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PHYSIOLOGY AND ENVIRONMENTAL RESTRICTIONS ON SKIPJACK TUNA,

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Physiological Effects Resulting in Variable Growth and Spawning Sequence

Probably the least understood processes in tuna biology are those relating growth, spawning and their environmental effectors. It is possible to examine some of the possibilities using first principles of energetics, from at least the cursory level I will develop here. The point being to stimulate discussion and perhaps to show that a little research in this area based on measurements of metabolites and respiration rates of the various genetic components over a season or two may yield significant information about the reproductive and growth processes of tunas in general.

Too often the collection of fisheries biological statistical data is limited to parameters which are easy to obtain, supposedly useful for long term comparison and handy for plugging into the well worn growth functions. Generally, this means the development of a growth curve from a data base formulated to generate a weight-length relation, and perhaps a ritualized collection and examination of gonad developments and size at maturity information. Little thought has been given to the existing modern biology and the potential for getting at the important and more valuable information which is cast away with the carcass after obtaining the fork length and sex. The lack of sophistication of fishery science relative to the other agricultural-productivity fields is amazing, to say the least. The general fishery biologists are sufficiently threatened by or ignorant of the modern biological sciences that they can be likened unto the clergy in the days of the renaissance, as they deliver their incantations about theoretical poobah and wave their symbolic  $C_{PUE}$  and  $L_{\infty}$  in vexation at the new knowledge and techniques. Perhaps a rigorous reevaluation

of the practicality of the CPUE models in tuna studies is overdue. Certainly no tuna fishery looks to have yielded any insights into its "dynamics" utilizing these hackneyed techniques.

Age determination, of course, is the key to much of the dilemma in deciding whether differential growth rates occur in complex tuna population structures. But even the age information cannot be interpreted without some fairly rigorous examination of the relative genetic homogeneity of samples. What in one case looks like highly variable data may indeed be distinguishable as two or more sets of extremely homogeneous data if the samples are stratified by genetic grouping. Complications of data collection and interpretation due to the selection or preference of specific environmental conditions by the fish strictly as a function of developmental state, or similar size group overlap of genetically distinct components are very probable given the complexity of tuna population structure. Several examples of this phenomenon <sup>in tunas</sup> are available. The solutions to biologically oriented tuna problems require intensive evaluation of sample homogeneity for all parameters to be appropriately evaluated. The problematic situation is that where several years of data have been collected ignoring this requirement there is generally a reluctance of the existing systems to accept the increased burden of multiple disciplinary sampling and the expense of analysis. Unfortunately, the value of the traditionally processed data in tuna biology is in most cases nil and/or not interpretable in any truly meaningful sense due to the unsuitability of the data to the processes which need to be defined (for example, take a good look at average weight of fish in the catch data for surface gear).

The virtual absence of information on the larval and young juvenile distribution of tunas precludes any description of spawning habitats or nursery grounds. The mobility of 50 cm tunas is such that even the slowest swimming

(T. obesus) compared to 67 Km/d for a 50 cm skipjack  
of the species groups, necessarily travels 27 km per day, for hydrodynamic stability and respiration purposes. Gonad maturation and post-spawner data summarizations typically have a 30 day time frame due to the typical sampling methods, resulting in a potential 500 to 1000 km error in spawning site definition, *for the slowest swimming of tunas.* The even more obscure aspect of not having the slightest sense of the relation of the spawners to the exploited populations tends to emphasize our ignorance and the weakness of any supposed exploited stock density dependence of recruitment.

Fisheries scientists assume a lot of limnological analogy exists in tuna physiology. Growth checks due to seasonal deprivation are highly unlikely in the tropical tunas due to their high mobility. The migratory behavior in pre-spawner age tunas appears to be a general characteristic. Why do these species migrate or at least concentrate in areas seasonally? It can't always be for the same reasons as salmonids for the simple reason that among tunas, the sexually mature migrator is the unusual case. The emergence of recruit tunas (generally at approximately 1 year of age) in areas of high productivity and high vulnerability probably indicates their ability to sense and climb environmental and/or food gradients. The cyclic nature of these appearances in some areas is certainly environmentally precipitated.

