ENSO IMPACTS ON PELAGIC ECOSYSTEMS IN THE EASTERN PACIFIC, WITH EMPHASIS ON FISHERY RESOURCES

by

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ENNIO IMPACTS ON PELAGIC ECOSYSTEMS IN THE EASTERN PACIFIC, WITH EMPHASIS ON FISHERY RESOURCES

1. INTRODUCTION

El Niño, today known as El Niño/Southern Oscillation (ENSO) is an aperiodic, large-scale oceano-atmospheric anomaly affecting the global atmosphere and the low and mid-latitude areas of the Pacific Ocean. This phenomenon has many and diverse ecological, economic and social consequences, particularly along the eastern boundary of the Pacific Ocean.

The 1982-83 ENSO event is recognized as one of the most intense events among those known to date. During its occurrence, numerous biological impacts were observed, recorded and studied. As a result of this, many research projects and monitoring programs were initiated, many of which were multidisciplinary efforts. The 1982-83 event probably generated more information than all previous events put together, contributing greatly to the knowledge of the mechanisms and effects associated with ENSO.
Among the contributions resulting from the 1982-83 event, a particular aspect worth noting is the generation of data applicable in studies of biological variability and in fishery management. For Barber and Chavez (1985), this event provided a natural experiment that illustrates some aspects of the relationship between ocean variability and the fluctuations of fish abundance. Wooster (1983) and Mysak (1984) have also emphasized that environmental changes in the eastern Pacific are likely to produce a significant portion of the observed interannual variability in fish populations. As evidence of this, Soutar and Isaacs (1974) and DeVries and Pearcy (1982) have shown that long before commercial fisheries had been established, certain species in the California and Humboldt system exhibited fluctuations in stock abundance.

Many new research and monitoring projects, developed or initiated during ENSO 1982-83, constituted detailed descriptions of changes in specific taxa or specific processes. However, only a few projects were opportunely started or continued as regional efforts in the eastern Pacific. For those reasons, the information obtained is difficult to compare. The works of Alvial (1985), Arntz (1986), Barber and Chavez (1985), Zuzunaga and Niquen (1985), Fiedler et al. (1986), and Pearcy and Schoener (in press) are attempts to integrate hypotheses on timing and cause-effect relations in the ecosystem from a more holistic point of view. This review paper is a new effort to gather, integrate and describe the principal documented impacts of ENSO on the pelagic upwelling ecosystem in the eastern Pacific.
boundary, principally in the Humboldt and California Current Systems. Most of the information comes from the 1982-83 event and complementary information from other previous events is also mentioned. Objectives of this paper are to show the biological impacts in relation with the principal environmental changes introduced by ENSO, and to discuss the probable mechanisms that govern their occurrences and interactions. Finally, the effects and consequences of ENSO on the management of pelagic resources will be discussed.
2.- PHYSICAL BASIS OF ENSO.

2.1.- GENERAL ASPECTS AND DEFINITIONS.

An adequate understanding of the ENSO impacts on the pelagic ecosystems in the eastern Pacific requires a clear identification of the principal climatic and oceanographic processes involved in the origin and evolution of this anomaly.

The El Niño event is a series of oceanic and atmospheric changes that, though concentrated in the Pacific off the west coast of South America, reach all the way across the Pacific to Australia and Asia and other remote regions. It coincides with major changes in atmospheric pressure patterns which are called the Southern Oscillation (SO) (Walker, 1924).

The SO is an oscillation of surface atmospheric pressure difference between the low pressure over the "maritime continent" centered on Indonesia, and the South Pacific high centered in the southeast Pacific. Berlage (1957), Troup (1965) and Bjerknes (1969) contributed to better understanding of the SO and its relation with fluctuations in tropical monsoon rainfall, as well as winter circulation anomalies over North America and other parts of both the Northern and Southern Hemisphere extratropics.
Southern Oscillation indices (SOI) are commonly used to represent the SO (Quinn, 1974, Quinn et al., 1978). Many indices have been suggested; the most widely used are comparisons between high and low pressure centers at Eastern-Darwin, Totegegie-Darwin, Rapa-Darwin, Hao-Darwin, and Tahiti-Darwin. The index changes occur in a seesaw fashion, one end of the seesaw being in the Australian-Indonesian region and the other in the southeast Pacific (Gill and Rasmusson, 1983). Thus, high values of the indices represent higher differences between the atmospheric pressure in the centers considered.

Although meteorologists had known about the SO for more than half a century, its relation to the oceanic El Niño phenomenon was not recognized until the late 1960’s (Rasmusson, 1986). It appears that most of the large short-term climatic changes, and their characteristic current and weather patterns over the lower latitudes of the Pacific Ocean, are associated with either the El Niño (low index) or anti-El Niño (high index) phases of the Southern Oscillation.

Originally the term El Niño referred to a warm current that sets southward each year along the coast of southern Ecuador and northern Peru during the southern hemisphere summer, when the southeast trade winds are weakest. Now, this term is reserved for the exceptional year phenomenon, and the new term ENSO (El Niño / Southern Oscillation) has been introduced for representing the short term climatic changes associated with a low index phase of the Southern Oscillation (W. Quinn, personal communication).
2.2.- ANTI-ENSO AND ENSO CONDITIONS.

When SO indices are high, the equatorial low is usually deep, the subtropical highs is strong (particularly the one in the south Pacific), and the trades and equatorial easterlies are strong. Under these conditions, equatorial oceanic upwelling is enhanced and the resulting cool equatorial surface waters cause an extensive equatorial Pacific atmospheric dry zone. This defines the anti-El Niño period.

Other conditions are also associated with the Anti-El Niño. The Humboldt Current System and South Equatorial Current are usually strong, and the North and South Equatorial Counter Currents are to a great extent weakened at the surface. Cool and nutrient-rich upwelled waters along the coast of Chile and Peru are also evident. The sea surface temperature (SST) along the equator in the Pacific Ocean is warm in the west and cold in the east. Wind stirring generates a well mixed surface layer, usually present to 150 m depth or more in the west, and shallower in the east, where it practically disappears near the coast of South America. In direct relation to this mixed layer, the thermocline slopes upward from the west to the east Pacific. On the other hand, sea level is higher in the west than in the east Pacific, because the trade winds driving currents along the equator build up an excess of warm surface water on the western side.
An additional oceanic current phenomenon occurs in the east Pacific between 3°N and 15°S and up to 140°W longitude. This region is colder than the mean SST of the tropics, due principally to cold water transported from the south by the Humboldt current. This surface water extends to the west as a tongue associated with the South Equatorial Current driven by the trade winds. This relatively cold flow is heated by the atmosphere at the equator, increasing in temperature before it reaches the western Pacific. Under these anti-El Niño type conditions (cool period, recently called the La Niña phase by Philander, 1985), rainfall over the central and western equatorial Pacific is abnormally low and rainfall over Indonesia and adjacent regions is usually enhanced during the east and southwest monsoons.

When SO pressure indices fall from peaks toward low values, the equatorial low is usually filling and moving eastward and the subtropical highs are weakening. As a result, the southeast trades and equatorial easterlies are relaxing and El Niño-type conditions set in. This event is also identified as El Niño phase by Philander (1985) or warm-episode by other authors. Under these conditions, equatorial upwelling diminishes in intensity or disappears, sea surface temperatures rise, the sea level increases at the eastern side along with a deepening of the thermocline, abnormally heavy rainfall occurs over the central and western equatorial Pacific, and an east monsoon drought usually affects Indonesia and adjacent regions.
With regard to the 1982-83 event, its manifestations appeared in spring of 1982, an unusual time considering the canonical event (Cane, 1983). At that time there were bursts of westerlies in the vicinity of the date line but in view of the variability of the winds in this area their significance was uncertain. By May, there was a noticeable SST anomaly and by July, the wind anomaly was sufficiently strong and persistent to cause the onset of the event at the equator. However, the usual precursors of an El Niño were absent. The easterlies were not especially strong and there was no tendency for the SST to be abnormally low in the east and high in the west. Sea level also did not build up in the western Pacific and the thermocline was not unusually deep there. A synthesis of the principal physical events observed during the El Niño 1982-83 is shown in Fig.1.

2.3.- THE MECHANISMS OF ENSO.

Since Bjerknes (1969) first suggested that El Niño corresponds to a large-scale oceanic phenomenon rather than a local one restricted to the west coast of South America, numerous investigations have contributed to the modern hypothesis about ENSO.

Today, as Enfield (1981) points out, Wyrtki's (1975) argument that El Niño is primarily an ocean wave dynamical response to trade wind forcing over the interior of the equatorial Pacific Ocean is broadly supported by theoretical and
**PRINCIPAL PHYSICAL EVENTS**

**ENSO- 1982-83**

<table>
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<tr>
<th>Spring 1982</th>
<th>Usual precursors absent</th>
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<tr>
<td>Spring</td>
<td>Bursts of westerlies</td>
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<tr>
<td>May 1982</td>
<td>(vicinity dateline)</td>
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<td>SUMMER 1982</td>
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<td>Early summer</td>
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<td>July 1982</td>
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<td>1983</td>
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<td>1st semester 1983.</td>
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**Fig.1.** Principal physical events during the 1982-83 ENSO.
numerical studies and by observational results. Wyrtki (1975) concluded that during the period of strong SE trades sea level rose in the western equatorial Pacific and that during the subsequent wind relaxation this zonal potential energy would be released in the west-to-east sea level downslope. Wyrtki argued that the energy release would take place initially in the mid-equatorial region of weakened winds and would propagate rapidly eastward in the form of a baroclinic disturbance, much like an equatorially trapped internal Kelvin wave. Upon arrival of the disturbance off South America, isotherms would deepen and a massive influx of warmer water would occur.

Theoretical and numerical models have also contributed to the conceptualization of the El Niño process. The papers from Lighthill (1969), Godfrey (1975), White and McCreary (1976), and Hurlburt et al. (1976) defined the wave dynamical process along the equator and in the eastern boundary. Results indicate that equatorially-trapped internal waves at a single frequency incident on the eastern boundary may be partially transmitted poleward along the coast in the form of coastal trapped internal Kelvin waves (Figs. 2 and 3).

The wave disturbance is confined to an equatorial band 5-6° of latitude on either side of the equator, as determined by the equatorial radius of deformation. Within less than a month the disturbance arrives at the eastern boundary and the pycnocline deepens as the disturbance spreads poleward into both hemispheres. Figure 4 shows the progression of an equatorially
REAR VIEW (LOOKING EAST)

EQUATOR

NORTH

SEA LEVEL

SOUTH

P1

P2

THERMOCLINE

U1

U2

OCEAN FLOOR

Fig. 2. Rear view of a Kelvin wave traveling eastward at equator.

(a) ONSHORE VIEW OF INTERNAL KELVIN WAVE TRAPPED AGAINST COASTAL WALL IN NORTHERN HEMISPHERE

(b) REAR VIEW OF WAVE PULSE

Fig. 3. Onshore view (a) and rear view (b) of a Kelvin wave traveling against coastal wall in NH. (After Wyrtki, 1966).
trapped Kelvin wave and resulting coastal Kelvin waves during a nine-month simulation period developed by O'Brien et al. (1981). The poleward propagation speeds of the leading edge (downwelling front) is equal to the Kelvin phase speed and is independent of latitude. On the other hand, the coastal internal radius of deformation, and therefore also the offshore width of the disturbance in the vicinity of the leading edge, decreases with increasing latitude.

Behind each advancing downwelling front there is an elongated zone where the pycnocline slopes sharply upward offshore. The quasi-alongshore front is continuous with the advancing downwelling front, and begins to advance offshore via internal Rossby wave propagation westward (Godfrey, 1975; Hurlburt et al., 1976; and Cane and Sarachik, 1977). The downwelling fronts continue propagating poleward and the thickened upper layer expands offshore in the coastal region. A westward propagating bulge corresponding to the effect of Rossby waves develops near the equator (Fig. 4). These waves propagate more rapidly at low latitudes, and as a consequence, at higher latitudes the rate of offshore migration of the alongshore pycnocline front is progressively less.

Gill and Rasmusson (1983) developed a simple model that explains the evolution of an event once it has started. It seems that once a region of anomalous convection in the atmosphere is established over the equatorial Pacific, there is a feedback
Fig. 4. Interface displacements depicting the progression of an equatorially trapped Kelvin wave and resulting coastal Kelvin waves during the first 9 months of model integration. Contouring intervals is 0.5 m; initial contours are ± 2.5 m so as to suppress the zero contour. Dashed (negative) contours indicate upwelling. Westward progression of an equatorial Rossby wave is evidenced in the height field.
(ASTER O'BRIEN ET AL., 1981)
process which can strengthen it. The westerly wind anomaly created to the west of the convection zone tends to drive a oceanic current downwind, causing the convection region to migrate eastward. The further it moves, the greater the anomaly because the contrast between the warm water pool temperature and the normal temperature gets larger with distance eastwards (Fig.5). When the wind stress anomaly is turned on, a surface current is driven downwind, heaping up water and deepening the thermocline ahead. This gives rise to a Kelvin wave (with positive sea level anomaly). A more slowly propagating planetary wave is reflected, adding to the sea level but subtracting from the zonal current. This model is in remarkable agreement with atmospheric and oceanographic observations such as wind, sea level and temperature anomalies along the equator and in the eastern boundary.

