OBSTINATE NORTH ATLANTIC BLUEFIN TUNA *(THUNNUS THYNNUS THYNNUS)* :
AN EVOLUTIONARY PERSPECTIVE TO CONSIDER SPAWNING MIGRATION

Phillipe Cury[1,4], Orlane Anneville[1], François Xavier Bard[2], Alain Fonteneau[1] and Claude Roy[3,4]

A tentative generalisation of the concept of "natal homing" (Cury, 1994) postulated that a newly hatched individual memorises early environmental cues, and that these later determine its choice of reproductive environment. This hypothesis may be viewed as an alternative hypothesis to the one generally accepted in marine ecology, in which it is assumed that an individual tries to select and track the optimal environmental conditions that will maximise its total reproductive output. It is considered in the context of bluefin tuna spawning migrations. Bluefin has the most temperate distribution, the most extensive geographic distribution and the greatest separation of spawning sites among the tunas, and is the tuna which is best able to feed in the remote and rich cold waters of the northern temperate areas. Migration routes of north Atlantic bluefin are postulated to have been developed during and after the ice ages in the northern hemisphere and it is proposed that bluefin still return to ancestral spawning areas despite having expanded greatly their foraging and overwintering areas to the extent that the two populations may mix in these areas. These evolutionary and ecological arguments reinforce the conclusion that spawning populations of north Atlantic bluefin should be considered as separate (two sub-populations) with minimum exchange, even though mixing does occur on the feeding grounds.

Une généralisation provisoire du concept de "retour au bercail" (Cury, 1994) postule qu'un individu nouveau-né mémorise au tout début de sa vie des indices environnementaux qui, plus tard, détermineront son choix d'environnement reproductif. Cette hypothèse peut être considérée comme étant une hypothèse alternative par rapport à celle qui est couramment admise en écologie marine, qui veut qu'un individu essaie de sélectionner et de suivre dans son environnement les conditions qui maximiseront son potentiel global reproductif. La première hypothèse est appliquée à la migration de reproduction du thon rouge. Le thon rouge est le thonidé qui présente la distribution la plus tempérée, l'aire de répartition géographique la plus ample, les lieux de ponte les plus écartés, et qui est le plus capable de se nourrir dans les zones riches éloignées et froides au nord et au sud. On postule que les circuits migratoires du thon rouge de l'Atlantique Nord se sont développés durant et après les périodes glaciaires dans l'hémisphère Nord, et on avance que le thon rouge reviendrait toujours vers ses lieux de ponte ancestraux, malgré l'importante expansion de ses zones trophiques et d'hibernation, au point qu'il se peut que les deux populations s'y trouvent mêlées. Ces arguments évolutionistes et écologiques étayent la conclusion selon laquelle la population de thons rouges géniteurs de l'Atlantique Nord devrait être considérée comme divisée (deux sous-stocks), avec un degré minime d'échange, même si le mélange se produit dans les zones trophiques.

1   ORSTOM-HEA BP 5045 Montpellier Cedex1. France.
2   ORSTOM BP 529, Papeete, Polynésie Française.
3   ORSTOM BP 70 29280, Plouzané. France.
4   University of Cape Town, Oceanography Dept., Rondebosch 7701, South Africa.

Una generalización provisional del concepto de "retorno al hogar natal" (Cury, 1994) plantea que un individuo recién nacido memoriza los primeros factores ambientales que, más adelante, determinan su elección de un entorno de reproducción. Esta hipótesis puede considerarse como una alternativa a la que está generalmente admitida en ecología marina, según la cual un individuo intenta seleccionar y buscar las condiciones ambientales que optimizan su reproducción global. Esta hipótesis se aplica a la migración reproductiva del atún rojo. Esta es la especie que tiene la distribución más templada, la distribución geográfica y separación entre las zonas de desove más amplia y es el túnido que tiene mayor capacidad de alimentarse en las distantes, ricas y frías aguas de las zonas templadas del norte. Se supone que las rutas migratorias del atún rojo del Atlántico norte fueron establecidas durante y después de las eras glaciares en el hemisferio norte, y que el atún rojo retorna a sus zonas de desove ancestrales, a pesar de haber ampliado mucho sus zonas tróficas y aquéllas donde pasa el invierno, hasta tal punto, que es posible que en las mismas exista una mezcla de las dos poblaciones. Estos dos argumentos relacionados con la ecología y la evolución apoyan el hecho de que las poblaciones reproductoras de atún rojo del Atlántico norte sean consideradas por separado (dos subpoblaciones) con un intercambio mínimo, a pesar de la mezcla que se produce en las zonas tróficas.

1. INTRODUCTION
OBSTINATE NATURE: A CONCEPTUAL FRAMEWORK FOR THE ANALYSIS OF MARINE FISH SPAWNING MIGRATIONS.

Demographic exchangeability of individuals is used commonly in most population models where individual members of a population can be aggregated into a single state variable representing population size. This contradicts, however, the basic biological fact that all individuals are unique (DeAngelis and Gross, 1992). Consequently, defining the degree of adaptability at an individual level should receive more attention in ecological and evolutionary studies as it has fundamental consequences on ecosystem predictability (DeAngelis and Gross, 1992). The usually accepted hypothesis about fish reproductive strategy postulates that an individual will try to select and track the optimal environmental conditions that will maximise its total reproductive output (Potts and Wootton, 1984). An alternative hypothesis was presented recently (Cury, 1994), that involves a tentative generalisation of "natal homing" within which homing is viewed as part of a continuum of reproductive strategies, all based on imprinting. This generalisation postulates that a newly hatched individual memorises early environmental cues which help in choosing its reproductive environment. Under this hypothesis, the same mechanism would account for successive generations that reproduce at the same geographic location (philopatry), or those that aim at a "moving target", i.e. a set of environmental conditions that do not have the same geographical coordinates (dispersal) (Cury, 1994). A theoretical functional dynamic mechanism has been advanced recently (Baras, 1996) that supports this generalisation and modelling at the level of the individual reinforces the importance of considering reproductive strategies in fish population dynamics (Lepage and Cury, 1996, 1997).

