FLUCTUATIONS IN ABUNDANCE AND AVAILABILITY
CAUSED BY BIOTIC FACTORS

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Abstract

In the study of fluctuations due to biotic factors it may be useful to replace the usual way of assessing separately the effects of different factors on the populations by a more synthetic approach, starting from the consideration of the whole ecosystem whose different structural elements (niches) are linked by feedback relations. A number of properties general to such systems can be applied automatically in any special case. Fluctuations may be internal to the ecosystem and then related only to availability, or they may mean a change in the composition of populations, as free oscillations (predator/prey oscillations) or as forced fluctuations imposed directly or mediatly by environmental (rhythmic) changes.

Sardines and related species belong to a low trophic level and to a juvenile stage in natural succession. Feeding, prolificity, and the survival curve indicates that sardines and allied species are well adapted to cope with fluctuations. Stable environments are somewhat detrimental to sardines, favouring competition by species better adjusted to more mature ecosystems. Alternative fluctuations between sardines and these species (anchovy, mackerel, etc.) are related to environmental changes, and free oscillations of the predator/prey type seem to be negligible.

Assuming random fluctuations in hatching or in recruiting, the dependence of the actual population upon the same population in the preceding year causes fluctuations in the stock, with more or less regular peaks every four to eight years. The amplitude and average period of such fluctuations is related to properties of populations. When composed of a higher proportion of old specimens with a longer average life span and lower prolificity fluctuations are of more limited range, of longer period, and are more sensible to overfishing.

The importance of year classes, assumed so far to be random, in fact may be related to certain factors. The problem is difficult, and the method of multiple regression does not always lead to correct prediction. Some clues are given by the existence of exceptional years, and also by the eventual synchronism of fluctuations in different places. The evidence furnished is meagre but points to plankton production, and hence to the availability and abundance of food as a major cause of fluctuation. Since inertia of seas can transform irregular yearly inputs and outputs of heat into more or less regular fluctuations by autoregression, the possible synchronism of short-term fluctuations may be accepted. These fluctuations are superimposed on slower changes common to widely separated areas, and due to general modifications in the physical properties of seas.

Spawning takes place when water conditions are suitable for the future brood. A certain amount of hydrographic heterogeneity is observed, but the timing mechanism is not understood. Occasional lack of synchronization may be a supplementary cause of variations in the stock.

Availability is related to changes in the internal distribution of the elements of the ecosystem. Fishing techniques have developed so that in pelagic fishes availability is proportional to shoaling propensity. Shoaling is certainly related to feeding reactions and to small scale heterogeneity in the distribution of physical properties of water and of plankton, but only scanty direct evidence is available.

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FLUCTUATIONS DE L'ABONDANCE ET DES RESSOURCES SOUS L'INFLUENCE DES FACTEURS BIOTIQUES

Résumé

Dans l'étude des fluctuations dues aux facteurs biotiques, il peut être intéressant de remplacer la méthode qui consiste à évaluer séparément les effets des différents facteurs sur les populations, par une méthode de synthèse en partant de l'examen de l'ensemble du système écologique dont les différents éléments sont liés par des rapports réciproques. Un certain nombre de propriétés, qui sont communes à des systèmes de ce genre, peuvent être appliquées automatiquement à tout cas spécial. Les fluctuations peuvent se produire dans le cadre du système écologique et ne porter alors que sur l'accessibilité, ou consister en un changement de composition des populations sous forme d'oscillations libres (oscillations prédateurs/proie) ou de fluctuations forcées imposées directement ou indirectement par des changements (rythmiques) du milieu.

Les sardines et espèces voisines appartiennent à un niveau trophique assez bas et à un stade de succession assez jeune. L'alimentation, les courbes de fécondité, de survie et autres caractères de la sardine et des espèces voisines montrent que leurs populations sont bien armées pour s'adapter aux fluctuations. Les milieux stables sont assez défavorables aux sardines car ils favorisent la compétition par des espèces mieux adaptées à des systèmes écologiques plus courts. Les fluctuations entre les populations de sardines et celles des espèces voisines (anchois, maquereaux, etc.) sont liées aux changements du milieu, et les oscillations libres du type prédateur/proie semblent avoir peu d'importance.

Si l'on admet des fluctuations au hasard du nombre d'individus qui entrent annuellement, la dépendance de la population actuelle par rapport à la même population de l'année précédente engendre des fluctuations de peuplement qui se traduisent par des périodes de pointe plus ou moins régulières, espacées par exemple de quatre à huit ans. L'amplitude et la période moyenne de ces hauts et de ces bas sont conditionnées par les propriétés des populations. Lorsque ces dernières comportent une proportion plus élevée d'individus âgés, dont la durée moyenne d'existence est longue et la fécondité faible, les fluctuations ont une amplitude moindre, une période plus longue et les populations sont plus sensibles aux effets d'une pêche excessive.

L'importance des classes d'âge que l'on supposait régies par le hasard, peut être en fait reliée à certains facteurs. Le problème est complexe et la méthode de la régression multiple ne permet pas toujours de faire une prévision correcte. On peut tirer certains indices de l'existence d'années exceptionnelles ainsi que du synchronisme éventuel des fluctuations en différents lieux. Les données dont on dispose sont rares mais indiquent que la production de plancton, et par suite la quantité de nourriture, constitue la cause principale des fluctuations. Étant donné que l'inertie des mers peut transformer par auto-régression l'irrégularité des quantités annuelles de chaleur absorbées et rayonnées en fluctuations plus ou moins régulières, on peut admettre la possibilité d'un synchronisme des fluctuations à court terme. Ces fluctuations se superposent à d'autres et qui sont dues à des modifications générales des propriétés physiques des mers.

La pente a lieu lorsque les conditions de l'eau sont favorables au développement de la génération future. Une certaine hétérogénéité hydrographique doit jouer dans ce cas, mais le mécanisme qui en provoque les manifestations successives n'est pas connu. Un défaut éventuel de synchronisation peut constituer une cause supplémentaire de variation de la population.

