REVIEW/SYNTHÈSE

The Monotypic Sardines, *Sardina* and *Sardinops*: Their Taxonomy, Distribution, Stock Structure, and Zoogeography

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This paper reviews the taxonomy, distribution, stock structure, biochemical genetics and zoogeography of the world's two subtropical sardines, *Sardina* and *Sardinops*. We conclude that both genera are monotypic and that the differences between populations of *Sardinops* in different current systems are not large enough to consider them distinct subspecies. Analysis of biochemical genetics information, fossil evidence, and present and paleoclimatic conditions suggests that *Sardinops* did not achieve its present distribution until the Pleistocene and that westward exchange of sardines via the northern and southern west wind drift regions is possible with present climatic conditions. Transequator exchange appears to be possible only during glacial maxima and only in the eastern tropical Pacific.

Notre étude fait le point sur la taxinomie, la répartition, la structure des stocks, la génétique au niveau biochimique et la zoogéographie des deux sardines subtropicales du monde, *Sardina* et *Sardinops*. Nous en concluons que les deux genres sont monotypiques et que les différences entre les populations de *Sardinops* dans les divers systèmes de courants ne justifient pas leur séparation en sous-espèces distinctes. L'analyse des données génétiques, des éléments fournis par les fossiles et des conditions présentes et paléo-climatiques semble indiquer que *Sardinops* n'a réalisé sa présente répartition qu'au pléistocène et que l'échange de sardines vers l'ouest via les régions nord et sud de dérive due aux vents d'ouest est possible dans les conditions climatiques actuelles. L'échange à l'équateur ne semble possible que pendant les maxima glaciaires et dans l'est du Pacifique tropical.

A small assemblage of species dominates the subtropical fish faunas of the world's eastern boundary currents (Bakun and Parrish 1980). The assemblage includes four types of small pelagic fishes; sardine (*Sardina* and *Sardinops*), anchovy (*Engraulis*), mackerel (*Scomber*), and jack mackerel (*Trachurus*). The same assemblage also dominates the epipelagic fish faunas of the subtropical portions of most of the western boundary currents. The most significant exception to this is the Gulf Stream region where sardines (*Sardina* or *Sardinops*) are absent and *Engraulis*, while abundant, is not a dominant species. The Brazil Current–Falkland (Malvinas) Current region also lacks *Sardina* or *Sardinops*, but the other types dominate the subtropical, epipelagic fish fauna in this region.

The four types account for about 30% of the world's catch of marine fishes. For most of the last 25 years either *Sardinops*

or *Engraulis* has supported the world's largest fisheries and *Sardinops* is presently the largest single component of the world's harvest of fishes.

There has been a long history of economic and scientific interaction between the major fisheries on this assemblage of fishes, both within geographical areas and among areas. Fishing vessels catching one of these fishes usually also catch the others. The world's trade in fish meal is dominated by these fishes and they comprise a large proportion of the world's canned fish. Information, technology and material used in the fisheries for these fishes has been transferred from one area of the world to another for many decades. For example, the development of the California pelagic fishery was heavily influenced by canning technology developed for sardines in Europe (Thompson 1921) and the round-haul nets used in the early

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California fishery were originally developed in Rhode Island, Italy, and Japan (Higgins and Holmes 1921; Scofield 1924). Much of the modern purse seine technology (Fry 1931), large-scale fish meal plants (Scofield 1921), and the first factory reduction ships (Scofield 1938) were developed in California. When the California sardine population collapsed much of the technology, and in many cases canning and fish meal machinery were transferred to South Africa, Peru, and Chile which fostered further development of both harvesting and processing technology. During the recent development of the Chilean sardine and jack mackerel fishery there were significant technological and investment transfers from South Africa. In Europe and Japan, where there were longer traditions of marine fisheries and local markets, development has had less interaction with other regions.

Transfer of research methodology and results between the research establishments in the various regions has also been extensive and continuous. However, whereas the transfer of methodology has been acccomplished very rapidly it is unclear whether the results from research in one area can be transferred to another area. One of the reasons for this is that there is an understandable tendency to assume that widely dispersed populations of admittedly very similar fishes (for example the various *Sardinops* populations) might be expected to have evolved adaptations which would be specific to their individual habitats. This assumption has been reinforced by the continued use of different species names in different regions.

With few exceptions, early taxonomists described a different species of sardine, mackerel, anchovy, and jack mackerel for each current system; in many cases they were originally described as different genera. Within each of the four groups of fishes the recent trend of taxonomy has been towards a reduction in the number of species. As will be shown later, in *Sardinops* there is a long history of publications documenting the fact that the "species" in different regions have no demonstrable differences. However, local scientific names continue to be used in most regions. In *Scomber* it is evident that there are only three species; *S. japonicus* which occurs in all of the major eastern and western boundary currents, *S. australasicus* which occurs in the Indo-Pacific (Kijima et al. 1986), and the temperate form *S. scombrus* which is found only in the North Atlantic (Collett and Nauen 1983). In *Engraulis* a separate species has been considered to occur in each current system and Nelson (1984) has suggested a separate subgenus for the forms in the California, Peru, and Falkland (Malvinas) currents. Also several taxonomic studies in progress suggest that *Engraulis* may be divided into two or three genera. In *Trachurus* the present taxonomic situation can only be described as confused, with papers that describe new species overlapping those that synonymize forms from widely dispersed areas of the world (Nekrasov 1978; Rytov and Razumovskaya 1984; Parrish 1989).

The question as to whether geographically isolated populations are distinct at the genus, species, subspecies, race, or fisheries stock level has significance far beyond the narrow range of taxonomy. If the distinctions among populations in widely separated current systems tend to be well below the species level, it is implied either that individual current systems are not closed systems for the species and that some exchange between current systems occurs or that the species has only recently (on a geological time scale) achieved its present geographical distribution. This would have great implications for research programs as diverse as evolutionary theory, zoogeography, ecosystem analysis, and fisheries management. In addition it would greatly enhance the value of interregional comparative analyses (Parrish et al. 1983).

In this work we have attempted to present the available taxonomic, genetic, geographical distribution, and stock structure information for one of these dominant and widespread ecotypes, the subtropical sardine, and to use this information to examine the degree of interchange which occurs among and within subtropical neritic regions of the world ocean.

Taxonomy

The Clupeidae are a difficult group to deal with taxonomically. Scores of genera and over 300 species have been described. A large proportion of these taxa has proved to be invalid and the status of other taxa is presently unresolved. One of the difficulties is that similar forms occurring in widely separated, but ecologically similar, regions of the world were originally described as separate species or even genera. As mentioned previously, local biologists continue to use old scientific names for many of these forms even after they have been shown to be indistinguishable from the forms in other regions. The sardines, or pilchards, are a good example of the present situation.

The North Atlantic–Mediterranean sardine, *Sardina pilchardus* (Walbaum 1792) was the first sardine to be described. It was originally described as *Clupea*, as were most of the *Sardinops* ecotypes described from 1842 to 1879. Valenciennes (1847) created the genus *Sardinella* to describe a tropical species of sardine, and for a few years some of the subtropical sardines were also referred to as *Sardinella*.

Gunther (1868) included all of the Clupeidae having a terminal mouth, minute or absent teeth, a complete midventral series of scutes, and an anal fin in the genus *Clupea*. Thus the subtropical sardines were included in the genus *Clupea* by most workers. Regan (1916, 1917), in his revisions of the Clupeidae, separated the sardines into a subtropical genus *Sardina* and a tropical genus *Sardinella*. Regan also examined sardines from all of the major subtropical areas of the world and decided that there were three species of *Sardina*:

1) *Sardina pilchardus*. With two subspecies; *S. p. pilchardus* off the Atlantic coast of Europe, from Portugal northwards to the British Isles, and *S. p. sardina* in the Mediterranean and off the Atlantic coast of North Africa.
2) *Sardina sagax*. With four widely separated populations; off the Pacific coast of South America, off the Pacific coast of North America, off Japan, and off South Africa.
3) *Sardina neopilchardus*. With populations off Australia and New Zealand and which Regan suggested was closely related to *S. sagax*.

Svetovidov (1952) in his extensive work on the Clupeidae repeatedly pointed out the close relationships between the "Clupeinea which migrate extensively and live mainly in the upper layers of the water (*Sardinops, Sardina, Sardinella*)." He notes the following unique characteristics which they share:

1) The dorsal fin is closer to the front of the body in *Sardina, Sardinops*, and *Sardinella*.
2) The lateral line canals on the head are most devloped in *Sardina, Sardinops*, and *Sardinella*.
3) The last two fin rays of the anal fin are elongated into lobes in *Sardina, Sardinops, Sardinella*, and *Clupeonella*.

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4) Individuals have dark lateral pigment spots on the body in *Sardina, Sardinops* and some species of *Sardinella* and *Harengula*.
5) There are two elongated scales on the base of the lobes of the caudal fin in *Sardina, Sardinops*, and *Sardinella*.
6) There are transverse striations on the body scales which are interrupted in the center in *Sardina, Sardinops*, and *Sardinella* and unbroken in *Harengula*.
7) There are radial striations on the operculum of *Sardina* and *Sardinops*.

The major characteristics which separate the three genera are:

1) In *Sardina* the body scales are variable in size with smaller scales hidden underneath the larger scales.
2) In *Sardinops* the gill rakers on the lower part of the gill arch decrease in size toward the corner of the arch and the rakers on the upper part of the arch overlap the rakers on the lower part.
3) In *Sardinella* there are bilobed dermal outgrowths on the vertical portion of the cleithrum and there are no striations on the operculum.