Many species of fish are well known for their homing migrations, e.g., salmon, herring (*Clupea harengus L.*), capelin (*Mallotus villosus*), shad (*Alosa sapidissima*), etc. (Harden Jones, 1968; Baker, 1981). Traditional knowledge states that the cod (*Gadus morhua*) off northern Norway migrate back to their exact place of hatching to reproduce. Different spawning stocks of cod were identified and traditional fishers know that overfishing of local stocks may result in total abandonment of certain spawning sites (Eythorsson, 1993). Scientific knowledge recognises the importance of homing for cod (Jakobsen, 1987) and the evidence of genetically discrete populations of haddock (*Melanogrammus aeglefinus*) in the North Atlantic (Jamieson and Birley, 1988; Zwanenburg *et al.*, 1992). However our understanding of the patterns and particularly the mechanisms of homing in fishes is derived from research on a very small number of species that reproduce at specific spawning grounds (Quinn and Dittman, 1992; Dingle, 1996).

For decades, ecologists have been collecting environmental and biological data on pelagic ecosystems. An impressive literature is now devoted to the analysis of the quantitative relationships between changes in pelagic fish populations and the environment (e.g. Cury and Roy, 1991; Durand *et al.*, in press). When studying the relationship between fish abundance and environmental conditions, it is often assumed that fish select the most suitable environmental conditions. The results, however, of field and genetic studies add complexity to any simple view of population dynamics and structures. Thus, despite the ability to induce spawning in some species, Blaxter and Hunter (1982) have noted a lack of understanding as to which environmental factors determine the onset and cessation of spawning in the sea. As another example of the added complexity, Hedgecock *et al.*, (1989) have reported genetic heterogeneity within the central Californian northern anchovy

stock (*Engraulis mordax*), that had been regarded previously as a panmictic population, which means that rather than being homogenous, anchovy stocks are in fact, a mosaic of "elementary" populations (Hedgecock, 1991). According to Mathisen (1989) the anchoveta stock (*Engraulis ringens*) off Peru consists of a large number of local subpopulations, each of which is adapted genetically to "home" to a different upwelling location and to spawn during a specific period of the year. European sardine populations (*Sardina pilchardus*) are traditionally assigned to six different "races"; however, further subdivisions have been identified according to spawning seasons that are separated by several months and which may define sympatric populations (Wyatt *et al.*, 1991). In a review on the Atlantic bluefin tuna (*Thunnus thynnus thynnus*), Mather *et al.* (1974, 1995) considered that "an infinite number of combinations of stocks, and degrees of mixing between them, might theoretically exist in the Atlantic and connected seas" and they concluded that "the problem of the stock structure is one of enormous complexity". Many examples can be found in the literature that emphasise the fact that fish populations are heterogeneous, even in an apparently homogeneous environment, and that this heterogeneity is likely to play a fundamental role in population dynamics.

Alternative views have been developed recently, that take into account qualitative changes and spatial constraints about what factors regulate marine populations. In his essay on population regulation, Sinclair (1988) considers that the life cycles and population patterns of sexually reproducing animals are defined in relation to particular geographical or spatial constraints that ensure persistence. Spatial processes do predominate in the regulation of marine populations and many examples support the discrete population concept (Sinclair and Iles, 1989). The generalisation of "natal homing" advanced by Cury (1994), recognises the importance of spatial constraints for sexual reproduction but also emphasises the role of learned components at the level of the individual. Each individual pelagic fish may tend to seek within its reproductive environment, the conditions that were imprinted as an egg (or larva?). This behaviour had been suggested for Atlantic eel by Kleckner *et al.*, (1983), and McCleave *et al.*, (1987) and for herring by Corten (1993). The reproductive strategies of marine turtles, salmon, herring, capelin, sardine or tuna are thus perhaps more similar than has been suspected.

This paper will not give any definite answers to the question as to whether the bluefin do or do not migrate to different locations to spawn. It presents a conceptual framework within which fish migrations may be analysed and knowledge assembled. This may be helpful in analysing complex migration patterns like those observed for bluefin, in organising facts and in determining the direction of future research. Some indirect evidence and some specific "knowns" are brought together in this paper to argue that bluefin may follow an individual-based reproductive strategy that results in a consistent and strong spawning site fidelity. For example, the possible consequences on fish population dynamics of paleoclimatological changes during the late quaternary are explored in order to give an evolutionary perspective to present reproductive migrations.