Figures 6 and 7 integrate graphically the Gill and Rasmusson model with the principal air-sea features along the equatorial and eastern Pacific Ocean during anti-ENSO and ENSO conditions.

According to Philander (1985), the most favorable time for a warm anomaly in the eastern equatorial Pacific to cause local heating and to amplify is early in the calendar year, when the ITCZ (Inter tropical convergence zone) migrates to its lowest latitude and when the SST is at the seasonal maximum. El Niño usually begins in April and May. Those are the months when the seasonal movement of the convergence zone in the west is from the
The feedback process

Fig. 5. The feedback process, according to the Gill and Rasmusson's (1983) model.
Fig. 6. Anti-ENSO conditions. High pressure system (1) parked over the eastern Pacific prompts trade winds to blow "downhill" (2) toward a wet low-pressure system over Indonesia (3) inducing a westward-setting current (4). Warm water piles up in the western Pacific (5). Cool subsurface water returns in an undercurrent (6); warm-water layer remains shallow off South America. (Based on Canby, 1984).

Fig. 7. ENSO conditions. In relation with the pattern shown in Fig. 2, the low moves eastward (7), and the high weakens (8). Trade winds falter and are replaced by east-blowing winds (9), causing the surface current to reverse (10) and warm water to surge toward South America in a phenomenon known as a Kelvin wave (11). (Based on Canby, 1984).
southern to the northern hemisphere. During El Niño, this northward movement is modified in an eastward direction (Philander, 1985). The seasonal movement of the convergence zone in the western tropical Pacific is back towards the southern hemisphere in December and January. This southward migration is remarkably regular and occurs even during El Niño when sea surface temperatures in the central and eastern tropical Pacific are exceptionally high. The rise of sea level in the western Pacific is associated with easterly winds that in turn are associated with the southward movement of the atmospheric convergence zone. This movement, which terminates El Niño and initiates La Niña (Philander, 1985), clearly demonstrates that sea surface temperature is but one of the factors affecting the movements of the atmospheric convergence zones. The factors other than SST that affect the convergence zones must be responsible for the westerly wind anomalies west of the date line at the beginning of El Niño and the easterly winds in that region at the beginning of La Niña.

According to Rasmusson and Carpenter (1982), the period of the Southern Oscillation is approximately three years. Philander (1985) has pointed out that this period is probably determined by the time it takes an unstable interaction to run its course through El Niño, a failure of the cold season in the east, and La Niña, an enhancement of the subsequent cold season in the east.
2.4.- DYNAMIC MECHANISM IN THE EASTERN PACIFIC.

The dynamic mechanism in the eastern Pacific was reviewed by Enfield (1981), who pointed out that, upon arrival of the perturbation at the eastern end of the equatorial waveguide, density structures in the east are depressed and the coastally trapped baroclinic disturbance that begins to propagate poleward into each hemisphere causes a series of changes behind the advancing front. The alongshore flow at the boundary reverses from equatorward to poleward and the isopycnal-deepening is confined to a coastal band which gradually widens as an alongshore isopycnal depression slowly migrates offshore via Rossby waves. Enfield (1981) concludes that the wave dynamical theory is consistent with the observational results.

Enfield and Allen (1980) and Chelton and Davis (1982) have shown the coherence between the high sea level fluctuations and El Niño occurrences in the eastern boundary. In addition, the ocean thermal structure anomalies observed off Peru along with the wind record analysis are consistent with the dynamical wave theory. In synthesis, other aspects deduced from observations and consistent with the theory are: 1) association of positive sea level anomalies with isotherm depression and mutual propagation poleward at large speeds; 2) increased sea surface temperature (SST); 3) the winds along the Peru coast remain favorable for coastal upwelling during ENSO occurrences; and 4) strong reversion of the normal equatorward flow (Smith, 1983; CPPS, 1984; Fonseca, 1985; Huyer and Smith, 1985b).
2.5.- ENSO IN THE CONTEXT OF LOW-FREQUENCY TRENDS.

During recent years there has been an increased interest in analyzing the SO-related short term changes (ENSO events) and a longer term climatic variation. The longer term climatic change was first reported at the Fourth Annual Climate Diagnostics Workshop (Quinn, 1979). The existing graphic trends showed that sea level pressures at Easter Island were falling while SST's were generally rising over the southeast Pacific. Quinn and Neal (1983) found since mid-1976 a shift in SOI anomalies. On the other hand, an apparent cumulative effect observed from the integrated index anomaly plots was also clear in the long term analysis. The exceptionally strong 1982-83 ENSO event appeared to result from the coincidence of the long term cumulative effect and the short term ENSO effect (Neal and Quinn, 1985).

The paleo-abundance of pelagic fish as recorded in anaerobic sediments off the coasts of the Californias and Peru-Chile tend to confirm long term fluctuations in the bioclimatological conditions, consistent with the ideas of long term climatic variations (Soutar and Isaacs, 1974; DeVries and Pearcy, 1982). These long-term trends could have great importance to biological systems of the eastern Pacific. Some of their implications, particularly for fisheries, will be discussed later in this paper.
3. THE PLANKTON COMMUNITY RESPONSE.

3.1. GENERAL CHARACTERISTICS.

The strong and recurrent alterations in the physical environment along the Eastern Pacific Boundary have an impact on the plankton community which has been especially evident in the upwelling ecosystems of the California and Humboldt Currents. According to Avaria (1985), studies on ENSO in the southeastern Pacific show that the effects of El Niño on coastal upwelling have a marked influence on the plankton community. Phytoplankton composition and abundance are altered in relation to ENSO events, principally off Peru. These alterations consist essentially of strong decreases in primary production, dominance of dinoflagellates in areas normally dominated by diatoms, and invasion of tropical and subtropical species into higher latitude waters. Although, coastal upwelling in the southeastern Pacific is highly variable, data generated by the Coastal Upwelling Ecosystem Analysis (CUEA) program off Peru confirm that this variability is increased during ENSO occurrences (Barber et al., 1985).

Clear indications of impacts on the ichthyoplankton were also reported in the southeastern Pacific since the 1972-73 event (Santander and Sandoval, 1985). The composition, dominance, diversity and abundance of species all changed. Cold-water species were negatively affected by the warm episodes while the warm-water species were favoured.
In the northern hemisphere, the California Cooperative Fisheries Investigations (CalCOFI) in the California Current provide a data set for the study of both the El Niño effects and the long term, low frequency variations. Large scale, low frequency biological and physical variations are spatially coherent over the entire current system (Bernal, 1979; Chelton, 1981; Bernal and McGowan, 1981; Chelton et al., 1982; McGowan, 1985). Physical and biological fluctuations are highly correlated in the low frequency part of the spectrum, demonstrating the occurrence of long-term events with strong impact on zooplankton biomass. A good example of this relation is the 1957-59 ENSO event.

In both hemispheres the phytoplankton records are relatively fragmentary and time series long enough for establishing the relationship with the physical changes do not exist. Just at the end of 1970's and 1980's some continuous monitoring programs were initiated in the southeastern Pacific under the support of ERFEN (Estudio Regional del Fenomeno El Niño) program (Avaria, 1984).

3.2.- THE EFFECTS OF THE 1982-83 EVENT.

During the second half of 1982 and the first quarter of 1983 clear changes were observed in the composition, distribution and standing crop of the phytoplankton in the southeastern Pacific (CPPS, 1984). A sharp decrease in the area of distribution of diatoms and an increase in the abundance and distri-
butional extent of warm water oceanic dinoflagellates were observed (Fig. 8). This situation sharpened during the second quarter of 1983.

In August of 1983 a return to more normal conditions was indicated by the decrease in oceanic dinoflagellate populations along the coast, the increase in diatom populations and the reappearance of some phytoplanktonic indicators in their usual areas. High chlorophyll concentrations also increased in small, narrow, coastal bands (CPPS, 1984; Avaria, 1984; Guillen, 1986). The reduction to a narrow coastal band approximately 50-75 Km in width is shown in Fig. 9, which is based on an integration of satellite information. A clear sequence of decreasing phytoplanktonic pigment around the Galapagos Islands as the El Niño event intensified was also shown (Feldman 1985).

McGowan (1985) found that in the northern hemisphere the first strong signal in the phytoplankton associated with the 1982-83 episode appeared in August 1983 off California, almost a year later than phytoplankton changes off South America coast (Alvial, 1985; Avaria, 1984). The nutricline off California was quite deep everywhere and sloped downward from a nearshore depth of 75 m, a very unusual pattern compared to that of previous years. Surface chlorophyll values were very low, and a subsurface maximum persisted until December 1983.
Fig. 8. Phytoplankton distribution in the ERFEN region.

Fig. 9. The area of the productive habitat derived from Nimbus-7 Coastal Zone Color Scanner images for the periods Dec73-Jan74 (darker shaded), Dec78-Jan80 (lighter shaded) and Dec82-Feb83 (enclosed by dashed line). The coast of South America is shaded black along the right hand edge of the image, and the Galapagos Islands are located on the equator at approximately 90°W.

From Feldman (1984)
Miller et al. (1985) also found a subsurface chlorophyll maximum over the Oregon shelf throughout the summer of 1983. The maximum occurred at a depth of 10 to 25 meters and extended all the way to shore. This pattern of distribution correlated well with non-upwelling conditions.

The abundance and composition of zooplankton also changed during the 1982-83 ENSO. According to the national reports in the Scientific Committee of ERFEN (CPPS, 1984), species associated with warm waters arising from the north dominated off the coast of Ecuador with a overall reduction in the biomass. Off Peru, biomass was reduced, meroplanktonic larval stages near coastal zones decreased and carnivorous zooplankton increased in equatorial and oceanic waters.

A general reduction in abundance of the zooplankton off Chile was also observed, with higher abundance levels concentrated along coastal bands. Copepods dominated the samples but tunicates, coelenterates and chaetognaths were also abundant. Zooplankters of oceanic and equatorial origin invaded the upwelling area from the beginning of the event, causing strong changes in diversity, species composition and biomass. Alvial et al. (1983) cited the massive invasion from the north of the jellyfish Chrysaora plocamia into northern Chile as one of the most remarkable and early indicators of this El Niño event. Along with jellyfish, high concentrations of crustaceans, chaetognaths and salps were also found.
In the northeast Pacific, McGowan (1985) pointed out that by midsummer 1983, the macrozooplankton biomass off California was greatly reduced. There was a depression of the normal summer peak, and the offshore maximum that usually coincides with the offshore chlorophyll maximum was totally missing. Over the Oregon continental shelf the overall density of zooplankton during spring and summer 1983 was low, about 30% of that in non-El Niño years (Miller et al., 1985). In April 1983 the fauna at both inshore and offshore stations was dominated by southern species.

3.3.- EXPLANATORY MECHANISMS.

Coastal upwelling processes are frequent and intense in the continental margins of the Humboldt and California Current Systems. Equatorward winds along these coasts produce both an equatorward and offshore flow of water in the surface layer. The surface waters are replaced by nutrient-rich waters upwelled from a depth of about one hundred meters. The supply of nutrients favour phytoplankton photosynthesis and increases the organic matter produced at the first trophic level. The variations of physical processes affecting the availability of nutrients in the euphotic zone will cause fluctuations in the primary productivity and will also impact the higher trophic levels (Fig. 10).

According to Barber et al. (1985) processes that depress the thermocline away from the surface layer (where adequate light is available for photosynthesis) will reduce the
primary productivity potential of an ocean ecosystem. Light decreases exponentially as a function of depth due to absorption and scattering. Thus, if the thermocline is deep and the mixed layer is thick, phytoplankton cells will spend less time in the upper depths favorable for the photosynthesis. This mechanism of regulation has been demonstrated by Alvial and Avaria (1982) for the coastal upwelling zone in the southeastern Pacific.

Regions of the ocean having a thermocline near the surface and a very shallow mixed layer are richer than other regions of the ocean because they provide optimal light and nutrient conditions for primary production and phytoplankton growth (Ryther, 1969).

The trade winds, blowing across the Pacific Ocean from east to west in the low latitudes, cause a rise in sea level in the western Pacific. As a dynamic compensatory mechanism, the thermocline remains shallow on the eastern side. The ocean thermal structure and the winds favor the regional upwelling process in the eastern tropical Pacific. Moreover winds blowing towards the equator along the eastern boundary of the Pacific induce a shoreward tilt of isopycnals and transport of water from depths of 40 to 80 m to the surface, causing the local coastal upwelling processes (Fig. 10).

