1974, Duffy 1980), and for South Africa (Crawford and Shelton 1978, Burger and Cooper, this volume). Although it has long been accepted that seabird reproductive success is sensitive to food availability (e.g. Ashmole 1971), this relationship has been difficult to demonstrate directly, due to lack of long sets of observations and difficulty in independently measuring food availability. Hunt and Butler (1980) have shown reproductive responses to southern California anchovy abundance in Western Gulls (*Larus occidentalis*) and in Xantus' Murrelets (*Endomychura hypoleuca*). Anderson *et al.* (1982) have shown that Brown Pelican fledging rates in southern California vary with anchovy availability. In Peru, fledging rates of guano birds during the intense fishery, 1966–71, were half the level observed during the early fishery, 1960–63 (Anonymous 1974).

Importantly, reproductive success may not vary smoothly with changes in food availability. Anderson *et al.* (1982) found that Brown Pelican fledging rates appear to decrease sharply below a threshold level of anchovy abundance. Using Ringed Turtle Doves (*Streptopelia risoria*) fed to satiation as controls, Keith (1978) found that if food were limited to 90% of that required for satiation, production fell to 50% of the central level. Production was near zero for birds restricted to 70% of the food required for satiation. If such a threshold response is common in seabirds, effects of lowered forage availability may be very difficult to predict unless the threshold level has been crossed and observed.

Animal populations are usually assumed to have some compensatory mechanism so that reproductive rates tend to increase as a response to lowered abundance. Such mechanisms are poorly documented for seabirds. Ashmole (1971) lists several likely mechanisms, but quantitative data are generally lacking. Again, without knowledge of compensatory capacity we cannot assess the resilience of seabird

populations to lowered food availability and possible consequently lowered bird abundance.

5.3. A simulation model

In view of our lack of knowledge regarding the mechanisms regulating seabird reproduction and abundance, it is difficult to predict the effects that particular fisheries may have on particular seabird colonies. However, there is enough information to construct a simple simulation of a hypothetical fishery-seabird interaction. To the extent that the component processes are reasonable models, the "predictions" of the simulation model may provide useful insight into the likely nature of actual fishery-seabird interactions.

The simulation model is intended to mimic fish and seabird dynamics, exemplified by the anchovy and the Brown Pelican in southern California. The model employs several functional sub-models representing components such as age structure, reproduction, and food supply. These sub-models are arbitrary; choices of functions and parameter values are subjective. Some parameter values are constrained by others due to mathematical necessity.

The life table of the model seabird has a constant survivorship schedule, but variable *per capita* reproduction (*R*). The Leslie matrix, which approximates that of the California Brown Pelican (see Anderson and Gress 1983), is as follows:

0	0	0	<i>R</i>
0.5	—	—	—
—	0.75	—	—
—	—	0.85	0.90

As is shown by the right-hand column, maturity is achieved at age four years. Subadults make no reproductive contribution. All adults experience the same survivorship and reproductive success; there is no maximum age constraint, but the average remaining life span of an adult is 10 years. Birds are censused at the time of fledging, and adult abundance at that time is considered equivalent to the number that attempted breeding.

The *per capita* reproductive rate is determined by $R = f(F)g(N)$, where $f(F)$ denotes a function of food availability, and $g(N)$ denotes a function of bird population size. In effect, the function $g(N)$ determines the maximum possible *per capita* reproductive rate averaged over all adults for a given population size, and the function $f(F)$ determines what portion of that potential maximum is realized due to the constraint of food supply. Note that *per capita* reproduction (here termed "reproductive success") is equivalent to the number of offspring fledged *per* breeding pair.

Two arbitrary functions, one linear and one non-linear, were used to model the effect of density or population size; both were calibrated to provide a replacement level of reproductive success (1.07) at a population size (*N*) of 1000 adults, given unlimited food availability, and to provide a maximum reproductive success (mean of all breeding birds, including survival to age one) of approximately 1.7 near zero density (Fig. 6). The parameter values chosen

here are arbitrary; no special significance should be attached to them. The linear model was as follows:

$$g(N) = 1.70 - 0.00063N \text{ if } 0 < N < 2698 \text{ and} \\ g(N) = 0 \text{ if } N \geq 2698$$

The latter constraint is necessary to prevent negative reproductive success. The non-linear model was in the form of a "reversed" logistic curve (Fig. 6):

$$g(N) = 1.72/[1 + \text{EXP}(0.00394N - 4.44)]$$

This shape of curve was chosen for two reasons. First, Murray (1979), Fowler (1981), and others have argued that many higher organisms, such as large mammals and birds tend to show density-dependent effects mainly at high population levels (close to carrying capacity). Second, it is unlikely that reproductive success would actually approach zero for populations in excess of carrying capacity, rather it should simply fall progressively farther below replacement.

The function used to model the effect of food availability must have a lower bound of zero, an upper bound of unity, and be capable of showing a threshold response at intermediate food levels. Again, a logistic function has these qualities (Fig. 7):

$$f(F) = 1.0/[1 + \text{EXP}(-4.39225 F/W)]$$

where F is a measure of food availability, scaled so that a value of $F = 0$ gives $f(F) = 0.5$. Parameter W controls the steepness of the threshold, so that if $W = 1$, $f(F)$ rises from 0.1 to 0.9 over the interval $F = [-0.5, 0.5]$, a "width" of one unit of F . Values of $W = 0.5$ and $W = 2$ reduce or expand the width of the threshold accordingly, while the centre of the response curve remains at $F = 0$.