2. BLUEFIN TUNA; SPAWNING, DISTRIBUTION, MIGRATION, STOCK STRUCTURE AND POSSIBLE RATES OF EXCHANGE BETWEEN THE SPAWNING AREAS

Fisheries catch statistics not only help to track changes in abundance of fish stocks but they also provide information on migration patterns and particularly reproductive migrations as fish tend to aggregate when they spawn and thus become more available to fisheries. The bluefin of the Atlantic Ocean is the largest and most long lived of the tunas with individuals reaching weights over 500 kg and an estimated maximum age of 30 years. It has been fished in the Atlantic Ocean since the most ancient times. Archeological studies have reported bluefin remains in a 8th millennium B.P. coastal pre-ceramic Neolithic site at Cape Andres Kastros on Cyprus (Desse and Desse-Berset, 1994a). Bluefin was exploited more than 3000 years ago by the Greeks, then by the Phoenicians, and subsequently by the Romans who set up active fisheries using large traps, around the Strait of Gibraltar. This exploitation pattern was continued until the early XXth century, all around the Mediterranean Sea. Since 1950, however, new fishing gears (hand-lines made of nylon thread, pole and line, purse seine, longline) offered possibilities for new coastal fisheries in the eastern and the western Atlantic. Bluefin tuna were sold on domestic markets as fresh fish with a small demand for canning. By 1960, the bluefin fisheries reached their maximal geographical extension (Fig.1), but, at the end of the sixties, two major fisheries disappeared; a longline fishery off Brazil, and a mainly purse seine fishery off Norway. The Japanese developed a longline fishery off Brazil in the late 1950s that initially targeted yellowfin (*T. albacares*) and albacore (*T. alalunga*) but later started to harvest bluefin in an area centred on the Equator between 25° and 30°W (Fig. 1). Bluefin became the dominant component of the catch, in terms of both weight and value and between 1963 and 1965, the longline catch from north of Brasil comprised 64% of the total landings from the Western Atlantic. The bluefin were large fish and were available all year, but apparently vanished from the area in the late 1960s. The bluefin fishery in the north-east Atlantic, off Norway, was also a major one during the fifties (an average 20% of the total bluefin Atlantic catch between 1951 and 1962) but bluefin disappeared from that area by 1965.

There are only two major areas where bluefin spawn; to the east, the south central Mediterranean Sea, particularly the Tyrrhenian and Ionian seas, and to the west, in the Gulf of Mexico and Florida Straits (Fig. 2). Some minor spawning areas may exist, such in the Black Sea but have never been proven fully. In the western Atlantic, bluefin spawn probably between mid-May and mid-June. In the Mediterranean, giant bluefin spawn in the last half of June and first half of July with younger adults, the "large fish" category, spawning throughout July and into August, and occasionally into September.

Depending on size, bluefin are encountered in different areas of the North Atlantic. This distribution was described by Rivas (1978) and a recent synthesis is presented in Deriso and Bayliff (1991). Mather (1962) and Rivas (1978) distinguished four size groups; age zero (less than 3kg),

juvenile (3-50kg), large (50-150 kg), and giant (over 150 kg). These groups migrate to a different extent, according to the marine seasons in the North Atlantic, with the larger fish migrating the furthest (Fig. 2). The migrations in the western Atlantic have been described by Mather *et al.*, (1974, 1995). After spawning in the Gulf of Mexico, large fish migrate through the Florida Strait and north along the coast of USA. The main feeding grounds are along edge of the continental shelf between Georges Bank and the Grand Banks of Newfoundland and into the Saint Lawrence estuary. In autumn, bluefin migrate southward, offshore from the American coast. Wintering grounds were believed to be in the Caribbean Sea, but the recent development of a winter longline fishery suggests that they could be located in the north central Atlantic between 60° and 40°N, to the east of the main track of the Gulf Stream. The present ICCAT delineation between the western and eastern stocks, at 45°W, runs to the west of this area.

In the east, young bluefin may or may not migrate from the Mediterranean at the end of their first year. A component leaves the Mediterranean through the Strait of Gibraltar for wintering grounds off Morocco. The next summer, these fish follow a migratory path off Spain to the Bay of Biscay. During subsequent years they migrate in summer to the feeding grounds located at the edge of the continental shelf in the Bay of Biscay and the Celtic Sea, and they winter off the saharo-moroccan coasts. The best known wintering area is around the Canary Islands and off the Saharan Banks (Santos Guerra, 1977). Large bluefin have been observed also from January to April in Azorean waters (Pereira, 1995). On reaching maturity, these eastern Atlantic bluefin migrate to the spawning grounds through the Strait of Gibraltar: they are named "atun de derecho" by Spanish traps fishermen. After spawning, they return to the eastern Atlantic ("atun de reves") and join the northward migration to the feeding grounds. The large fish can endure colder waters, reaching, as observed during the 1950s, the North Sea and the Norwegian coast, as far as Cape North.

The other component of the bluefin spawned in the Mediterranean stays in that sea, apparently never leaving. In summer, bluefin of all sizes are observed in the northern Golf du Lion (Farrugio, 1981), in the Adriatic, the Aegean Sea and the Sea of Marmara. The Black Sea was, in the past, a feeding area, but it is less important now because of the collapse of the anchovy biomass, the main prey species (Zaitsev, 1993). The bluefin of the Mediterranean and adjacent seas can winter in the relatively warm waters of the southern Mediterranean and Ionian seas.

Some movement between the two sides of the Atlantic has been shown by the results of tagging experiments carried out over nearly thirties years. The 1994 Report of the Standing Committee on Research and Statistics (SCRS) of the International Commission for the Conservation of Atlantic Tunas (ICCAT) summarises (ICCAT, 1995) the tagging-recoveries on each side of the Atlantic:

West Atlantic: Tagged 31,746; recovered 4,376 of which 72 were from the eastern Atlantic.