L'accessibilité est liée aux changements intervenus dans la répartition interne des éléments du système écologique. Les techniques de pêche se sont développées de telle sorte que les disponibilités de poissons pélagiques sont proportionnelles à la propension de ceux-ci à se grouper en bancs. La formation des bancs est certainement conditionnée par les réactions des poissons à la nourriture disponible et à une hétérogénéité limitée de la répartition des propriétés physiques de l'eau et du plancton, mais on ne possède encore que peu d'éléments pour étayer cette hypothèse.
FLUCTUACIONES EN ABUNDANCIA Y ASEQÜIBILIDAD CAUSADAS POR FACTORES BIOTICOS

Extracto

Al estudiar las fluctuaciones debidas a factores bióticos, es aconsejable prescindir del sistema acostumbrado de ir analizando separadamente la acción de diferentes factores sobre una población, para adoptar un punto de vista más sintético, partiendo de la consideración de un ecosistema formado por una serie de unidades (nichos) unidas unas con otras por circuitos recurrentes o relaciones de retroalimentación. Ciertos número de propiedades comunes a todos los sistemas se pueden aplicar luego automáticamente a cada caso particular. Las fluctuaciones pueden ser internas al ecosistema y entonces afectan solamente a la asequibilidad, pero también pueden significar cambios en la composición total de la población, no en la simple distribución de sus elementos, y entonces tienen la forma de oscilaciones libres (como las que se establecen entre depredador y presa) o de fluctuaciones forzadas por cambios del ambiente, que pueden actuar directamente o a través de uno o más niveles bióticos.

Las sardinas y especies afines corresponden a un nivel trófico bajo y a etapas primitivas o juveniles de la sucesión ecológica. El modo de alimentarse, la fecundidad, la mortalidad y otros caracteres no enseñan que sus poblaciones estén perfectamente adaptadas a experimentar considerables fluctuaciones cuantitativas. Es más, si el ambiente se hace más constante, ejerce una acción nociva sobre las poblaciones de sardinas y especies afines, pues favorece la expansión de otras especies mejor adaptadas a ecosistemas de carácter más maduro. Las fluctuaciones alternan entre sardinas y otras especies (anchoa, jurel, etc.) más que una competencia dentro de un mismo nicho, representan cambios en las condiciones de ambiente. Oscilaciones libres como las que se establecen en los sistemas formados por un depredador y su presa pueden tener poca importancia.

Si suponemos fluctuaciones al azar en la cantidad de huevos avivados o en la de individuos reclutados y, además, reconocemos que la población de un año depende en parte de las características que tenía la población en el año precedente, llegaremos a comprender la existencia de aperiodos regularidades en las fluctuaciones que ofrece la población, en la que, en virtud de un sencillo mecanismo, pueden aparecer máximos ordinariamente separados entre sí por cuatro a ocho años. La amplitud y el período medio de estas fluctuaciones dependen de propiedades de las poblaciones. Si están compuestas por una elevada proporción de individuos viejos, o la edad media es elevada, o la fecundidad es baja, las fluctuaciones se mueven entre límites más próximos, son de período más largo y más afectables por la pesca intensiva.

Lo dicho vale aceptando que la importancia de las sucesivas clases anuales varía al azar, pero en realidad ella depende de factores determinados, aunque difíciles de precisar. El método de las regresiones múltiples puede conducir a conclusiones engañosas, inutilizables para la predicción. Algunos indicios útiles derivan de la existencia de años excepcionales, que permiten relacionar una clase anual muy notable con cierta característica local. También tiene valor el estudio del sincronismo entre las fluctuaciones de áreas alejadas. Los datos señalan que la producción de plancton y cantidad de alimento presente en el agua son factores fundamentales de las fluctuaciones. Puesto que la inercia del agua del mar puede transformar una serie irregular de ingresos y salidas anuales de calor en fluctuaciones, si no regulares, por lo menos con "picos" cada un número medio de años, no repugna aceptar por esta causa un posible sincronismo entre las fluctuaciones de la producción de plancton en áreas alejadas. Estas fluctuaciones de corto período se sobreponen a otras más lentas, éstas comunes a áreas muy distantes y producidas indudablemente por cambios más pausados en las propiedades físicas de los océanos.

La prena parece estar sincronizada con ciertas propiedades del agua, en virtud de un mecanismo desarrollado bajo la guía de la selección natural y que consigue que las crias se desarrollen bajo condiciones propicias. Al parecer, las condiciones para la puesta incluyen cierto grado de heterogeneidad hidrográfica. El fallo de semejantes mecanismos, por falta de correspondencia entre características físicas y bióticas que suelen ir asociadas, puede ser una causa suplementaria de variaciones irregulares.

La asequibilidad se relaciona con cambios en la distribución de los individuos en el seno del ecosistema. La pesca de las especies pelágicas se ha organizado de tal modo, que la máxima asequibilidad coincide con la máxima realización de la tendencia a formar grandes cardúmenes. Ciertamente, esta tendencia se relaciona con la alimentación y con el grado de heterogeneidad hidrográfica y planctónica a pequeña escala. En aguas estabilizadas, mas heterogéneas, se forman cardúmenes; en los momentos de mezcla y homogeneización, los peces se dispersan. El "atmósfera" nictemeral complica estos fenómenos. Las migraciones no son más que cambios en la posición de los cardúmenes y en la tendencia a formar cardúmenes, a lo largo de las costas, y pueden considerarse, igualmente, como cambios internos al ecosistema y, que por tanto, afectan intensamente a la asequibilidad.
THE ECOSYSTEM APPROACH

1.1 Introduction

The ordinary approach to the study of dynamics of fish populations is to consider a unispecific population and to assess quantitatively by analysis the actions of other species, including man, and of different environmental factors. In this rather clumsy procedure one soon loses sight of the system as a whole and the question arises whether such a method is suitable for sardine research, notwithstanding its evident utility for species which stand at the end of food chains and where removal of individuals by fishing is an important regulatory factor.