Thompson (1926) in a morphological comparison of the European sardine (*S. p. pilchardus*) and the California sardine, which he called *Sardina sagax*, described a number of characteristics which could be used to separate the species. Hubbs (1929) used Thompson's results to establish a new genus, *Sardinops*, in which he included Regan's *Sardina sagax* and *Sardina neopilchardus*. His new genus was based on the six characteristics listed below:

1) In the American species there is usually a row of dark blotches behind the head, typically not apparent in the European.
2) The scales in the American species are arranged in a regular order, whereas the European are irregular with each alternating row not being nearly overlapped by the one in front.
3) The ventral scutes are weaker and less keeled, and have less expanded bases than the European species.
4) The gillrakers on the lower limb, unlike the European species, are shortened at the angle of the arch and they differ markedly in number at comparable sizes. In addition the upper limb folds down over the lower limb near the angle and there are differences in the minute processes on the gill rakers.
5) The interopercle is more expanded and widely exposed behind the preopercle.
6) The opercular ridges (and preopercle edge) are strongly oblique instead of being nearly vertical.

Hubbs (1929) examined *Sardinops* from California, Chile, Japan, and Australia and although he found no differences between these forms and even mentioned that "The distinctness of *Sardinops caerulea* is particularly doubtful," he differed from Regan (1916) and Thompson (1926), and used different scientific names for the populations in each of the major current systems in which the form occurs. Therefore the accepted usage for *Sardinops* became as follows:

1) *Sardinops sagax* (Jenyns, 1842)   Chilean
2) *Sardinops melanosticta* (Temminck & Schlegel, 1846)
                                                  Japanese
3) *Sardinops ocellata* (Pappe, 1853)   South African

4) *Sardinops caerulea* (Girard, 1854)   Californian
5) *Sardinops neopilchardus* (Steindachner, 1879) Australian

A number of taxonomic studies have been carried out comparing various populations of *Sardinops*. Thompson (1926) found no significant differences in sardines from California, Japan, and Peru. Taranets (1938) was unable to find significant differences between the Japanese and California sardines and suggested that the two forms were subspecies. He also found that Japanese and California sardines had keel scales that were essentially the same as those in *Sardina*, thus invalidating one of the characteristics Hubbs (1929) used to create the genus *Sardinops*. Fowler (1941) agreed with Regan (1916) in including the South American, Californian, South African, and Japanese forms as a single species; however, he considered the use of the genus *Sardina* invalid and suggested that the proper name for all of the subtropical sardines was *Arengus*. The usage of the generic name *Arengus* was, however, not picked up by most authors. Amemiya and Tamura (1943) concluded that the degree of difference between the Japanese and California sardines was no more than typically occurs within a single species. Hildebrand (1946) examined *Sardinops* from Peru and California and found differences which he considered significant only at the subspecies level.

Svetovidov (1952) considered all of the populations of *Sardinops* to be the same species, *Sardinops sagax*. He also stated that *Sardina* often has lateral pigment spots and pointed out that this is a characteristic which it shares with *Sardinops* and *Sardinella*. This invalidated another characteristic which Hubbs (1929) used to establish the genus *Sardinops*.

De Buen (1958) examined sardines from Chile, Peru, and California and used the results of Thompson (1926) and Hildebrand (1946) to propose that there were three subspecies of sardines in the eastern Pacific:

1) *Sardinops sagax musica*   Chile
2) *Sardinops sagax sagax*   Peru
3) *Sardinops sagax caerulea*   California

However, Saez (1980) showed that there is no reason to distinguish between two subspecies for the Peru Current and based on meristic and morphometric evidence he concluded that the populations of sardines distributed along the coast from Ecuador to Chile comprise a single subspecies, *Sardinops sagax sagax*.

In contradiction to the studies listed above, species synopses for *Sardinops sagax* (De Buen 1960), *Sardinops caerulea* (Ahlstrom 1960), *Sardinops melanosticta* (Tokai Regional Fisheries Research Laboratory 1960), *Sardinops ocellata* (De Jager 1960; Matthews 1960), and *Sardinops neopilchardus* (Blackburn 1960) were presented at the *World Scientific Meeting on the Biology of Sardines and Related Species* which was held in Rome in 1959. The taxonomic sections of these species synopses did not contain a single piece of evidence suggesting that the various forms were indeed separate species and most of the synopses quoted one or more of the above works which state that differences between the various geographically isolated forms are too small to consider them as separate species. Nevertheless they were given their traditional species names; this appears to have been influenced by the fact that at that time a review of *Sardinops* was apparently underway at the Scripps Institution of Oceanography. Ahlstrom (1960) stated that conclusions then permissible from this study indicated that all cur-

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rently recognized species would be synonymized under the name *Sardinops sagax*; only *neopilchardus* from Australia and New Zealand appeared to merit subspecific rank. This study, apparently by Hubbs, was never published and presently the traditional species names are used, with the exception that the California form is now considered to be *S. sagax* (Robins et al. 1980) and the Russians consider the Kuroshio form to be *S. sagax* (Kenya 1982).

Much of the differentiation of the Clupeidae has been associated with variations in the gill arches in association with adaptations to feeding (Nelson 1967). Nelson suggests that overlapping gill rakers, in some, and the mediopharyngobranchial in all alosins seems to place this subfamily at a higher level of specialization than that of the Clupeinae. Nelson points out that some of the more advanced Clupeinae (*Sardinops* and *Sardina*) have both overlapping gill rakers and a mediopharyngobranchial and that several others (*Sardinella* and *Opisthonema*) have a mediopharyngobranchial. Nelson also suggested that based on similarities in gill arch structure *Sardinops* and *Sardina* are closely related forms and probably should be recombined in a single genus. More recently Whitehead (1970) suggested that Svetovidov's solution (i.e. to recognize five subspecies of *Sardinops*) seemed to be the best.

The history of taxonomy in the sardines suggests that it is easier, and much more acceptable, to describe species than to synonymize them. In spite of the fact that no one has been able to find a characteristic feature with which to separate the various *Sardinops* populations, many workers dismiss contrary evidence such as Svetovidov's (1952) work with comments such as "There is evidence of a 'lumper' at work here!" (Culley 1971) and continue to use individual species names for each of the sardines in each major current system. The fact that the American Fisheries Society (1960) had accepted *Sardinops sagax* as the correct scientific name for the Pacific sardine for more than a decade before Culley's work was published also did not deter him from using the name *Sardinops caerulea* for the California population. Geographic distance rather than meristics, morphometrics or genetics appears to have been the major characteristic utilized in the definition of the presently accepted species of *Sardinops*.

Distribution

One of the most significant features of the sardines is their extensive anti-tropical distribution. *Sardinops*, or *Sardina*, occur in all of the eastern boundary currents and in the western boundary currents of the Indo-Pacific. When their population level within a current system is high they dominate the entire neritic zone of the current system from approximately the area of the west wind drift to the subtropical convergence. When their population level is low their distribution is greatly reduced and they are at times totally absent from areas which are productive fishing areas during periods of high abundance.

Canary Current

It is generally accepted that there are two subspecies of *Sardina* in the North Atlantic and Mediterranean. *Sardina pilchardus pilchardus* occurs off the Atlantic coast of Europe to southern Norway (59°N) (Riedel 1960) and *S.p. sardina* occurs in the Mediterranean and in the Atlantic off North Africa and off the Azores (Fig. 1). However, the distribution of *S.p. sardina* around and north of the British Isles appears to be asso-
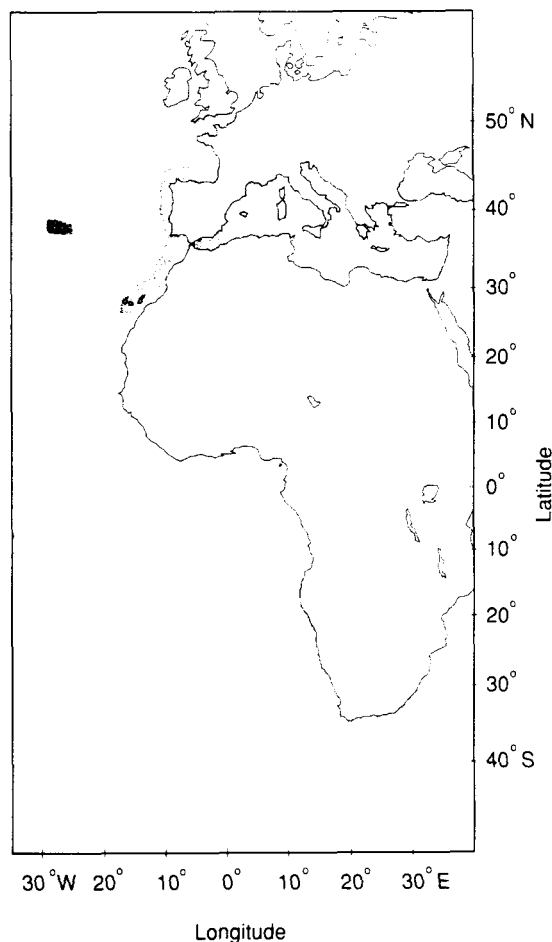

FIG. 1. Distribution of *Sardina* and *Sardinops* in the Atlantic at low abundance (dark shadiong) and the increase in range that occurs at high abundance (light shading).

ciated with warm periods and increases in its' abundance (Demir and Southward 1974; Binet 1986; Southward and Boalch 1986). In the past *S.p. sardina* extended to as far south as Cap Blanc (21°N) but it was not abundant south of Cape Bojador (26°N); however, during the mid 1970's there was a large increase in sardines south of Cape Bojador and in association with this increase sardines were taken as far south as the Bay of Goree, Senegal (15°N) (Boely and Freon 1980).