East Atlantic: Tagged 9,736; recovered 431 of which 17 were from the western Atlantic.

In spite of some differences in the modalities (size, season, place), the overall balance of these results indicates low exchange between the East and the West Atlantic. Moreover, the pattern of transatlantic migrations over time seems irregular. This holds true particularly for juvenile bluefin. A clear example is the recovery in 1966, of 14 young bluefin aged 2 and 3 years-old, in the inner Bay of Biscay. These fish had been tagged just one year earlier in the New York Bight (Mather *et al.*, 1967). A large number of such young bluefin had been tagged in the years immediately prior and after the 1965 season, but this cluster of transatlantic recaptures is the only one observed. Such irregularity of transatlantic recoveries suggests random movements by strays guided by unusual oceanographic features, rather than regular migration.

Other sources of information about exchange rates are inconclusive so far. Neither biometric nor biochemical studies have provided conclusive evidence in regard to identifying whether there is one or more stocks of bluefin tuna in the Atlantic Ocean and adjacent seas. The biochemical studies now available are, admittedly, of a preliminary nature (Graves *et al.*, 1995) and were based on samples which were not sufficiently numerous to provide definite results. As pointed out by the National Research Council of the USA (NRC, 1995) genetic studies may not be very conclusive, because only a few exchanges between reproductive populations could be sufficient to pool genes and mask genetic difference. The proportions of micro-elements (Sr/Ca, stable isotopes of oxygen, Hg traces, etc.) in otoliths were originally proposed by Calaprice (1986) as a possible mean to identify where bluefin had been, but up to now some very preliminary studies have not provided any conclusions. This appears, however, to be potentially a promising line of research and in the end could provide quantitative estimates of exchanges by year. Infestation rates by parasites were also proposed as a mean to analyse migrations, as were counts of the scars left by bites of the small pelagic shark *Isistius brasiliensis*, which is a tropical species, (Parin, 1966) as these could indicate migrations to the tropical waters (Hester, 1996). Up to now, however, no meaningful results from such studies have been reported.

When populations on both side of the Atlantic were abundant, a feeding area where western and eastern bluefin tuna seem to have mixed regularly together was in the southern part of the North Sea, off Norway. Fishermen harvesting herring (*Clupea harengus*) in the Northern Channel, the North Sea and off the Norwegian coast, observed during the 1930s, large bluefin feeding on herring schools. This fact led to a directed bluefin tuna fishery using purse seines and handlines, from 1950 to 1964. Hamre (1959, 1960, 1962, 1963) describes the major Norwegian fishery which at times extended nearly as far north as Cape North, and yielded an annual average catch of 9,300t of bluefin between 1950 and 1962. He reported the recovery of bluefin that had been tagged in the USA, as well as of fish tagged in traps (almadrabas) close to the Strait of Gibraltar. In addition, bluefin tagged off Norway were recovered in the Spanish traps. Two simultaneous events may explain the disappearance of large bluefin from this northern area (Tiews, 1964): possible changes in the oceanographic

conditions (Binet, 1988) and change in the pattern of the fisheries in the Bay of Biscay, as fishing by baitboats on juvenile fish developed by the early 50s (Bard *et al.*, 1978). Hamre concluded that large bluefin from the West Atlantic followed the Gulf Stream during the trophic migration to boreal waters rich in food, especially small pelagic fish. Mather (1962) reports the recapture of two large bluefin tagged off the USA and recovered less than 4 months later off Norway. It is thus quite possible that the abundance of small pelagic fish (herring, capelin, mackerel) in the North Sea and off Norway, in summer (August, September) generates a common feeding area for bluefin spawned on both sides of the Atlantic. Tiews (1963), using observed differences in the condition factor (K) as an index of transatlantic migration, estimated the average component of western bluefin in the Norwegian catches to be 12%. Recently a longline fishery for large bluefin has been developed around the Faeroe Islands in summer (ICCAT, 1996b). This may be an area where large and giant size bluefin from west and east could forage together on the rich supply of small pelagic species.

The bluefin wintering areas are less known than the summer feeding areas. The reason is that prior to the eighties, except for the fishery off NE Brazil, winter fisheries for bluefin were minor and coastal. The recent development of long lining for bluefin during the winter suggests that the wintering area could be widespread and it is not impossible that the area could be continuous, straddling the Atlantic, south of latitude 40°N.

As the knowledge increased about the extent of the migrations, and the existence of two distinct spawning zones, questions were soon raised about the population structure of the Atlantic bluefin and consequently about the most suitable management units. The alternatives considered were a single stock, two independent stocks, two stocks with a regular rate of exchange, or two stocks with random exchange. Rivas (1978) proposed the existence of a single population of bluefin in the Atlantic, and presented a model of the migration patterns and life cycle. In particular, he considered that only the young adults (50-150 kg) spawn in the Mediterranean, and that when older, as the larger so-called "giants", bluefin spawn in the Gulf of Mexico. An alternative hypothesis would be to consider two independent populations. The ICCAT accepts currently, a model of two populations rather faithful to their spawning grounds, which constitute, in effect, two stocks with low exchange. The strongest arguments in favour of two separate populations are:

• Two spawning areas well separated, where ripe males and females are observed, and even mating has been seen (Arena, 1979);

• Eggs and larvae identified in plankton catches in the Gulf of Mexico (Richards, 1976) and in the western Mediterranean (Piccinetti and Piccinetti Manfrin, 1979);

• Spawning seasons differing only by one month (May-June in Gulf of Mexico, June-July in Mediterranean;

• Slight differences in the early growth rates;

• Separate nursery areas for small fish (age group zero) either in the Gulf of Mexico and Florida Straits, or in the western Mediterranean, at the same time;

• Absence of any other demonstrated major area of reproduction, despite intensive research, particularly in the eastern Atlantic, outside of the Mediterranean Sea. This is particularly relevant since spawning could occur theoretically anywhere where sea surface temperature is warmer than 22°C, and this is the common feature of all the spawning areas known for the other species of tunas.