When an ENSO event takes place, the thermocline in the eastern region becomes deeper, sea level rises and the mixed
layer warms. In addition, the trade winds weaken and regional upwelling may diminish and even stop. Along the coast, the equatorward winds driving coastal upwelling in general remain the same (Enfield, 1981; Smith, 1983), but the water entrained by the upwelling circulation contains fewer nutrients and is warmer. As the thermocline is depressed with the passage of the Kelvin wave, nutrient-rich source waters are deepened and upwelled water will be warm and nutrient-poor. Thus, El Niño decreases the nutrient supply to the surface which, in turn, causes primary production to decrease proportionally (Fig. 11). There are some data which support the hypothesis that the interannual nutricline variability is the causal process for interannual biological variability in the eastern Pacific (McGowan et al., 1985; Guillen, 1986). However, the effects of advection cannot be ignored in the low frequency changes (Roesler and Chelton, in press).

From the impacts analyzed above, it is derived that the physical alterations introduced by ENSO into the eastern Pacific affect phytoplankton communities principally by diminishing population growth rates, causing changes in community structure (making dominant those taxa better adapted to the "new" warmer and more oligotrophic conditions) and by introducing changes in distribution of some populations. Changes in zooplankton abundance and community composition can result from either: 1) a change in the physical conditions in a given location, or 2) advection into waters having different characteristics. The second has significant implications for the survival of eggs and larvae of pelagic species, with important consequences for fishery resources.
Coastal upwelling off South American coasts under non-ENSO (top diagram) and ENSO (bottom diagram) conditions. North-blowing winds (1) and the earth's rotation push warm surface waters westward (2), and colder, deeper waters high in nutrients replace them (3). These support plankton (4), in turn eaten by fish. Dead plankton are recycled (5), and the system sustains itself.

When El Nino strikes, winds, westerly water flow, and coastal upwelling remain (bottom diagram). However, the upwelling is contained within the surface layer of warm water. Nutrients are not cycled upward. Plankton thins, and fish are impacted with the consequences discussed in this paper. (Adapted from Canby, 1984).
4.- THE ENSO IMPACTS ON NEKTION.

The following impacts of ENSO on nekton are considered:
* Changes in trophic relations.
* Changes in distribution.
* Changes in abundance.
* Changes in body condition and growth.
* Changes in reproduction and early life history.

4.1.- CHANGES IN TROPHIC RELATIONS

The reduction of the standing stock and production of the phytoplankton and the consequent low abundance of zooplankton result in reduced food availability for zooplankton and planktivorous nektonic animals and for early life stages. Most investigators think that reductions in fish abundance during ENSO are caused by decreases in primary productivity that affect the entire food web. Mysak (1984) thought that the availability of food is one of the most important factors affecting fish abundance and migrations.

During the 1982-83 event, a 5-to-20-fold reduction of primary productivity was estimated in the normally eutrophic upwelling areas of the southeastern Pacific (Barber and Chavez, 1983). Chilean pilchard or sardine (Sardinops sagax) stayed in coastal bands of relatively high plankton concentration. Jack mackerel (Trachurus murphyi) disappeared from the catch in Peru.
in December 1982, between the time when hake (*Merluccius gayi*)
and sardines left the coastal zone. This timing accords with the
alteration of the habitat of the three species by El Niño.
Species that prey on jack mackerel, such as bonito (*Sarda
chiliensis*), dorado (*Coryphaena hippurus*), and yellowfin tuna
(*Thunnus albacares*) became more abundant close to the coast.
Apparently anchoveta (*Engraulis ringens*) suffered from reduction
of phytoplankton, a key factor of larval survival of this
species.

Arntz (1986) noted that the food of pelagic fishes
during ENSO was impoverished. Anchovetas and sardines replaced
the phytoplankton in their diets with zooplankton, mainly
copepods. Jack mackerel and mackerel (*Scomber japonicus*) often
switched to mesopelagic fishes in oceanic waters because
anchoveta, their staple food, were scarce.

Sanchez de Benites et al. (1985) pointed out that hake
consumed more crustacean food, which showed that these fish were
feeding closer to the sea floor than under non-ENSO conditions,
when they live in the water column and feed on pelagic fishes.
Lorna (*Sciaena deliciosa*) and sharks, according to the same
authors, decimated anchovetas which had withdrawn to the sea
floor. Hake and gurnard (*Prionotus stephanophrys*) stomachs even
contained bathypelagic fish normally living off Central America.
In general, the food of demersal fishes appeared to be more
diversified and abundant during ENSO, contrary to that of pelagic
fishes, reflecting improved feeding conditions at the sea floor (Arntz, 1986).

Both species of pinnipeds in Peru, the sea lions (Otaria byronia) and fur seals (Arctocephalus australis), normally feed on anchoveta and were therefore affected during the 1982-83 event. The feeding trips of females fur seals were prolonged to about 5 days, instead of the normal 2-3 days, and larger fish (sardine, jack mackerel) were taken. As a consequence of food shortage, large numbers of pups died when they could not obtain sufficient quantities of their mother's milk.

According to Bailey and Incze (1985), a major effect of ENSO in the northeastern Pacific is the reduction in the production of food for planktivorous life stages of fishes. This is best documented for the California Current System where El Niño results in reduced planktonic production. During the 1982-83 El Niño off California, the reduction of plankton abundance resulted in diminished growth rates of adult fishes such as anchovy (Engraulis mordax) and rockfish (Sebastes spp.). Changes in zooplankton species composition due to enhanced poleward flow and/or onshore transport during an ENSO event could be important to larval fishes, which depend on certain species or sizes of microzooplankton for food (Bailey and Incze, 1985). Changes in zooplankton composition were reported by Miller et al. (1985), off the Oregon coast.
TABLE I. Summary of ENSO impacts reported in this paper on trophic relations (cases and references are not exhaustive and their locations do not show correspondence among them).

<table>
<thead>
<tr>
<th>IMPACTS</th>
<th>CASES</th>
<th>REFERENCES</th>
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<tbody>
<tr>
<td>FOOD REDUCTION</td>
<td>* Planktivorous fishes</td>
<td>Barber &amp; Chavez (1983)</td>
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<tr>
<td></td>
<td>* carnivorous fishes</td>
<td>Mysak (1984)</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Bailey &amp; Incze (1985)</td>
</tr>
<tr>
<td>FOOD INCREASE</td>
<td>* Demersal fishes</td>
<td>Sanchez de Benites et al. (1985); Arntz (1986)</td>
</tr>
<tr>
<td>FOOD TOTAL SHORTAGE</td>
<td>* Sea lions and fur seals</td>
<td>Barber and Chavez (1983)</td>
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<tr>
<td></td>
<td></td>
<td>Arntz (1986); Alvial (1985)</td>
</tr>
<tr>
<td>FOOD ALTERATIONS</td>
<td>* sardine and anchoveta</td>
<td>Arntz (1986); Sanchez de Benites et al. (1985)</td>
</tr>
<tr>
<td>(CHANGE IN DIETS)</td>
<td>* hake</td>
<td></td>
</tr>
<tr>
<td></td>
<td>* jack mackerel and mackerel</td>
<td></td>
</tr>
<tr>
<td></td>
<td>* sea lion and fur seals</td>
<td></td>
</tr>
<tr>
<td></td>
<td>* lorna and sharks</td>
<td></td>
</tr>
<tr>
<td></td>
<td>* gunard</td>
<td></td>
</tr>
<tr>
<td>FOOD DISPLACEMENTS AND PREDATOR</td>
<td>* Jack mackerel attracting bonito, dorado, &amp; yellowfin</td>
<td>Arntz (1986); Pearcy and Schoener (in press)</td>
</tr>
<tr>
<td></td>
<td>* Small fish attracting rockfish and saury to coastal waters</td>
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</table>
Pearcy and Schoener (in press) pointed out that perhaps the invasions of some oceanic and offshore fishes in the north-eastern Pacific were related to a changes in the availability of prey populations between inshore and offshore waters.

A summary of the trophic alterations mentioned above, including examples and some references, is shown in Table I.

4.2.- CHANGES IN DISTRIBUTION.

The distribution of nektonic species during ENSO events are affected by habitat reduction within an area, passive transport of early life stages, and invasions of highly migratory species. With the warming of the waters, invasions of diverse tropical and subtropical oceanic fish was observed off Ecuador, Peru and Chile. Skipjack (Katsuwonus pelamis) and large dorados or palometas (Coryphaena hippurus) were taken by hook and line a few kilometers from the coast. Sierra (Scomberomorus maculatus sierra), yellowfin tuna (Thunnus albacares) and bonito (Sarda chilensis) were also abundant (CPPS, 1984; Alvial, 1985; Arntz, 1986). A variety of sharks, such as hammerhead sharks (Sphyrna spp.), mako sharks (Isurus oxyrhynchus), and large eagle rays (Mylobatis spp.) and mantas (Manta hamiltoni) were observed unusually close to the coast. In addition, mullets (Mugil spp.) increased in abundance.
Some of the invaders, like bonito and dorados, contributed considerably to the total fish landings in northern Chile and Peru. Velez and Ceballos (1984) and Velez et al. (1985) counted 51 fish species, most of them in the port of Callao, which had extended their distribution area during ENSO 1982-83, either from the north to the south or from oceanic to neritic waters. Kong et al. (1985) recorded 51 non-autochtonous fish species (grouped in 31 families) in northern Chile, the most austral region strongly affected by this event. Among them 29 were recorded for the first time in Chile and the remainder had only been cited occasionally.

The 1982-83 ENSO event also changed the distribution pattern of the sardine. They virtually disappeared from Ecuadorian waters and became concentrated off southern Peru and northern Chile. In this latter region, sardines were concentrated near the coast in association with lower temperatures (CPPS, 1984; Castillo and Guzman, 1985; Martinez et al., 1985; Zuzunaga and Niquen, 1985). Moreover, this species was found at greater depth in the more oceanic zones (Castillo and Guzman, 1985). Torres et al. (1985) concluded that the patterns of migration observed in the presence of the 1982-83 El Niño differed notably from those that occurred in 1984.

Arntz (1986) pointed out that during 1982-83 sardines migrated south, whereas in former ENSO events they only moved inshore or withdrew to deeper waters. This fact may be associated with the greater intensity of ENSO 1982-83. A large part of the
population may have left Peruvian waters by the end of summer 1983 and entered Chilean waters (Canon, 1985; Martinez et al., 1985). Many of those that left Peru may have died when surface waters warmed or, like anchoveta, they may have stayed close to the sea floor. During the second half of 1983 sardines gradually returned to their usual area of distribution (Arntz, 1986).

Anchoveta changed distributions in three basic ways. Many of them withdrew to the remaining upwelling areas near the coast. A second group descended to deeper waters where little food was available. By the end of 1982, anchovetas suspended their vertical migrations altogether, and remained close to the sea floor, always below 40-50 m and in some cases even below 100 m. The third part of the population migrated southward at an early stage and constituted the bulk of survivors of the Peruvian stock (Arntz, 1986).

Jack mackerel are widely dispersed under anti-ENSO conditions, with the highest concentrations found off southern Peru-northern Chile (Zuzunaga and Niquen, 1985). In northern Chile their distribution during the 1982-83 event was scattered, with only small areas of high concentration near the coast and a greatly enlarged depth distribution following the isotherms of 14° to 18°C (Castillo and Guzman, 1985). Off Peru, during the highest intensity of the event (March of 1983), the concentration of jack mackerel increased close to the coast and they were found in deeper waters, like anchovetas and sardines. This species was
also found farther north during 1982-83, being caught commercially for the first time in history in the coastal zone of Ecuador (CPPS, 1984).

Mackerel and jack mackerel had similar distributions before the maximum intensity of the 1982-83 event. In March-May 1983, centers of higher concentration were located in northern Peru, with higher concentrations close to the coast. In September 1983 they were widely dispersed, with abundance highest off northern Peru.

Changes in distribution, density and availability of demersal fish were recorded in waters of the continental shelf off northern Ecuador. At the onset of the event, some fishes immediately migrated to the south (Arntz, 1986). According to Barber and Chavez (1983), the first species to respond was hake. Apparently this relatively large and motile bottom dwelling fish moved down the continental slope, staying with the cool water to which they are adapted.

Among the invertebrates, some species increased their distributional ranges, especially in the north part of the Humboldt Current System. Under normal conditions, shrimps are not caught at all in the upwelling area south of 6°30'S. However, during the last event, at least 3 species were found more than 1500 km south of their usual geographic range. By far the most important of the species was the titi shrimp (Xiphocanopus riveti) which extended its area into northern Chile, like langos-
During ENSO swimming crabs (Fam. Portunidae) were found in high concentrations off Peru, south of their normal distribution areas. At the same time catches declined off Ecuador. *Euphyllax dovii* was the most important immigrant into Peruvian waters. Among the mollusks, individuals of the benthic *Aplysia* spp. were frequent off Iquique (Soto, 1985), probably as the result of transport of early life stages toward the south rather than active migration of adult individuals.