An interesting dichotomy in migratory species is the partitioning of energy for either migration or spawning. The problem is that the spawning behavior and the shift in energy requirements must be stimulated by the abundance of food and the appropriate environmental milieu. Migration can be of several types, (e.g. short term-short distance for optimization of food availability; long term-long distance seasonal responses to food or spawning site availability; generally short term, long distance responses to locate appropriate spawning or feeding environments). The long distance migrations during the short term

are probably the most energy requiring (see Sharp & Dotson - in Press). The other two modes can be facilitated by ocean currents or just minor directed orientations, not requiring energy above the typical or basal swimming levels and may account for the movements typical (or necessary) to obtain sufficient "spare" energy to get to the spawning mode. I suspect that the long distance migrations are typical of "growth" facilitating behavior. These movements probably reflect the necessity and successfulness of juveniles and pre-spawners to seek out and utilize the high productivity oceanic regions. Here the fish graze heavily and the growth rate is maximized. Rapid growth is necessary for several biologically sound reasons. For example, the scombrids are opportunistic feeders and are not ecologically separable at their immature sizes, so that rapidly obtaining the appropriate size for optimum utilization of the later developing niche stratification adaptations (Sharp and Pirages, in press) is a pre-requisite to obtaining sufficient spare calories to provide for gonad maturation and egg development. The importance of physical environmental parameters to rapid growth and development is easily shown. One of the readily recognized principles in biology today is that involving temperature dependent respiration rate,  $Q_{10}$ . I can see very little available physiological stratification in specific tunas below the 55-70 cm total length range to allow them to effectively hold a unique niche. The process of obtaining this size range rapidly would be facilitated by high ambient temperatures. The effective collection of spare energy (above basal requirements) for egg development and spawning is an effective driving motivation in natural selection for diversity in adapting to the non-tropical environments (Sharp and Pirages, in press). This is of course exemplified in the scombrid phylogenetic process having resulted today in

two terminal species of note, the skipjack, K. pelamis, and the Atlantic bluefin tuna, Thunnus thynnus thynnus which will be contrasted in a later section.

#### Physiology and Environmental Restrictions on Skipjack Tuna

The dangers of generalizing the physiological concept of a tuna species, in particular skipjack are manifold. The only available data on physiological parameters for skipjack are those collected at Honolulu, Hawaii on specimens representing either the northeastern and/or northwestern Pacific subpopulation. The general respiration requirements and temperature "preference" data are likely to be slightly more restricted at the low end of the physiological scales ( $O_2$  and temperature) for these particular skipjack populations than the colder water inhabitants observed off New Zealand and Southern Australia. On the other hand the very warm water skipjack from off Papua New Guinea and the western equatorial (including the Kuroshio) oceanic region would very likely be restricted to warmer temperatures and higher oxygen levels than even the Hawaiian type fish due to the relatively higher temperatures and metabolic rates which they would experience and have adapted to.

It is perhaps presumptuous to generalize from the available data and therefor necessary to accept the typical boundary conditions for fishing success in each of the potential subpopulation centers as representative of their respective preference values. This approach has been successfully applied in species-wise comparisons of estimated lower oxygen and temperature ranges for yellowfin, albacore, and bigeye tuna with the relative successfulness of longline and/or surface gear for areas where the thermal and oxygen profiles are known.

Activity related respiration requirements are estimable from swimming energetics relations (Sharp and Francis 1976), but subject to scrutiny once again due to the fact that the hydrodynamic characteristics employed in the energetics equations for skipjack were collected from those same subpopulations represented in Hawaii. Significant differences in these characteristics (lift surface, fat content, etc) would be expected among the various racial or physiological types. Even minor variations in these characteristics would be particularly important in estimating skipjack energetics due to the relatively unbuffered condition of the bouyancy in this species as compared to other tuna and tuna like species (e.g., no gas bladder).

So what then can we say about skipjack in the equatorial and southern Pacific Ocean relative to the Hawaiian data base. I think that in order to answer this question we must break the population structure down into the potential fundamental units. If significant stratification of environmental characteristics exists for the regions of maximum availability of these units, then we have perhaps answered another question, or at least posed it for the first time. Namely, what are the environmental variations which correspond to the stock structure stratifications as implied from gene frequency data? Presumably these are physiologically significant parameters. That there is a direct link between environmental preferences, tolerances, and genetic structure does not seem an unlikely assumption.

What I propose to do is present the most recent evaluation of the subpopulation data from genetic studies, and to relate these data to the distribution of populations over environmental realms to evaluate potential interactions, where they might be found.

### Hypothesized Subpopulation Structure

In this exploration of potential subpopulation structure I will include data collected from 1966 to the present by Dr. Fujino, and data<sup>that</sup> I have collected over the last two years. I will primarily utilize data sets where eighty or more fish were collected in single samplings. In my own studies, generally, the samples represent single schools and as near 200 individuals (or 400 genes) as were available for sampling. The samples collected since 1966 have come from diverse sources, usually commercial catches, and include some research cruise material. With the recent development of commercial fisheries in Papua New Guinea, New Zealand, and the interest in the western Pacific by U.S. purse seiners, the availability of large samples has grown over the last several years. The importance of the large sample to population stratification is a point I have developed and iterated far too many times to dwell on in this discussion.