Under this working hypothesis, it is important to consider the biological significance of the sporadic exchanges that have been shown by tagging, when building up a conceptual model for assessment and management advice (ICCAT, 1995. See vol. 2 p.122-127). The implications of the migration patterns are important, especially in the ICCAT context, because during the past fifteen years the development of the fisheries on each side of the Atlantic has diverged substantially, and the apparent rate of exploitation of the various size groups is now very different. Since 1982, ICCAT recommendations for the management for bluefin have increasingly taken into account the hypothesis of two well-separated stocks and the management rules applied are by now very different in the east and in the west. In the western Atlantic, where recruitment to the bluefin stock seems to have declined greatly, more rigorous management rules were applied sooner, in order to restore the spawning biomass. This restoration has, however, been very slow (ICCAT, 1995, 1996b). Recruitment in the West Atlantic is still apparently low, but it is not clear whether the recruitment levels presently observed in the west are really low in comparison to previous levels and are thus a consequence of a recruitment overfishing, or correspond more simply to the low size of the western stock. It is striking to observe that the western stock has never yielded the large catches of bluefin that have been seen in the Mediterranean, where up to 20,000 tons have been taken annually for centuries (Doumenge, this volume).

3. POSSIBLE IMPLICATIONS OF HISTORICAL GLOBAL CLIMATIC VARIATION FOR SPAWNING LOCATIONS

As has been seen, the bluefin is the biggest of all tunas and has the most temperate distribution, and it is the only tuna which is able to feed in the distant and forage-rich cold waters of the northern areas. In this sense, the bluefin is different from all the other tunas. It must, obviously, find an appropriate place and time period to reproduce. Few experiments have been performed at the level of the individual to analyse any exchange between reproductive zones and no data exist to examine the possible deterministic influence of any imprinting on bluefin migration. What is known has been observed mostly at the population(s) level (and "population" means here a group of individuals which may or may not reproduce together). Due to their extensive movements into areas that would be sub-optimal for a tropical tuna, appropriate spawning areas and time-windows are certainly not numerous.

The latitudinal distribution of marine species may be the result of past climatic changes (Fields *et al.*, 1993; Crame, 1993) and the existence of refuge areas during the last glaciation may help in understanding present distribution patterns (Maley, 1989; Blondel, 1995). This concept will be explored in the context of bluefin spawning in the eastern Atlantic being confined to the Mediterranean, and the possibility that this reflects the impact of the last Ice Age.

Oxygen and carbon isotope analyses of benthic and planktonic foraminifera from the Mediterranean basins have proved to be useful in establishing an isotopic stratigraphy, and in recognising major paleohydrographic events in that Sea since the Neocene. During the cold (10,000 years BP), glacial (18,000 BP) and postglacial episode, the general pattern of ^{13}C contrasts with the global pattern reported for the open ocean, and demonstrates that the Mediterranean hydrology and its geochemical records have been influenced strongly by local climate.

Historical oxygen isotope patterns for the world's oceans show globally synchronous geochemical events and these are seen also in the Mediterranean historical oxygen isotope patterns. The boreal glaciations can be recognised in the Miocene and Pliocene oxygen isotope records, respectively at about 14 and 24 million years BP. The transitions between glacial and interglacial stages of the Quaternary period are identifiable easily in Mediterranean deep seabed cores. Generally, the global trend of the isotopic signal is preserved, but the details of the isotopic stratigraphy have been modified with reference to microfaunal data. In fact, the nanoplankton assemblages show little variation throughout the Quaternary, which implies that temperature differences were not very marked (the differences were lower than those determined by oxygen isotope analyses). This observation is confirmed by results from CLIMAP (Climap Project Members, 1976) that indicate changes of 1° to 2°C. The results of investigation of the micro-factor and nannofossils show clearly that temperature changes were not the most important factor, but rather that this was the variation in the influx of Atlantic water during glacial and interglacial periods.

The Pleistocene was marked by a series of glacial and postglacial periods, but in the Mediterranean Sea, the nannoplankton assemblages show little variation. The assemblages in the western Mediterranean are typical of the temperate zone with a predominance of *Syracosphaera pulchra*, *Gephyrocapsa ericsonii*, *Helicosphaera carteri*, *Cyclococcolithus leptoporus*, *Emiliania huxleyi* and *Coccolithus pelagicus*. The nannoplankton assemblages in the eastern Mediterranean are characterised by species of the subtropical zone, with *Oolithotus fragilis*, *Umbellosphaera tenuis*, *Umbilicosphaera mirabilis*, *G. oceanica*, *Discosphaera tubifera* and *Umbellosphaera irregularis*. This difference between the western and eastern Mediterranean is due to the greater influence of Atlantic water in the western part.