In 1982-83 marine turtles became extraordinarily frequent in the fishermen’s catch off Peru and off northern Chile (Arntz, 1986; Alvial, 1985) suggesting a southward migration. With regard to mammals, at the beginning of the event the fur seal *Arctocephalus australis* was detected off northern Chile (Alvial et al., 1983). Torres (1985) suggested that the presence of *A. australis* to 23°S off northern Chile could be a result of initial effects on important components of their food, such as cephalopods and anchovetas, in the Peruvian waters.

In the Northeast Pacific, analogously to the Southeast Pacific, strong northward migrations were detected. Active swimmers such as mackerel, bonito, yellowtail (*Seriola lalandi*), Pacific barracuda (*Sphyraena argentea*), and white seabass (*Atractoscion nobilis*) migrated into northern waters. These movements were probably triggered by the poleward advection and warm waters
in the southern region of the California Current System (Huyer and Smith, 1985a; Pearcy and Schoener, in press).

The displacement of oceanic species toward the coast was also reported in the northern hemisphere (Pearcy and Schoener, in press). Blue shark (*Prionace glauca*), pacific saury (*Cololabis saira*), ocean sunfish (*Mola mola*), thresher shark (*Alopius vulpinus*) and Pacific pomfret (*Brama japonica*), were reported frequently in coastal waters during the summer of 1983.

According to Mysak (1984), numerous exotic warm water species of fish, birds and turtles were sighted off British Columbia, many in inshore waters, during spring-summer of 1983. Larger pelagic organisms such as the market squid (*Loligo coalescens*) decreased in catches off Oregon but increased in both Puget Sound and Alaska (Pearcy and Schoener, in press).

Pacific mackerel (*Scomber japonicus*) and jack mackerel (*Trachurus symmetricus*) increased greatly off Oregon and Washington in 1983-84, reflecting latitudinal movements. Inshore displacements like those observed in the southern hemisphere could also influence the availability of these species close to the coast. Another pelagic species, the bonito, was caught by commercial fishermen off Oregon in substantial numbers during the summer of 1983 (Pearcy and Schoener, in press), constituting another unusual record which had an equivalent in the southeast Pacific.
TABLE II. Summary of ENSO impacts reported in this paper on distribution (cases and references are not exhaustive and their locations do not show correspondence among them).

<table>
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<tr>
<th>IMPACTS</th>
<th>CASES</th>
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<tr>
<td>POLEWARD EXTENSIONS OF DISTRIBUTION</td>
<td>* Tropical and subtrop.</td>
<td>Pearcy et al. (1985)</td>
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<tr>
<td>RANGES</td>
<td>fishes.</td>
<td>Soto (1985)</td>
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<tr>
<td></td>
<td>* Sardine and anchovy.</td>
<td>Canon (1985)</td>
</tr>
<tr>
<td></td>
<td>* Swimming crabs</td>
<td>Martinez et al. (1985)</td>
</tr>
<tr>
<td></td>
<td>* Turtles</td>
<td>Castillo &amp; Guzman (1985)</td>
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<td></td>
<td>* Fur seals</td>
<td>Kong et al. (1985)</td>
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<tr>
<td></td>
<td>* Mackerels, bonito</td>
<td>Pearcy et al. (1985)</td>
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<tr>
<td></td>
<td>* Pacific barracuda</td>
<td>Pearcy &amp; Schoener (in press)</td>
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<tr>
<td></td>
<td>* Red crabs</td>
<td>Arntz (1986)</td>
</tr>
<tr>
<td></td>
<td>* Market squids, etc.</td>
<td>Barber &amp; Chavez (1983)</td>
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<tr>
<td></td>
<td></td>
<td>Zuzunaga &amp; Niquen (1985)</td>
</tr>
<tr>
<td>COASTWARD EXTENSIONS OF DISTRIBUTION</td>
<td>* Skipjack</td>
<td>Pearcy &amp; Schoener (in press)</td>
</tr>
<tr>
<td>RANGES</td>
<td>* Dorado</td>
<td>Barber &amp; Chavez (1983)</td>
</tr>
<tr>
<td></td>
<td>* Sierra</td>
<td>Arntz (1986)</td>
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<tr>
<td></td>
<td>* Sharks, mantas</td>
<td>Pearcy et al. (1985)</td>
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<tr>
<td></td>
<td>* Yellowfin</td>
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<td></td>
<td>* Bonito, sunfish</td>
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<td></td>
<td>* Sardine, anchovy</td>
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<tr>
<td></td>
<td>* Mackerels</td>
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</tr>
<tr>
<td></td>
<td>* Sea hare, etc.</td>
<td></td>
</tr>
<tr>
<td>RANGES</td>
<td>* Fur seals</td>
<td></td>
</tr>
<tr>
<td>VERTICAL MIGRATIONS</td>
<td>* Anchoveta,</td>
<td>Castillo &amp; Guzman (1985)</td>
</tr>
<tr>
<td>RANGES</td>
<td>* Jack mackerel,</td>
<td>Arntz (1986)</td>
</tr>
<tr>
<td></td>
<td>* sardine,</td>
<td></td>
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<tr>
<td></td>
<td>* mackerel</td>
<td></td>
</tr>
<tr>
<td>GENERAL INCREASE OF DISTRIBUTION</td>
<td>* Jack mackerel</td>
<td>CPPS (1984)</td>
</tr>
<tr>
<td>RANGES</td>
<td>* Shrimps</td>
<td></td>
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<tr>
<td></td>
<td>* mackerel</td>
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<tr>
<td>ALTERATIONS OF MIGRATIONS</td>
<td>* Tuna</td>
<td>Yamanaka (1984)</td>
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<td></td>
<td>* Salmon</td>
<td>Smith (1985)</td>
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<td></td>
<td></td>
<td>Pearcy &amp; Schoener (in press)</td>
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<td>IATTC (1984, 1985)</td>
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</table>
Among the invertebrates, pelagic red crabs (Pleuroncodes planipes), were found far north of their usual range off Baja California during several ENSO events, including the 1982-83 ENSO (Schoener and Fluharty, 1985; Pearcy and Schoener, in press). Pearcy et al. (1985) reported the sea hare (Aplysia californica) out of its usual range. This species was found in Yaquina Bay at Newport, far north of its normal northern range limit in southern California (J. Sonor, personal communication). Several sightings of the leatherback turtle (Dermochelys coriacea) were reported in the summer of 1983 from the outer Washington coast. Both species were reported far to south off South America, indicating poleward movements in both hemispheres.

A summary of the impacts on distribution, including some examples and references, is shown in Table II.

4.3.- CHANGES IN ABUNDANCE

Changes in abundance as a consequence of the strong alterations induced by ENSO are not separable from the other impacts considered in this paper. For this reason, this section includes only those impacts that affected mortality and had a relatively immediate effect principally on the abundance of commercially important species.

The pelagic resources of the Southeast Pacific have been important to the world fishery catch in the past 25 years.
In 1970 this fishery represented 22% of the world’s maritime catch in terms of volume. The industrial fishery, which was initiated at the beginning of the 1950’s in the coastal zones of Peru and Chile, was based primarily on anchovy until 1972. After that year, other species were harvested including Chilean pilchard, jack mackerel, and mackerel. According to Avaria (1986), the impacts of ENSO on these fishery resources have been different for each of the events that took place after 1950. The 1957-58 episode affected the behavior and distribution of the anchoveta without affecting its abundance. The 1965 event produced a drastic decline in the anchoveta catch but the effect was short-lived and the catch levels soon recovered and even increased. The 1972-73 ENSO impact was more severe and lasted longer. Adverse environmental conditions and overfishing apparently produced the collapse of the anchoveta fishery. The low intensity event of 1976 accelerated the decrease of the remaining anchoveta population and increased the abundance of other species (Fig. 12). The anchoveta fishery has never recovered to its former level, although the fishery of other pelagic species, particularly sardine and jack mackerel, has increased (Avaria, 1986).

During the 1982-83 event, anchoveta practically disappeared from the coast of Chile and could be found only in very restricted areas off the Peruvian coast. The decreased abundance estimated from catches is evident for Peru and Chile in Fig. 12. In the first month of 1984, the catches off the Peruvian coast were very low and a recovery of the population was not observed. Massive mortalities were observed in Peru (Barber et al., 1985)
Fig. 12. Cambios en los niveles anuales de captura de anchoveta, sardina y jurel considerando años de ocurrencia de "El Niño" (Modificado de Jordán, 1983).

Fig. 12. Annual changes in the catch levels of anchovy, sardine and jack mackerel in Perú and Chile, considering "El Niño" years. 1964-1983 (Modified from Jordán, 1983).

(ITEM AUA:6,1985).
and in northern Chile. Yanez et al. (1986) pointed out that the anchoveta fishery collapsed in the region as a consequence of intensive exploitation and environmental fluctuations. However, they note an increase in eggs and larvae of this species during 1985-86, which could be associated with diminishing sardine abundance after the last ENSO episode.

For the southeast Pacific, Arntz (1986) reported that during 1982-83 the total sardine biomass declined by almost 20% due to loss of body weight and increased natural mortality. Nevertheless, because of the changes in distribution, the sardine landings in Chile increased 47% in terms of weight and 105% in terms of number of fish. Average length of sardines caught in northern Chile decreased between the first and second halves of 1983 and increased drastically in 1984, when the values were approximately the same as the average for the period 1980-82 (Martinez et al., 1985).

In 1986, the anchoveta catch in Chile was at a record high of 1.34 million tons (Martinez, 1987), making this species the second in importance (Fig.13). In addition, the size increased notably in 1986. Fig. 14 shows the increase observed since June 1986. On the other hand, the number of small individuals of Chilean pilchard greatly increased (Fig. 15). This latter fact and the diminishing abundance of pilchard observed in recent years indicate that this resource is being overexploited (Martinez et al., 1987).
Fig. 13. A: Catch evolution in northern Chile. B: Monthly catches in 1986; Catches obtained with, 1) up to 50 cubic meter-capacity purse seiners; 2) up to 140 cubic-meter and 3) obtained with all the fleet.

Fig. 14. Size of the anchovetas caught in 1986 in the Iquique zone.
Fig. 15. A: Size composition of the sardines catches between Arica (18°20' S) and Antofagasta (24°S); B: Percentage of individuals with size lesser than 27 cm; C: Mean length of spawning.

From Martínez et al. (1983)
The population size of jack mackerel apparently stayed constant during the last event, but the changes in horizontal and vertical distribution influenced the availability of the resource, resulting in reduced catches off Peru and Chile (CPPS, 1984; Castillo and Guzman, 1985).

Mackerel was the dominant species in the Ecuadorian pelagic fisheries until February of 1983. Then, it diminished and it was practically absent during April-August. Its abundance stayed constant in Peru and decreased in Chile (CPPS, 1984). Unusually high commercial catches of dorado, bonito and yellowfin tuna in northern Chile were another indicator of the strong alteration introduced by the last ENSO event. In relation with these changes in abundance introduced by El Niño, Alvial (1985) concluded that decreased catches of these species along with sardine, and increased catches of jack mackerel in Iquique (Chile), marked the end phase of the 1982-83 event. Another recorded change was the increase in shrimp catches in Colombia, Ecuador and northern Peru, and an increase in abundance of Octopus spp. on the northern Chile coast (Alvial, 1985; Arntz, 1986).

The pups of Otaria flavescens, the common seal present on the coast of Iquique, died in large numbers from poor nutrition, especially between January and March of 1983. Barber and Chavez (1983) reported that all the Galapagos fur seal pups (Arctocephalus galapagoensis) born in 1982 died by March 1983.
Many of the pups and some of the adults of the California sea
dlion (*Zalophus californianus*) and fur seals and sea lions on the
southeastern coast of Peru died also. Another case of massive
mortality was the marine iguana (*Amblyrhynchus cristatus*) in the
Galapagos Islands. They suffered a 45% mortality between July
1982 and July 1983, and the surviving adults showed a mean weight
loss of 30%, a result of higher water temperature and decreased
salinity killing the seaweeds which are the iguana's normal food
(Arntz, 1986).

In the northeastern Pacific the market squid (*Loligo opalescens*) was the most numerous squid species off Oregon be-
Rockfish and Pacific herring (*Clupea pallasi*) which are charac-
teristic of cold water also decreased in relative abundance
during 1983-84. On the other hand, dogfish (*Squalus acanthias*)
increased in abundance during 1983-84 compared to other years.
The most notable change, however was for Pacific mackerel and
jack mackerel. In 1983-84 these species became the most commonly
captured nekton in the purse seine samples (Pearcy and Schoener,
in press). High abundances of mackerels in waters off Oregon and
Washington also persisted into 1984. Another pelagic species
that registered an increase was bonito. Increased catch of ocean
sunfish (*Mola mola*) and the Pacific saury were reported off the
Washington coast during the 1982-83 episode (Schoener and
Fluharty, 1985).
Salmon were also affected by El Niño events. Low landings of coho salmon occurred after each of the three strong ENSO (Schoener and Fluharty, 1985). The low number of 3-year old coho salmon off Oregon and California (42% of predicted) was apparently the result of an extraordinarily high mortality of maturing fish during their final year in the ocean (Pearcy et al., 1985). The return of chinook salmon to many areas of Oregon and California was reduced. Besides the unprecedented mortality of adult coho in the Oregon-California region in 1983, the mean size of adult salmon was reduced.