As the author is less familiar with the field of fisheries research than with that of general marine ecology, the starting point will be a search for what Slobodkin (1958) has called "metamodels" large enough to predict the behaviour of any specific community - an approach that is more synthetic, more interested in a dynamic than a kinetic angle, and also speculative enough to explore new outlooks.

1.2 What are fluctuations in a fishery?

Fluctuations in a fishery are irregular departures from the average catch per unit of effort; as fluctuations by definition do not consistently follow a trend, the ecologist, aiming to cope with the ups and downs, searches indefatigably for cycles.

Ecosystems are very complicated structures, and it is almost impossible to identify the causes of fluctuations and classify them as abiotic, biotic, and human. A certain overlap in these categories is inevitable.

1.3 Organization of the ecosystem

Ecosystems result from the integration of populations of different species in a common environment. They rarely remain steady for long, and fluctuations lie in the very essence of the ecosystems and of every one of the unispecific populations.

An ecosystem is: (a) a reticulated path of energy flow, and (b) the material base that is the carrier of the energy flow, a "machine" built by discontinuous and reproducible units. Relations between these organisms may be of a complementary (predator/prey) or competitive nature.

It has often been remarked that "density dependent" factors in populations, the only ones capable of regulating numbers, involve some form of feedback. Between species linked by complementary relations, feedback is negative and stabilizing, or compensatory, so that the structure is maintained, e.g., the increase of a predator or fishing effort means a decrease of prey or of the fished stock, which later turns into a decrease in the number of predators. Feedback in partial systems involving competing individuals is null or positive, information is gradually lost and the structure simplified up to a single species per niche, according to Gause's law. Species that compete, without negative feedback between them, belong in the same niche.
Every niche may be appraised quantitatively as a number and class of individuals or simply as biomass (B, e.g., as dry weight); it affords the channel for a limited flow of energy. This energy may be conveniently evaluated as net productivity (P), or as the excess of synthesized organic matter that is forwarded to other niches. This is what happens when the ecosystem is steady and there is a turnover of individuals.

Productivity decreases necessarily in the successive niches linked in a food chain, but biomass does not necessarily do so. Quotient P/B is higher in niches of a low trophic level (primary producers) than in a high trophic level (carnivores). The quotient P/B is directly related to the mortality rate and to the rate of dissipation of energy. In every niche, along natural succession, quotient P/B decreases. A higher productivity implies a rapidly falling survival curve of the species.

Populations not well regulated by feedback and at the mercy of density independent factors may fluctuate around an average situation, fixed by the temporal pattern of environmental change.

In a preliminary approach it would seem advisable to leave aside stochastic questions and state the problems in deterministic terms; it is soon evident that in low level niches of ecosystems subjected to strong fluctuation, random values and configurations may assume real importance.

1.4 The changing ecosystem

The regular and irregular changes that an ecosystem experiences over a period of time may be summarized as shown in Table I.

Maturity can be compared not only in corresponding or homologous niches or successive ecosystems, but also in a single or actual ecosystem where niches of a higher trophic level have a more mature character. Less mature ecosystems or parts of ecosystems "export" production to more mature adjacent systems. As a general rule, fluctuations in more mature niches are of smaller amplitude and longer period. Plankton is a less mature community than benthos on soft bottom, which in turn is less mature than hard bottom benthos.

2 GENERAL PROPERTIES OF THE ECOLOGICAL NICHE TO WHICH SARDINES AND RELATED SPECIES BELONG

2.1 Place in succession

Multiple criteria established by the study of connections of clupeid populations in natural ecosystems permit us to predict types of fluctuations in sardine fisheries. This first step is necessary before planning a research program and before constructing detailed quantitative models.
Table I

DIAGRAM OF THE REGULAR AND IRREGULAR CHANGES IN AN ECOSYSTEM

<table>
<thead>
<tr>
<th>Ecosystem in an ideal steady state</th>
<th>Real ecosystem</th>
<th>Action of environment</th>
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<tbody>
<tr>
<td>Average frequencies of reproduction and death constant in time. In every species individuals move at random through space.</td>
<td>Internal rhythms. Synchronization in reproduction and death, and orientation and synchronization of movements. Free oscillations arising from inertia and time lag in the feedback systems (predator/prey oscillations) Forced fluctuations (eventually regular oscillations) imposed by environmental changes, either (a) directly, or (b) indirectly, at other biotical levels. Short and repeated successions</td>
<td>Environmental rhythms (a) Nyctemeral (b) Tidal (c) Monthly (d) Yearly (e) Multiannual, in part due to inertia in the system atmosphere/seas, in a balance of irregular inputs and outputs of heat (f) Random fluctuations (g) Secular climatic trends</td>
</tr>
<tr>
<td>Regulation of numbers by efficient feedback systems. Net rate of increase of all species null.</td>
<td>Entrainment of free oscillations by forced oscillations and general adjustment of the rhythmicity of ecosystems to environment. (Reactions of organisms)</td>
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Sardina and Sardinops, more than Sardinella, are pelagic fishes limited to coastal waters, and to environments subjected to an annual cycle, with phytoplankton production concentrated in a few peak periods. They are found in areas which are periodically enriched usually by upwelling, and which export organic production to neighbouring areas.
Sardines and related species belong to ecosystems in the juvenile or primitive condition that have relatively short food chains. In more mature communities, niches in a higher trophic level are better furnished. Hanaoka (1953) found that the percent of ichthyophagous fishes is positively correlated to the "oceanic" conditions of Japanese bays; these conditions were measured by size, depth, and similarity of salt content with offshore waters.

Fluctuations imposed by an unstable environment arrest the advance of succession, and the ecosystems remain in a juvenile state. A more stable situation (i.e., a series of years with less important environment fluctuations or with a major influence of offshore water) may be detrimental to species adjusted to thrive under changing conditions (i.e. Sardina), favouring the competition of species such as Sardinella, Engraulis encrasicolus, Trachurus, Scomber colias, common in offshore waters and in coastal areas with a narrow shelf.