It is difficult to assess the relative importance of spawning grounds due to the lack of synoptic, large-scale egg and larval surveys covering major segments of *Sardina's* range; however, spawning takes place over a wide portion of *Sardina's* range. In the European Atlantic region spawning appears to be concentrated in the northern Bay of Biscay and the western side of the English Channel (Demir and Southward 1974). Franco and Lago de Lanzas (1976) report spawning grounds off the Cantabric coast in northern Spain, and Atunez, et al. (1973) report

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spawning off central Portugal. In the Mediterranean "junior stages are found in all sardine areas," according to Larranetta (1960), who lists a large number of spawning areas where young stages are at high concentrations.

Bravo de Laguna et al. (1976), analyzed seasonal migration and maturity stages, and suggest that in the Moroccan area the principal *Sardina* spawning occurs between Cap Juby (28°N) and Agadir (30°N). Little evidence is available for the Saharian region; however, spawning has been reported in the region (Domanewsky and Barkova 1976).

Benguela Current

According to Davies (1956) the range of *Sardinops* in southern Africa extends from Baia dos Tigres, Angola (16°S) around the Cape of Good Hope (35°S) to Durban, South Africa (30°S) (Fig. 1). Spawning grounds are located in the area between Cape Frio (19°S) and Walvis Bay (24°S) (King 1977a) and on the Agulhas Bank (35°S); however, before the decline in landings in the latter area, older sardines also spawned in the area west of St. Helena Bay (32°S) (Shelton 1981).

California Current

In the California Current system *Sardinops* occurs from southern Baja California (23°N) to southeastern Alaska (57°N) and in the Gulf of California (Fig. 2). During the peak in the fishery in the 1930's annual catches in excess of 100 000 tons were taken in Canada; however, with the total collapse of the fishery in the 1950's and early 1960's the range decreased markedly and sardines were virtually absent from the area north of Point Conception (34°N) from the mid-1960's until the early 1980's when a minor recovery of the population resulted in the occurrence of sardines as far north as San Francisco (38°N). Spawning grounds are located from the Southern California Bight (34°N) to southern Baja California (23°N) (Kramer 1970) and in the central portion of the Gulf of California (26–29°N) (Sokolov 1974).

Peru Current

The early literature gives the distribution of *Sardinops* in the Peru Current region from Secchura, Peru (5°S), and around the Galapagos Islands (Hildebrand 1946; Alverson and Shimada 1957) to the Gulf of Arauco (37°S) in Chile (Delfin 1900; Mann 1954). Other authors point out that sardine did not extend south of Coquimbo (30°S) during the late 1950's and early 1960's (De Buen 1958; Brandhorst 1963). During the 1970's sardine abundance increased in the Peru Current region and its range now extends from the equator (0°S) in Ecuador (Garcia 1983) to Chiloe (42°S) in Chile (Serra 1986) (Fig. 2). According to Santander and Flores (1983) spawning grounds off Peru are centered at 5–12°S. Off northern Chile, spawning is centered at 18–26°S and a separate spawning area now occurs from 34–39°S, near Talcahuano (Serra 1983). Paleosediment analyses also suggest that sardines have had population centers in northern Peru (7–10°S) and northern Chile (17–22°S) and a population minimum in central and southern Peru (11–16°S) during much of the Holocene (DeVries and Pearcy 1982).

Kuroshio Current

In the Kuroshio Current region *Sardinops* occurs from south of Japan (29°N) to the east coast of Kamtchatka (54°N) (Tokai Regional Fisheries Research Laboratory 1960) (Fig. 3). During
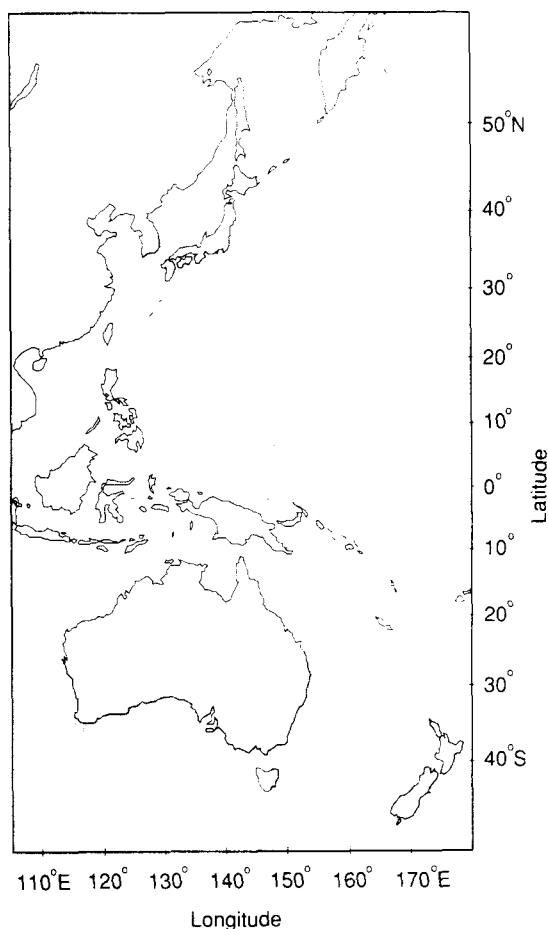

Fig. 2. Distribution of *Sardinops* in the eastern Pacific at low abundance (dark shading) and the increase in range that occurs at high abundance (light shading).

the 1930's when population levels were high the spawning grounds of the Japanese sardine were concentrated in the area around southern Kyushu (29–33°N); sardines from this area migrated northwards throughout the Sea of Japan, along the Pacific coast of Japan to Hokkaido and through the Tsugaru Straits (Nakai 1952). During the 1940's sardines markedly declined in the landings and the fishery was greatly reduced in the northern portion of its range around northern Honshu and Hokkaido, being primarily restricted to the western Sea of Japan and East China Sea; spawning was concentrated in the Sea of Japan northwest of Kyushu (33–35°N) (Nakai 1960). The fishery recovered during the late 1970's and the recovery was associated with recolonization of the spawning grounds around southern Kyushu, a major increase in spawning grounds on the Pacific Coast of Honshu (30–36°N) and the redevelopment of the fishery in northern Honshu and Hokkaido (Tanaka 1983; Watanabe 1983). During the recent period of high abundance, sardines were taken in the Kuroshio Extension at 171°E,

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The observed variations in the geographical distribution of sardine stocks associated with changes in population size have a similar pattern in each of the current systems where sardines have been heavily exploited (and therefore extensively studied). Sardine spawning grounds have been abandoned as populations decreased in size, or colonized as population size increased, or both. In the Canary Current increases in population size of the Sahara sardine stock was associated with the establishment of a "new stock" in Senegal (Freon and Stequert 1979). The higher latitude distribution of sardines in the Atlantic, i.e. in the English Channel, occurs in association with increased population size (Binet 1986; Southward and Boalch 1986). In the Peru Current increases in the population size in Peru and northern Chile were associated with records of spawning as far north as the equator and with colonization of 'new' spawning grounds in the Talcahauno, Chile region (Garcia 1983; Serra 1983). In the California Current an extreme decrease in the population size resulted in the abandonment of most of the northern range of the California stock. In the Kuroshio Current sardines abandoned much of their range and spawning grounds when the population declined and then several years later recolonized much of their former range and spawning grounds as the population size increased; however, the geographical distribution of biomass and the relative importance of different spawning grounds during the population resurgence was considerably different from that of the previous population maximum (Kondo 1980; Watanabe 1983). The present (1987) spawning range and geographical distribution has returned to very nearly that of the 1930's (T. Kawasaki, Tohoku Univ. Sendai, Japan, pers. comm.).

An outstanding feature of *Sardinops* is the similarity in the timing of extremely large, multi-decade population fluctuations occurring in the Kuroshio, Peru and California current systems (Shuntov and Vasilkov 1982; Kawasaki 1983). As shown above, these fluctuations also resulted in extensive alterations in the geographical distribution of *Sardinops* in each system.

Stock Structure

The stock concept has been interpreted in several different ways in marine fishes. The concept had its inception in studies which demonstrated morphological differences between geographic areas and has become an important organizing principle in the design of research and formulation of management policies by fishery agencies (Cushing 1968). With the realization that morphological variation may merely reflect the response to geographic variation in environmental conditions, and with the development of biochemical methods capable of detecting Mendelian variation, considerable effort has been directed toward using genetic methods, such as protein electrophoresis, to search for discrete stocks (e.g. Allendorf and Utter 1979; Ihssen et al. 1981). The rationale for using genetic methods was that stocks were thought to be reproductively isolated from each other to some degree by distance or by barriers to migration such as warm or cold current systems. Reproductive isolation between stocks is thought to lead to genetic differentiation which is potentially detectable by biochemical methods.

The term "stock" is used differently by different workers. It has been used by some to designate a biologically significant unit; others use the term merely to designate artificial subdivisions of fish into geographic or political areas. For purposes
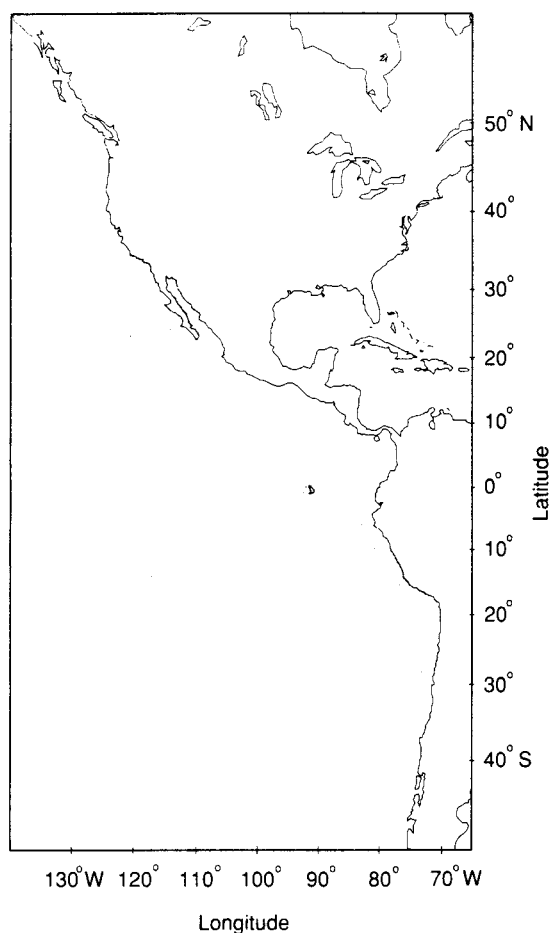

FIG. 3. Distribution of *Sardinops* in the Indo-Pacific at low abundance (dark shading) and the increase in range that occurs at high abundance (light shading).

approximately one third (2800 km) of the way across the Pacific (Kenya 1982).