At the outset I would like to make clear that the results of my studies are supportive of the general conclusions arrived at by Dr. Fujino. The only significant qualification I would add to his results where our studies overlap, are that in the northwestern, southwestern and equatorial regions there is significant heterogeneity of the within area exploited skipjack stocks of a genetically distinguishable nature. Also in the Honolulu, Hawaii fishery the large sample data yield similar results. The statistical problems inherent to small sample-replication methodology are particularly apparent when these data are contrasted with large samples collected simultaneously from the same time area strata, and quite evident when contrasted to data from a truly homogeneous fishery as exemplified by the New Zealand material in the following description of the area-wise data sets.

Recent Large Sample Collections - Serum sterases only, where the designation

Est 2 is the same gene product described by Fujino (1972) as  $E_{SJ}^1$ .

Papua New Guinea

	N		pooled $\chi_1^2$ , Total $\chi_9^2$	Heterogeneity $\chi_8^2$
A	N=143	.661		
B	N=162	.632	2.4	19.4
Y	N=144	.653	(NS)	$p < .025$
Z	N=179	.743	( 2 p values $p_1 \sim .64$ and $p_2 \sim .74$ )	

Marianas

John Fowler N=135 .693

New Zealand

(1-49	(N=49)	.56		
(50-103)	(N=53)	.58	(very homogeneous data set)	
(104-131)	N=97	.58		
NZ-A	N=195	.53	$\bar{p}$ value $\sim .57$	
NZ-B	N=195	.59		
S-2-18	N=145	.56		
S-2-23	N=196	.59		
F4-7**	N=119	.54		

Eastern Pacific

Northern area:

Taurus B	N=146	.50	
G-2	N=198	.46	
KC	N=134	.48	
KB	N=140	.45	
KA	N=150	.52	
MK-D	N=189	.48	$\bar{p} \sim .47$
MK-A	N=199	.46	
LB-65*	N=193	.48	

Southern Area - Ecuador

Ec-B	N=199	.41	
Ec-C	N=197	.37	2 $\bar{p}$ values: $\sim .38$ and $.47$
Ec-D	N=198	.37	
Ec-G	N=200	.47	



<u>Hawaii*</u>		Est $2=E_{SJ}^1$	
21	N=120	.46	
22	N=100	.60	
23	N=96	.59	
25	N=86	.31	?      2 $\bar{p}$ values: ~.47 and .59
26	N=100	.41	
27	N=99	.59	
28	N=98	.48	
29	N=90	.46	
30	N=95	.44	
31	N=98	.52	
32	N=97	.47	
33	N=92	.58	
34	N=100	.48	

<u>Japan*</u>			
1	N=96	.64	
2	N=95	.58	
5	N=82	.68	
7	N=129	.71	2 $\bar{p}$ values: ~.60 and .68
8	N=96	.59	
9	N=95	.62	
10	N=92	.61	
11	N=96	.64	
12	N=97	.62	
13	N=97	.57	
14	N=96	.63	

<u>Palau*</u>			
1	N=81	.66	
2	(N=65)	.70	
3	(N=74)	.77	
4	(N=76)	.72	2 $\bar{p}$ values: ~.73 and .66
5	(N=74)	.71	
6	(N=71)	.70	
7	(N=65)	.75	
9	(N=78)	.76	
11	(N=77)	.64	
13	N=86	.65	
14	N=90	.65	
15	N=88	.69	

\* = K. Fujino data on file at La Jolla NMFS laboratory

The small sample data (N<<80) collected and compiled by Fujino (not shown here) are useful in comparison to the large sample data to show the wide statistical variability inherent to small samples. When sampling

true replicates of homogeneous units one would expect there to be a normal distribution about population characteristic means, even with small samples. In turn this is the unlikely situation due to the facts that schools are not necessarily genetically homogeneous, and that there is very little expectation for areas of relatively high commercial productivity to comprise only one genetic unit. Data collected from commercial sources of skipjack and yellowfin support these conclusions. The only region of relative genetic homogeneity I have observed, or had sufficient samples to say without doubt that this is the case is the New Zealand skipjack catches for 1976.