At the end of the last glaciation, during the Würm (18,000 BP), the sea level was 120m below the current level. The Mediterranean basin was very reduced and the straits were much narrower. The Strait of Gibraltar was only 10km wide and 164m deep and the Strait of Sicily was a narrow lane, 35km long and 210m deep. During this time, the Mediterranean Sea concentrated salts and the hydrology showed strong contrasts (Doumenge, 1995).

In winter, in the Occidental Basin, the water was clearly colder (below 7°C at the north and between 9° and 10°C elsewhere) than that of the Levantine Basin. The presence of a north/south hydrodynamic front (Rhodes to lyboegyptian frontier) caused by cold water coming from the Black Sea, explained this contrast. The front isolated the Levantine Basin, which in consequence had winter temperatures greater than 14°C (and as high as 21°C). During warm events, the water was 20°C to 26°C, subtropical conditions which allowed relic flora and fauna (*O. fragilis*, *U. tenuis*, and the tropical species *U. irregularis*) to survive (Blondel, 1995). The central basin was greatly reduced and had similar conditions to those of the occidental Mediterranean (13°C to 18°C in winter and 18°C to 24°C in summer). This pattern of temperatures explains the actual distribution of some species. Many species, particularly land plants, found refuge in the warmest area.

Thiede (1978) reconstructed the glacial Mediterranean paleo-oceanography using the planktonic foraminifera, and deduced the sea surface temperatures. These ranged from 13°C in the Alboran Sea to 18°C in the Levantine Sea during the winter and from 19°C to 26°C respectively, in summer. An influx of cool, fresh surface water from the Aegean Sea disturbed this gradient in the eastern Mediterranean. It is also notable that conclusions about higher sea-surface temperatures in the glacial Balearic basin are supported by the virtual absence of the polar planktonic foraminiferan *G. patchyderma*. Marine species of holococcoliths are common in Quaternary Mediterranean, Red Sea and Gulf of Mexico sediments, but are rare or absent in the Atlantic. During each glaciation, the Mediterranean refuge permitted the survival of the European flora and fauna as well as the survival of the North Sea species. The fast rise in the sea level and the postglacial global warming changed drastically the environmental conditions and caused reduction of "cold" species and the spread of subtropical ones. The period of heavy rains, "the deluge", produced a low-salinity surface layer in the East Mediterranean (Rossignol-Strick *et al.*, 1982).

On the basis of these evolutionary and ecological facts, a simplified scenario of bluefin migrations may be proposed. An adequate place to spawn did not exist in the open North Atlantic during the Pleistocene glaciations (1,800,000 to 10,000 BP), and bluefin found shelter at that time in the Mediterranean and in the Gulf of Mexico where water temperatures, water salinity and associated environmental conditions were suitable for this species. The actual spawning locations in the Mediterranean Sea fit quite well with a past trade-off between a preference for higher temperatures and avoidance of low salinity gradients and sapropel formation (Rossignol-Strick *et al.*, 1982). The eastern Mediterranean basin was the most favourable in terms of temperature during and after the late quaternary, but unfavourable in term of stratification. In contrast, the western Mediterranean part was favourable in terms of salinity but had low summer temperatures. Reproductive activity of the bluefin would

have been confined to the central part of the Mediterranean Sea (Tyrrhenian Sea and Balearic Sea) where sub-optimal but adequate conditions did exist with respect to temperature and salinity. Fish were restricted to these spawning zones for a long time, but as the waters warmed the distribution increased. However, as homing is an important element of the spawning migration, bluefin still use these locations for reproduction. From time to time, strays migrate from one spawning zone and may reproduce in the other but, as noted with the tagging experiments, these events appear to be rare and sporadic (Cury, 1994; Lepage and Cury, 1997). The strategies for spawning and feeding are different and while spawning zones are localised and recognised precisely by the spawners, feeding zones may be more variable and be shared at certain time periods by all bluefin.

4. IMPLICATION FOR MANAGEMENT AND SCIENTIFIC RESEARCH

The mixing of two populations of bluefin in the feeding and wintering areas is not incompatible with an "obstinate" return to the spawning grounds. However, exploitation in the areas of mixing, such as the Faroes feeding grounds or a common wintering area, would justify the concerns within the ICCAT about the effect on the bluefin population on the other side of management rules applied on only one side of the Atlantic (ICCAT, 1996b). The most important question in this regard is the size of the spawning biomasses of bluefin reproducing in the Mediterranean and in the Gulf of Mexico respectively, and their interrelationship, if any. If they are independent as argued in this paper, the estimation of the rate of mixing as a result of any straying between the two reproductive areas is important. This information is essential also to understand better the biological potential for a recovery of the western stock. The incorporation by fisheries scientists of fisheries history (anecdotes such as the local extinctions documented here) into the present models would help evaluate the true disappearance of resources and the ecological cost of fisheries (Pauly, 1995). Unfortunately the standard method presently used in the stock assessment, the Virtual Population Analysis or VPA, can only estimate, in the best case, the number of large tunas in each area, not the number of fish that will spawn there. More research is required on the east-west migrations of bluefin tuna and on their fidelity to spawning in the area of their origin. It is likely that intensive research using a large array of modern research techniques, such as the biochemistry of hard parts, genetics, and pop up and archival tags, could provide the answers to most of those biological questions which are critical to the management and conservation of many marine species (Ryman *et al.*, 1995; Cury and Anneville, 1998) and particularly of Atlantic bluefin tuna.