Food availability is modelled as a serially correlated, normally distributed random variable with unit variance (Fig. 7). This simulates the approximately normal probability distribution and temporal structure seen in log-transformed anchovy abundance from previous models (Fig. 2). Serial correlation was obtained by use of the recursion algorithm (Yevdjovich 1966),

$$F_t = \rho_s F_{t-1} + r_t (1 - \rho_s^2)^{1/2}$$

where F_t is log food availability in year t , ρ_s is serial correlation coefficient, and r_t is an independent normal $N(0,1)$ random number for each year. This food-availability model does not specify whether a single-species or a multiple-species forage-base is represented. Both cases should behave similarly, except that a multiple-species forage-base may have a relatively smaller variance. It is unnecessary to consider a range of variances in the model food supply because equivalent effects can be obtained by varying the threshold steepness or "width" parameter W in the function $f(F)$.

This model of food availability has a mean value of zero. The effect of changes in mean food supply, perhaps due to fishery or other impact, is modelled by adding an appropriate constant. For example, because F is in logarithmic units, halving of the average food availability can be simulated by adding $\log_e(0.5) = -0.69$.

The model is implemented with an initial equilibrium population structure of 535, 268, 187, and 1000 for ages one, two, three, and adult respectively. As a result, random variability is not seen in the adult abundance until 4 years have elapsed. Due to the high survival rate of adults, the initial abundance of adults may influence results for decades, especially if the initial abundance is far from the eventual equilibrium.

The simulation model was used in two ways. The first way was to follow the time-course of adult bird abundance starting with initial conditions, giving a qualitative impression of patterns and trends. The second way was to determine probability distributions at long-term equilibrium. In the latter case, the simulation was run for 500 years

Figure 6

Alternative linear and non-linear models for maximum average reproductive success (function $g(N)$, see text). Success is equivalent to the number of offspring fledged per breeding pair