I propose that one can hypothesize the existence of at least five genetic units in the Pacific Ocean from existing genetic data. These components can be identified from the distribution of the large sample esterase 2 gene frequencies ( $Est\ 2 = E_{SJ}^1$ ) and the locations of collection of individual samples. The hypothesized structure is diagrammatically expressed in Figure 1. The creation of set boundaries or range limits is artificial and presumptions for several reasons, primarily due to the dependence of the ranges of the individual ~~populations~~ <sup>ranges</sup> on the oceanic conditions. These physical features are notoriously unstable and vary within a year as well as between years, so as to make the cartographic expression of such limits tenuous at best.

I do not intend to dwell on the genetic story more than to say that the New Zealand skipjack exploited in 1976 is statistically a different population from any other described previously, including the two from the eastern Pacific Ocean whose ranges are centered far into the central Pacific Ocean. These two populations overlap extensively, but represent two separate breeding units. There is no reason to expect that the western equatorial Pacific warm water region and the cooler region off Japan should comprise a single habitat. The large samples collected from the two areas are

statistically heterogeneous and bimodal with respect to the frequency of the esterase 2 allele supporting the hypothesis that there are at least two western Pacific populations (Fujino 1970).

To summarize, there are at least five genetic units in the exploited Pacific skipjack population which are geographically associated in varying degree. These can be related to habitats which are distinctive in areas where sufficient data are available, and the intent of this discussion is to explore the basis for this apparent stratification by examining the environmental parameters characterizing these several regions, and the zones of confluence or overlap of genetic components.

## Environmental Characteristics and Skipjack Subpopulations

A compilation of the summarized monthly 5° square oceanographic observation data for the Pacific Ocean was made from the extensive data files of the National Oceanographic Data Center. As the two variables temperature and oxygen are the significant physiological effectors in the physical-chemical data base, their pairwise relation was deemed to be the most likely useful data to work with. The species-wise limitations in skipjack for these two parameters appears to be 15°C and around 2.5 ml O<sub>2</sub>/liter<sup>1/</sup>. The northern Pacific skipjack appear to aggregate at interfaces of rapidly changing thermal structure about the 20°C isotherm. This value is analogous to the 23°C isotherm aggregation behavior of yellowfin school fish in the eastern Pacific, which has been very useful in defining the vulnerability of yellowfin to surface gear (Sharp 1976). The oceanographic data are summarized such that the average sea surface temperature, mixed layer depth, thermocline gradient strength, and depths of isotherms by 1°C intervals to 450 meters are available for fast processing. Oxygen data at each isotherm depth were also compiled.

A graphic presentation of three sets of the oceanographic features is provided. The monthly average strata<sup>1</sup> (Figures 2 January - December) include A. The depth of the 15°C isotherm (to 200 meters) which is the presumed lower tolerance temperature for long term exposure of any skipjack tuna; B. The sea surface temperature by 3°C intervals from 29°C downward (in the eastern Pacific the 28°C isotherm

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1/ Oxygen sensitivity data were provided by Dr. Dizon and Dr. Gooding of the NMFS laboratory in Honolulu.

was plotted to show the region of maximum temperature in cases where the 29°C water was not evident); and C. The limiting features for skipjack vulnerability to existing surface fishing methods are indicated simultaneously by showing the 20°C isotherm and oxygen structure corresponding to maximum fishing depths of modern purse seine gear. Where the 20°C isotherm is shoaler than 80 meters (design fishing depth of the 40 fathom purse seine) a vertical hatching is used. The northern and southernmost boundaries of the continuous line show the surface emergence of that isotherm, indicating that no commercial quantities of skipjack would be expected to be available outside of the enclosed range, except perhaps in the southwestern Pacific. The dashed line encloses the 2.5 ml/L oxygen level areas shoaler than 80 meters and the cross hatching represents the zones where oxygen levels below this value are encountered above 50 meters, indicating a severe limitation due to skipjack respiration requirements in these shoal areas.

Where oxygen becomes limiting, typical fish behavior is to pump more water over the gills, utilizing the opercular apparatus. Tunas, however, have to swim faster to achieve the same goals, thereby increasing their respiratory demands, a non-useful solution to the problem if a more oxygenated water source is not immediately available. One can also see where the additional problem of heat production via the increased swimming activity in these areas characterized by limited oxygen availability could compound the problem as these zones are also very warm relative to the general habitat, and may result in severe thermal stress to active skipjack, resulting in even greater respiratory demands.

Each of the described parameters is in constant flux within the year and also between years to some extent. The most stable areas with respect to these features are probably found in the mid Pacific and may indeed account

for the apparent offshore concentrations of reproductive activity, and even more likely it probably accounts for the migratory tendencies of the various components toward the productive edges of their habitat for pre-reproductive grazing for growth and fat storage.