Australia and New Zealand

Much less information is available on sardine distribution and its variability in Australia and New Zealand than in the other systems due to the lack of a significant fishery. Blackburn (1960) reported the northern limits of the range of sardines in Australia to be 24°S on the west coast and 25°S on the east coast. Their range extends south to southern Tasmania (43°S) and Baker (1972) reported their distribution from 34°S to 46°S in New Zealand (Fig. 3). No extensive egg and larval surveys have been carried out in the Australian and New Zealand region and the distribution of spawning of sardines in the region is not well known; however, Blackburn (1960) shows the breeding range nearly equaling the geographical range in Australia, whereas in New Zealand spawning is concentrated in the area between the North and South Islands near 40°S.

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of this review we will use the term stock in its biological sense as an extension of the genetic concept of a population; that is as an aggregation of fish which may or may not be genetically discrete from other aggregations of fish, but one which is isolated, on at least a decadal time scale, from other aggregations.

In each of the major current systems in which sardines occur it is presently believed that there are several stocks. This belief is partially due to the presence of several geographically separated spawning grounds; however, in many cases stocks have been identified by differences in meristic or morphological characteristics such as the number of vertebrae, the number of gill rakers, or differences in body proportions. In most cases these differences appear to be small enough so that it is impossible to determine whether they are caused by developmental responses to variations in the environmental conditions present in the different spawning and nursery grounds or by differences in gene pools. As will be demonstrated later, sardines from high or low latitude regions of different current systems often tend to be more alike in these characteristics than are sardines from high and low latitude areas within a current system. This is not uncommon as a negative correlation between the number of vertebrae and the temperature of their habitat has been found in a number of Clupeids (Muzinic 1960). It also should be noted that it is not possible to use average values such as those derived from meristic or morphometric characteristics to determine the degree of annual admixture between the populations in different spawning areas. In addition, in a few of the current systems some electrophoretic and serological studies of sardine stocks are available.

The following sections review the current knowledge of the stock structure in the regions in which *Sardina* or *Sardinops* occur.

Canary Current

Sardina pilchardus is the most studied of the sardines; an extensive review of the geographical variations in its meristic and morphometric characteristics has been published by Freon and Stequert (1979). The two currently accepted subspecies, which are based parimarily on the number of gill rakers, both occur in the Atlantic. *Sardina pilchardus pilchardus* is generally considered to occur off western Europe, and *S.p. sardina* occurs off North Africa and in the Mediterranean. Determination of the stock structure within the Mediterranean appears to be quite controversial, based on quite small scale geographical features, and a solution was beyond the language skills and endurance of the present authors. In the Atlantic there appears to be some consensus on stock structure.

Bravo de Laguna (1983) points out that *Sardina* extends from Dogger Bank in the North Sea to Cap Vert in Senegal. In this large area Andreu (1969) and Furnestin and Furnestin (1970) distinguished the following geographical stocks.

1) The septentrional Atlantic stock which occurs from the North Sea (57° N) to the Cantabric coast of Spain (43°N). (Vertebrae 52.0)[1]

2) The Iberian or meridional Atlantic stock which occurs from the Cantabric coast to the Straits of Gibraltar (36°N). (Vertebrae 51.2)

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[1]Vertebrae counts were made in different ways by different authors. We have standardized the counts to that suggested by Hubbs and Lagler (1947), (ie. the hypural plate is counted as one vertebrae).

3) The Moroccan stock which occurs from Cap Spartel (36°N) to Cap Juby (28°N). (Vertebrae 51.0)

4) The Saharian stock which occurs from Cap Juby (28°N) to Levrier Bay (21°N). (Vertebrae 50.3)

On the basis of the number of vertebrae, electrophoretic differences, and growth differences it has also been suggested that three stocks exist off North Africa (Anon. 1978):

1) A stock near Casablanca (34°N).
2) A stock between Safi (32°N) and Cap d'Anlou (30°N).
3) A stock between Ifni (29°N) and El Ayoun (27°N).

Bravo de Laguna (1983) analysed the results of hydroacoustic surveys and seasonal migrations of sardines off North Africa and concluded that sardines between Safi and El Ayoun might belong to the same stock. He also stated that there was not enough evidence on sardines south of Cap Bojador (26°N) to assess the stock structure in this region.

Analyses of all of the information available on biometric and meristic characters, electrophoretic studies, spawning areas and periods of reproduction, growth studies and distributions observed during hydroacoustic surveys have recently led several workers to suggest that there are three stocks off North Africa (Belveze and Erzini 1983; Rami 1984):

1) Casablanca stock (36°N to 33° 30'N).
2) Moroccan stock (32° 30'N to 27°N).
3) Saharian stock (26°N to 21°N).

Beginning in about 1970 there were increasing amounts of sardines caught along the coast of Mauritania between the latitudes of about 16°N to 26°N and since about 1974 sardines have been taken as far south as Senegal (Anon. 1978). Freon and Stequert (1979) present very convincing evidence that the expansion of the population has resulted in a new stock off Senegal. They also present evidence which places the separation of *Sardina pilchardus* into two subspecies based on the number of gill rakers or vertebrae in doubt. Their fig. 8, which shows the relationships between the number of gill rakers and total length for sardines taken at a wide variety of locations, clearly demonstrates that although there is a strong tendency for the Atlantic, European sardines to have a larger number of gill rakers than the Atlantic, North African and Mediterranean sardines, this is not always the case. For example, sardines taken near Casablanca which are supposedly *S.p. sardina*, the subspecies with the smaller numbers of gill rakers, actually have the largest number of gill rakers of any of the locations. Sardines from their proposed Senegalese stock also have very large numbers of gill rakers. The number of vertebrae appears to be a good characteristic in separating the two stocks of *S.p. pilchardus*; however, the number of vertebrae in *S.p. sardina* taken in most of the Mediterranean areas are intermediate between the two *S.p. pilchardus* stocks and the rest are similar to the Iberian stock or have even fewer vertebrae.

In summary, there appears to be at least four stocks of *Sardina pilchardus* in the northeastern Atlantic. The most likely expansions from the four stock descriptions of Andreu (1969) and Furnestin and Furnestin (1970) given above are the possibility of two Moroccan stocks as suggested by Belveze and Erzini (1983) and Rami (1984), the possibility of a Senegalese stock which is separate from the Saharian stock as suggested by Freon and Stequert (1979) and a stock in the Azores.

Benguela Current

On the west coast of southern Africa, the Benguela upwelling system may act to some degree as a barrier to migration between sardines off Namibia and those of the southern portion of South Africa. The region of maximum upwelling, which lies between the two regions, may reinforce reproductive isolation between the two regions as it has temperatures which are below the minimal temperature needed for normal sardine larval development (King 1977b). Davies (1956) suggested that there was only a single stock based on small regional differences in the numbers of verbebrae. Newman (1970) concluded, on the basis of tagging experiments, that there was little exchange of individuals between the Walvis Bay fishery in Namibia and the Cape fishery in South Africa. The presence of two widely separated spawning grounds, sharp differences in historical landings in the two areas, and Newman's work led to the general acceptance of the two-stock concept in southern Africa (Butterworth 1983; Crawford et al. 1983):

1) Cape stock (34°S). (Vertebrae 51.2 to 51.4)[2]
2) Walvis Bay stock (22°S).

These stocks have been the subject of three genetic studies using electrophoretic methods. Thompson and Mostert (1974) examined three samples extending from Namibia to the west coast of South Africa for geographic variation at a single locus encoding an esterase enzyme. Allele frequency differences in that study suggested that regional genetic differences may exist between the two areas. Le Clus (1978) searched for geographic variation among five samples taken from the Namibian stock and also detected a significant degree of heterogeneity. In both of these studies, however, there were significant departures from Hardy–Weinberg proportions; these could have resulted from three effects. The first is that the samples may have included individuals from two or more genetically differentiated stocks (the Wahlund effect). The second is that an undetected null or silent allele was present which produced the apparent excesses of homozygotes in the samples. The third is that the phenotypic variation may not have been under simple genetic control. Spurious electrophoretic bands can appear through storage and handling effects (Utter et al. 1979). In the latter two cases any attempt to infer genetic differences between stocks using the data is invalid.

In the third study, Grant (1985b), examined the variation in 30 protein coding loci for six samples extending from 19°N in northern Namibia to 26°S on the south coast of South Africa. Four proteins (excluding esterase) were sufficiently polymorphic to make statistical tests of geographic structure, but no significant differences in allele frequencies were detected among the samples. A gene diversity analysis (Nei 1973) indicated that 99.5% of the total genetic variation that was detected in the samples was contained, on average, within each location. Only 0.5% of the total variation was due to allele-frequency differention among the locations that were sampled. The lack of regional differentiation implies either that there is sufficient migration between the stocks to prevent genetic differentiation or that reproductive isolation between the stocks has occurred

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[2]Average vertebrae counts for the Cape stock were given by Baird (1971) as 49.2–49.4. According to P. Shelton (Sea Fisheries Institute, Capetown, South Africa) these counts did not include the urostyle or hyperal plate; for comparative purposes we have therefore increased the counts by two.

only recently, and insufficient time has elapsed for significant differences in allele frequencies to appear. The former explanation is more likely.