As a wound inflicted on the body of an organism establishes a rejuvenated area of regeneration, any disturbance of an ecosystem or of a part of an ecosystem results in an increase of productivity and leads to a less mature state. Fisheries cause a rejuvenation of populations, which affects the whole ecosystem.

2.2 Trophic level and trophic relations

Etmnalosa and Brevoortia are exclusively filter feeders (Bainbridge, 1957) and sardines and allied species belong also to a relatively low trophic level. Young Sardina and Sardinops up to about 40 mm in length (about four months old) have underdeveloped gillrakers and are dependent on the active capture of copepods and small planktonic larvae. Later, they ingest an increasing proportion of microplankton, screened by the rakers. In Sardinops melanosticta this way of feeding continues till the fish reaches 150 mm in length (Yamashita, 1955; Yasuda and Hiyame, 1957); in a specimen of 120 mm, the area of gillrakers amounts to 7.2 cm² and can filter about 270 litres per day (Yoshida, 1955; Yoneda and Yoshida, 1955); as a first approximation it may be accepted that filtering capacity is proportional to the squared length. When Sardina and Sardinops reach a certain size, filter feeding in most environments is insufficient for sustained growth. Increasing quantities of small animals are selectively taken; at least Sardina pilchardus eats almost anything (Scoultier, 1934; Massut, 1946, etc.). Sardinella aurita and Sardinella longiceps (Nair and Subrahmanyan, 1955) also filter microplankton and snap small prey.

Feeding and shoaling may be related. In general, shoal forming is less common in animals actually competing for food. Fishes, when shoaling, feed automatically; either there is plenty of food, or they do not feed at all. Some data point to the existence of a more active feeding during daytime in Sardina and Sardinops. It may be that fishes looking for prey then disperse over the bottom, and shoal, especially at night, when filtering.

There seems to be general agreement regarding change in types of food and feeding habits according to age groups. Data reported by Nakai (1960) on Sardinops melanosticta do not support the hypothesis of a diel periodicity in feeding.

Intensity of feeding and the abundance of the food supply may indirectly control the tendency to aggregate and the speed of exploration. It is logical to assume that speed increases
when water leaves less material over the gillrakers. Further research on this subject would be advisable.

As sardines are microphagous animals, able to exploit the ample resources of plankton production, they may be compared to whalebone whales. Whales have a tremendous exploratory power and congregate where plankton yields a good food supply. Compared with whales, sardines appear to be poorly fitted, but we have no literature to prove the point.

The seas have a rich small-scale structure in the distribution of properties of water and of plankton. Shoaling of fishes, if related to exploration and to the best utilization of resources of lower trophic levels, has to keep causal connections with small-scale configurations in the distribution of the properties of the seas. A general rule in ecology is that information accumulated by a species provides a short circuit for random exploration; it is not compatible with the manifested workings of natural selection to suppose that sardines are devoid of direct and indirect means to aggregate in places where feeding may be more effective.

If a considerable increase is observed in the number of fishes feeding on sardine, a weakening of fluctuations follows, and a step forward is taken in the succession; for this very reason, sardines are liable to be gradually replaced by species of a more "mature" character. Populations of sea birds feeding on sardines and related species can search a vast area, looking for the proper places to feed, and thus the inconveniences of local fluctuations are avoided. Birds develop in great numbers only where intense upwelling is a regular phenomenon and assures a sufficient food supply.

2.3 Prolificity and development

The breeding, growth and survival curve of sardines and allied species conform to a low level and primitive niche. The number of eggs spawned by a female in a season divided by the cube of the total length of the female in cm ranges from seven to 12 (Sardina pilchardus, Sardinops ocellata, Sardinops caerulea). In such prolific species, census of eggs and larvae may give a fair estimate of the population density. Perhaps fecundity can vary independently of size, as demonstrated by Bagenal (1957).

Anadón (1954) believes that the fecundity of Sardina pilchardus of northwest Spain is higher than that of Sardinops caerulea of California, as it is related to a shorter average life span. The expression \( \int e^{-rt} dt = 1 \) (\( t_p \) = probability of life at age \( t \), \( n_t \) = fecundity at age \( t \), \( r \) = net rate of increase) relates fecundity to the survival curve; the steeper portions of this curve cover the so-called "critical periods" of high mortality (Marr, 1956).

Eggs hatch in two to three days and sardines attain a total length of 110 to 140 mm at the end of the first year; in general, they are then able to spawn. Although the life span may be ten and more years, growth is very slow after the first three to four years, and the bulk of the populations is made up of young individuals. The turnover in weight per year, P/B, is higher than in most fishes; it is between 0.75 and 1.

Data point to a total yearly mortality of 50 to 80 per cent of which about half, and very often much less than half, is accounted for by fishing.
By analogy with equivalent organisms in other ecosystems it can be assumed, as a working hypothesis, that sardines and related species are very euryoic; that, either as a primitive or as a neotenic trait, they have a notable somatic plasticity (vertebral fluctuations); that tendency to genetic differentiation of populations is not high, and that direct responses should prevail over endogeneous rhythms (Margalef, 1959). Sardine populations are naturally adapted to change and only in fluctuating conditions can display their superiority (cf. Nicholson, 1957). The foregoing ideas are simple suggestions for research in comparative evolution of clupeids.