The important issues to be considered from the data sets include the concept of vulnerability as a function of environmental profiles as discussed in the 1974 and 1975 Annual Reports of the IATTC and as presented at the 1974 Annual Tuna Conference at Lake Arrowhead, and 1976 Annual Japanese Tuna Conference at Shimizu (Sharp 1976). The physiological requirement for oxygen by skipjack tuna is apparently a more significant delimiting factor in the eastern Pacific than it is almost anywhere else in the Pacific Ocean. Other regions however, have more extensive areas of far warmer water than is characteristic of the eastern Pacific. In fact a great percentage of the total skipjack catch in the Pacific Ocean comes from areas where the water temperatures are rarely below 28°C. Oddly enough the virtual absence of catch in similar temperatures in the eastern Pacific can likely be attributed to the shallow oxygen minimum layer, and perhaps only secondarily to the temperature - heat production-dissipation problem hypothesized earlier by Barkley, Neill & Gooding (see Kearney's M.S.)

Examples of expendable bathythermograph (XBT) tracings for three peripheral areas in the Pacific Ocean are provided to show the relative differences. The eastern Pacific Ocean can be stratified into two types of fishing areas, one as exemplified by Figure 3A shows the thermal profile in the Baja California area during a noted "good skipjack bite" Figure 3B is the thermal profile in the relatively anoxic zone just north of 10°N and west of 87°W in an area of good yellowfin school fish availability. Figures 3C and 3D show traces at 2°N 144°E and 9°N and 146°E respectively. No schools larger than 3 tons were

sighted in this area which were not associated with floating debris. The successfulness of purse seine gear in this area for skipjack or yellowfin is poor and virtually dependent upon aggregating devices for effective fishing. The lack of a well defined mixed layer in the latter tracing indicates one of the major differences to be found in the thermal structure of this region of the Pacific Ocean, and not in the central or eastern portions.

If indeed there is a temperature aversion in the north and southeastern Pacific populations it is probably compounded by the oxygen picture as the overall respiration rates should rise with temperature in these areas, causing even more severe demands on the fishes respiration requirements and heat dissipating capability. A manuscript describing the heat production and dissipation process in tuna-like fishes by Sharp and Vlymen (in review) indicates that heat build-up in tunas occurs at all sizes above 2 kg. at swimming speeds greater than about  $1.5 \text{ ms}^{-1}$  (3 knots) and that activities necessary to provide the minimum swimming speed to maintain hydrostatic equilibrium in a 50 cm skipjack generates about a  $4^{\circ}\text{C}$  temperature excess (ambient-body temperature differential). Increase in activity above these levels rapidly produces greater differentials. If the lability of skipjack neural tissue or enzymes is noticeable at body temperatures of  $35^{\circ}$  to  $40^{\circ}\text{C}$ , one can quickly see that a skipjack swimming in  $29^{\circ}\text{C}$  water must effectively dissipate the physiological heat produced or limit its activity to near basal levels. This indicates a likely role of genetically determined morphological and biochemical strategies in coping with the diverse environments among different geographical races. That the eastern Pacific skipjack may be averse to the higher temperatures is not unreasonable, and indeed the gene frequency data may indicate a closer relation of the two eastern Pacific races to the

cold water tolerating New Zealand stock than to the warm water preferring components in the eastern Pacific. As we have only recently begun evolving the relationships necessary to examine the stratification of the Pacific skipjack races, much more study is necessary before the picture will be any clearer. Once again I must reiterate the importance of not generalizing from one component to the next and certainly not from one species to even a closely related species if the behaviors are distinctive.

As I have approached the tuna genetic picture, phylogeny, morphology and biochemistry from a comparative aspect, further examination of racially specific behavior and affinities will follow a similar pattern. Hopefully in the near future we will be able to add columns of comparative data to the ones I propose to be contrastable now.

In the following table I have listed five specific properties of the commercial activities and schooling behavior of skipjack in the general areas of the five hypothesized genetic components in the Pacific Ocean.

TABLE

Exploited group	Average school size	Bait fishing method	Mixed layer depth in fishing areas	Optimum temperature range of commercial activity
Northeastern Pacific	5-25 tons	stop schools with bait	30-100 m	20-26°C
Southeastern Pacific	1-25 tons	walking schools	30-100 m	20-28°C
New Zealand	10-30 tons	stop schools with bait	20-90 m	17-23°C
Papua New Guinea Solomon Isl.	10-15 tons (?)	drift into schools	100-300 m	28-30°C
Northwestern Pacific	3-10 tons	walking schools	50-200 m	20 to 28°C (?)