California Current

It has been generally accepted that there are at least three stocks of *Sardinops* in the California Current system and a fourth has been proposed (Radovich 1981). Clark (1947) used vertebral counts to demonstrate that sardines in Baja California differed from those further north. Clark and Janssen (1945) and Janssen (1948) used tagging studies to show that there was significant intermixing of sardines between northern Baja California and California and between California, Oregon, Washington and British Columbia. McHugh (1950) found morphometric and meristic differences between sardines in southern Baja California and those to the north. Vrooman (1964) separated the California Current sardines into the following three subpopulations based on serological differences, and he also noted that the number of vertebrae differed between the three subpopulations:

1) Northern stock, from northern Baja California (30°N) to Alaska (55°N). (Vertebrae, 51.44)
2) Southern stock, off the Pacific coast of Baja California (23–30°N). (Vertebrae, 51.36)
3) Gulf of California stock (23–31°N). (Vertebrae, 51.04)

The ranges of the southern and northern stocks appear to overlap seasonally by at least 400 km; southern stock fish were taken as far north as San Pedro, California (34°N) and northern fish were taken as far south as San Quintin Bay, Baja California (30°N); however, it appears that both groups move north or south at about the same time of year with no overlap of the stocks (Vrooman 1964).

In contradiction to Vrooman (1964) recent morphological and biochemical genetic studies have not revealed genetic variation between sardines from central California, the Pacific side of southern Baja California and the Gulf of California (Hedgecock et al. 1985).

Radovich (1962, 1981) postulated that the sardines off the Pacific Northwest (Oregon to Canada) and southern California were somewhat distinct, either genetically or due to a strong tendency for fish to favor areas in which they were born. He pointed out that sardines in the Pacific Northwest were larger and older than those in southern California and that there were differences in the growth patterns on scales from fish in the two areas. The occasional presence of spawning and occurrences of young-of-the-year sardines in the Pacific Northwest (Walford and Mosher 1941) also gives some credence to separation of sardines in the southern California and Pacific Northwest areas. However, the relatively small proportion of young fish in the Pacific Northwest fishery (Radovich 1981) and the rapid movement of tagged fish between the Pacific Northwest and southern California can be used to argue against a separate far northern stock (Janssen 1938). Marr (1960) and Murphy (1966) both rejected the existence of a far northern stock.

Peru Current

The stock structure of sardines in the Peru current system is presently no better understood than that of the other systems and it is further complicated by the recent high population levels which have resulted in a geographical expansion of the range and also apparent recolonization of spawning grounds which

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were not occupied in the decade prior to the population expansion. There is no conclusive evidence regarding the fishery stock units but there could be three or possibly five stocks based on the spacial pattern of spawning:

1) Northern stock(s), from southern Ecuador (1°S) to central Peru (15°S). The Galapagos Islands may have a separate stock.
2) Central stock, from southern Peru (15°S) to northern Chile (25°S). (Vertebrae 50.87)
3) Southern stock(s), off Coquimbo, Chile (30°S). (Vertebrae 51.15) Off Talcahuano, Chile (37°S).

Supporting evidence for the stock structure of sardines in the Peru Current system is quite limited. Hildebrand (1946) found differences in the number of dorsal rays, 17–20 in Peru vs 15–18 in Chile, and in the relative length of the head, 3.3–3.7 head lengths is the standard length in Peru and 3.48 in Chile. De Buen (1958) gave the following differences between the sardines in Peru and Chile; length of the head 27–28.5% of the standard length in Peru and 25.5–26.1% in Chile, predorsal distance 47–50% of standard length in Peru and 45.1–47.6% in Chile.

Brandhorst et al. (1965) analyzed sardines from Arica, Chile (18°S) and from Coquimbo, Chile (30°S). They found that the mean number of vertebrae were 50.874 ± 0.034 at Arica and 51.153 ± 0.070 at Coquimbo suggesting stock differences may occur between these two regions. The recent expansion of sardines into the Talcahuano region of Chile (37°S) probably occurred from sardines in the Coquimbo region (30°S). The presence of spawning at this new location may indicate that the populations of sardines in these two regions are at least partially independent.

Another feature in the Peru Current is that large geographical dislocations of sardines have been observed in association with El Niño events. Before 1983 the main concentrations of sardines were in northern and central Peru and in northern Chile (Zuta et al. 1983; Serra 1983); however, during the first quarter of the El Niño year of 1983 there was an influx of sardines into southern Peru. It is assumed that these fish were primarily from northern and central Peru, but it is possible that fish from northern Chile also moved into southern Peru as suggested by tag recoveries and spacial distributions shown by hydroacoustic surveys. The Ecuadorian sardine fishery suffered a sharp decline as sardines migrated south into Peruvian waters, apparently avoiding the high water temperatures caused by the same El Niño event (Anon. 1984). Evidence from "normal" years suggests that the abundance of sardines in northern Chile shows a seasonal pattern with peak abundance occurring during the winter spawning season and much lower abundance during the summer and fall (Serra and Tsukayama 1988).

Tagging experiments have shown that during the 1982–83 El Niño there were movements of sardines from both northern and central Peru into Chile (Torres et al. 1984). Maximum movement observed was from approximately 9°S to 30°S (over 2000 km). In other years, tag recoveries suggest that fish move seasonally to and from northern and central Chile (i.e., from 18°S to 30°S) with southward recoveries at a maximum during the summer and northward recoveries at a maximum during the winter.

When the available evidence is viewed as a whole, it is obvious that there is considerable evidence for intermixing of fish from central Peru to Coquimbo, Chile. It is likely that definitive analysis of the stock structure in the Peru Current will only be possible when properly designed biochemical genetic analyses have been carried out.

Kuroshio Current

The number of sardine stocks in the waters associated with the Kuroshio Current system has been the subject of considerable debate. The number of stocks proposed to inhabit the area has varied from one (Nakai 1952, 1962) to five or seven (Uda 1960).

According to Nakai (1952), during the period of high abundance in the 1930's the spawning grounds of the Japanese sardine were heavily concentrated in the area around southern Japan (29–33°N); sardines from this area migrated northwards throughout the Sea of Japan, along the Pacific coast of Japan and through the Tsugaru straits. Based on this information he suggested that there was only one stock.

According to Uda (1960), Aikawa and Konisi (1940) considered that there were two stocks.

1) Sea of Japan stock. (Vertebrae 51.75 ± 0.45)
2) Pacific stock. (Vertebrae 51.46 ± 0.55)

Based on the time sequence of catch data, Uda (1960) divided the population into five or seven principal groups for which he suggested that there were spawning grounds corresponding to the various groups but he did not identify the locations.

According to Kondo (1980), after the population size declined in the 1940's it became apparent that there were four subpopulations of the Japanese sardine; however, Kondo presents no documentation for these four subpopulations:

1) Kyushu subpopulation: Spawns along the Western coast of southern Japan) Kyushu to San-in district) and occupies the area from the East China Sea to the Western part of the Sea of Japan.
2) Japan Sea subpopulation: Spawns around the Noto Peninsula (Ishikawa Prefecture) and occupies all of the Sea of Japan.
3) Ashizuri subpopulation: Spawns along the Pacific coast of southern Japan (Kyushu and Shikoku).
4) Pacific subpopulation: Spawns in the Pacific waters along Honshu.

Watanabe (1983) stated that there are two subpopulations on the Pacific side of Japan. However, his statements suggest that the Japanese perspective of subpopulations is quite different from the concept of stock used in this review. For example, he stated that it is assumed that one of the major reasons for the burst in the spawning in the Ashizuri subpopulation was the substantial immigration of parental fish, especially the 1977 and 1978 year-classes from the Pacific subpopulation. He further stated that it is apparent that a substantial amount of the larvae of the Ashizuri subpopulation have been transferred and therefore recruited to the Pacific subpopulation and that intermingling of juvenile and adult fish has widely taken place between the two subpopulations after the expansion of the distribution range in each.

We were unable to find evidence from tagging, biochemical analyses, or traditional taxonomic studies on which to base an analysis of stock structure in the Japanese region. However, the available literature suggests considerable intermixing of sardines throughout the Kuroshio Current region, particularly when abundance is high.

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Australia and New Zealand

Blackburn (1960) suggested that two well-separated winter spawning and two well-separated summer spawning regions occur in Australia. On "the assumption that sardines spawn only once a year for a period of a few months only" he proposed that there were four reproductively isolated populations in eastern Australia, possibly two in western Australia and one in New Zealand. In view of recent evidence on spawning frequency of sardines (Alarcon et al. 1984) and the fact that spawning has been observed for extended periods in sardine populations from many areas of the world, our interpretation of Blackburn's (1960) data is that there are four stocks with spawning grounds in the following areas:

1) Western Australia, 27–35°S. (Vertebrae 50.86)[3]
2) Southern Queensland to southern New South Wales, 27–36°S. (Vertebrae 50.89)
3) Victoria, Tasmania, and South Australia, 34–41°S. (Vertebrae 50.83)
4) New Zealand, 35–46°S. (Vertebrae 51.39)

Discussion of Stock Structure

The concept that populations of fishes are subdivided into discrete stocks has a substantial appeal to those responsible for fishery management. Stocks of various species of fishes have been defined by geographic differences in meristic and morphological characters, by regional differences in population parameters, by physiology and behavior, by the results of tagging experiments and by physical oceanographic features (Ihssen et al. 1981; Iles and Sinclair 1982). With the development of such molecular methods as protein electrophoresis and the restriction enzyme analysis of DNA, it became possible to search for genetic differences between the putative stocks which had been defined by non-genetic methods. In the genetic stock concept, stocks are viewed as collections of individuals of a species which freely interbreed. In reality, individuals in the same species do not always freely interbreed because factors external to their genetic systems prevent them from physically mixing. The most important of these are isolation by geographic distance and physical barriers to migration, both of which can lead to some degree of reproductive isolation between local groups of fish. This reproductive isolation may lead to subsequent genetic divergence through natural selection or genetic drift.