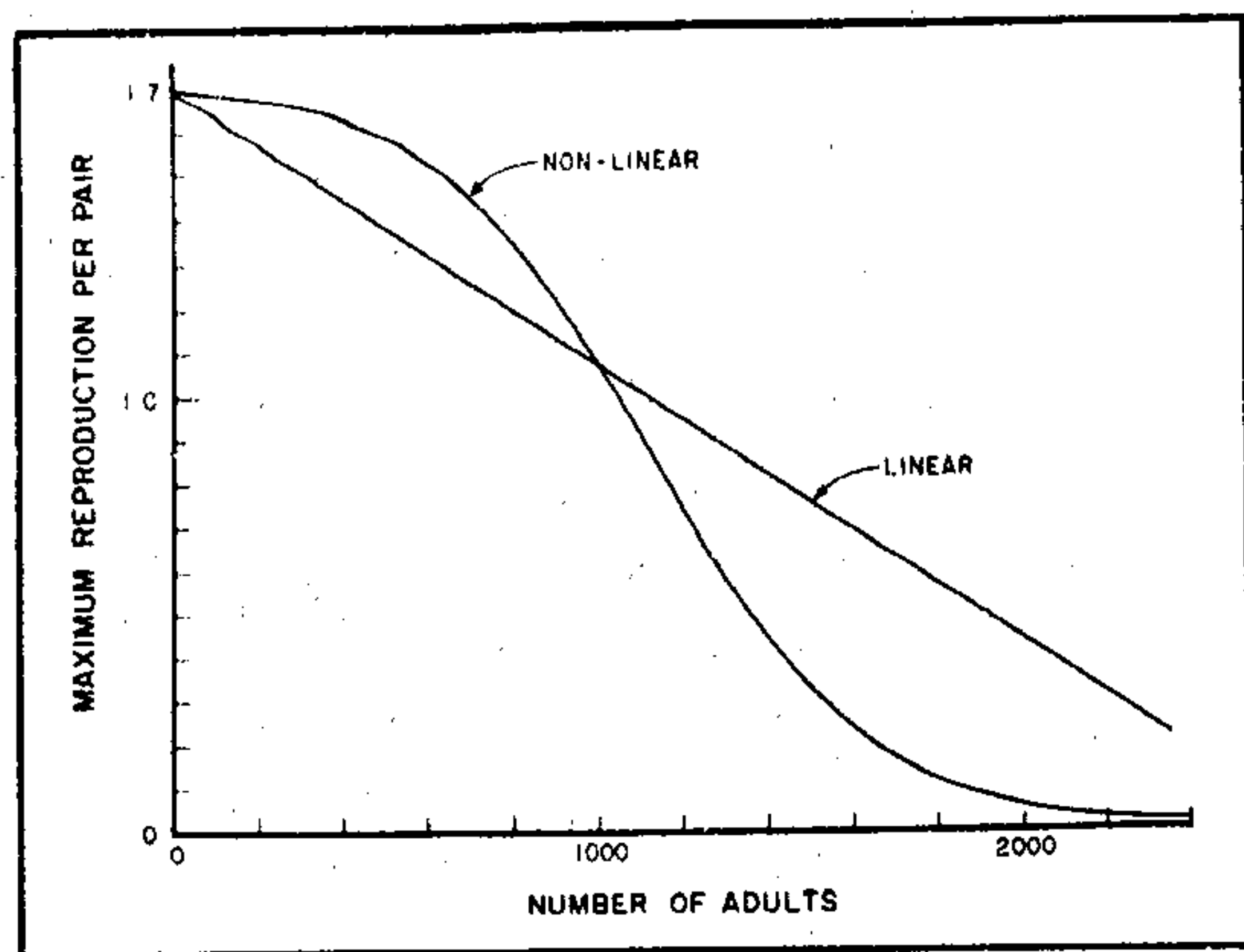
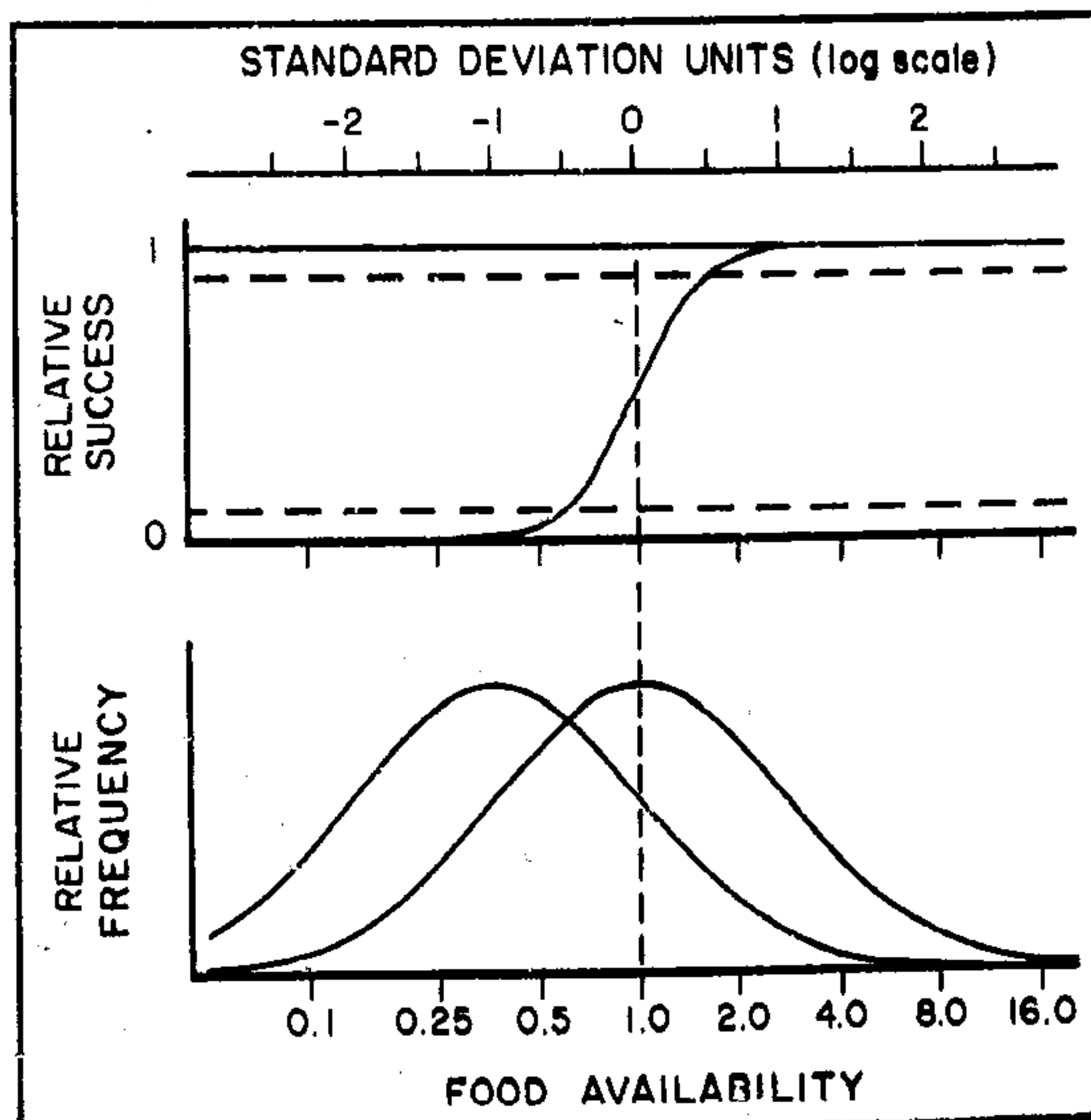


Figure 7

Upper diagram: Food availability threshold ($W = 1$) for relative reproductive success (function $f(F)$, see text). Horizontal dashed lines are 0.1 and 0.9 levels. Lower diagram: Probability distributions of relative food availability ($\sigma = 1$). Right probability curve represents possible virgin distribution ($\bar{F} = 1$), left probability curve represents possible distribution under exploitation ($\bar{F} = 0.37$). Note that food availability is arbitrary