The genetic flow and degree of differentiation and the structure of populations are important in assessing the ecology and evolution of sardines and sardine-like fishes. Sprague (Ahlstrom, 1960) has detected some heterogeneity in the distribution of blood groups in Sardinops caerulea. Free complexes of amino-acids in muscular tissue are influenced by food and perhaps by other factors; a genetical local differentiation in relation to them has not been definitely proved. The dependence of meristic characters in particular the vertebrae, on environmental factors, of which temperature is the most important, seems established (McHugh, in Ahlstrom, 1960). However, sometimes even with decreasing temperatures there is a decrease in vertebral numbers in batches of fishes born successively in a season (Sardina pilchardus); in other fishes, bigger eggs produce larvae with an average higher number of vertebrae. Many workers are convinced that sardines spawn many times in a season, and perhaps the size of eggs is not only related to temperature but also to the ordinal number of the spawned batch to which they belong. In this connection, local and time differences in the average size of eggs of sardines should be studied in the manner of the research done on the anchovy by Demir (1959).

The problem of plasticity versus stabilization in the development of sardines is complex: its understanding lies in the study of local differentiation. However, the species seem to be well adjusted so as to resist fluctuating conditions and to be integrated in ecosystems of only relatively low maturity.

2.4 Competition

In the relevant ecosystems, competition is indiscriminate and assumes the form of a brutal dominance, based on prolificity; it is only in more integrated and mature ecosystems that we observe subtler actions, based on metabolic efficiency.

The only serious competitors of sardine and related species are the filter feeders, such as pelagic tunicate (Salpae), which are capable of massive multiplication.

There has been question of a certain alternation in the fluctuations of Sardina pilchardus and other species, such as Clupea sprattus, Trachurus trachurus, Engraulis encrasicholus (de Buen, 1927, 1929, 1932; Navaz, 1946; Anadón, 1950; Mužinić, 1958). Full competition is not necessarily at the base of such reciprocal fluctuation, since the different populations involved are comparable quantitatively only when allowing for the tenfold larger sardine population. Such alternate fluctuations reflect rather a change in the conditions of life, since there is a certain ecological segregation: Clupea sprattus prefer water of lesser salinity, and in the Baltic its periods of abundance coincide with abundant runoff (1903-38, 1924-36, 1950-57; Nikoleav, 1958); Engraulis and Trachurus favour more oceanic and stable conditions so that competition would be established only with the older sardines. Biologically, these fishes play the role of indicator organisms rather than that of true competitors.
TYPE OF FLUCTUATIONS TO BE EXPECTED AND COMPARISON WITH EMPIRICAL DATA

3.1 Relative importance of different causes of fluctuations

Sardines are dependent on plankton, but feeding of fishes does not provide a sufficient feedback for the stabilization of phytoplankton production. In any case, the rate of multiplication of plankton and sardines would impose free oscillations of a very short period, which would affect plankton but not fishes.

Since the superior trophic levels of the ecosystems to which sardines and allied species belong are poorly developed, interaction with ichthyophagous fishes plays a minor role in the observed fluctuations (free oscillations of a period of more than a year). Moreover, many predatory fishes are migratory and prey in a complicated pattern upon different populations of sardines. Adult sardines swallow their own eggs and larvae; cannibalism may be a minor cause of free oscillations (Anadón, 1954).

Schaefer (1954) explores the possibility of explaining fluctuations in sardine populations by the interaction of sardine and man, but damage caused by fishing is rarely serious, since sardine populations easily recover, even when subjected to a continued fishing effort. Oscillations of the predator/prey type, originating in a feedback system of sardine to man, should be of a longer period than the observed fluctuations. But fishing means a rejuvenation of ecosystems and accelerates random fluctuations by shortening the average life span of fishes.

The changes of biomass and availability in sardines and related species are considered to be the result of forced fluctuations, imposed by environmental changes, more than of internal rhythms, or changes in local distribution, or of oscillations in overfishing. Nakai (1960) suggests that a reduction of the population may accelerate reproductive maturity as a sort of intraspecific regulatory mechanism.

We may conclude that biotic fluctuations in the sardine populations are related principally to changes in the supply of basic food. Phytoplankton production is probably the more important cause of fluctuations as it is dependent on abiotic factors, and an indirect relation exists between abiotic environment and sardine populations. It is generally agreed that the quantity of adequate food may be of maximum consequence in the first period of the life of sardines, and that such a relation between sardine populations and plankton may be established through a more or less efficient complex of synchronizing mechanisms.

3.2 Fluctuations in the stock resulting from autoregression and random variations in recruitment

Palmgren (1949) discussed the possibility that regular cycles originate from autoregression, or the interaction of climatic random changes and the influence of the population density in the preceding year.

Let us consider four year classes and suppose that differences in availability are not important, that mortality after recruiting is nearly constant, say 66 per cent a year, and that
the weight of fishes doubles in a year. We can start with a series of random numbers (x) taken from the tables of Fisher and Yates, as 36, 42, 56, 96, 38, 49, 57, 16, 78, 9, 44, 84, 82, 50, 83, 40, 96, 88, 33, 50, 55, 59, 48, 66, 68, 83, 6, 33, 42, 96, 64, 75, 33, 97 .... With these numbers we can obtain a second series, representative of the weight of the catches in successive years, computing every term as:

\[ x_{n} + \frac{2/3}{x_{n-1}} + \frac{2/3}{x_{n-2}} + \frac{2/3}{x_{n-3}} : \overline{152}, 144, 134, 135, 87, \overline{129}, 78, 103, 141, 157, 156, \overline{178}, 142, 164, \overline{206}, 146, 145, 129, 128, 120, 141, 151, \overline{165}, 111, 94, 91, 141, 157, \overline{173}, 140, 172 .... , \]

with peaks distributed every four to eight years.

The average period and amplitude of the fluctuations are related to the range of variation of the independent random variable and to the way of combining the random terms. Summation over a longer series of terms makes fluctuations more regular and smooth. In species of lower prolificity, the dependence of a number of offspring on a number of parents (Ricker, 1954) contributes to fluctuations.

Very different amplitudes of the fluctuations in different areas of the range may be found in the same species: in Lynx canadensis there are 100:1 in north, 50:1 in centre, and 20:1 in southern British Columbia (Dymond, 1949, in Andrewartha and Birch, 1954). In sardine populations, the ratio between maximum and minimum catches may reach 40 or more (Sardinops caerulea of California, Sardina pilchardus in northwest Spain), six to 15 in most situations (e.g. Sardinops melanosticta), and lower values in Mediterranean populations of Sardina pilchardus.