The degree to which genetic differentiation among populations is realized varies according to the life history patterns which affect migration and gene flow among populations. Theoretical studies have shown that only a small amount of gene flow is sufficient to prevent genetic differentiation through genetic drift between populations (Wright 1940; Kimura 1955). Populations of freshwater fishes are isolated by physical barriers to a much greater degree than marine fishes. For instance, in freshwater fishes inhabiting lakes or geographically isolated river systems, the amount of the total genetic variation in a species which is due to population differentiation generally ranges between 15 and 20% (Gyllensten 1985). The remaining intraspecific diversity is contained within populations. In anadromous fishes, such as salmon and sea run populations of trouts, between 5 and 10% of the total genetic variation is due to dif-

[3]The number of vertebrae given one higher than that reported by Blackburn (1960) as he did not count the hypural plate.

ferences between populations (Ryman 1983). Anadromous fishes are less restrained by barriers to migration than are purely freshwater fishes and thus show a greater degree of similarity between populations.

Marine fishes show an even greater degree of similarity between populations because of the large potential for gene flow through unrestrained adult migration or passive drift at the egg and larval stages. In a study of 10 species of near-shore fishes located along the Pacific coast of California and Mexico which had different life-history patterns, Waples (1987) found a negative correlation between dispersal capability and the amount of genetic differentiation among populations. On average, only 4% of the total genetic variation in a species was due to genetic differences among populations. One exception in Waples' study was a species lacking a pelagic larval stage for which 56% of its total variation was due to population differences. In other studies of near shore fishes which spawn benthic eggs less than 2% of the total variation over large areas (1000–3000 km) was due to regional differences (Atlantic herring (Clupea harengus) Grant 1984, Ryman et al. 1984; and Pacific herring (C. pallasi) Grant and Utter 1985).

Epipelagic or benthic marine fishes which spawn planktonic eggs into coastal current systems show an even greater degree of similarity between populations. Anchovies (Engraulis, Grant 1985b), Atlantic mackerel (Scomber, Jamieson and Smith 1987), hake (Merluccius, Grant et al. 1987), deepwater snapper (Pristipomoides, Shaklee and Samollow 1984), damselfish (Stegastes, Shaklee 1984), to mention a few neritic marine fishes that have been studied with genetic methods, typically exhibit virtually no genetic differences among locations. Usually much less than 2% of their total genetic diversity is due to regional differences. All of these results clearly demonstrate the homogenizing effect that gene flow has on the genetic stock structure of marine fish populations over large areas.

Grant et al. (1987) have further argued that genetic differences among stocks of marine fishes are unlikely to appear over short periods, on an evolutionary time scale, because genetic drift is unimportant in very large populations. Even for populations which become completely isolated from one another, at least N generations (where N = population size) must pass before any substantial divergence is likely (Kimura 1955). Since the population sizes in the dominant marine fishes tend to be very large, on the order of at least $N = 10^7$ individuals, genetic drift is not an important differentiating force.

Both the foregoing theoretical considerations and previous attempts to find discrete genetic stocks in marine fishes in general, and in southern African sardines in particular, suggest that it is unlikely that sardines within the individual current systems are subdivided into genetically definable stocks.

Speciation

One of the intriguing aspects of the subtropical sardines (Sardina and Sardinops) is that over much of their range they have few marine Clupeid competitors. In fact, the only other marine Clupeid genus which can be classified as subtropical is Brevoortia which occurs in the subtropical northwestern and southwestern Atlantic, the only subtropical, neritic systems in which sardines do not occur. However, the tropical sardine (Sardinella) co-occurs with Sardina off northwestern Africa and in the Mediterranean.

The subtropical regions are not the only ones with limited Clupeid faunas. There are only two marine sub-polar clupeid

| 18 MY | 11 MY | 3.2 MY |
| Tethys Separation | Miocene Cooling | Closure of Ithmus of Panama |

S. caerulea
S. ocellata
S. melanosticta
S. neopilchardus

Sardina pilchardus
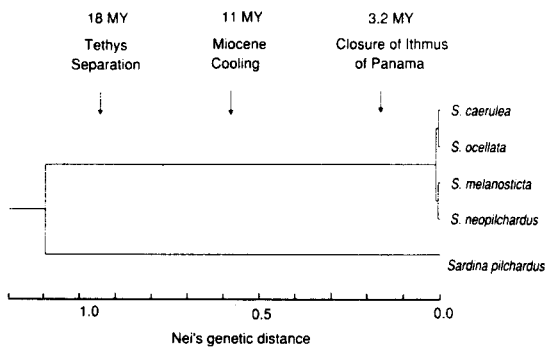
1.0   0.5   0.0
Nei's genetic distance

Fig. 4. A UPGMA cluster analysis of Nei's genetic distances (Nei 1972) between geographically isolated populations of *Sardina* and *Sardinops*. Genetic distances are based on data for 29 protein coding loci. Positions of paleo-events are based on an assumed relationship of 19 million years per 1 unit of Nei's genetic distance.

genera, *Clupea* and *Sprattus*, and these have very different distributions, co-occurring only in the northeastern Atlantic and the subpolar portion of South America. We note that according to Whitehead (1964) the taxonomic status of *Clupea bentincki* from South America is still not well resolved. There are, of course, a number of estuarine or anadromous Clupeid populations which are restricted to subtropical and subpolar regions (i.e. *Alosa, Pomolobus, Ramnogaster,* and *Clupeonella*).

Sardinops is unique in that the ecotypes which occur in widely separated current systems exhibit very limited meristic or morphometric diversification, the meristic variations of stocks within the various current systems have a similar latitudinal pattern, and each current system is considered to contain a number of fishery stocks which collectively comprise a very large biomass and occupy a huge geographical area.

It is possible, of course, that the forms in the various current systems look alike but have considerable genetic diversification at the physiological level. Recent biochemical genetic analyses (Grant and Leslie, unpubl. data), however, suggest that the morphological similarity between taxa appears to result from an underlying genetic similarity and not from convergent evolution in response to similar selective regimens in the various current systems.

Grant and Leslie analyzed tissue samples of four of the nominal species of sardines from Japan (*Sardinops melanosticta*), Australia, (*Sardinops neopilchardus*), California (*Sardinops caerula*), southern Africa (*Sardinops ocellata*), and a single species of sardine from Europe (*Sardina pilchardus*). Standard starch gel electrophoretic methods were used to analyze the gene products of 29 enzyme encoding loci. The Mendelian natures of the banding patterns on the gels were inferred according to the criteria outlined in Allendorf and Utter (1979). Allele frequencies were calculated from the resulting genotypic data and used to calculate Nei's (1972) genetic distances between each pair of taxa. Phenetic relationships among the taxa were then inferred using the unpaired group method of cluster analysis (UPGMA) (Fig. 4).

There are two important features of these results. The first is that there is a large genetic distance between the European sardine and the remaining taxa of sardines. The average genetic distance between the European sardine and the remaining sardines was 1.10, a value that is typical of genetic distances

between well-differentiated genera in the same family (Thorpe 1982). This confirms the taxonomic separation of the European sardine (*Sardina*) from all of the remaining sardine taxa (*Sardinops*). The second important feature of these results is that there is very little genetic differentiation among taxa in the genus *Sardinops* even though they are separated by very large geographic distances. Genetic distances between the taxa represented by the four samples ranged from 0.002 to 0.009 and are more typical of genetic distances between conspecific populations rather than between species or even between subspecies (Thorpe 1982).

Other than the major division between *Sardina* and *Sardinops*, the cluster analysis of genetic distances did not reveal any apparently meaningful relationships among these taxa. The relationships among the four nominal species of *Sardinops* shown in the phenogram are most likely due to sample effects of the allele frequency data and cannot be taken as reflecting true biogeographic or phylogenetic relationships. Thus the lack of anatomical, morphometric and meristic differences between the *Sardinops* populations in widely dispersed regions of the world is reinforced by a corresponding lack of differences at the biochemical level.

We therefore conclude that *Sardinops* is a monotypic genus as proposed by Svetovidov (1952), and that *Sardinops sagax* is the correct scientific name for the populations in the Agulhas, Benguela, California, Kuroshio, and Peru Currents as well as for the Australian and New Zealand populations. The type specimen is *Clupea sagax* Jenyns, from Darwin's collections, and the description of the species is the original description (Jenyns 1847) plus the material presented by Hubbs (1929) in his description of the genus. *Sardinops melanosticta* (Temminck & Schlegel), *Sardinops ocellata* (Pappe), *Sardinops caerula* (Girard), and *Sardinops neopilchardus* (Steindachner) become synonyms of *Sardinops sagax* (Jenyns).

Biogeography

Discussions of biogeography and speciation are heavily dependent upon the biases of the individuals concerned and before proceeding further we will state our biases in regard to the biogeographic principles under which we are interpreting the sardine data. Firstly, we assume that speciation occurs predominantly as a result of isolation in allopatry (Futuyma and Mayer 1980). This is especially true for epipelagic fishes where it would be difficult to imagine the formation of ecotypes, for instance, within the ranges of species which have extensive migrations. Secondly, allopatric isolation can occur as a result of vicarious events which subdivide a species distribution by superimposing a barrier to migration somewhere within the species range or by dispersal into previously uninhabited areas. Probably the best example of the former with respect to marine fishes is the formation of the Isthmus of Panama. For the latter, the best example is the dispersal of Atlantic or Arctic Ocean fishes into the Pacific, or vice versa, when the Bering Strait opened in the late Pliocene. Thirdly, we must assume that the biogeographic relationships among the various sardine taxa have resulted from historical events in the past and are not wholly the result of present oceanographic features.