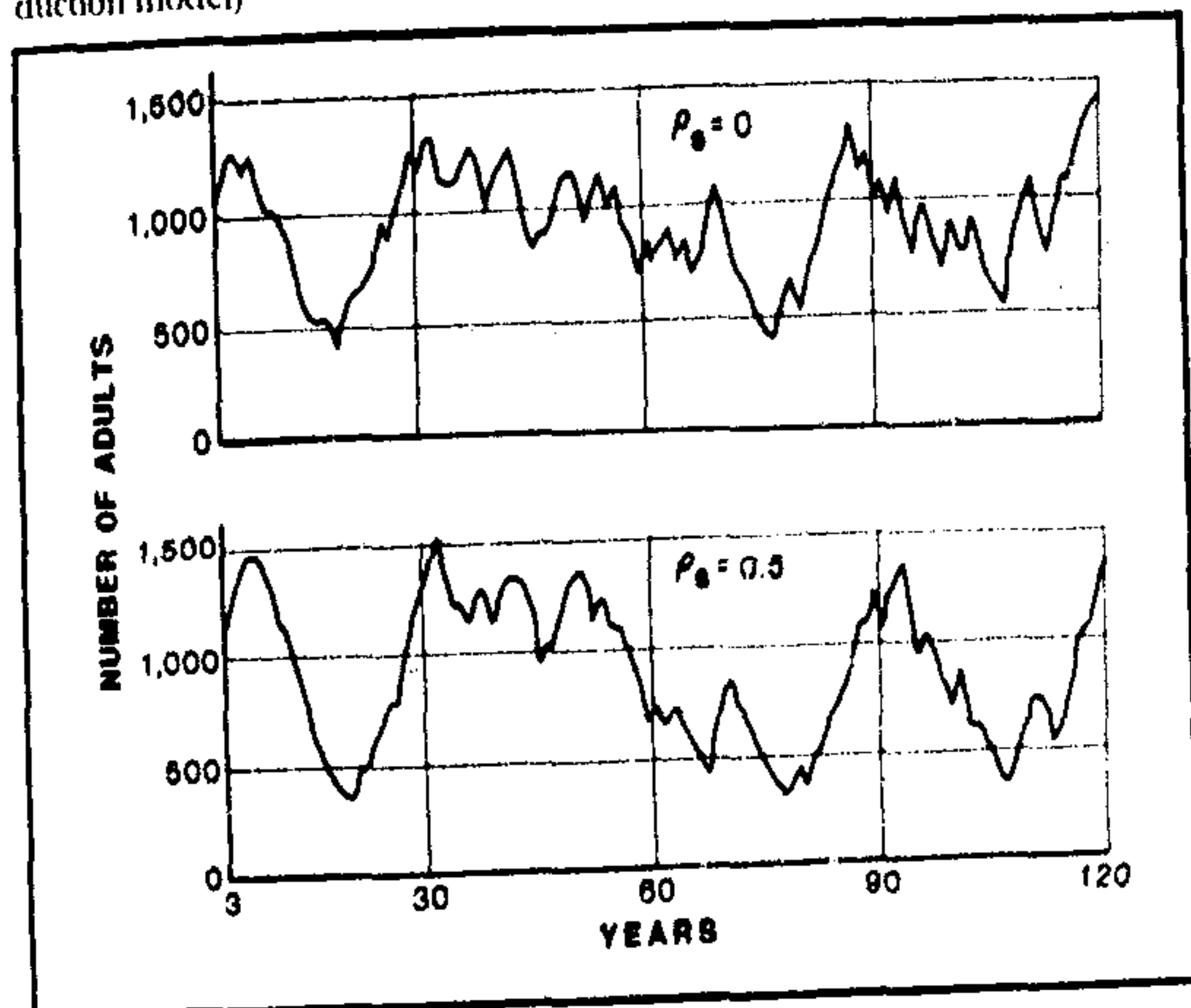
to establish equilibrium before monitoring the results. All simulations used the same series of random numbers (r_t).

5.4. Simulation results

This model was designed to investigate the fundamental question of how seabird abundance may vary as a function of characteristics of seabird food supply. Although

Figure 8

Simulated time-series of seabird abundance for two levels of serial correlation (ρ_s) in food availability ($\bar{F} = 1$, $W = 1$, $\sigma = 1$, non-linear reproduction model)



the mean level of food availability is probably the most important factor, the variance and serial correlation of the food supply also impact the bird population.

As described earlier, serial correlation is a measure of similarity of food availability in successive years. The effect of serial correlation of the food supply can be seen in comparative population trajectories (Fig. 8). Increased serial correlation preserves the overall pattern, but the excursions to high and low levels of abundance become more severe. The equilibrium probability distributions (Fig. 9) show that the bird population varies only moderately about the mean for a serially uncorrelated food supply, but in the presence of serial correlation there are occasional excursions to near-extinction. The long-term mean abundance is only slightly affected by serial correlation, as the magnitude and duration of excursions to high and low abundance nearly balance.

The effect of variance in food supply has surprisingly similar effects to those of serial correlation (Fig. 10). High variance (equivalent to a very sharp threshold) generates high population variability, whereas low variance enables the population to remain near mean abundance. Again, the effect of increased population variability is only a slight lowering of long-term mean abundance. The above simulations were for a mean food abundance centred at the mid-threshold level. Clearly, the effective variance in bird response will decrease as the mean food abundance moves above or below this threshold level. In effect, the birds will more consistently be successful or unsuccessful. If a sharp threshold response to food availability is to be expected for seabirds, these results indicate that its delineation is very important to predicting fishery impacts.

