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INTERNATIONAL SYMPOSIUM ON MIDDLE-SIZED PELAGIC FISH. *C. BAS, J.J. CASTRO and J.Mª. LORENZO (eds.).*

Ecological structures: expansion and replacement*

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SUMMARY: From an ecological point of view, the middle-sized pelagic fish, specially *Trachurus* spp and *Scomber* spp, are located between the little-pelagic fish (pilchards and anchovies) and the big migrators ones (tuna and related species). Its ecological rol has been considered as a particular level between the zooplanktivorous fish and the strictly piscivorous ones. These species have a global biomass between the other two groups of fish, that is to say, less that the little one and more than the big one. It is necessary to consider three distinctive aspects of the middle-sized pelagic fish: 1st. Its longevity with several age-groups in the different stocks of these species. 2nd. Its trphic plasticity, and 3rd. the high swimming capacity and resistant. As results of these three characteristics the populations of these species show a high stability and a major capacity of expansion, occuping, by replacement, the niches leaved by the over-exploited little-sized pelagic fish species. The total catches of pelagic fish species, in a high scale, do not show this capacity of replacement in a clear way. The analysis of specific fisheries shows that when the biomass of the little-sized pelagic fish decreased, it is followed by a significative increase of the middle-sized pelagic fish biomass. These are several fishing grounds in the world that have experimented a collapse of stocks of little-sized fish and quick rise, in biomass, of the middle-sized ones. The fisheries off the namibian coast are anexcellent example. In this area the fisherie on *Sardinops ocellata* collapsed and was follow by a strong increase in catches of *Trachurus trecae* and *T. capensis*. The japanese fisherie of *Sardinops melanosticta* has experienced a significative decline compensate by a high expansion and increase in catches of *Scomber japonicua*. If a longer longevity with a more age-groups in the population mean a higher stability, the wide trophic spectrum (zooplankton and small fish, and even phytoplankton) capacitate to these species to be much more competitives than other fish species during low favourable trophic conditions. The high swimming capacity, in the horizontal and vertical planes, facilitate to search for food in a more extensive areas, than that covered for the little-sized pelagic fish strongly dependents of the productive areas on the shelf (upwelling). As a result of all these characteristics,the middle-sized pelagic fish species show an important and quick expansion of their populations, occuping the depletioned zones and support a high fishing presure.

Key words: Food spectrum, life span, geographic distribution, migrations, expansion and replacement.

RESUMEN: ESTRUCTURA ECOLÓGICA: EXPANSIÓN Y REEMPLAZAMIENTO. – Desde un punto de vista ecológico, los peces pelágicos medianos, en particular *Trachurus* spp. y *Scomber* spp., se situan entre los pequeños pelágicos (sardinas y boquerones) y los grandes migradores (túnidos y especies parecidas). Su papel ecológico les situa entre los peces zooplanctívoros y los estrictamente piscívoros, con cierta mayor afinidad con los primeros. Su biomasa global se situa entre los dos grups mencionados: menor que los primeros pero muy superior a los segundos. Es necesario considerar tres aspectos característicos de los peces pelágicos medianos: 1°. Su longevidad, con varios grupos de edad en los diferentes stocks. 2°. Su plsticidad trófica, y 3° la alta capacidad natatoria y su resistencia. Como resultado de estas tres características las poblaciones de estas especies muestran una alta estabilidad y una mayor capacidad de expansión, ocupando por reemplazamiento, los nichos desocupados por los pequeños pelágicos sobreexplotados. La captura total de peces pelágicos no muestra esta capacidad de reemplazamiento de forma clara. El análisis de pesquerías concretas muestran que cuando decrece la biomasa de los pelágicos pequeños, se observa a continuación un incremento significativo de la biomasa de los pelágicos medianos. Hay varias zonas de pesca que han experimentado un colapso de los stocks de pequeños pelágicos y un rápido incremento de la biomasa de los pelágicos medianos. La pesquería namibia es un buen ejemplo. En ella colapsó *Sardinops ocellata* y siguió un fuerte aumento de las capturas de *Trachurus trecae* y *T. capansis*. La pesquería japonesa de *Sardinops melanosticta* también experimentó un declive significativo compensado por una expansión e incremento de las capturas de *Scomber japonicus*. Su mayor longevidad con un mayor número de grupos