The Inter-American Tropical Tuna Commission (IATTC) has, over the last 25 years, been investigating the possible effects of El Niño episodes on tuna abundance and availability and the vulnerability of tunas to capture by purse seiners. For each year from 1960 through 1984 data on skipjack and yellowfin catches, fishing effort, and the environment have been summarized from logbook records. These have been analyzed for three important fishing areas: the inshore coastal area of Ecuador and northern Peru, the Costa Rica dome (CRD) area, and the area within a triangle between Cape San Lucas, Cape Corrientes (Mexico), and the Revillagigedo Islands, centered at 19°N-110°W (IATTC, 1984; 1985). During prolonged El Niño episodes, such as occurred in 1957-58, 1969, 1972, and 1982-83, the availability of tunas was reduced in the tropical eastern Pacific, especially off Ecuador. In the 1982-83 ENSO event the catches and effort in the yellowfin and skipjack fisheries were reduced in the CYRA (Commission's yellowfin regulatory area), and many large seiners moved to the
western Pacific, where good catches were obtained. Changes in both the environment and in the catches along the coast of Ecuador and northern Peru appear to have been similar before and during the last two El Niño events. Catch per unit effort (CPUE) and effort decreased dramatically during ENSO events in this area of the Pacific.

In the Costa Rica Dome zone, the 1982-83 ENSO caused weak westerly winds, high sea levels, weaker-than-normal upwelling, and reduced nutrient enrichment and primary production. The CPUE of yellowfin tuna was well below the 1962-1984 mean during most of 1983. In contrast, the CPUE of skipjack was near or above normal during about half of the year. After April 1984 the wind directions were more similar to the long-term mean than were those in 1983, and the CPUE of yellowfin in 1984 was greater than in 1983, reaching a peak in April during a period when the wind speeds dropped, SSTs were slightly above normal, and easterly winds strengthened sharply as they had at the end of 1983. It appears that in 1982-83 skipjack were more available to the purse seiners around the CRD than were yellowfin. When El Niño conditions relaxed, yellowfin were more available to the purse seiners than were skipjack.

In the third important fishing area, centered around 19° N, pelagic red crabs are a principal source of food for both skipjack and yellowfin. Because pelagic red crabs are plankton feeders they tend to live associated with the western edge of
TABLE III. Summary of ENSO impacts on abundance reported in this paper (cases and references are not exhaustive and their locations do not show correspondence among them).

<table>
<thead>
<tr>
<th>IMPACTS</th>
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<th>REFERENCES</th>
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<tr>
<td><strong>DECREASE OF ABUNDANCE</strong></td>
<td>* Anchoveta</td>
<td>Alvial (1985)</td>
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<tr>
<td></td>
<td>* Sardine</td>
<td>Martinez et al. (1985)</td>
</tr>
<tr>
<td></td>
<td>* Sea lion, fur seals</td>
<td>IATTC (1984 &amp; 1985)</td>
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<tr>
<td></td>
<td>* Marine iguanas</td>
<td>Yanez et al. (1986)</td>
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<td></td>
<td>* Skipjack, yellowfin</td>
<td>Avaria (1985)</td>
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<tr>
<td></td>
<td>* Squid</td>
<td>Barber et al. (1985)</td>
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<td></td>
<td>* Rockfish</td>
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<td></td>
<td>* Coho, pink and chinook salmon</td>
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<tr>
<td><strong>INCREASE OF RELATIVE ABUNDANCE</strong></td>
<td>* Shrimp</td>
<td>Arntz (1986)</td>
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<td></td>
<td>* Octopus</td>
<td>CPPS (1984); Alvial (1985);</td>
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<td></td>
<td>* Dorado</td>
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<td></td>
<td>* Bonito</td>
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<td></td>
<td>* Dogfish</td>
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<td></td>
<td>* Sunfish</td>
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<tr>
<td></td>
<td>* Jack mackerel</td>
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<tr>
<td></td>
<td>* Pacific mackerel</td>
<td></td>
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<tr>
<td><strong>MASSIVE MORTALITY</strong></td>
<td>* Sea lions</td>
<td>Barber et al. (1985)</td>
</tr>
<tr>
<td></td>
<td>* Fur seals</td>
<td>Barber &amp; Chavez (1983)</td>
</tr>
<tr>
<td></td>
<td>* Marine iguanas</td>
<td>Arntz (1986)</td>
</tr>
<tr>
<td></td>
<td>* Coho salmon</td>
<td>Pearcy &amp; Schoener (in press)</td>
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<td></td>
<td>* Anchovy</td>
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coastal upwelling centers. In most years the California Current moves southeast along the coast of Baja California, inducing upwelling and transporting red crabs and plankton southward. In El Niño years, however, the California Current weakens and moves offshore. Near the coast of Baja California in those years the Davidson Current becomes predominant, transporting warm water and red crabs and other sub-tropical species northward. During the 1982-83 El Niño, red crabs were found in large numbers along the west coast of United States. During 1983, both the skipjack and yellowfin CPUE's were below the long-term mean, except that the yellowfin CPUE reached the mean at the middle and at the end of the year. During the first half of 1984 the prevailing winds were from the northwest, just as they had been in 1983, but the wind speeds were weaker than in 1983. The CPUE for yellowfin in 1984 was well above normal all year except in August, when fishing was greatly curtailed due to frequent tropical storms. Skipjack CPUE was below the normal levels, but this probably was due to decreased effort during 1984 caused by a diminished market demand (IATTC, 1985).

A summary of the impacts on distribution is presented in Table III, along with some examples and references.

4.4.- CHANGES IN BODY CONDITIONS AND GROWTH

Mujica et al. (1985) found that the condition factor $b$ ($b$, in the equation $W = aL^b$) of sardine in northern Chile during 1982-83 was clearly lower than those recorded under normal
oceanographic conditions. The values of b decreased to the north. Zuzunaga and Ñiquen (1985) also reported a decrease in the condition factor for sardine off Peru.

Romo (1985) reported a strong reduction in the lipid content of fishmeal (principally from sardines), a decrease in oil production, and an increase in the percentage of the ash content of fish meal. Romo believes that in periods of low food availability fish preferentially use their more saturated lipid fraction for their metabolic requirements and accumulate non-saturated fatty acids. She also found that in 1982-83 the lipid content increased geographically from north to south and returned to approximately normal values in 1984.

Arntz (1986) pointed out that many pelagic fish suffered great losses of body weight during the 1982-83 ENSO. In the most severe case, that of the anchovy, this loss amounted to 30% for individual fish. Sardines lost weight over a relatively broad range. Jack mackerel and mackerel weighed about 10% less than in earlier years.

Aguayo et al. (1985) concluded that the growth rate of sardine and jack mackerel was low during 1982-83 based on growth rings in otoliths. According to Barber et al. (1985) hake may have suffered reduced growth between November 1982 and January 1984 because of the sparse food in deep water. Interestingly, hake were the first fish to leave the northern Peru region but
TABLE IV. Summary of ENSO impacts on physical conditions reported in this paper (cases and references are not exhaustive and their locations do not show correspondence among them).

<table>
<thead>
<tr>
<th>IMPACTS</th>
<th>CASES</th>
<th>REFERENCES</th>
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<tbody>
<tr>
<td>REDUCTION OF CONDITION FACTOR</td>
<td>* sardine</td>
<td>Mujica et al. (1985)</td>
</tr>
<tr>
<td>DECREASE IN LIPID CONTENT</td>
<td>* sardine</td>
<td>Romo (1985)</td>
</tr>
<tr>
<td>REDUCTION OF GROWTH RATE</td>
<td>* anchovy</td>
<td>Francis (pers.comm.)</td>
</tr>
<tr>
<td></td>
<td>* jack mackerel</td>
<td>Aguayo et al. (1985)</td>
</tr>
<tr>
<td></td>
<td>* hake.</td>
<td>Barber et al. (1985)</td>
</tr>
<tr>
<td></td>
<td>* sardine</td>
<td>Fiedler et al. (1986)</td>
</tr>
<tr>
<td></td>
<td>* maturing coho</td>
<td>Pearcy et al. (1985)</td>
</tr>
<tr>
<td>REDUCTION OF BODY WEIGHT</td>
<td>* anchoveta</td>
<td>Zuzunaga &amp; Niquen (1985)</td>
</tr>
<tr>
<td></td>
<td>* sardine,</td>
<td>Arntz (1986)</td>
</tr>
<tr>
<td></td>
<td>* jack mackerel</td>
<td>Johnson (1984)</td>
</tr>
<tr>
<td></td>
<td>* mackerel</td>
<td>Pearcy et al. (1985)</td>
</tr>
<tr>
<td></td>
<td>* coho salmon</td>
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the last to return once the physical conditions had returned to normal.

In the Northeast Pacific a reduction of the growth rate in hake was evidenced during the El Niño period (R. Francis, personal communication). Fiedler et al. (1986) reported that the growth rate of juvenile and adult anchovy was slowed in the northeastern Pacific. Pearcy and Schoener (in press) reported that the growth rates of juvenile coho in the ocean during 1983 were similar to other years in spite of the abnormally low survival of coho smolts in this period.

A summary of the impacts observed in terms of changes in body conditions and growth is presented in Table IV, along with some examples and references.

4.5. - CHANGES IN REPRODUCTION AND EARLY LIFE HISTORY

Low values of the gonadosomatic index of sardine were associated with the occurrence of ENSO in northern Chile (Mujica et al., 1985). These results were consistent with the diminishing in the condition factor above mentioned for this species. Distributional changes in eggs and larvae of sardine were evident and areas of relatively high concentration of both were observed. Mujica et al. (1985) estimated that a high mortality rate occurred either at the last stage of egg development or at early larval stages. Retamales and Gonzalez (1985) found no secondary maximum in spawning during February-March 1983 (the principal
spawning period is in winter-spring). In addition, they found a high percentage of atrecic oocytes in the different stages of gonadic maturity. The principal spawning in 1983 showed low percentages of spawning and gonadosomatic indices were inferior to those registered in 1982. In 1984 this species exhibited a recuperation of the mentioned index, active vitelogenesis and permanent spawning (Retamales and Gonzales, 1985).

Although sardines spawned successfully off Peru at the beginning of the 1982-83 event, subsequent spawnings were restricted to just a few areas between November 1982-March 1983 (Santander and Sandoval, 1985). The summer spawning of this species practically disappeared off Peru and the winter spawning was considerably reduced during ENSO conditions (Zuzunaga and Niquen, 1985).

The spawning of anchovy off Peru ceased in December 1982, instead of March as in normal years, and became restricted to small, nearshore areas. Eggs and larvae of anchoveta reached the lowest density off Peru since 1966 (Arntz, op cit.). According to Santander and Sandoval (1985) anchoveta was the species most affected by the 1982-83 event. Areas of larval distribution were reduced and practically disappeared during 1983.

Arntz (1986) pointed out that the general deterioration of physical conditions had a serious impact on the spawning of
anchovies and sardines. Santander and Sandoval (1985) attempted to classify the ENSO impacts on reproduction of the principal pelagic fishes in the southeastern Pacific. According to them, the species that inhabit the coastal cold areas and are winter-spring spawners, like anchoveta, are negatively affected by ENSO events. Species like the sardine, that inhabit mixed-waters and spawn during winter-spring are not as affected by strong or moderate events, like those of 1972 and 1976, and can be favoured by them. However, these species are negatively affected by very strong events like that of 1982-83.

According to Avaria (1985), the large alterations in the spawning and the high mortality of larvae and juveniles of sardines could have repercussions on the recruitment to this fishery during subsequent years. Sardines, unlike anchoveta, have a longer life cycle, with recruitment between the fourth and fifth year of age. These fish remain in the fishery for 10 to 11 years with many age groups supporting the fishery. Therefore the effects of poor recruitment during one year will have less effect on the fishery for sardines than for anchoveta (Avaria, 1985).

Santander and Zuzunaga (1984) believed that the spawning of mackerel and jack mackerel were normal during the 1982-83 event, and may have even increased. They believed that the ichthyoplankton of these species were favored by this event.

In the Northeast Pacific, Johnson (1984) and Pearcy and Schoener (in press) reported that coho salmon off Oregon had

Specific fecundity for anchovy was low in 1983 off Southern California due to an unusually high proportion of young females in the spawning stock. Yolk-sac larvae mortality was abnormally high in the spring of 1983, probably as a result of predation (Fiedler et al., 1986). Low recruitment in this species in 1983 was caused by a combination of factors: low specific fecundity, high mortality of yolk sac larvae, and possibly high predation pressure (Fiedler et al., 1986).