There are several predictions from population genetics theory and interpretations of biogeographic data in other species that may bear on explaining why there are so few species of sardines. Both theoretical (e.g. Templeton 1980a,b) and paleobiographic (e.g. Jablonski 1986) studies suggest that speciation

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is more likely to occur in species with highly subdivided population structures, in which the average genetic distance between populations is large, than in species acting like a single panmictic population because of large amounts of gene flow. Theory suggests that genetic changes occur through natural selection and random genetic drift and that change can be much more rapid in small populations than in large populations, and these genetic changes can lead to intrinsic reproductive barriers between populations and to the formation of new species.

Genetic studies of most epipelagic marine fishes (see earlier discussion of stock structure) show that there is generally very little genetic subdivision within the range of a given species. In addition sardines have a number of behavioral characteristics which would tend to reduce their speciation rate. Sardines make extensive migrations and alter their geographical distributions in association with fluctuations in abundance or environmental perturbations. They have extended spawning seasons with multiple spawning; some spawning is observed all year in many of the warmer spawning grounds. Thus there is extensive opportunity for interbreeding between fish from different geographical areas within a current system. In addition, as previously mentioned, sardines have extremely large populations. Sardines must therefore be included in the category of species that are not likely to speciate within an individual current system. Thus we do not see sympatric or parpatric species of sardines which can be interpreted to have arisen in situ.

On a broader geographic scale there are two problems requiring explanation. One is to explain the major phylogenetic subdivision between the European sardine (*Sardina pilchardus*) and the remaining taxa in the genus *Sardinops*. The other is to explain why the populations of *Sardinops* in widely separated current systems are genetically so similar.

Before attempting to answer these two questions, it would be useful to put the biogeographic and speciation events of these taxa into a temporal context. A genetic distance can be used to estimate in a rough way the time since divergence between two related taxa (Grant 1987). Empirical calibrations of genetic distance suggest that a Nei genetic distance of 1.0 is approximately equal to 19 million yr of divergence time. However, comparisons of genetic distances between pairs of related fish taxa separated, for instance, by the Isthmus of Panama 3.1 million yr ago, show that there is a large error associated with any estimate of time. Therefore it is better to use the estimate of genetic distance along with its standard error to estimate a period of time when divergence was most likely. For the *Sardina*–*Sardinops* split with $D = 1.10$ (SE 0.26) this period of time extends from 16 to 26 million yr before the present; or from the end of the Oligocene to the mid-Miocene. For the various *Sardinops* splits the average D value was 0.005 (range 0.002–0.009) and the average standard error was 0.004 (range 0.002–0.008). Using the average D value and the average standard error the time of divergence of the *Sardinops* populations would have occurred from 19 000 to 171 000 BP. Both dates are in the late Pleistocene. The last glacial period is considered to have peaked about 18 000 BP and the last interglacial period was about 125 000 BP.

Given the present-day location of *Sardina pilchardus* and the apparent length of time that they have been separated from *Sardinops*, we suggest that the closure of the Tethys Sea in the late Oligocene by the colliding continental plates of Laurasia and Africa (King 1983) served as a vicariant event leading to the separation of the ancestral sardine taxa into two isolated populations. *Sardina* was then derived from the North Atlantic population and *Sardinops* from the Indo-Pacific population.

Sardina is presently restricted to the subtropical portion of the northeastern Atlantic and the Mediterranean. The absence of *Sardina* from the northwestern Atlantic, if indeed it ever existed there, could be explained by local extinction during Pliocene or Pleistocene cooling. During periods of cooling the North Atlantic was characterized by large-scale intrusions of cold polar water and during the Pleistocene much of the North Atlantic was repeatedly covered by an ice sheet (Kellogg 1980). Latitudinal isotherms were much compressed during these cooling episodes (CLIMAP 1976) and habitat alterations could have easily led to the extinction of *Sardina* in the northwestern Atlantic. The dispersal capability of *Sardina* is apparently not great enough for it to have made the upstream, westward transit across the mid-latitude Atlantic since the last glacial maxima; nor has its temperature tolerance permitted it to colonize the northwestern Atlantic by westward advection around the polar, northern rim of the North Atlantic or along the North Atlantic equatorial current.

The task of explaining the biogeographic origins and distribution of *Sardinops* is much more difficult. The minor genetic distances between populations in different current systems suggest two general hypotheses:

1) There is ongoing migration between the various current systems which keeps the populations so genetically similar.
2) *Sardinops* achieved its present distribution as the result of Pleistocene climatic changes, in which case there were probably exchanges between current systems at some time during each glacial cycle.

Before developing these hypotheses it should be noted that the earliest time that *Sardinops* could have achieved its present distribution was probably during the late Miocene. The middle Miocene fish fauna of California is quite well known and Jordan (1921) points out that, with few exceptions, the middle Miocene fauna is similar to the present subtropical fauna of California. One of his exceptions is "There are no anchovies, sardine, or true herring, the numerous herring-like forms being all of rare or extinct types." We note that the striations on the opercular bones of *Sardinops* and *Sardina* make them particularly easy to identify as fossils. It should be noted that Fitch (1969) found the otoliths of the northern anchovy, *Engraulis mordax*, and the Pacific herring, *Clupea pallasi*, but not *Sardinops* in three Pliocene deposits and numerous Pleistocene deposits. The earliest recorded occurrance of *Sardinops* in the California Current region is from Holocene sediments off Vancouver Island which were dated between 8 850 and 9 840 yr BP (Casteel 1975). The earliest recorded occurrance of *Sardinops* in the Peru Current region is not much earlier; (i.e. between 11 400 and 11 700 yr BP, DeVries and Pearcy 1982). However, we were unable to find any studies of the Miocene–Pleistocene marine fish fauna of this region.

To evaluate the first hypothesis it is necessary to evaluate the probability of exchanges of sardines between current systems under the present climatic conditions. Sardines are highly migratory, epipelagic plankton feeders and it is certainly within the realms of possibility that they could simply swim across an ocean. For example, tagged sardines have made one-way migrations between southern California and Canada (1850 km) in as little as 103 d (Jannsen 1938). On the other hand they do not occur in the northwestern or southwestern Atlantic.

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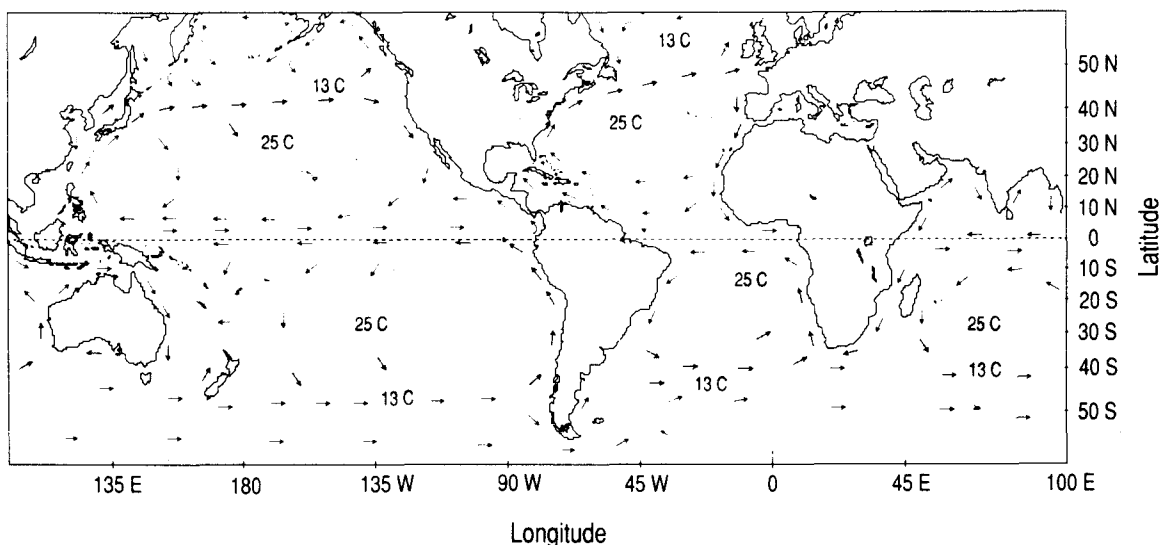*Can. J. Fish. Aquat. Sci., Vol. 46, 1989*

FIG. 5. Major ocean circulation features and area with summer sea surface temperatures between 13 and 25°C (shaded). Based on charts in Sverdrup et al. (1942).

The biomass levels of sardines within each of the major current systems for which population estimates exist, have at times exceeded several million tons. At these biomass levels there are undoubtedly millions of larval and juvenile sardines swept offshore and lost to the neritic populations each year. It is therefore possible that sardines could be passively advected from one current system to another.

The temperature tolerance of adult Sardinops is from 7 to 27°C (Tokai Regional Fisheries Research Laboratory 1960; Ahlstrom 1960) and most spawning occurs at temperatures of 13–17°C (Ahlstrom 1960). In all of the regions in which it occurs the high and low latitude edges of the normal range of Sardinops (Fig. 1–3) are well described by the summer 13 and 25°C isotherms (Fig. 5). This is well within the range of sea surface temperature (SST) occurring in the mid-latitudes but SST at low and high latitudes (Sverdrup et al. 1942) is near or exceeding lethal temperatures for sardines. Of course sardines could feasibly avoid the high equatorial SST by staying in the thermocline to avoid thermal stress. However, the interaction between the increased metabolic rates that would occur at higher temperatures and the lower food availability which occurs in tropical waters would be a severe limitation to sardine survival in equatorial and central water mass regions.