Amplitude of fluctuations is related to the important quality of the niche or of the ecosystem that we have called maturity. Mediterranean populations of Sardina pilchardus are in a more mature state than populations of the Galicia coasts. Mature populations, less prolific and with a longer life span, do not follow environmental changes so quickly, their fluctuations are of longer period and smaller amplitude, and are more sensible to overfishing.

Random dispersal movements from spawning centres makes the proportion of older individuals increase with distance. Fluctuations are expected to show a corresponding local diversity, that is, greater differences between maximums and minimums and a shorter average period close to the spawning areas, and the consequences of fishing can be expected to be more serious in the peripheral regions. Complications are introduced by movements of some fishes that recombine different groups of the total population at random with restrictions imposed by the general pattern of physical conditions.

We have assumed fluctuations based on irregular or random factors, that, notwithstanding, should have a certain average time between peaks. The periodicity may be reinforced by entrainment of eventual free oscillations, and also by the physical factors responsible for vertical mixing and phytoplankton production which themselves may represent an autocorrelated series with peaks every few years, as manifested also in the discontinuity of deep-water movements (Cooper, 1955).

Many of the papers presented at this Meeting offer examples of fluctuations with peaks separated by five to ten years (e.g. Brazil, Morocco, Portugal, Turkey). Lack of synchronization between the peaks suggests autoregression and random changes in the environment.
"Random" means here that environmental changes are so complex that the probability of coincidence in separated areas is very small.

3.3 Fluctuations in brood strength, and survival rate

We have now to look for the causal determination of the seemingly random numbers that we combine in our summatory expressions - in other words, we now proceed to the interpretation of the strength of the year classes (as hatched or as recruited individuals) and of the yearly values of the mortality rate. An assessment, of course, is far beyond the scope of this paper.

The relation between the obtained series of numbers and certain system of biotic and abiotic properties of the sea has to be established either by (a) searching for empirical correlations between brood strength or mortality and selected hypothetical agents, or (b) proceeding to a logical and experimental analysis of the acting factors, despite poor quantitative correlations.

The method of multiple regression was successfully used by Riley (1939) in general problems of plankton production, and in fisheries research by Doi (1955) and Tham (cited by Hardy, 1958), but has many pitfalls. Given a limited number of points, often no more than ten, and a sufficient number of variables, it is always possible to obtain a good correlation with reasonable accuracy. The same may be said of more elementary methods.

But significant correlations may be biologically inoperative (Bell and Pruter, 1958). A critical study is necessary to ascertain the meaning of regressions. In most instances, prediction fails, and we are then forced to enlarge the first scheme, introducing new parameters and changing constants. This happened in studies on the relation between phosphate concentration in surface waters and the quantity of young fishes, and in our research work on the relations between wind and surface temperature as indicators of upwelling and standing crop of phytoplankton, although both adduced relations have a logical background of causal relations.

Inaccuracy of predictions is most likely to occur when presumed causal factors are selected by "intuition" without previous basic study.

As for the method of analysis of series with mechanical or electrical auto-correlators, a serious limitation exists in the sense that historical phenomena cannot be related to the simple addition of different independent functions; the sum in a precedent moment is what matters.

3.4 A few positive indications

Now and then unique situations occur where an obvious factor overcomes the combination of all other random, or unknown, effects; for example, the winter of 1950-51 was exceptional along the Castellón coasts (west Mediterranean). A very strong upwelling was ascertained by different methods, and the high-standing crop of phytoplankton has never since been equalled. The annual class of Sardina pilchardus born that season was also excellent and has been adopted by Gómez Larraneta and co-workers as index 100 for evaluating the precedent and posterior
year classes. This is a strong argument for the relation between plankton production and sardine breeding success, but adjustment in subsequent years was not good, as is seen from the following figures:

<table>
<thead>
<tr>
<th>Season</th>
<th>1951</th>
<th>1952</th>
<th>1953</th>
<th>1954</th>
<th>1955</th>
</tr>
</thead>
<tbody>
<tr>
<td>Relative value of the year class of Sardina pilchardus</td>
<td>100</td>
<td>92</td>
<td>60</td>
<td>55</td>
<td>88</td>
</tr>
<tr>
<td>Average biomass of phytoplankton from December to May; pigment units/m³</td>
<td>3,850</td>
<td>1,970</td>
<td>3,060</td>
<td>2,750</td>
<td>2,730</td>
</tr>
</tbody>
</table>

Similar conclusions may be drawn from the relations between the survival of Sardinella longirostris and the density of phytoplankton (Panikkar, 1952; Nair and Subrahmanyan, 1955). The hypothesis of Nair and Subrahmanyan that fluctuations of the most important element of phytoplankton, Fragilaria oceanica, are due to periodic asexual processes, is not in agreement with general experience; if nutrients were sufficient and Fragilaria were not increasing, other diatoms would flourish and the diatom bloom would continue anyway.

Possible synchronism between fluctuations in different areas merits careful study. Even if the peaks every four to eight years derive basically from random causes, there may be perhaps a basic common cycle affecting the seas as a whole, originating in the interaction of inertia of water and random inputs and outputs of heat. Moreover, some exceptional years may affect the cycle of production in far apart areas, and result in a relative synchronism of fluctuations for a certain period of time.