Changes in composition of larval fishes off Oregon was indicative of larval transport from offshore waters. Larvae normally associated with waters approximately 40 Km from shore increased in abundance in coastal waters (Brodeur et al., 1985; Pearcy and Schoener, in press). Thus, northern anchovy, unfrequently collected inshore in other years, were the dominant fish larvae in 1983.

Bailey and Incze (1985) analyzed the effects of ENSO on the early life history and recruitment of fishes of temperate waters. They pointed out that the abundance of eggs and larvae depends partly on the response of spawning adults to warming and other environmental changes. ENSO events appear to have disastrous effects on recruitment of some stocks in some areas, especially those living near the southern end (northern end in
TABLE V. Summary of the ENSO impacts on reproduction and early life history (cases and references are not exhaustive and their locations do not show correspondence among them).

<table>
<thead>
<tr>
<th>IMPACTS</th>
<th>CASES</th>
<th>REFERENCES</th>
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<tr>
<td>ALTERATIONS OF EGGS AND LARVAE</td>
<td>* Sardine</td>
<td>Pearcy &amp; Schoener (in press)</td>
</tr>
<tr>
<td>TRANSPORT AND DISTRIBUTION</td>
<td>* Anchovy &amp; anchoveta</td>
<td>Mujica et al (1985)</td>
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<tr>
<td></td>
<td>* Mackerel</td>
<td></td>
</tr>
<tr>
<td></td>
<td>* Jack mackerel</td>
<td></td>
</tr>
<tr>
<td>ALTERATIONS OF EGGS AND LARVAE</td>
<td>* Sardine</td>
<td>Arntz (1986);</td>
</tr>
<tr>
<td>ABUNDANCE</td>
<td>* Anchoveta</td>
<td>Santander &amp; Sandoval (1985)</td>
</tr>
<tr>
<td>EGGS AND LARVAE</td>
<td>* Sardine</td>
<td>Fiedler et al. (1986)</td>
</tr>
<tr>
<td>MORTALITY</td>
<td>* Anchovy</td>
<td>Mujica et al. (1985)</td>
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<tr>
<td></td>
<td>* Anchoveta</td>
<td>Avaria (1985)</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Santander &amp; Sandoval (1985)</td>
</tr>
<tr>
<td>FECUNDITY ALTERATIONS</td>
<td>* Sardine</td>
<td>Retamala &amp; Gonzalez (1985); Arntz (1986);</td>
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<tr>
<td></td>
<td>* Anchovy</td>
<td>Pearcy &amp; Schoener (in press); Fiedler et al.</td>
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<tr>
<td></td>
<td>* Coho salmon</td>
<td>(1986).</td>
</tr>
<tr>
<td></td>
<td>* Jack mackerel</td>
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</tr>
<tr>
<td></td>
<td>* demersal fish</td>
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<tr>
<td>RECRUITMENT ALTERATIONS</td>
<td>* Anchovy</td>
<td>Avaria (1985); Fiedler et al. (1986); Bailey</td>
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<tr>
<td></td>
<td>* Sardine</td>
<td>et al. (1986); Bailey and Incze (1985).</td>
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<tr>
<td></td>
<td>* Anchoveta</td>
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the southern hemisphere) of their geographical range, such as cod off the Canadian coast. On the contrary, ENSO sometimes appears to be good for some subtropical stocks spawning at the northern end (southern end in southern hemisphere) of their range, such as sardine and jack mackerel off California during both, 1958-59 and 1983 ENSO events. On the other hand, El Niño often, although not always, causes poor year classes in anchovy, a pattern that has also been observed in the Peruvian region.

A summary of the impacts of ENSO on reproduction and early life history is presented in Table V, along with some examples and references.
5. ENSO IMPACTS AND IMPLICATIONS ON PELAGIC FISHERIES.

I will discuss the short-term and long-term impacts and implications of ENSO on fisheries. Short-run impacts consist essentially of population level alterations that persist for only a few years. The long-run impacts involve changes in the community structure that may persist for periods of many years. ENSO events involve several levels in the spectrum of response of the biological systems, from microscale spatio-temporal processes that affect the early stages of life history up to large scale processes related, for example, to recruitment alterations, species succession and community changes that tend to persist a very long time.

5.1.- SHORT-TERM RESPONSES.

Short-term responses can be grouped as those related to changes in abundance and catchability, both key factors in the exploitation and management of these pelagic resources.

5.1.1.- Changes in abundance.

ENSO can cause both almost immediate and delayed alterations in biomass abundance of the stocks. Fast responses are generated by changes that affect mortality rate, growth rate and body conditions. Alterations in abundance introduced in a given area by changes in distribution will be discussed further in the section on changes in catchability. The second type is
represented by a more delayed effect on recruitment as a consequence of the alterations that affect reproduction and early life stages.

Fast responses

The strong alterations induced by ENSO may affect the natural mortality rate of impacted pelagic species, as has been reflected by mortalities observed in anchoveta and sardine in the southeastern Pacific (Arntz, 1986), and by increases in coho salmon mortality in the northeast Pacific (Pearcy and Schoener, in press). Fishes that retreat into small water bodies in which favorable conditions remain can be trapped in them as the ENSO event evolves, increasing the mortality rate of the stock. Moreover, predation rates may change as predator and prey distribution and abundance become altered during ENSO. An example is the strong increase in abundance reported in Pacific mackerel, which prey on northern anchovy, during ENSO occurrences (Huppert, 1981). Food availability for planktivorous fishes also changes during an ENSO event often, reducing growth rates and biomass levels. Hence, changes in mortality rate will vary with the intensity of the event, and it will affect the different species in different ways, depending on their susceptibility to environmental perturbations, including predators and changes in the quality and amount of food.
Models developed for most of the pelagic fisheries in the eastern Pacific have assumed a constant natural mortality rate for biomass. However, adverse physical conditions can have a direct impact on fish when they exceed the tolerance limits of the fish.

Effects of different natural mortality rates and carrying capacities, analyzed through a stochastic model for the northern anchovy fishery, show that a decrease in carrying capacity results in corresponding decreases in average catch and average spawning biomass. Average economic return is sharply affected and decreases more than average catch itself due to increased cost of harvesting in the face of a lower abundance (Huppert, 1981). In some cases, as occurred with temperate demersal fishes during the last event in the southeastern Pacific, the food availability apparently increases in terms of diversity and total abundance (Arntz, 1986), and the net effect in those circumstances would be an increased carrying capacity for the period of time in which those conditions persist.

Lower growth rates and condition factors have also been reported in some species including anchoveta, sardine and hake. These effects diminish the biomass and may change the chemical composition of fishes and fish meal. A reduction in lipid content will affect the efficiency of fish meal and fish oil production.
Delayed responses

Year class strength of many stocks of fishes is thought to be determined during early life history stages, with the conditions before spawning determining the quantity and viability of eggs (Lasker, 1985). During the weeks following hatching, survival success may be determined primarily by the coincidence in time and space of feeding larvae and a food supply of adequate concentration and quality (Bailey and Incze, 1985; Lasker, 1985). In the absence of such a supply, larval growth is retarded and vulnerability to predation is increased. The coincidence in time of abundance of a predator and prey is governed by the timing of spawning, hatching, primary, and secondary production. The coincidence in space is governed by the physical processes of advection and diffusion. In both cases, the coincidence is in large part a product of environmental variability. Thus, recruitment is not just a simple function of spawning stock size. The relative size of a cohort is also determined by feeding and predation rates in a variable environment.

According to Bailey and Incze (1985), the general potential effects of the environmental anomalies introduced by ENSO events on early larval stages of temperate marine fishes are changes in: 1) distribution of migratory species immediately before or during spawning; 2) fecundity of spawning fish; 3) physiological condition of eggs and larvae; 4) transport of eggs and larvae, and 5) the predator-prey community to which eggs
and larvae stages are exposed. These authors concluded that the potential mechanisms of impact of ENSO conditions on recruitment success of fish can be grouped by the migratory behavior of species. So, it is possible to distinguish sedentary or "homing" species and "nomadic" or migratory species of fish.

For sedentary or "homing" species, which remain in or return to the same area regardless of El Niño (like many coastal species), there can be a direct physiological impact of temperature on fecundity, timing of spawning and condition of spawned eggs. Temperature will affect rates of development and metabolism of eggs and larvae. Changes in abundance, temporal variation of species composition and/or changes in temporal dynamics of the prey community can be expected, due either to the intrusion of different water masses or the effect of increased temperature on local species assemblages. This could affect spawning of fish, depending on the nature of the adult’s diet and patterns of energy storage and mobilization for reproduction. After spawning and hatching of eggs, the quantity and the type of prey could affect larval feeding conditions. Planktonic predators also may change because of a new water mass or because of local warming, and these changes have the potential to affect egg and larval stages. A summary of the potential effects of ENSO conditions on sedentary or "homing" species is presented in Table VI.

For "nomadic" species of fish, physiological impacts of temperature could be minimized or avoided by migration into
places with appropriate conditions. Spawning could take place in a different water mass and/or at different latitudes than usual. The planktonic and nektonic communities encountered by the spawned eggs and larvae of these species may or may not be unusual, depending on whether the migration occurred within a water mass or in a different one. The latter condition could result in alteration of predator-prey relationships and production dynamics for eggs and larvae. If a northward migration (southward in the southern hemisphere) occurs within the same mass of water there will be an opportunity of colonization of new areas (successful recruitment). However, this extension may be only temporary if conditions become hostile to the eggs and larvae after ENSO subsides, as frequently occurs. A summary of the potential impacts of ENSO conditions on nomadic or mobile species is shown in Table VII.

The dependency of recruitment on natural environmental fluctuations induced by El Niño seems to be unquestionable. Therefore, models are needed that take into account this dependency of recruitment on environmental physical variability. Two ways in which this can be done are: 1) developing the necessary functions to account for this dependency and including them in the models, and 2) introducing stochastic terms that reflect the environmental variability.

Huppert (1981), analyzing the effects of different recruitment functions in a northern anchovy model, demonstrates the effects of uncertainty (environmental variability) in these
### TABLE VI
Summary of potential effects of El Nino conditions on sedentary or "homing" species.

1. Impact of elevated temperatures on spawning effort
   - fecundity
   - timing of spawning
   - condition of eggs

2. Effect of changes in food abundance on spawning effort
   (depends on nature of prey and spatial and temporal pattern of energy storage and mobilization for spawning)

3. Elevated temperature effects on eggs and larvae
   - physiological tolerance
   - development time
   - metabolism

4. Indirect effects of elevated temperatures on eggs and larvae:
   predator and prey communities
   - abundance
   - species composition
   - timing

5. Effects of new water mass on eggs and larvae
   - same as above

6. Effects of migratory vertebrate predators that follow ocean warming, and which may feed on eggs and larvae
   - timing
   - new species

---

### TABLE VII
Summary of potential effects of El Nino conditions on highly migratory (nomadic) or mobile species.

These species may minimize adverse physiological impacts of elevated temperatures on adults, but there are costs, including:

1. Extra energetic expenditure on migration which may affect spawning effort
   - fecundity
   - timing of spawning
   - condition of eggs

2. Spawning may take place in a different water mass than usual
   - predator and prey communities may be different (abundance and species composition)
   - local dynamics (timing) may be different

3. Spawning may take place further poleward
   - opportunity for "colonization" or "expansion" may be successful or unsuccessful
   - new interspecific interactions
   - colonized area may be physically inhospitable after El Nino conditions subside

---

*From Brady and Jepson (1985).*
models. Fig. 16 shows that the biomass at time $T$ generates the recruitment at the time $T+1$ through the function labeled $A$ (a recruitment function derived from the logistic model). The straight line out of the origin labeled "replacement" represents the total loss of adult biomass due to natural causes in a year. If the size of recruitment equals the total mortality, the population just maintains itself; hence the term "replacement". In Figure 16 it is possible to see that in this particular model, for spawning biomasses below 4.2 million tons (equilibrium level), the recruitment exceeds the replacement level and therefore net growth occurs. The same figure shows that the estimated stock-recruitment relationship $A$ is not a very close "fit" to the 15 observations shown on the diagram. Thus, the statistically fitted equation can be used to make conditional predictions, but with a "high degree of uncertainty". An alternative method of recruitment tested by Huppert (1981), labeled $B$ in the figure, could not be distinguished statistically from the original logistic based model with a reasonable degree of confidence. In any case, a wide range introduced by the uncertainty persists, and management of the northern anchovy and other pelagic fishes must recognize the "level of uncertainty" in population models as a result of environmental variability.

Effects on dynamic population models

In light of the facts discussed above, it is reasonable to question the deterministic single-species population
Figure 16 Alternative stock-recruitment models. Model A is the logistic model, and Model B is the modified constant Recruitment Model.

Figure 17 Comparison of predicted with observed anchovy population sizes, including a plot of residuals.