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de edad en la población conlleva una mayor estabilidad, su más amplio espectro trófico (zooplancton, pequeños peces y aun fitoplancton) posibilita que estos peces sean más competitivos que otras especies durante los periodos con condiciones tróficas poco favorables. Su alta capacidad natatoria, tanto horizontal como vertical, facilita la búsqueda de alimento en áreas más amplias que las ocupadas por los pequeños pelágicos, fuertemente dependientes de las zonas productivas en la plataforma continental (afloramientos). Como resultado de todas estas características, los peces pelágicos medianos muestran una importante y rápida expansión de sus poblaciones, ocupando zonas agotadas y pueden soportar una alta presión pesquera.

Palabras clave: Espectro trófico, longevidad, distrbución geográfica, migraciones, expansión y capacidad de reemplazamiento.

INTRODUCTION

Middle pelagic fishes - horse mackerel, mackerel, etc., together with the smaller tuna species - occupy an intermediate position in the trophic structure of the pelagic ecosystem, between the small pelagic fishes - pilchard, anchovy, sardinella, etc. - feeding on plankton, particularly small plankton such as small copepods, nauplii, and the like and the large pelagic migratory fishes - tunas and swordfishes - feeding on larger prey, especially fishes and pelagic cephalopods.

The category of middle pelagics groups a number of fish families (BEN-TUVIA, A., this volume). The most important families are the Scombridae and Carangidae (COLLETTE, B.B. and C.E. NAUEN, 1983). The former family includes the most important scombrid fishes: *Scomber*, *Rastrelliger*, *Scomberomorus*, and *Acanthocybium*, together with small migratory fishes: *Sarda*, *Auxias* *Euthynnus*, and *Katsuwonus*. Important members of the carangid family include *Trachurus*, *Decapterus* (SILLET, R., 1989; CALKIN, T.P. and W.L. KALVE, 1963; MATSUMOTO, W.M.R., A. SKILLMAN and A.E. DIZON, 1986), *Caranx*, and *Salar* (SHAMEEM, A. 1986; SHAW, R.F. and D.L. DRULINGER, 1990). Although aggregations of *Scomberomorus* are small, the species are widely distributed in different oceans (COLLETTE, B.B. and J.L. RUSSO, 1985; BARRIEN, P. 1987; FONTELES-FILHO, A.A., 1988).

The food spectrum is closely tied to areas of very high productivity, but the relationship is looser and less direct than that for the small pelagics. Certain species of the genus *Trachurus* form high concentrations of biomass, e.g., *Tr. symmetricus* from Chile and Peru (PARRISH, R.H. and J. MENDO, 1987) to the Central Pacific Ocean. *Scomber japonicus*' important capacity for expansion is also noteworthy (HUNTER, J.R. and C. KIMBELL, 1985). In contrast, *Scomber scombrus* is restricted to the North Atlantic and Mediterranean Sea (BAS, C., 1959, 1960 and 1967).

In these fishes aggregations normally comprise a single species or genus. Some *Scomber japonicus* individuals may often be found in shoals of *Scomber scombrus*. The situation is similar for *Trachurus*, especially in interaction zones between two different species. Coexistence of *Scomber scombrus* and *Clupea harengus* is common in the North Atlantic (PILCHER, T.J., A.E. MAGURRAN and L. EDWARDS, 1985).

The general location of the most highly productive upwelling regions is well known: California, Peru, Cape Blanco, the Benguela, Western Japan, etc. (Fig. 1). The structure and dynamics of these productive areas also present certain well-known variations in oceanographic conditions. Such variations bring about very important changes in the biomass production of small pelagic fishes. The most important effects of the variations relate to food availability in response to changes in environmental conditions.

Small pelagics respond immediately to such environmental fluctuations. Changes in fish abundance or availability are intensified by these species' high reproductive potential and fast growth rates, capable of producing very large increases in biomass under favourable conditions. At the same time, these stocks are quite unstable because of the very low correlation between spawning stock biomass and recruitment in any given year. Fluctuations in stocks of anchoveta off Peru, pilchard (*Sardinops ocellatus*) in the South Atlantic, and pilchard (*S. melanosticta*) off Japan are prime examples of the situation just described. The sharp fluctuations in biomass for these fish stocks under unfavourable environmental conditions can be attributed to the low flexibility of their food estrategy the low number of age groups present in the population, and small pelagics' limited migratory capacity, all of which contribute to the highly variable abundance of small pelagic fish populations. All these factors are weaker in middle pelagic fishes.