Figure 9

Long-term probability distributions of simulated seabird abundance for three levels of serial correlation, (ρ_s) in food availability ($\bar{F} = 1$, $W = 1$, $\sigma = 1$, non-linear reproduction model). The arrow indicates mean abundance

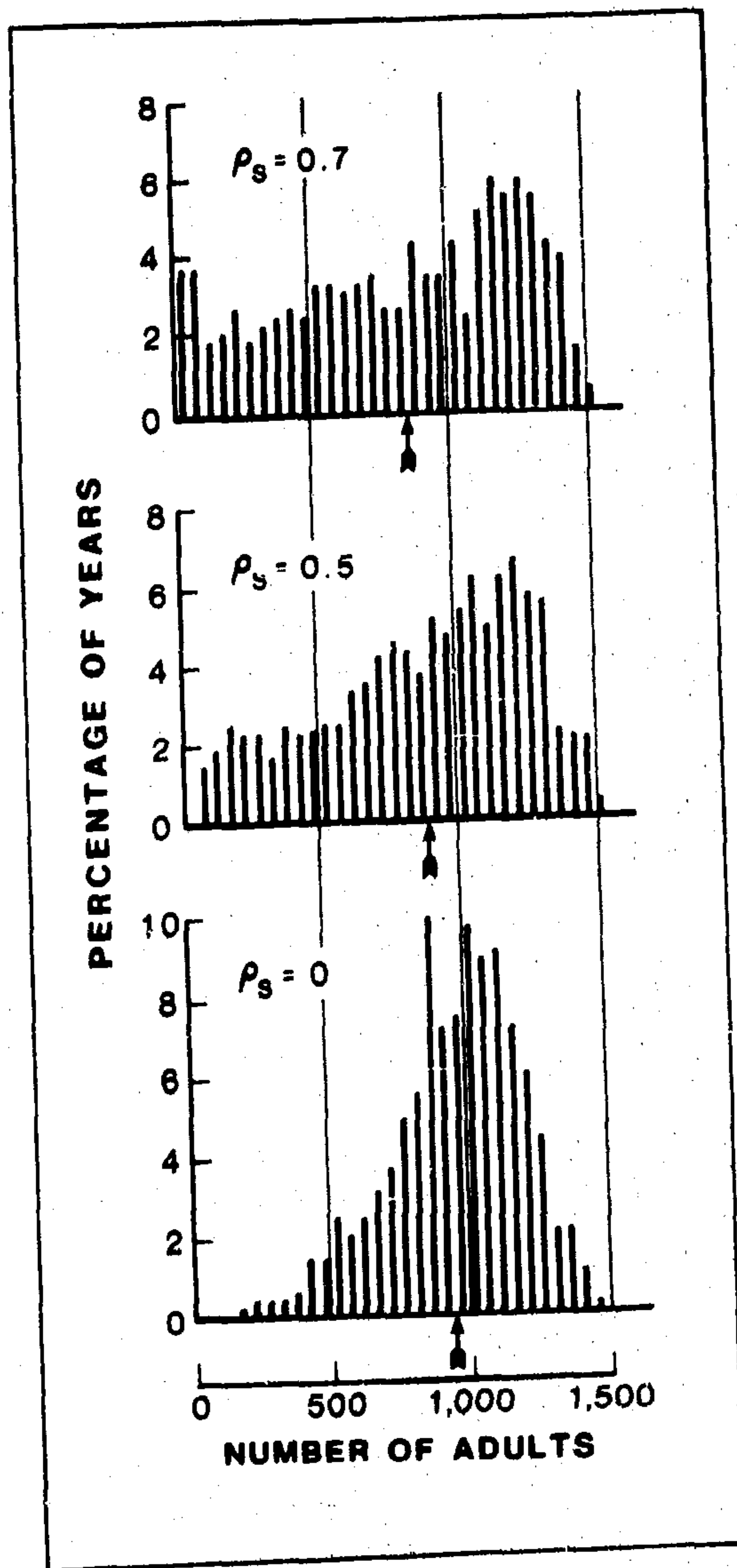
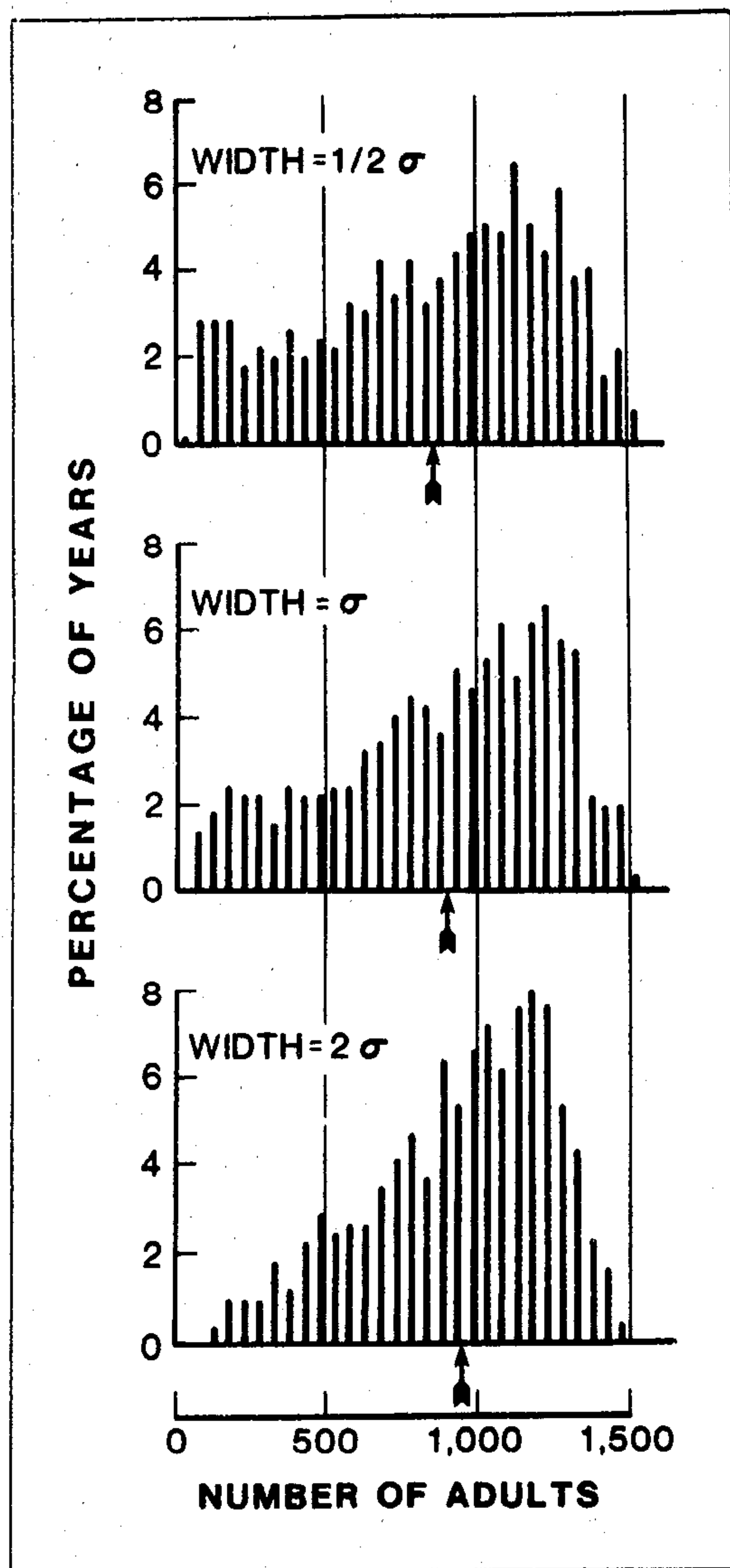