Légends des figures

Figure 1.   Prise totale de thon rouge dans l'Atlantique de 1956 à 1993 par carré de 5°x5°.

Figure 2.   Distribution, migrations et lieux de pêche au thon rouge dans l'Atlantique.

Leyendas de las figuras

Figura 1.   Captura total de atún rojo en el Atlántico entre 1956 y 1993 por cuadrículas de 5°.

Figura 2.   Distribución, migración y zona de desove del atún rojo en el Atlántico.
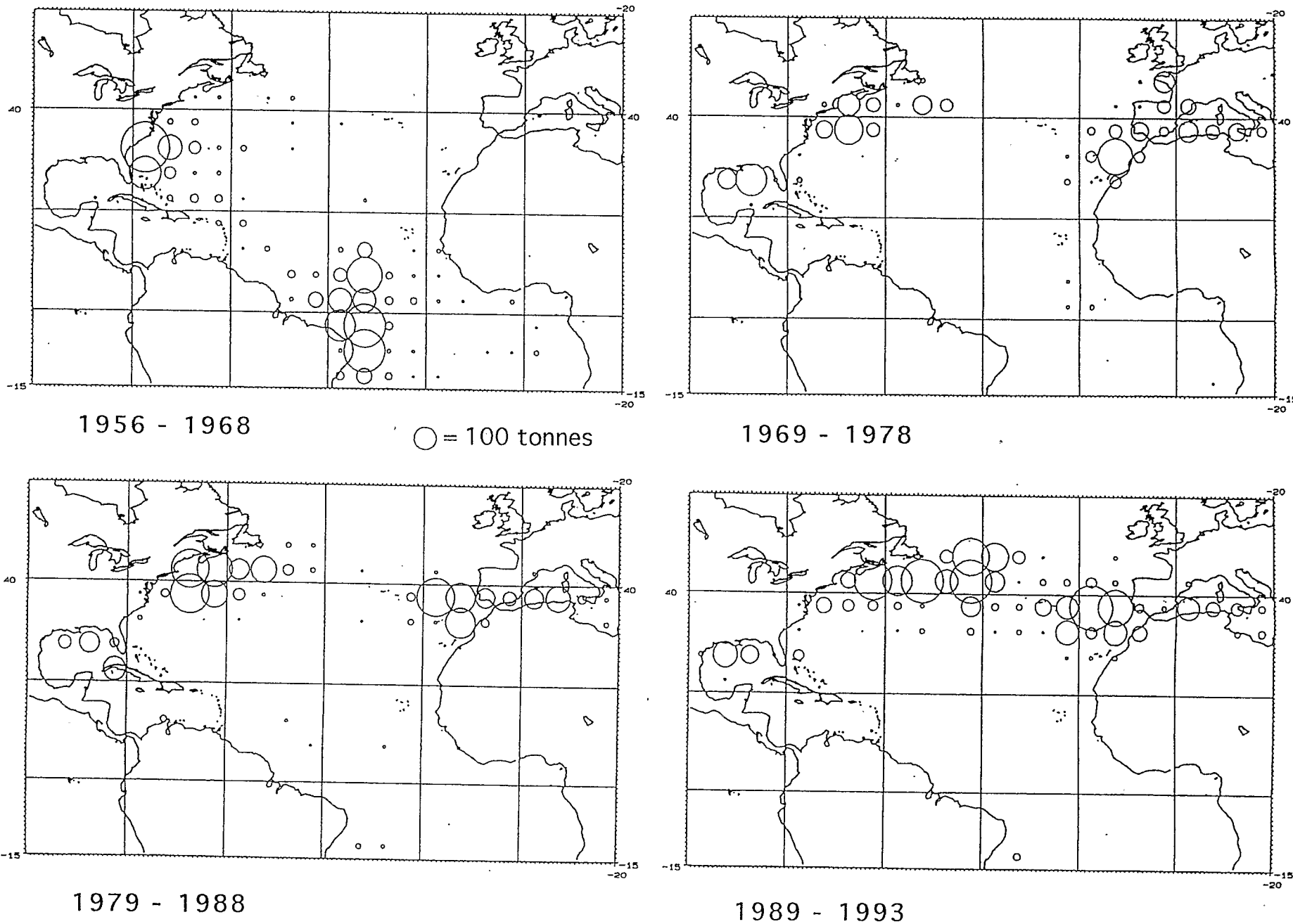
1956 - 1968