The observations or characteristics from outside of the eastern Pacific are based primarily on discussions with scientists working in the fishery areas and the environmental profile data compiled for this study, and may require modification from more intensive evaluation. I do, however, see a few interesting characteristics which may indicate affinities such as the aforementioned cooler water preferring types. The schools in areas with very deep mixed layers tend to be smaller on the average than those from the more compressed mixed layer areas. The two cooler water areas are fished by attracting and stopping the schools with bait, whereas the southeastern and northwestern skipjack schools are generally moving continuously and the vessels forced to "walk" along with them. The Papua New Guinea fishery technique requires that the ships wake not be encountered by the schools for best catches.

The average school size variation is probably analogous to the data from the small yellowfin schoolfish studies in the eastern Pacific showing that average school sizes increased with a decrease in habitat depth in small time area strata. This phenomenon is likely a function of the interaction rate of schools in a constrained volume. For example, the more small schools there are travelling into or migrating through a small volume the more likely they are to aggregate into larger units. This property is probably also why large yellowfin schools tend to be genetically heterogeneous. Similar phenomena would be expected to occur in skipjack and other tuna-like species.

#### Conclusions

The skipjack racial stratification appears to be based on physiological adaptation to either tropical and temperate temperatures. The giant bluefin tuna, in all its splendor, exemplifies the ability of a tuna species to cope

with ocean temperatures from 5°C to 31°C, without any apparent genetic population differentiation. The biological efficiency of this system epitomizes the selection process for the individuals to handle great environmental diversity as opposed to the rather narrow niche or habitat of the early and pre-thunnid species.

The skipjack is the analogous species in the pre-thunnid group and exemplifies the stringent requirements imposed by selection to obtain the great step between the two groups. I have labeled the morphological and distributional properties of the family Scombridae in Table 1. The skipjack is analogous to the two early thunnids, T. tonggol and T. atlanticus, except the two Thunnus species are not notorious migrators, and they prefer warm coastal waters to the open ocean. Neither the early thunnids nor skipjack obtain sizes over 30 kg typically. All of these example species coexist regularly with more than one other species of related scombrid. The first Thunnus species, phylogenetically speaking, to obtain large size (>100 kg) is T. albacares, and this event is paralleled by the development of a large gas bladder and a shift to the lateral vascular pathways (Graham, 1975, Sharp and Pirages in press, Sharp and Vlymen in review) at approximately the same time developmentally (at 2-5 kg). These two features provide the means for physiological stratification of the genus from the tropics into the temperate water tolerance, and, later phylogenetically, preference for cooler water. Here, the point is to bring out the precise limitations on skipjack, namely the ability to handle the physiological stresses of relatively wide temperature variability but not the lower oxygen levels associated with high temperatures in some parts of the ocean. Where skipjack are certainly mobile in the horizontal and vertical senses, they are severely limited in their requirements for oxygen on temperature tolerance

as compared to the Thunnus group due to their relatively small size and high density (Sharp 1976).

The lack of bouyancy is the primary cause of the requirement for more oxygen by skipjack. They are obliged to swim faster to stay in the water column than are those species with gas bladders and/or high fat contents (Magnuson 1970 and 1973). The fat content of a fish with the migratory properties of skipjack is going to fluctuate dramatically in time as a function of the migratory status of the individuals. The pre-spawner necessarily must yield to their spawning motivations and curb the relatively energetically expensive migration impetus. In areas where the habitat is perpetually warmest ( $>28^{\circ}\text{C}$ ) one would expect migratory activity to be slight compared to the cooler areas, due primarily to the higher overall respiratory rates of the fishes in the warmer habitats. If the  $Q_{10}$  of respiration in skipjack were exponential (where  $Q_{10} = 2$  the respiration doubles with each  $10^{\circ}\text{C}$  increase) then the respiration for the New Zealand fish whose habitat appears to be centered about  $18^{\circ}\text{C}$  would be about 23% lower than the Hawaiian group at  $20^{\circ}\text{C}$ . The Papua New Guinea - Solomon Islands stock's respiration would be double the New Zealand fish and 79% higher than the Hawaiian stocks, leaving comparatively little energy to spare for migration or growth or spawning, assuming similar ingestion rates, food availability, and no acclimation effects.

Considering this information has advantages when one tries to interpret the lower apparent growth rate of the skipjack in Papua New Guinea's  $28^{\circ}\text{C}$  or warmer habitat. Comparative respiration values of representatives of the various habitats would certainly help in the interpretation of the physiological bases for the apparent population stratification. The seasonal monitoring of such data could also be useful in defining the migration-spawning dichotomy.