Figure 10

Long-term probability distributions of simulated seabird abundance for three threshold sensitivities (widths) to food availability ($\bar{F} = 1$, $\sigma = 1$, $\rho_2 = 0.5$, non-linear reproduction model). The arrow indicates mean abundance



Variance and serial correlation of the food supply appear to have little effect on the long-term mean bird abundance, however the mean food supply itself has the anticipated relationship to mean bird abundance. Mean bird abundance declines as mean food availability declines (Fig. 11), but there is an unexpectedly sudden drop in mean bird abundance near the critical food level causing extinction. This sharp drop is more severe for the non-linear model than the linear model, apparently due to the non-linear response having exhausted its compensatory capacity

near the virgin level (see Fowler 1981). On an arithmetic scale, the drop is more precipitous than on the logarithmic food-availability scale of Figure 11.

The virgin level of food abundance is defined only relatively in this model. Several possibilities can be examined. In terms of fishery impact, it is useful to assume that a "well-managed" fishery will reduce fish availability to about one-half its unexploited level. In the face of such a fishery impact, the bird population will survive if the unexploited food level is above about 1.4 relative units (Fig. 11), assuming no serial correlation of food supply. This result suggests that those seabird populations showing sporadic reproductive success under pre-fishery conditions may be severely impacted by a fishery on their food supplies. Unfortunately, many seabirds outside of Peru seem to fall into this category.