From Hjort (1921).
dynamic models in the eastern Pacific pelagic fisheries. The question then is: How can these models be replaced, taking into account the elements of uncertainty and complexity introduced in these fisheries by ENSO variability? What is the feasibility of applying holistic and stochastic approaches in these fisheries?

Holistic comprehensive models should be developed, incorporating those variables which clearly have a role in regulating the fish biomass fluctuation. Laevastu (1985) pointed out that single purpose models ignore crucial complexes and present bogus answers. The development of holistic approaches will provide results that are more consistent with the reality of systems that are impacted by environmental changes. The generation and application of these approaches are feasible today because of the recent development of computational tools capable of dealing with the level of complexity involved. Laevastu and Larkins (1981) provide an example of a dynamic marine ecosystem model that includes environmental processes, permits simulation of the steady state, and considers the dynamic of the standing stocks of species in space and time as affected by inter-specific interactions and the activities of man (e.g., fishing). Models such as this require a great deal of theoretical support in order to define the functions involved in the model. Commonly these data bases do not exist, or are available in only a few aspects. Ecosystem approaches in the eastern Pacific should be focused in specific areas, modelling the fluctuations of the relevant taxa in relation to all factors that have an influence on the abundance of the resources, i.e., those that directly affect the
stock abundance itself (dynamics of the stock), and those that affect its displacements and that indirectly alter its abundance. Of course, this task requires a clear definition of the physico-biological, inter-specific, and fishery-biological interactions, which so far is almost impossible.

With regard to the second approach in modelling, a good example is a stochastic model developed for the northern anchovy fishery by the Pacific Fishery Management Council (1978). Fig. 17 shows the plot of the logarithmic of observed biomass against the logarithmic of biomass predicted by the model. The values of the residuals are plotted against the predicted biomass, showing that the model is a fair descriptor of the relationship over the range of biomasses observed. Since a stochastic error term is introduced in the biomass estimation, a stochastic model for recruitment could be then obtained. Essentially, this stochastic model works using a matrix containing the probabilities that a population of observed size \( B_i \) at time \( t \) will become a population \( B_j \) of observed size \( B_j \) at time \( t+1 \). The probabilities of each possible transition are associated with the corresponding error term \( e_{ij} \), which is from a hypothetically normal distribution. Thus, these models do not have just one response associated with a set of conditions but many probable responses according to some probabilistic function. The transition probability matrix of this model can be used for several purposes. In general, any probability vector associated with the vector of discrete observed population sizes \( B \) can be multiplied by the transition proba-
ability matrix to obtain a new vector of probabilities reflecting the likelihood of observing the corresponding population sizes in the following year, and so on. In particular, this model has been used to examine the impacts of alternative quota formulas in the long-term. Huppert et al., (1980) ran a simulation of one thousand years for each of 70 different quota formulas. For each simulation, three important characteristics of the fishery were obtained as outputs: average annual quota, average potential net economic yield, and the number of years with the quota equal to zero. Thus, a simulation model based on a stochastic approach demonstrates its utility in obtaining long-term estimations of management impacts in a changing environment.

How then can we apply the MSY concept in pelagic fisheries that undergo strong environmental variability? According to Huppert (1981), one immediate consequence of the stochastic recruitment is that the concept of sustainable yield is inapplicable. Although the peak of the yield curve may occur at some given level, this level of yield is in no sense sustainable. Huppert (1981) found that harvesting MSY year after year can be expected to severely deplete the population within a short period of time. Populations fluctuating due to environmental conditions will become unstable under either constant fishing effort or constant catch policies (Beddington and May, 1977).

Notwithstanding that the development of holistic and stochastic approaches can improve our knowledge and prediction of fish population dynamics, some important questions remain. How
do major changes of very low-frequency occurring in the eastern Pacific impact pelagic fisheries? Do these fisheries move from one equilibrium state to other, with alteration of the species structure and functional relationships? Are these changes of catastrophic character and do they have profound implications for management? How does El Niño relate to these low frequency trends? These aspects will be discussed further in the section on analysis of the long term.
5.1.2.- Changes in catchability.

In addition to variations in abundance introduced by ENSO events, variations in catchability also have strong management implications.

Considering the catch equation:

\[ C = qfn \]

where,

- \( C \) = quantity removed by fishing or catch,
- \( q \) = catchability coefficient,
- \( f \) = effort,
- \( N \) = fish abundance,

it is possible to deduce:

\[ \frac{C}{f} = \frac{q}{N} \]

and introducing CPUE (catch per unit effort), then:

\[ \text{CPUE} = \frac{C}{f} \]

therefore,

\[ N = \left( \frac{1}{q} \right) \text{CPUE} \]

So, the catchability coefficient \( (q) \) is presumed to be constant and knowing CPUE, \( N \) can be estimated.

But is \( q \) really a constant value? Much evidence shows that this coefficient is not constant in pelagic fisheries, especially in those exposed to strong environmental variability, such as fisheries in the eastern boundaries of the Pacific Ocean.
Gulland (1983) mentioned five patterns of change in catchability: 1) cyclical changes in time; 2) trends in time; 3) changes related to the total amount of fishing; 4) changes related to stock abundance; and 5) random variations.

Changes related to stock abundance, which occur during El Niño events, can be the most serious type of changes in catchability, since they can partly or wholly obscure what is happening to the real abundance of the stock. In the extreme case, if catchability is inversely proportional to the abundance, then:

\[ \text{CPUE} = qN \]

and

\[ q = a/N \]

therefore,

\[ \text{CPUE} = a \]

where \( a \) is a constant.

Gulland (1983) gives an example that supports this supposition. In a purse-seine fishery, the catch per set of the net might appear to be a suitable measure of CPUE. If, however, as the stock decreases the number of schools decrease but the size of the schools remains constant, and each set takes one complete school, then clearly the CPUE is equal to the school size and is constant. The catchability, i.e., the proportion of the total stock taken by a unit of effort (one set), is inversely proportional to the number of schools. If these assumptions are correct, then ENSO episodes that reduce stock abundances could
simultaneously cause an increase in catchability. However, this relationship between stock abundance and schooling behavior clearly needs more research in order to define the mathematical functions.

Much variation in catchability is random or related to physical variability. Fluctuations in weather and sea conditions can result in good or bad catches in specific periods. The El Niño phenomenon represents another kind of random fluctuation of catchability, which can seriously affect fisheries. For example, one effect of the 1972-73 and 1982-83 ENSO events was that the stocks of anchoveta and sardine were concentrated in small strips near the coast in the southeastern Pacific. This fact allowed good catches to be maintained off Peru in 1972 even when the stock was rapidly declining. This delayed recognition of the serious situation and the adoption of appropriate measures by the Peruvian government.

In these fisheries, a monitoring survey repeated at regular intervals and using constant methods from year to year could provide an index of abundance that is free of the difficulties caused by possible changes in the catchability coefficient $q$. However, to provide more and better information is costly, and at some point the marginal cost of more information must exceed its marginal value. The decision for intensifying the monitoring should rest in a simple economic analysis like that proposed by Huppert (1981), in which the increase in EMV...
(expected monetary value) is compared with the increased cost at successive levels of monitoring precision in a given fishery.

Highly migratory species are a special case of alteration in catchability within the fisheries of a country. The timing and routes of migration of species may be affected by ENSO occurrences, changing catchability in some particular areas and times. The highly migratory fishes often constitute shared resources between different EEZ’s and/or between EEZ’s and the high seas. Changes in catchability demonstrate the necessity of cooperative research and management efforts between countries in order to avoid over-exploitation and the eventual collapse of the fisheries. The Law of the Sea establishes that the conservation, development and optimum utilization of the transboundary stocks and highly migratory species must be shared between the states concerned, but special provisions are not available to regulate catches. Direct cooperation, or cooperation through adequate international organizations, is urgent, particularly in light of the effects introduced by ENSO in the productive ecosystems of the eastern boundary currents in the Pacific.

5.2.- ENSO IMPACTS IN THE LONG-TERM CONTEXT.

Quinn and Neal (1983), analyzing a 120 year record of Southern Oscillation-related activity along the west coast of South America, noticed significant decreases in the frequency of occurrence of moderate/strong El Niños and in the related
abnormally heavy amounts of Chilean subtropical rainfall over the past half century. In a more recent investigation, Quinn and Antunez (1986) noted significant long-term climatic changes over a four and a half century record of El Niño activity. Since 1976 the SO index has been unusually low. This has coincided with weakened southeast trade winds as observed in marine weather data from merchant ships, reduced upwelling, and above normal SST’s along the equator in the eastern tropical Pacific. The weak trade winds piled up less than normal amounts of water in the western Pacific and, as a result, thermocline depths there have been shallower than normal, while in the eastern tropical Pacific they have been deeper than normal (McLain, 1984). Quinn and Neal (1983) suggested that these oceanographic changes played a significant part in the decline of anchoveta off Peru and northern Chile and in the increase of other species such as sardine and jack mackerel.

These changes have also been noticed in the Northeast Pacific. Associated with the 1976 shift in the SOI was a shift in the pattern of SST anomalies over the Northeast Pacific. MacLain (1984) pointed out that the pattern of SST anomaly has two general types: 1) a pattern called "warm-cold" or WC pattern, with above normal SST’s in a large area north of Hawaii and below normal SST’s along the coast from the eastern tropical Pacific to the Gulf of Alaska or even the Bering Sea, and 2) a "cold-warm" or "CW" pattern with generally below normal SST’s north of Hawaii and above normal SST’s along the coast. During periods when the
SOI anomaly has been positive, the SST anomaly pattern has often
been of the WC type. Consistently since the summer of 1976, when
the SOI fell the SST anomaly pattern shifted to the CW type, and
has remained generally of that type into the 1980's. The change
in the SST pattern involved a shift in the atmospheric
circulation over the North Pacific Ocean with a eastward shift of
a ridge of circulation. Associated with the shift in 1976, the
winds off California have been more southerly and precipitation
over California and the southwestern U.S. has been above normal

The more southerly component of winds in winter since
1976-77 has had an effect on the Ekman transport, which has been
more onshore. ENSO conditions in 1976-77 and 1982-83 caused
northward propagating baroclinic waves with a deepening of the
density structures. McLain (1984) pointed out that a combined
result of these processes, along with the general warming of the
coastal waters, caused above normal subsurface temperatures and
deeper than normal isotherms along the coast since 1976. Sea
level data show a pattern similar to that of subsurface tempera-
ture, with sea level generally above normal each winter since
1976.

McLain (1984) pointed out since 1976 that biological
productivity in the California Current region apparently has
been below normal because of reduced nutrient supply in the
surface waters. This is related to other biological effects,
e.g., a decrease in kelp growth off San Diego, declines in the
marine survival of Oregon and California coho salmon, decreases of albacore catche along the west coast, and the shift in the migration route of maturing Fraser River sockeye salmon.

The low frequency biological variability in the Northeast Pacific has been reflected in the zooplankton biomass fluctuations. Bernal (1981), analyzing CalCOFI data, found that these fluctuations are coherent with interannual changes occurring in the California Current System. Soutar and Isaacs (1974) and DeVries and Pearcy (1982) demonstrated long term variations in the estimated abundance of the dominant pelagic fishes in the California Current and Humboldt Current systems based on fish remains preserved in marine sediments.

The evidence of long-term trends in the eastern Pacific have estimulated the development of models that attempt to represent these trends using simulations. Ka-Ming Lau (1985) developed and discussed the elements of a theory of the long term variability of ENSO. He hypothesized that the occurrence of the ENSO is the result of an inherent instability in the tropical ocean-atmosphere triggered by stochastic forcings. The effect of this forcing is to allow the release of the instability in the system at different times of the year. However, even in the presence of stochastic forcing, triggering of instability in the system will be favored during specific phases of the annual cycle when its amplitude is close to the threshold value for the instability. The results of the simulation show that the model
output pattern and the SOI anomalies for a 50-year segment are correlated, confirming that air-sea interaction, seasonal cycle and stochastic intraseasonal forcings are key factors in leading to the long term behavior of the tropical ocean-atmosphere system.

Steele and Henderson (1984) modelled long-term fluctuations in fish stocks. They combined a simple ecological model that produces two equilibrium states with low frequency stochastic input to show that the observed time sequence in regional fish stocks as those in the eastern Pacific can be reproduced. The model combines the classical logistic growth formula with an S-shaped predation function. After the numerical simulations, it was concluded that unlike the deterministic case, the response is no longer dependent on initial conditions and the model responds only to the variability. A second result is that there appears to be a narrow range of frequency where the system makes the transition from a single equilibrium state to a two-valued system. With low-frequency inputs and large carrying capacity values the model switches in a way that is qualitatively similar to the changes that have been observed, showing changes in abundance with intervening periods of about 50 years. It also shows that the consequences of environmental and fishery factors can be similar and that small or gradual changes in the environment can produce sudden and dramatic consequences. The effects of a decrease in carrying capacity derived from an increase in fishing effort appear to significantly increase the frequency of the changes in abundance, which would imply that the
traditional steady-state assumption for management is no longer appropriate in these fisheries. A succession of species may be associated with the ecological jumps between the equilibrium states shown by this model, particularly considering the magnitude of these alterations. In a fluctuating environment which shifts between equilibrium states that represent markedly different conditions, it may be expected that the species present in the two different equilibrium states would have different strategies for facing the natural constraints.