The main differentiating factors distinguishing middle pelagics from small pelagics are: a broader food spectrum; a geographic distribution less closely

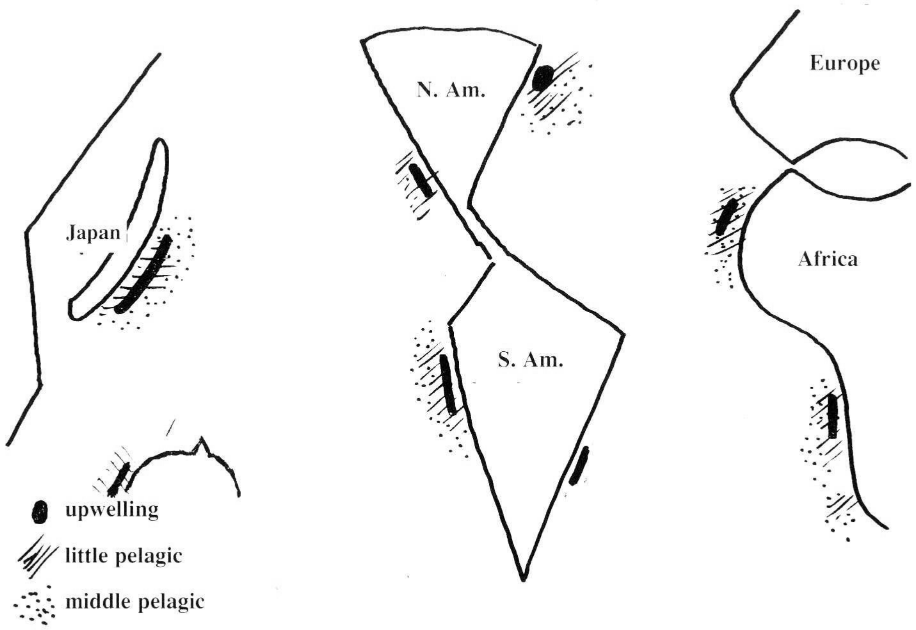

FIG. 1. – Oceanographic distribution of the more important upwelling zones and the small ad middle pelagic fishes.

tied to high primary production zones; longer life spans; and horizontal and vertical migratory capacity (Fig. 2).

FOOD SPECTRUM

The feeding strategy of middle pelagic fishes differs considerably from that of small pelagics. First, their food spectrum is substantially wider. This factor helps make them less vulnerable to the sharp fluctuations affecting the zooplankton. Large copepods, and the mesozooplankton in particular, are major contributors to the diet of middle pelagics and are consistently very abundant. On the whole, the most important food sources of middle pelagic fishes are quite stable, particularly as the components of the diet move further away from the more basic trophic levels. Thus, from a dietary standpoint, middle pelagics enjoy access to more stable food sources as well as larger quantities of food. Additionally, these species' food sources have wider spatial distributions less closely restricted to areas of high productivity. The large biomass of *Trachurus symmetricus murphyi* in Central Pacific waters is supported by the high abundance of small oceanic fishes that carry out large nychthemeral migrations (KONCHINA, Y.V., 1990; SANCHEZ, G. and P. MUCK, in press). *Scomber scombrus* and *S. japonicus* feed

PELAGIC FISHES

Small Pelagic Fishes

Food: narrow spectrum.

Mobility: strongly related to upwelling zones.

Migratory capacity: little.

Age: few groups of age, short life span.

Middle Size Pelagic Fish

Food: more plasticity in the food spectrum.

Mobility: more mobility; vertical and horizontal.

Age: major longevity and major number of age groups.

FIG. 2. – The more important characteristics of small and middle pelagic fishes.

on copepods, though mysids are the most important contributors to the diet off the Canary Islands (CASTRO, J.J., 1991) and euphausiids play this role in other seas. Off Peru *S. japonicus* feeds on the meso and macroplankton (KONCHINA, Y.V., 1990). In the English Channel *S. scombrus* first feeds on copepods in May/June and then switches to larger crustaceans until November (WALLACE, P.D., 1991).