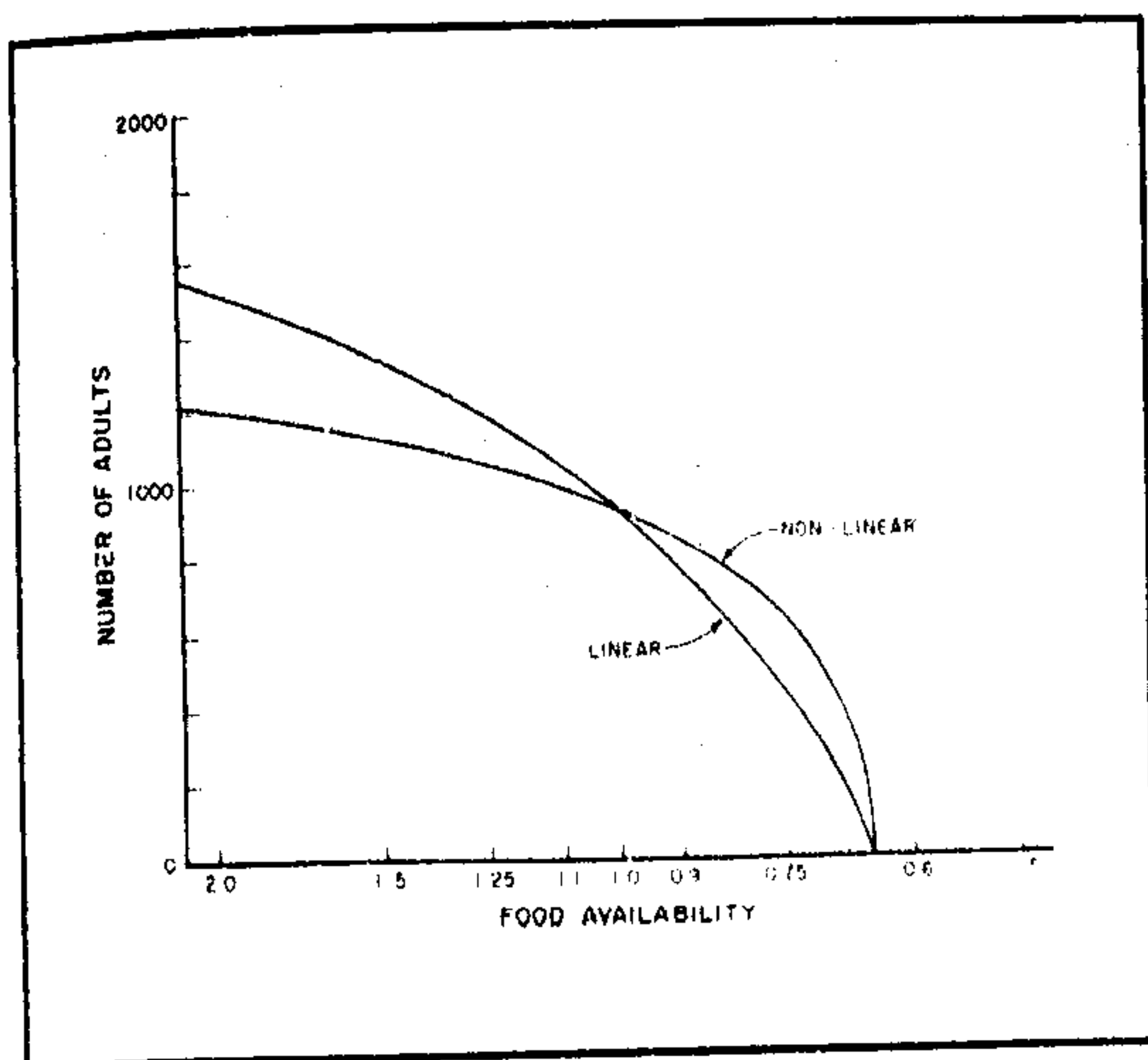
Although it is clear from Figure 11 that the model seabird can exist on a mean relative food availability of 1.0, but will become extinct on a mean food supply of 0.5, this fact would not immediately be clear from an abundance monitoring program. I simulated an example based on 120 years of seabird abundances for these two mean food levels and an initially pristine bird population: the patterns obtained were disturbingly similar (Fig. 12). Because of high serial correlation, the true long-term trend tends to be masked by prolonged variability at intermediate time scales of decades. In both cases there would be apparent cause for alarm during the first 20 years of the fishery, but the birds would stage an apparent recovery due to a more favourable environment over the subsequent 30 years. From abundance alone, it would not be apparent for over 60 years whether the population is viable. Prediction of fishery impact will require detailed studies of seabird population dynamics as well as improved fishery models. Unfortunately the long trends in seabird and fish populations associated with high serial correlations indicate that short-term studies are likely to miss upper or lower ranges of abundances which may be important to understanding long-term dynamics.

Many modifications of this simple model are possible, and until most of the reasonable cases have been examined, it would be unwise to attempt broad generalizations. It is not within the scope of this paper to attempt such a complete investigation. Other life tables have not been considered here because it would be difficult to establish a simple standard of comparison. Higher adult survival rates would require lower average reproductive success to maintain comparable population levels. However, the nature of such a change is easy to anticipate. In this model, bird abundance behaves as a moving average of fish availability, with exponentially declining weights. Higher survival would increase the span of time over which averaging occurs, and would tend to decrease the variability of seabird abundance.

Simulation modelling of a Peruvian seabird population may require three modifications. The probability distribution of the food supply should reflect sudden declines typical of El Niño; this pattern is not well modelled by the simple serial correlation algorithm used here. Also, predation pressure from the seabirds themselves might modify the availability of food. Finally, the life table would have to contain variable survival rates, perhaps dependent on food availability, to reflect the mortality that occurs during El Niño events. These investigations are beyond the scope of the present paper.