Monitoring the seasonal changes in variability of the length-weight relations, fish densities, and fat contents among the various exploited components could provide the information necessary to define spawning and migratory seasonality.

I hope that this cursory discussion of tuna, and in particular skipjack, physiology and genetics will provide the impetus to broaden the scope of research in the near future so that a significant improvement can be made in the assessment and understanding of tuna population biology. The present system of body counts, catch rates and simplifying assumptions is clearly inadequate for a realistic description of tuna populations. I feel strongly that sufficient evidence and inferences are available to proceed to the next phase for description and interpretation of relative population parameters utilizing data on the environmental and racial stock levels, which would be far more defensible and realistic than the presently utilized tautologies.

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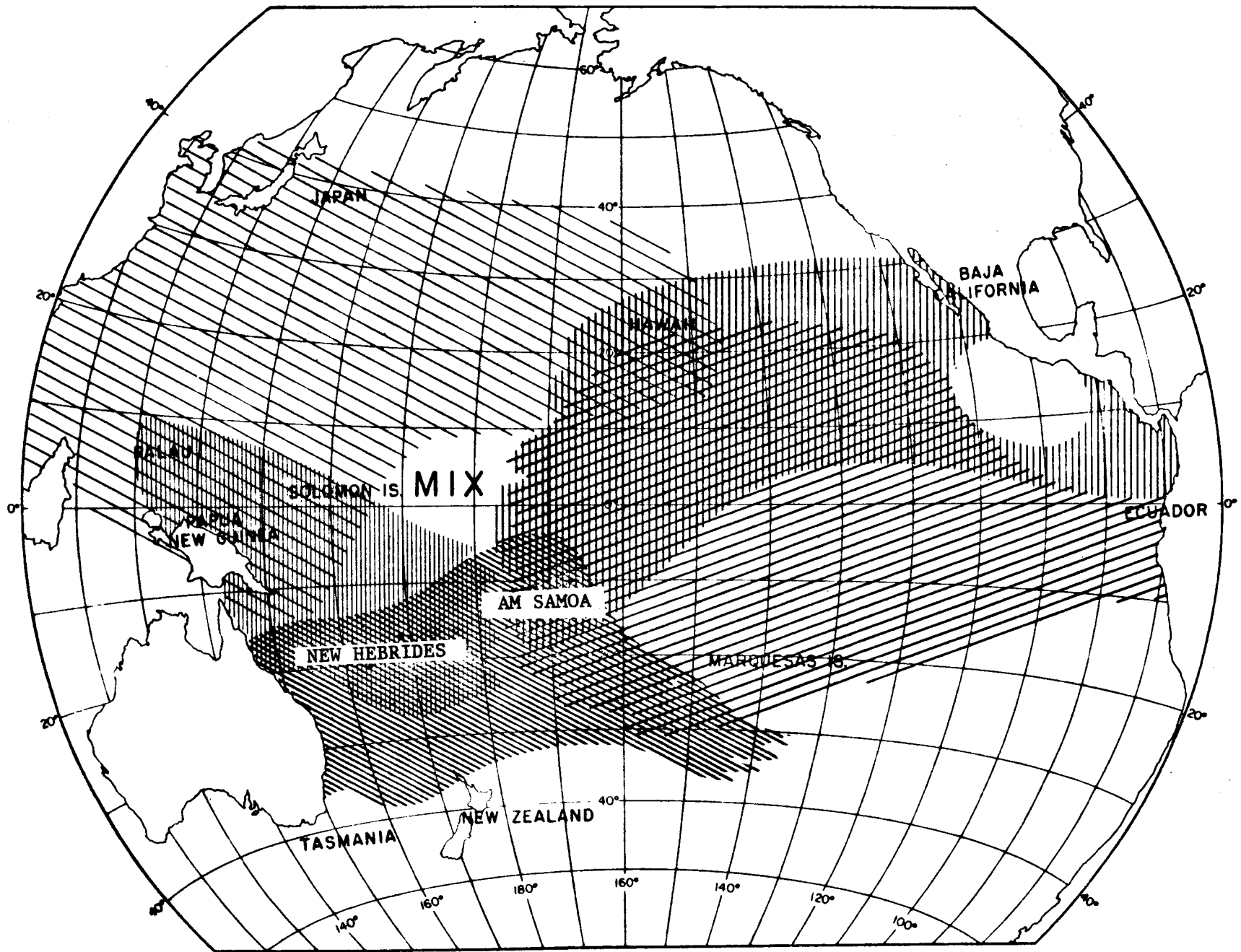
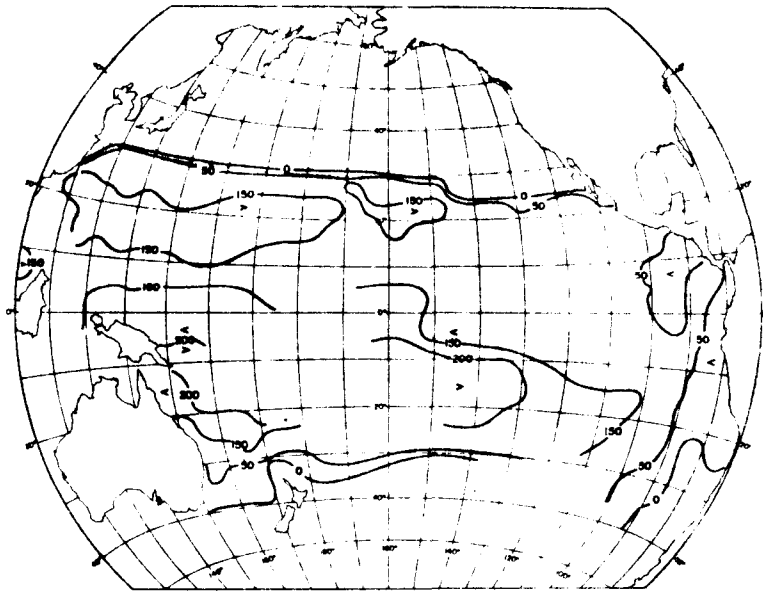