The larger middle pelagic fishes, e.g., *Scomberomorus*, base their diets on the small pelagics - carangids, clupeids, engraulids - and on crustacean larvae, and to a lesser extent on squids (MENEZE, M.F. de, 1969-1970; NAUGHTON, S.P. and C.M. SALOMAN, 1981; FINUCANE, J.M., C.B. GRIMES and S.P. NAUGHTON, 1990).

Finally, small tunas feed on clupeoid fishes to the northeast of Santa Margarita Island, and clupeoids are also the main food source for *Euthynnus alletheratus* and *Auxis thazard*. RAMOS, A.J.S. (1992) reported that *Scomber japonicus* is a major contributor to the diet of *Katsuwonus pelamis* off the Canary Islands.

LIFE SPAN

Another very important characteristic of these species is their greater longevity. Consequently, middle pelagic fish populations contain more age groups than the populations of small pelagics. Generally speaking, fluctuations in biomass in small pelagics are the result of the presence or absence of a single very abundant age group from a year with strong annual recruitment. In middle pelagic fishes, which have a larger number of age groups, the existence of two or more strong age groups is common, a situation that contributes to the stability of these species' populations. Within this greater stability there is still some scope for biomass fluctuations, e.g., in the Mediterranean mackerel, *Scomber scombrus*, whose populations follow a seven-year cycle of fluctuations.

The genus *Trachurus* is the main contributor to the global biomass of middle pelagics, with the genus *Scomber* a secondary contributor. The result is minor variability in overall biomass levels. Some differences between *Trachurus trachurus* and *Tr. symmetricus* are discernible (ALEKSEEV, F.E., 197). Size at first spawning differs in different species: in *Scomber japonicus peruanus* it ranges from 25 cm FL to 28.9 cm FL. The growth parameter values for *Scomberomorus commerson* are K = 0.38, L_∞ = 177.5 off SE India (THIAGARAJAN, R., 1989) but K = 0.4699 and L_∞ = 126.37 off the coast of Natal (GOVENDER, A., 1994). *Rastrelliger kanagurta* exhibits a slower growth rate (UDAPA, K.S. and C.H.K. BHAT, 1984).

GEOGRAPHIC DISTRIBUTION

The world's main concentrations of small pelagics coincide with the major upwelling regions. The middle pelagics present a very similar though wider distribution; the biomass of *Scomber scombrus* attains high levels in the North Atlantic region, but distribution is non-homogeneous. BARRIEN, P. (1990) showed that the biomass of this species in the NW Atlantic is 10 times higher than the biomass off Great Britain. *Trachurus trecae* presents very high concentrations off Cape Blanco, *Tr. capensis* and *Tr. trecae* off Namibia and South Africa. *Tr. symmetricus* and *Tr. murphyi* inhabit the SE Pacific Ocean and represent a very interesting case on account of their oceanic distribution between Chile and New Zealand (JONES, J.B., 1990). Off Japan *Tr. japonicus* and *Scomber japonicus* contribute to very high middle pelagic fish biomass levels. Aggregations of *S. japonicus* near the thermocline form in response to the intrusion of the cold waters of the Oyashio current below the warm waters of the Kurashio current (HIRAI, M., 1991). Environmental conditions may contribute to the higher biomass levels and large cohort size in this species (HONNA, M., Y. SATO and S. USAMI, 1987; NISHID, H. and G. HASEGAWA, 1994), which may also be responsible for changes in the growth pattern recorded in 1991-1992 and 1993.

Changes in the abundance of *Trachurus japonicus* in the Niigat and in the Eastern, North, and Central China Sea are probably also caused by changes in environmental conditions. Still, *Scomber japonicus* is the middle pelagic fish species with the widest distribution range, and the species is present in nearly all the world's oceans. Although the genera *Trachurus* and *Scombrus* are the most abundant middle pelagics, this group also contains other, less important, though still significant, representatives: *Scomber australasicus*, *Rastrelliger* sp., *Scomberomorus* sp., *Decapterus* sp., *Caranx* sp., etc. *Rastrelliger kanagurta* and *R. faughni* form small populations in the Indian Ocean, the latter in association with *Scomberomorus commerson* (DEVERAJ, M., 1983); GNAMAMUTHU, J.C. and K.G. GIRISTALLABHAN, 1984; LABLANCHES, 1988). *Decapterus kurroides* and *D. tables* are common near the Zambezi River mouth (SOUSA, M.I., 1989).