The theory of r and K selection (MacArthur and Wilson, 1967) is consistent with the variations of life history parameters in fishes, as demonstrated by Adams (1980), and is applicable to the analysis of the long term variability in the eastern Pacific. This theory is based on two assumptions about the allocation of a population’s resources between competitive and reproductive functions. The first is that there is a positive relationship between the amount of resources spent on an offspring and the fitness of that offspring. The second assumption is that any species has only a fixed amount of resources available. The criterion for success in natural selection is the number of the surviving offspring that a parent produces. Thus, the best reproductive strategy is a compromise between two conflicting demands: production of the largest possible total number of offspring (r-selection), and production of offspring with the highest possible fitness (K-selection).
In the case of marine fishes, a species which is exposed to a large component of non-selective or catastrophic mortality would be selected for characteristics that increase number of progeny (i.e., an r strategist) and has features summarized in Table VII. In environments with more predictable mortality, the species would be selected for characteristics that increase competitive ability. In this case, a different set of attributes are associated with K-strategist species (Table IX).

The r and K strategists present clear differences in outputs when they are simulated using dynamic fishery models (Beverton and Holt yield-per-recruit equation and Schaeffer’s surplus production model). Thus, in fisheries based on K selected species, the maximum yield per recruit would occur at a lower level of fishing mortality and at later age at first entry than in fisheries based on r selected species. However, K selected species will have fewer total fish than r selected species. On the other hand, they would be much more sensitive to overfishing both in terms of fishing mortality and age at first entry. As in the yield per recruit analysis, the maximum yield occurs at a lower fishing mortality for the K selected species than for the r selected species. The K selected species are reduced to levels lower than the maximum sustainable yield by much more rapidly than the r selected species. The life histories of K selected fishes are also more complicated, and they have strong interspecific relationships, usually of competitive character.
**TABLE VIII.**—Summary of hypothetical $r$ and $K$ correlates in life history parameters of fishes.

<table>
<thead>
<tr>
<th>Characteristics</th>
<th>$r$ selected</th>
<th>$K$ selected</th>
</tr>
</thead>
<tbody>
<tr>
<td>Body size, $L_x^1$</td>
<td>Small</td>
<td>Large</td>
</tr>
<tr>
<td>Maximum age</td>
<td>Low</td>
<td>High</td>
</tr>
<tr>
<td>Age at first maturity</td>
<td>Low</td>
<td>High</td>
</tr>
<tr>
<td>Natural mortality, $M$</td>
<td>High</td>
<td>Low</td>
</tr>
<tr>
<td>Growth rate, $k^1$</td>
<td>High</td>
<td>Low</td>
</tr>
</tbody>
</table>

*The parameter from the von Bertalanffy growth equation was used to represent the actual characteristic.*

**TABLE IX.**—Predicted signs of correlation matrix of life history parameters in fishes.

<table>
<thead>
<tr>
<th>Characteristics</th>
<th>$L_x^1$</th>
<th>Maximum age</th>
<th>Age at first maturity</th>
<th>$M$</th>
<th>$k^1$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Body size, $L_x^1$</td>
<td>1.0</td>
<td>+</td>
<td>+</td>
<td>–</td>
<td>–</td>
</tr>
<tr>
<td>Maximum age</td>
<td>1.0</td>
<td>+</td>
<td>–</td>
<td>–</td>
<td>–</td>
</tr>
<tr>
<td>Age at first maturity</td>
<td>1.0</td>
<td>+</td>
<td>–</td>
<td>–</td>
<td>–</td>
</tr>
<tr>
<td>Natural mortality, $M$</td>
<td>1.0</td>
<td>1.0</td>
<td>+</td>
<td>1.0</td>
<td>+</td>
</tr>
<tr>
<td>Growth rate, $k^1$</td>
<td>1.0</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

*The parameter from the von Bertalanffy growth equation was used to represent the actual characteristic.*

From Adams (1980).
Fisheries based on more r-selected species present the opposite tendencies. They will be more productive, and they allow fishing at younger ages and at higher levels of fishing mortality. They should also recover more rapidly from overfishing. These species usually constitute fisheries of a boom and bust nature, and for that reason the most efficient form of harvesting these fisheries would be fleets which are able of switching between a number of target species relatively quickly.

Another important influence of r-K strategies on fisheries is related to predictability. Fisheries based on more K selected species, in contrast to the boom and bust nature of r selected fisheries, will be characterized by relatively stable population sizes and therefore catch levels. Predictions could be made with a relatively higher degree of accuracy.

Long-term trends may affect life history patterns of the species inhabiting in east Pacific. Thus, and considering the characteristics of the environmental changes, the alterations in the pelagic communities would be consistent with the r-K theory. The cold-trends, likely would be related with the dominance of r-selected species, such as anchoveta, and would show boom-bust r selected fisheries with the characteristics described above. An example of this period was 1925-1976, when the number of moderate/strong ENSO events was considerable less than during the previous 1864-1925 warm phase (Quinn and Neal, 1983), and anchoveta in Peru reached high abundance levels. This
species collapsed between 1972-76 when a transition into a warm period started and the effects of fishing pressure became evident. Since then, an increase of more K-strategist species such as the sardine began, along with a depletion of anchovy and the development of environmental conditions that characterize warm periods. A higher frequency of moderate/strong ENSO events during this later stage is expected to maintain the general warm conditions for around 50 years. In summary, a warm trend in the eastern Pacific associated with more stable conditions (less environmental variability), deepening of the thermocline in the eastern Pacific, and reduced nutrient supply and relatively low primary production would favour the dominance of more stable but less productive fisheries. During this warm period there would also be evident a poleward extension of tropical and subtropical pelagic ecosystems, which would cause "tropicalization" of higher latitude ecosystems. The alternation of anchoveta and sardines as dominants in the pelagic communities in the southeastern Pacific is consistent with these changes. In fact, these species probably compete in the ecosystem, so that under cold-trend conditions the anchoveta have certain advantages over the sardine, a situation that is reversed during warm-periods when the sardine is favoured. Considering the biological characteristics of these species (especially their tolerance ranges) and their responses to environmental variability, warm conditions may be more drastically negative for anchoveta than the cold conditions are for sardine. The dominance of the sardine during warm trends would rest more on a drastic decrease of anchoveta than on a drastic increase of sardine. This kind of
relationship would be analogous to the ecological process observed in phytoplankton successions between diatoms and dinoflagellates in environments that exhibit strong environmental variability with alternation of unstable and stable conditions (Alvial and Avaria, 1982).
6.- SUMMARY

The following summary about the principal ENSO impacts on the eastern Pacific pelagic systems is mainly based on the information provided by the strong 1982-83 ENSO event, even though data from previous events have also been considered in the analysis. Because of that, many generalizations contained in this summary about the ENSO impacts correspond to strong events, like 1982-83, and some of them would be qualitatively or quantitatively modified, or absent, for moderate or weak events. Inasmuch as this summary contains information previously referenced in this paper, citations are omitted here.

The eastern boundary Pacific Current systems are affected by an aperiodic ocean-atmosphere anomaly known as the El Niño/Southern Oscillation (ENSO). This air-sea perturbation originates westward in the equatorial region and propagates eastward as a wave dynamical response to the trade wind weakening, impacting the coast of South America and then propagating poleward along the eastern boundary. These ENSO events alternate with anti-ENSO in the Pacific Ocean.

ENSO events cause strong alterations of the environmental conditions in the eastern Pacific, which are more marked in the equatorial region and decline toward higher latitudes. The principal changes are: increase in sea level, increase of SST, isotherm deepening, poleward transport of warm surface water,
onshore transport of oceanic waters in some high latitude zones, and upwelling of warm-oligotrophic water instead the cold-eutrophic water.

The pulses introduced by ENSD influence the plankton communities in the eastern Pacific, affecting their composition, abundance, and productivity, especially close to the equator. A "tropicalization" of the higher latitude communities is evident due to invasion of warm, tropical and subtropical species. At higher latitude, onshore displacements of oceanic species may also occur. The decrease in primary production in the usually productive waters of the upwelling systems in the eastern tropical Pacific can be explained by the combined effect of the reduction of nutrient supply from the deep layer due to weakened upwelling, and the deepening of the thermocline. Along the coast toward higher latitudes, the reduction is apparently clearly associated to a decrease in the nutrient supply caused by the upwelling of warmer oligotrophic waters transported from the equator to higher latitudes. In addition to the physical reasons, the presence and dominance of warm water species with slower growth rates than the usually dominant diatoms also contributes to the diminishing of primary production in the coastal upwelling areas of both Current systems.

Changes in zooplankton abundance and community composition can result from either: 1) a change in the physical conditions in a given location, or 2) advection into waters having
different characteristics. The second has significant implications for the survival of eggs and larvae of pelagic species.

The nekton respond to ENSO episodes with changes in trophic relations, distribution, abundance, body conditions (and growth), reproduction and early life history. Some of the most notable impacts within these categories are summarized below.

The reduction in primary production has an effect on the entire trophic chain, causing a general reduction of food availability for nektonic organisms. Trophic alterations are evident in early life history stages which undergo the consequences of a reduction in plankton abundance and changes in its composition. Partial or total diet modifications are evident in some species. The changes in distribution apparently are the result of active migrations in the case of species that are highly mobile and also a consequence of passive transport of early life stages. The displacements of tropical and sub-tropical species toward higher latitudes is noticeable. Likewise, intrusions of oceanic species toward the coast is common in both hemispheres. Alterations in distribution caused by the ENSO anomalies as well as the impacts on growth (decrease) and mortality (increase) affect the abundance of some species in given areas along the eastern pacific. Apparently the combined effect of ENSO and overfishing can cause the collapse of some sensitive fisheries, as occurred with the anchoveta off Peru between 1972-76. During ENSO events oceanic and warm water fishes increase their relative abundance onshore. A reduction in the condition
factor in clupeoid fishes along with a reduction in lipid content are due probably to the decreased food availability and the extra energetic cost demanded by their increased migrations. Several species of fishes exhibit losses of body weight and reduced growth rates. With regard to changes in reproduction and early life history, low values in the gonadosomatic index occurred in the sardine and the anchoveta. Likewise, the spawning of both species was reduced. Apparently larval mortality rates increase in some relatively coastal spawners due to the increased abundance of predators in the spawning and nursery areas.

The short-term ENSO impacts on pelagic fisheries can be divided into changes in abundance and in catchability. Within the first it is possible to distinguish between fast and delayed responses. Fast responses are associated with changes in natural mortality rate, growth rate, carrying capacity and body condition. The impacts demonstrate that these factors are not constant but they are strongly influenced by the changing environmental conditions. In the delayed impacts, represented by recruitment, the changes introduced by ENSO also make clear that recruitment is not just a function of the size of the spawning stock, and therefore, physical variability should not be ignored. As a result, the application of classical deterministic models in the management of these fisheries is questionable, and must be be replaced by approaches that comprehensively incorporate the key functions that represent the environmental effects on the stock, or approaches that at least incorporate uncertainty in the form
of stochastic terms. The current levels of theoretical knowledge of the systems in question make the second option feasible e.g. the stochastic simulation model of the northern anchovy fishery. Such models could be used in assessing the long-term impacts of alternative management measures.

The strong variation in catchability introduced by ENSO can cause serious errors in using CPUE in stock assessment in these fisheries. Therefore, the implementation of systematic monitoring surveys of pelagic resources is essential and should be balanced against the expected monetary value of the fishery at different levels of monitoring precision.

The alteration of the timing and routes of migrations of the highly migratory species during ENSO events emphasize the need of international cooperation in research and management. This is the only way of dealing adequately with transboundary stocks that undergo the effects of a highly variable environment in the context of current international regulations.

Analysis of the fisheries in the eastern Pacific requires the consideration of the long-term alternation of cold and warm trends that affect this region, and that are characterized by low and high frequencies of moderate/strong ENSO events, respectively. These periods could result in two different equilibrium stages in the pelagic ecosystem associated with specific environmental conditions. The application of the r-K theory into this long-term variability allows the hypothesis that a warm-
trend would be characterized by higher proportion of K-strategists species of fishes, which result in fisheries with relatively high maximum yield per recruit, low total standing stock, stable abundance, and high sensitivity to fishing pressure. The maximum equilibrium yield in these fisheries would occur for older fishes and at lower levels of fishing mortality. Conversely, cold-trends would be characterized by higher proportion of r-selected species of fishes which would determine fisheries presenting opposite tendencies than those of K-strategists in terms of the features above mentioned.
LITERATURE CITED