Figure 11

Long-term mean simulated seabird abundance in relation to mean food availability (\bar{F}) for two alternative reproduction models ($W = 1$, $\sigma = 1$, $p_r = 0.5$, non-linear reproduction model)



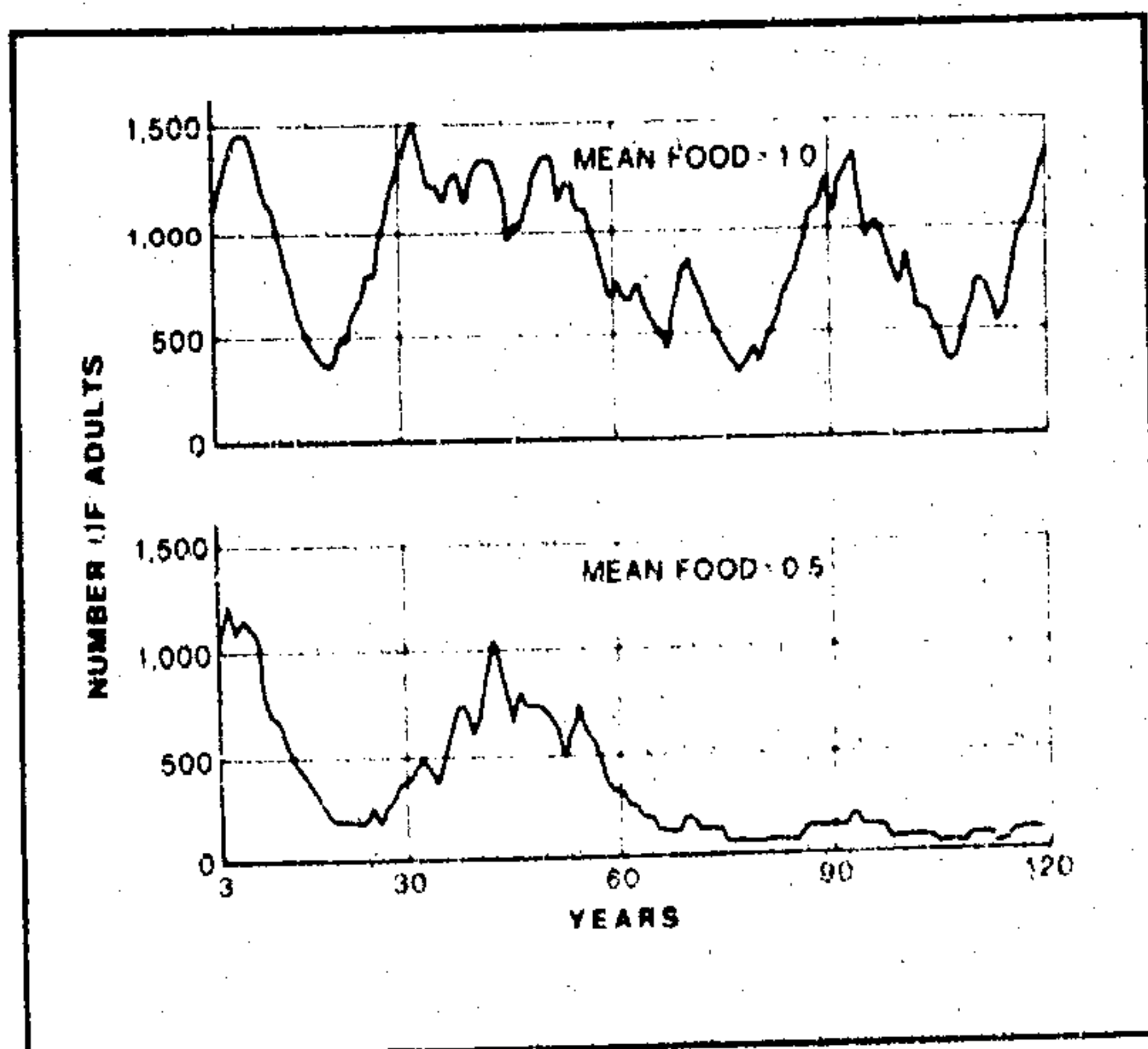
6. Conclusion

The relationship between seabird abundance and fishery activity cannot be considered outside the context of natural patterns of forage availability. Those patterns are superficially similar in California and Peru, but Peru is different in two important, interrelated respects. In the absence of an intense fishery, forage availability is much higher in Peru, but the episodic occurrence of El Niño causes more severe shortages than are observed in California. Because of these differences, the potential impacts of fisheries on seabird abundance are not necessarily comparable. The California and Peruvian fisheries are likely to impact the life table and regulatory mechanisms of the seabirds in different ways.

As more details of seabird life history and population dynamics become known, it may be possible to construct more useful models of seabird-fishery relationships. Also, improved models of the erratic temporal and geographic behaviour of the fish resources should improve the utility of seabird-fishery interaction models. The present attempt relies on an overly simple "black box" representation of these important components. The results of this exercise are suggestive, but should not be taken without reservation; yet the indication that seabirds may be slow in overall population response, but very sensitive to chronic forage depletion, should be considered in the determination of optimum fishery yields. The long life span of seabirds may allow sufficient time to gain understanding of trophic interactions so that appropriate action may be taken before species are actually endangered by prolonged reproductive difficulties. The developed countries are showing increased concern for maintaining the diversity of species in the natural environment. Let us hope that this trend reflects a movement toward human cultural maturity rather than a passing luxury allowed by inexpensive fuel and relatively abundant food.

Figure 12

Simulated time-series of seabird abundance for two levels of mean food availability (\bar{F} = mean food, $W = 1$, $\sigma = 1$, $p_r = 0.5$, non-linear reproduction model)



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