Such other species as *Caranx ignobilis* and *C. memphycus* also form small populations (SUDERKUM, A.E., J.D. PARRISH, R.L. RADZKE and S. PALSTON, 1991). The influence of ocean currents on the distribution pattern for the ichthyoplankton and consequently for adult populations is a major factor.

MIGRATIONS

The ability of medium pelagic fishes to carry out large migrations is another important characteristic of these species. Unlike the small pelagics, they perform not only horizontal migrations but vertical migrations as well. Consequently, they occupy very broad ranges, as already pointed out above. As postlarvae and early juveniles, they tend to dwell in small groups inshore (CASTRO, J.J., 1991). At a size of 12-14 cm in length, they migrate to offshore waters over the continental shelf, where they continue growing to the size at first reproduction. Afterwards, these species migrate to oceanic waters, where they may live out the greater part of their life span. At the same time, these fishes also carry out vertical migrations related to reproductive processes (C. BAS, 1960) (Fig. 3). The different fishing strategies employed during the year, bottom trawling or purse-seining at the surface, are linked to this annual migratory activity. A normal feature of the vertical migrations is that fishes tend to attain deeper depths with age, down to 300 m in older specimens. The migratory capability of these species is a very important factor underlying the bioecological stability of middle pelagic fish populations.

In the New Scotland region the first catches of *Scomber scombrus* are made in May. Catches are large at first and then decrease as the fish migrate to other areas (GREGOIRE, F. and K. FITZGERALL, 1991). Similar situations occur for *Trachurus trachurus* in the Bay of Biscay and the English Channel (HOLZLOENHNER, S., 1991). *Scomber japonicus* migrations are related to environmental conditions (SATO, Y., 1990). *Scomber scombrus* in the North Sea may come from the western stock, because the age of individuals is greater than the estimated age for the eastern stock (IVERSEN, S.A. and D.V. SKAGEN, 1989). *Scomber japonicus* migrate from northern to southern Japan out into the Pacific Ocean along both the western and Pacific coasts of Japan (HASEGAWA, S., T. NASAW and M. WATANABE, 1994). Mackerel migrate from Korea Bay off the east coast of China in April. They then travel to the southern coast of Korea and perhaps to the South China Sea in July-October. Migratory routes between China, Japan and Korea are known to exist (LIMBUNG, D., K. HAYASHI and Y. MATSUMIYA, 1988). Spring migrations of *Scomberomorus niphonius* have also been observed (WEI, SHENG, ZHOU and BINBIN, 1990).

DISCUSSION

The foregoing characteristics considered above point up these species' ability to maintain populations that are highly stable in space and in time. As a consequence, middle pelagic fishes are able to expand and occupy ecological niches when the pre-

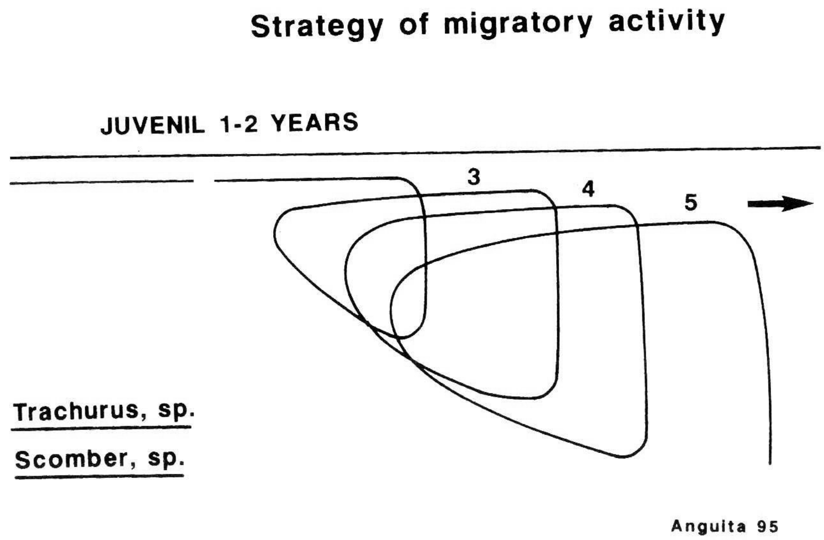

FIG. 3. – Pattern of migratory routes of the middle pelagic fishes along age.