The most likely exchange of sardines between current systems, with the present climatic conditions, would appear to be a mid-latitude crossing from a western boundary current to an eastern boundary current via one of the west wind drift regions. Recent research on the near surface currents of the North Pacific, using drifting buoys, has shown that the average transit time across the North Pacific going east in the mid-latitudes and west in the equatorial regions is approximately the same, 700 d (McNalley et al. 1983). Sardines often live for up to 10 yr and 5-yr-old fish are quite common. It is thus feasible that there could be passive advective exchanges within an ocean basin gyral system. The major limitations to this type of exchange would appear to depend on the availability of food

and encounters with predators. Sardines are essentially planktivorous species which feed on both phytoplankton and zooplankton. McGowan (1972) has described the biogeography of the major zooplankton faunal assemblages in the Pacific. He describes a "transition zone" fauna which is distributed along the warm side of the subarctic convergences associated with the west wind drift. It is obvious from a comparison of the distributions of McGowan's faunal assemblages with that of Sardinops that, in the Pacific, Sardinops populations are centered in the neritic boundaries of the transition zone fauna. This implies that sardines could remain within the transition zone fauna if, for example, they were advected eastward from the Kuroshio Current to the California Current via the North Pacific Current (i.e., the west wind drift region) but not if they were advected westward from the California Current to the Kuroshio Current via the North Pacific Equatorial Current or via the Alaska and Oyashio Currents (Fig. 5).

In this regard, Kenya (1982) has reported finding commercial quantities of sardines along a large portion of the Kuroshio extension; sardines were taken as far east as 171°E. This is approximately 2800 km from the spawning grounds of southern Honshu and approximately one third of the way across the Pacific. Kenya also found young-of-the-year sardines as far east as 166°E in July. Thus it is likely that during the Holocene there has been frequent eastward, advective mixing of sardines from the Kuroshio Current to the California Current via the west wind drift region and, by analogy, between the southern African, Australian, New Zealand, and South American populations.

Conversely westward, advective exchange via the equatorial currents would be very unlikely as it would have to occur at near lethal temperatures and within zooplankton faunas in which sardines do not normally occur. Westward, advective exchange via the Alaska Current would presently be impossible as temperatures are near, and seasonally below, the sardine's temperature tolerance range, and there is no comparable subpolar gyre

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in the southern hemisphere. Westward mid-latitude exchange, via the northern and southern hemisphere west wind drift regions, would also be very unlikely as it would have to occur against the prevailing currents (Fig. 5).

Exchange of sardines between the southern and northern hemispheres would also appear to be very difficult as present sea surface temperatures near the equator are higher than those in which sardines normally occur and, for the most part, the present large scale circulation patterns would tend to hinder exchanges between the northern and southern hemispheres. If transequator exchanges are possible under the present climatic conditions they would be more likely to have occurred on the eastern edges of the oceans rather than the western edges . There are two principal reasons for this; the eastern edges of the tropical oceans are cooler than the western edges and the eastern boundary currents advect cool (sardine rich) water towards the equator whereas the western boundary currents advect warm (sardine poor) water away from the equator.

The most likely area for transequator exchanges with the present climatic conditions is the Eastern Tropical Pacific. In the eastern Pacific *Sardinops* occurs to southern Baja California (24°N) in the California Current and to the equator in both Ecuador and the Galapagos Islands. *Sardinops* does not presently occur in the Eastern Tropical Pacific; however, it can at times survive there as fishing vessels have successfully transported it from the Galapagos Islands to the Central American tuna fishing grounds as live bait (Alverson and Shimada 1957). Present SST in the Eastern Tropical Pacific (Sverdrup et al. 1942) is near the lethal limit for sardines; however, the prevailing nearshore currents would favor dispersal from the Peru Current to as far north as southern Mexico. Seasonally, currents are favorable as far as 28°N in the Gulf of California (Baumgartner and Christensen 1985). Conversely southern dispersal from the California Current to the Peru Current would be hindered by the prevailing currents.

The second area in which transequator exchanges might occur with the present climatic conditions is in the Guinea Current region. *Sardina* presently occurs as far south as 15°N in the Canary Current and *Sardinops* occurs as far north as 16°S in the Benguela Current. Sea surface temperatures over most of the Guinea Current region (Sverdrup et al. 1942) are near or above the lethal limits for sardines. The region has somewhat lower SST in August with SST over some of the area below 25°C: however, at this season SST in the area between the Canary and Guinea currents is above 27°C. The prevailing current in the Benguela and Canary Currents is equator-ward. Sardines could therefore possibly be advected to the equator; however, once across it they would have 15 degrees of latitude to cross, against the prevailing currents at near-lethal SST, before reaching sardine habitat in the opposite hemisphere. Thus transequator exchanges in the Atlantic appear to be impossible for either *Sardina* or *Sardinops*.

The second hypothesis is supported by the fact that the apparent time of divergence between populations in the different current systems is placed in the Pleistocene, a time of both global oceanic cooling and warming that would have enhanced migration from one current system to the other. We note that the genetic distance of 0.003 between the Japanese and Californian sardine populations is on the same order of magnitude or less than genetic distances observed between eastern and western Pacific ocean populations of Pacific herring, *Clupea pallasi* (Grant and Utter 1984), and Pacific cod, *Gadus macrocephalus* (Grant et al. 1987).

Eastward exchange between western and eastern boundary currents during the Pleistocene would have been possible with the same explanations as those given above for the present climatic conditions. It is likely, however, that conditions are more favorable at some stages in the glacial cycle than at others. Westward exchange during glacial maxima via the equatorial currents would have been nearly as unlikely as at present as there is little temperature difference in the tropics between glacial maxima and minima (CLIMAP 1976). However, there is considerable difference between temperatures at glacial maxima and minima in the subpolar regions (CLIMAP 1976) and paleosediment analyses show that the North Pacific subpolar gyre is an area with maximum faunal changes between glacial maxima and minima (Ruddiman 1985). Westward exchange may, therefore, have been possible in the North Pacific via the Alaska Current when conditions were warmer than at present (i.e., in the Pliocene or during extreme interglacial periods during the Pleistocene).

The evidence discussed earlier suggests that with the present climatic conditions transequator exchanges of sardines are not possible anywhere except in the Eastern Tropical Pacific, and they would have to be considered very unlikely even there. However, recent evidence from oxygen isotope and radiolarian analyses of ocean cores suggests that at the last glacial maximum (18 000 yr BP) the August 25°C isotherms were displaced southwards to southern Mexico (18°N) and northwards to southern Costa Rica (8°N) and maximum mean SST in the eastern tropical Pacific was only 26°C (Ruddiman 1985). Jones and Hassen (1985) suggest that contact between the Tethys-derived coral fauna in the Caribbean and Tropical Pacific was lost in the late Pliocene, following development of the Panama land bridge, and the virtual extinction of the eastern Pacific coral reef fauna ensued during Pleistocene glaciations. There is, therefore, considerable evidence that implies that climatic conditions in the Eastern Tropical Pacific would have been cool enough to allow *Sardinops* from the Peru Current to cross to the California Current during Pleistocene glacial maxima.

In summary we suggest:

1) Eastward, advective exchange of *Sardinops* between western and eastern boundary current systems via the west wind drift regions and within the transition zooplankton faunal zones is possible with the present climatic conditions.
2) Westward, advective exchange of *Sardinops* from the California Current to the Kuroshio Current via the subpolar gyre is not presently possible, but it would have been possible during the late Miocene and early to mid-Pliocene when sea surface temperatures were warmer than those that have existed since the onset of northern glaciation in the late Pliocene. It may also have been possible during extreme interglacial maxima.
3) Westward, advective exchange is and was not possible via the equatorial currents due to their high SST and different zooplankton fauna.
4) Westward exchange, against the prevailing current, is and was not possible within the west wind drift regions.
5) Trans-equator exchange is only possible in the eastern Pacific and is most likely to occur during glacial maxima.

If the above statements are accepted, then it can be postulated that the present distribution of *Sardinops* was derived from the Indo-Pacific segment of the original Tethys sardine population. *Sardinops* is most likely to have achieved its present distribution by first dispersing from the southern Indian Ocean to

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Australia, New Zealand, and Pacific South America via the southern hemisphere west wind drift. The absence of *Sardinops* in the southwestern Atlantic Ocean can be explained by the fact that *Sardinops* from the Benguela Current would have to move against the west wind drift current to colonize the region and *Sardinops* from the Pacific could not reach the region as the southern tip of South America extends into water that is too cold for *Sardinops*.

The present southern hemisphere distribution was probably achieved by the late Miocene or early Pliocene, a period when ocean temperatures were decreasing and oceanic productivity was increasing. In the eastern Atlantic, paleo-oceanographic reconstructions show that, although there was considerable cooling in temperate areas, Pleistocene equatorial waters remained nearly as warm as present day equatorial waters (Thunell and Belyea 1982). Indeed, there is no evidence to show that *Sardinops* (or *Sardina*) crossed the equator in this region. The colonization of the North Pacific apparently did not occur until after the closing of the Isthmus of Panama and the onset of extensive northern hemisphere glaciation in the late Pliocene; it is most likely to have occurred in the Pleistocene when the minimum ocean temperatures associated with a glacial maxima would have resulted in climatic conditions which would most favor the dispersal of *Sardinops* from the Peru Current to the California Current. There is a possibility that *Sardinops* achieved its present distribution by reaching the Kuroshio Current, via the North Pacific subpolar gyre, in the late Pliocene; however, this probably occurred during an extreme interglacial period in the Pleistocene.

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