◯ = 100 tonnes

1969 - 1978

1979 - 1988

1989 - 1993

Figure 1. Total bluefin tuna catch in the Atlantic between 1956 and 1993 by 5° square.
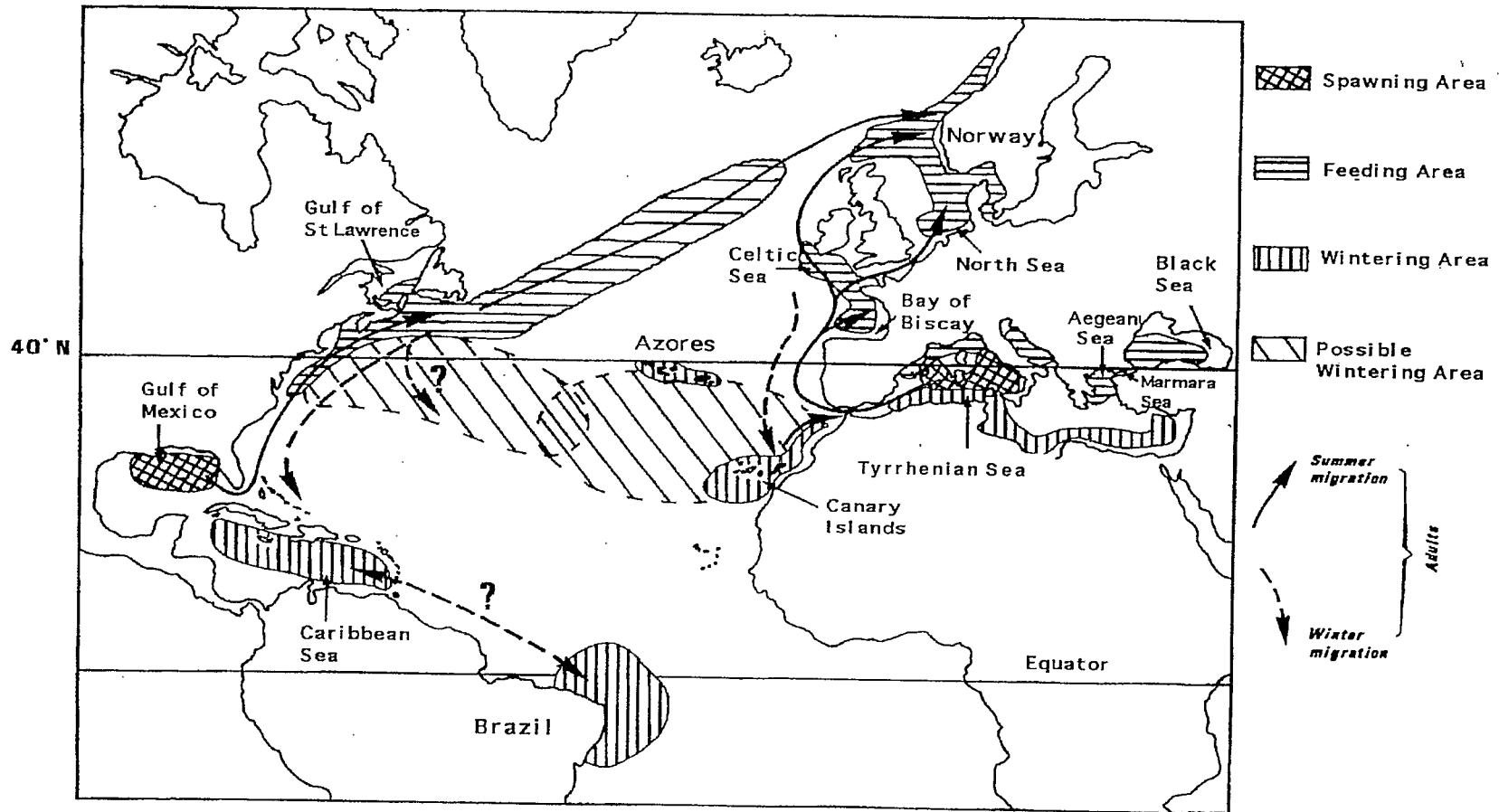
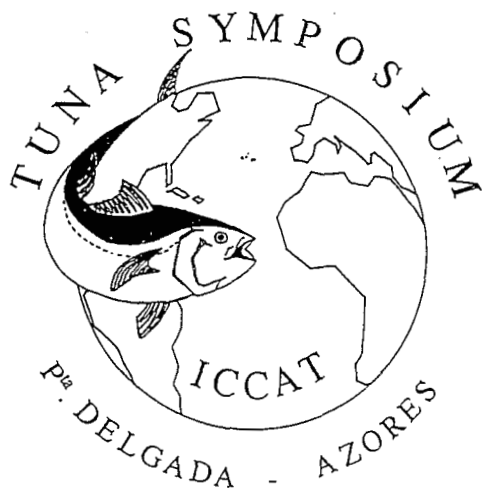**Figure 2.** Distribution, migration and spawning grounds of the bluefin tuna in the Atlantic.

ICCAT TUNA SYMPOSIUM

SYMPOSIUM ICCAT SUR LES THONIDES

SIMPOSIO ICCAT SOBRE TÚNIDOS
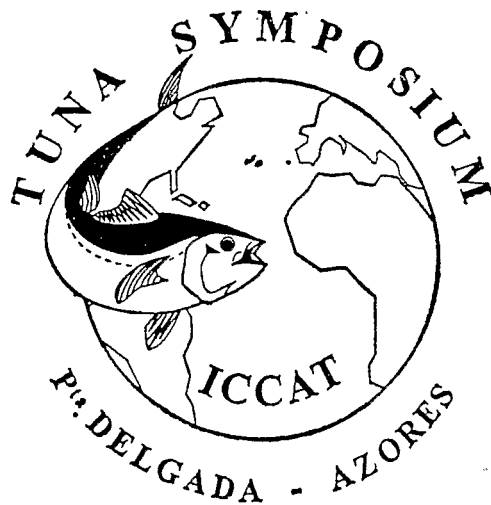
1998

PROCEEDINGS OF THE ICCAT TUNA SYMPOSIUM
ACTES DU SYMPOSIUM SUR LE THON ORGANISE PAR L'ICCAT
ACTAS DEL SIMPOSIO ICCAT SOBRE TÚNIDOS

PART / PARTIE / PARTE 1

Edited by

James S. Beckett