vious occupants, generally small pelagics, undergo a decline or collapse for any of a variety of reasons. In such situations middle pelagic fish populations, in particular *Trachurus* sp. and *Scomber* sp., have been observed to increase in biomass quickly and occupy the free space. This expansion and occupation is a result of the above-mentioned attributes of these species, in particular their high biological stability and large growth potential when situations unfavourable to the original occupants prevail. Replacements of this type have taken place in many areas of high productivity. In Japan the pilchard *Sardinops melanosticta* suffered important fluctuations and underwent a sharp decline between 1950 and 1970 (Fig. 4). A series of very strong year-classes then caused

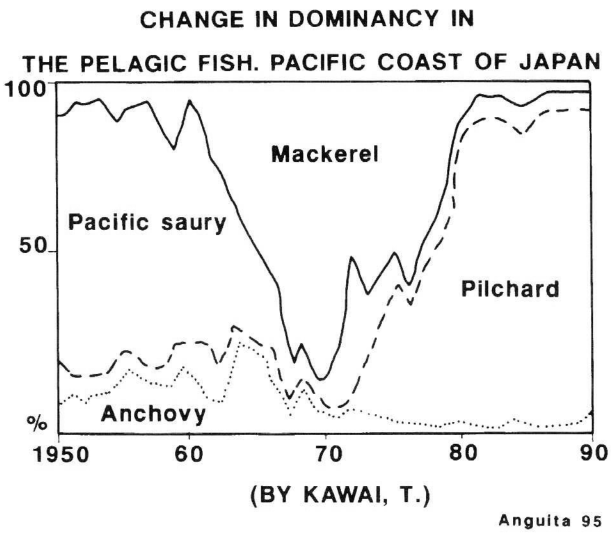

FIG. 4. – Changes in the composition of the pelagic fishes in the japanese zone.

the biomass to rise to around 4 000 000 Tm in 1985, after which it decreased again (KONDO, K., 1980; KAWASAKI, T. 1983). An important increase in the middle pelagic fishes - first *Scomberesox* and then *Scomber japonicus* - was observed when the pilchard population was in decline. The decrease in the pilchard stocks was related to a disturbance that affected the warm Kurashio current flowing northwards along the east coast of Japan. Between 1959 and 1962 the Kurashio current was displaced from its normal route by a cold-water mass located inshore (Fig. 5). The high productivity generated by the friction between current water and shelf water decreased, leading to a consequent decline in the biomass

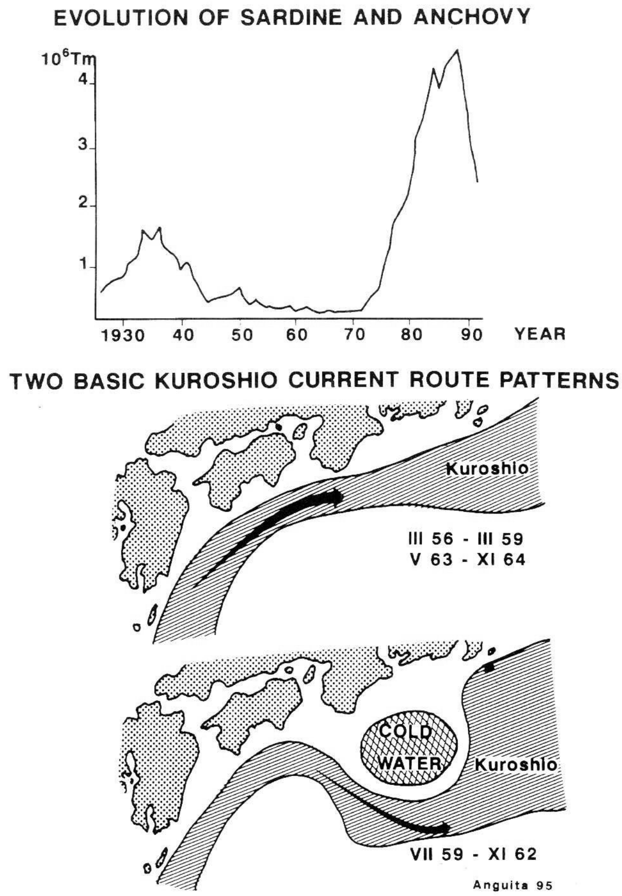

FIG. 5. – Environmental changes in the Kurashio current (Japan). The cold watter mass explain the variations in the fish abundance (by Kawai, T.).