In Sardina pilchardus of northwest Spain (Vigo), the peak catches occurred in 1937, 1944, 1951 and 1956; in Marín, a few kilometres away, 1931, 1937, 1939, 1945, and 1947 produced very good year classes (Anadón, 1954); Sardinops caerulea of California presented peaks in 1934-35, 1941-42, and 1949-50; Sardinella in Israel in 1935, 1940, 1944 and 1951 (Ben-Tuvia, 1957) and, in India in 1927-28, 1949, 1953 and 1957. The remarkable thing is that maximum peaks are generally separated by a period averaging about seven years, as are fluctuations of physical characteristics in some notable places, e.g. in "El Niño" off the coast of Peru (Schweigger, 1954; Posner, 1957) with peaks in 1923-26, 1930-31, 1939-41, 1948-49 and 1951-53 or, by another count, in 1891, 1911, 1918, 1925, 1932 and 1939, these fluctuations were reflected also in the local populations of anchovies.

These local short-term fluctuations are interconnected with trends or fluctuations of longer period. A general decrease of stocks started in 1938 and was particularly rapid around 1946. A similar pattern pertained in northwest Spain (Sardina pilchardus), in California (Sardinops caerulea), and in Japan (Sardinops melanosticta, Kurita, 1957; Uda, 1957, etc.).
The similarity of pattern is indicative of common causes of basically abiotic origin, reflected also in other biotic changes. The effects of overfishing as a detrimental factor are generally dismissed by authors (Anadón, 1954; Kurita, 1957).

It seems that the reduction of sardine populations is related to an increasing influence of warm and offshore waters, favouring more mature and less productive ecosystems. Fischer-Piette (1958) assumes a "meridionalisation" of the coastal communities of northwest Spain, which started around 1932-33 and lasted until about 1950; it was followed by a "septentrionalisation" which is now in operation. The sediments of the Ria de Vigo provide us with a record of past events in the form of plankton remains and plant pigments. An important change was recorded some 20 years ago (Margalef, 1956, and unpublished), when a decrease of sardine populations and the acquisition of a more southern character by coastal communities coincided with a strong decline in the number and average size of Melosira sulcata, the invasion of Thalassiosira rotula, and other signs of decreased circulation and production, and more lasting stability periods. In northwest Spain, changes in availability may be as important as changes in stock, since traditionally fishing is almost limited to the Rias.

A relation with basic phytoplankton production seems clear, but exact quantitative correlations cannot yet be established. We are only beginning to realize that sardines are a part of complex ecosystems.

There is a certain parallelism in the trends manifested over a period of years. Recent progress in physical oceanography, based mainly on the results of the International Geophysical Year, will surely provide a new basis for discussion.

3.5 Timing and locating mechanisms in spawning

It has been suggested that induction to spawning may be related to a certain temperature, in most cases, between 14° and 18°C; photoperiodicity seems less probable, owing to the wide range of spawning time, which often lasts about eight months. In Sardinia pilchardus, Sardinops caerulea and Sardinops melanosticta, of the northern hemisphere, spawning is centered around winter and spring; Sardinops ocellata of South Africa and Sardinops neopilchardus of Australia spawn in about the same months and in the austral summer. The existence of subpopulations with different spawning time, as suggested by Andreu (1955) in Sardinia pilchardus, if confirmed, would help disentangle the spawning mechanism.

Analysis of data shows that temperature cannot be a decisive factor leading to spawning. In most species spawning lasts a considerable part of the year and takes place under very different temperatures. This is true at least in Sardinops caerulea and Sardinia pilchardus, but in these species the possible existence of subpopulations with a different spawning reactivity has been assumed. If such were the case, this would afford a mechanism enabling genetic differentiation; it has been found that different Indian species of Sardinella spawn in different seasons (Nair, 1960). The observation of Devanesan and Chidambaram (1948, reported by Nair, 1960) made on Sardinella longiceps, that spawning is concentrated around the day of the new moon, suggests a possible occurrence of time mechanisms based on light perception, but examination of empirical data relative to other species does not lead to the acceptance of photoperiodicity. Unfortunately, no spawning has so far been induced through experiments. Nair
points to a possible influence of the monsoon on the spawning of Sardinella, possibly through the action of a complexity of ecological factors. Spawning of _Sardina pilchardus_ on the north-west African coasts occurs later in summer and at higher temperatures than in the Mediterranean (Furnestin and Furnestin, 1959): in such places there is upwelling in summer. Of course, spawning areas can only be hydrographically and geographically defined.

Production of phytoplankton is dependent on enrichment and turbulence and is related to temperature only in an indirect way since most species are euryterm. My personal impression is that temperature has to be played down also in other fields of marine ecology. If one remembers that Sardinops and Sardina live in similar latitudes and that spawning is generally more or less associated with vertical mixing, we can readily accept that spawning occurs under relatively similar temperatures. Sardine spawn in most areas after feeding over the bottom at the end of a planktonic cycle and before or just at the beginning of a new cycle introduced by upwelling or vertical mixing. Carotenoids, or other active substances in the food, may also be operative.

Spawning shows a synchronization with phytoplankton production that correlates more or less well (Barnes, 1957). Spawning of _Sardina pilchardus_ starts before strong upwelling, at least in the western Mediterranean. Data on the same species in the Adriatic also seem to support the view that spawning is not linked to actual upwelling (Gamulin, 1954); this is to be expected, since small zooplankton, the food of larvae, is very scarce in upwelled water. In California, a positive correlation was found between importance of upwelling and spawning (California Cooperative Sardine Research Program, 1950-52), but in a later report (1958) the opinion is sustained that excessive upwelling has been detrimental to sardine stocks.

Any efficient synchronization mechanism between spawning time and increase of mixing or upwelling must work so that sardines spawn in patches of stabilized water, rich in zooplankton, but with spatial and temporal proximity to upwelled water, so that young fishes, when a few centimetres long, can feed adequately and survive in good numbers. Spawning of sardines, then, would be more efficient when associated to areas of hydrographic heterogeneity, such as can only be common in bays, between islands, or over a shallow shelf.

Although sardines are not aggregated at spawning time, eggs are usually highly concentrated, often over a thermocline in water rich in zooplankton. The young are dispersed, carried by currents, and often found in upwelled water rich in phytoplankton. Most data confirm the existence of a certain amount of hydrographical heterogeneity in and around the places of spawning. Shoaling behaviour takes place later.