of small pelagics. This was accompanied by an important increase in the biomass of middle pelagics thanks to the aspects of their ecological behaviour already discussed above. Other alterations in the contact front between the warm Kurashio current and the cold Oyashio current gave rise to fluctuations in the biomass of the pilchard, *Sardinops melanosticta* and *Clupea pallasii* populations. These environmental variations would appear to be responsible for the populational changes, e.g., a drop in spawning stock biomass, etc. Excessive fishing pressure may bring about similar responses. These two adverse factors working together can lead to very dangerous situations - collapse - as a result of a combination of low recruitment and high catches.

Another very important area of high primary production is located off southern Angola, Namibia, and the Atlantic coast of South Africa, the Benguela upwelling region, with very large pelagic fish populations. Until 1969-1970 the pilchard, *Sardinops ocellatus*, produced the highest yields, with maximum yearly catches of nearly one million tons. From that time on, the time series of catch data shows a constant decrease, especially off Namibia, where the pilchard population collapsed. During that same period there was a large increase in the biomass of anchovy off South Africa, an important centre of secondary upwelling. Comparison of the catches of pilchard and horse mackerel, *Trachurus capensis*, off Namibia show that the decline in *Sardinops ocellatus* was offset by a sharp increase in *Trachurus capensis* (CRAWFORD, R.J.M., 1988; LAEVASTU, T., 1993; LAEVASTU, T and F. FAVORITE, 1988) (Fig. 6). The situation was very similar to the

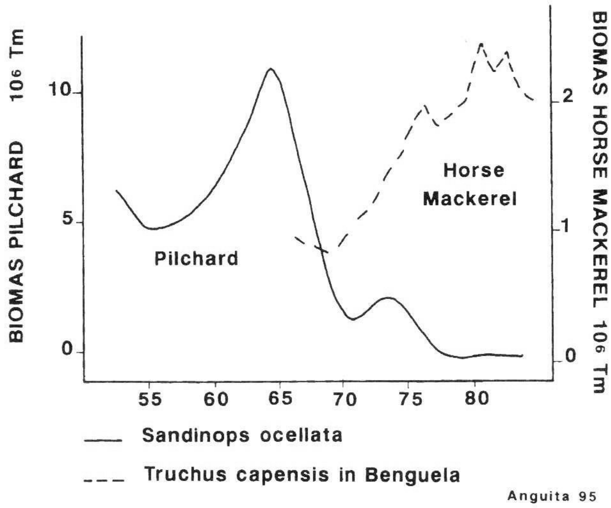

FIG. 6. – Changes in the composition of the pelagic fishes in the namibian zone (from Crawford).

one off Japan for *Sardinops melanosticta* reported above: intrusion of warm water from Angola raised the temperature of the coastal waters where the small pelagic fishes lived and displaced the Benguela current supporting the high productivity in the vicinity of Cape Frio (17º S). The situation off Namibia was the inverse of the situation off Japan, but the outcome of the alterations in environmental conditions was the same: an increase in the population of middle pelagic fishes when the environmental situation was unfavourable for small pelagics.

Similar situations have been observed in other regions. In the Spanish Bay of Biscay, anchovy and sardine are replaced by *Trachurus* (VILLEGAS, M.L. and J.L. LOPEZ-ARETA, 1988). Similar effects have been reported for five other pelagic fishes (SILVERT, W. and R.J.M. CRAWFORD, 1988). The same alterations observed off Japan and Namibia may also occur off Chile and Peru.

Thus, their considerably migratory ability, their less restricted food spectrum as compared to that for small pelagics, and their moderately long life spans with scope for two or more strong cohorts enhance the biological survival capability of middle pelagic fishes and the stability of their populations.

Comparison of the global catch data on small and middle pelagic fishes clearly demonstrates that on the whole the stability of middle pelagics is a more important factor than the greater biomass of small pelagics. Collapses in the biomass of small pelagics have been followed by increases in the biomass of the middle pelagics. Japan, Namibia, and other regions have furnished very clear examples. Although the ecological stability of middle pelagic fish populations is extremely important, in certain circumstances heavy fishing pressure may cause serious declines in the populations of these species.

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