Let us speculate further: if a definite spawning stimulus has been selected and a convenient regulating mechanism fixed by evolution, the population becomes adjusted to spawn under certain conditions. In the course of time, the ordinary association between starting stimulus and efficient food supply may break down at certain points. Disruption of a timing or anticipatory mechanism may result, for example, in good plankton production and bad spawning, with an apparent discontinuity in the work of the mechanism of fluctuations.
FLUCTUATIONS IN AVAILABILITY

4.1 Ecological meaning of availability

Every species uses stored information to reduce the exploration that is necessary to obtain food. In the course of evolution, the information becomes organized as a pattern of endogenous rhythms, instincts, etc. The development of fisheries has experienced a similar evolution. Through trial and error, fishing gear and methods have evolved towards obtaining the maximum catch at lowest cost. Pelagic fisheries have been generally adjusted to exploit big shoals, and when fishes do not conform to this distribution, or do not adopt it when stimulated by light, it is assumed that they are less available.

Availability is related to internal rhythms of the ecosystem, that in time change the probability of finding individuals in a certain point of space. Many aspects of aggregation are related to species ethology (Breder, 1954; Kuroki, 1953; Morrow, 1948; Parr, 1927; Verheijen, 1958, etc.), and others to environment.

4.2 Small scale hydrographic structures, plankton heterogeneity and shoaling

Marine fronts, like atmospheric fronts, develop small scale vortexes near the boundary structures; the careful study of coastal waters has uncovered a vast amount of unsuspected hydrographical heterogeneity. Sardines are bound to such coastal waters, and it is probable that spawning is especially efficient when associated with a certain type of heterogeneity.

Shoals of fishes may be guided by many different factors, biotic and abiotic, to place themselves in the best conditions for feeding, just as herring aggregates in patches of Calanus (Cushing, 1955). Published data, mostly indirect (Pack, 1956; Yokota et al., 1953) suggest that development of a thermocline, stabilization of water and "maturity" of ecosystems, lead to an increasingly contagious distribution of individuals and shoals, that is, to bigger shoals in the sardine and related species. In periods of mixing, on the contrary, hydrographic and planktonic heterogeneity is lost or less persistent and shoals break down and disperse; the effect is reinforced if fishes feed better close to the bottom. So far, no causal explanation of such behaviour is available.

Nychtemeral rhythms increase the complexity of the rhythms of longer period affecting the spatial structure of the ecosystem. Moreover, it seems that the movement of shoals is not always related to hydrographic or planktonic heterogeneity. The whole problem is extremely complex; we would add only that distribution of fishes has more to do with small scale heterogeneity of the seas than is generally recognized, and that our Institute has started working along these lines.

In Sardinops ocellata, du Plessis (1960) has found very suggestive positive correlations between plankton, temperature, and availability over a period of seven years. South African investigations may help to clarify mechanisms also operating in other areas with more complex overall relations. Spawning intensity is negatively correlated with availability. Also in the Mediterranean, the development of a thermocline, a higher temperature near the surface, leads to the aggregation of fishes, facilitating fishing or increasing availability, and is opposed

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to the mixing which favours the success of spawning.

Catches of sardine in the Marmara Sea are positively correlated to the sea level (Artüz, 1960). If a higher sea level indicates a stronger flow of water of low salinity and a more active circulation, there is perhaps here a parallel to the "Ría" of Vigo, where the influx of Atlantic water and a stronger circulation is generally followed by the apparition of sardines.

4.3 Migrations

Migrations in sardines and related species are equivalent to shoaling, and to dispersion and movement of shoals, on a larger scale than so far discussed - that is, on a scale that goes beyond the average range of action of a fishing fleet based in one harbour. But it is often inoperative to study pelagic populations with reference to a co-ordinate system based on land.

In relation to availability, migrations generally take the form of a drifting of the shoals or of the shoaling tendency along coasts, complicated by a steady dispersal of the growing individuals from spawning areas to more peripheral situations, to the no-man's-land that constitutes the boundaries between different units of population.

5 REFERENCES


Andreu, B., Consideraciones ecológicas sobre la sardina gallega. Inst. Invest. pesq. II. Reun. Product. pesq. 65-70


Breder, C.M., Equations descriptive of fish schools and other animal aggregations. Ecology, 35: 361-70

California cooperative oceanic fisheries investigations, Progress reports 1953-58

California cooperative sardine research program, Progress reports 1950-52


de Buen, F., Sustitución alternativa de las especies emigrantes. Bol. Pesca y Caza, Madr., 135


, Nuevos datos sobre la alternancia en los peces emigrantes. An. Univ. Madr., Ciencias, 1(2)


Hardy, A.C., 1958, Toward prediction in the sea. In: Perspectives in marine Biology, a symposium, ed. by Buzzati-Traverso, Berkeley Univ. California Press, 159-86


Margalef, R., 1956, Paleoecología postglacial de la ría de Vigo. Invest. pesq., 5: 89-112

Margalef, R., 1959, Ecología, biogeografía y evolución. Rev. Univ. Madrid, 8: 221-73


Palmgren, P., Some remarks on the short-term fluctuations in the numbers of northern birds and mammals. Oikos, 1: 114-21


Ricker, W.E., Effects of compensatory mortality upon population abundance. J. Wildlife Mgmt., 18: 45-51


1284
Schaefer, M.B., Some aspects of the dynamics of populations important to the management of the commercial marine fisheries. Bull. interamer. trop. Tuna Comm., 1: 26-56

Schweigger, E., Ensayo sobre las variaciones periódicas de la temperatura del mar y sus ciclos en el norte del litoral peruano. Bol. cient. Comp. adm. Guano, 1(2): 5-20


Tokai Regional Fisheries Research Laboratory, Synopsis on the Biology of Sardinops melanosticta (Temminck and Schlegel). In: Proceedings of the World Scientific Meeting on the Biology of Sardines and Related Species. Species Synopsis (6)