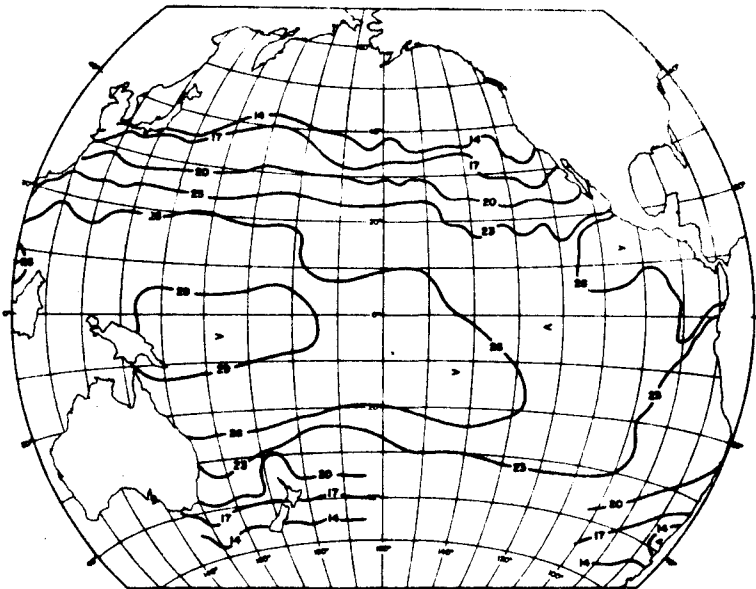
FIGURE 1

FIGURA 2  
JANUARY

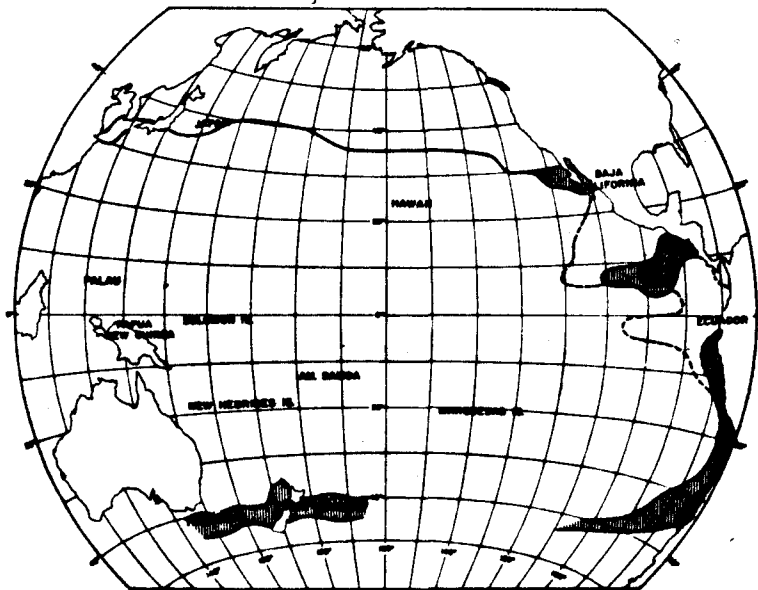
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B.

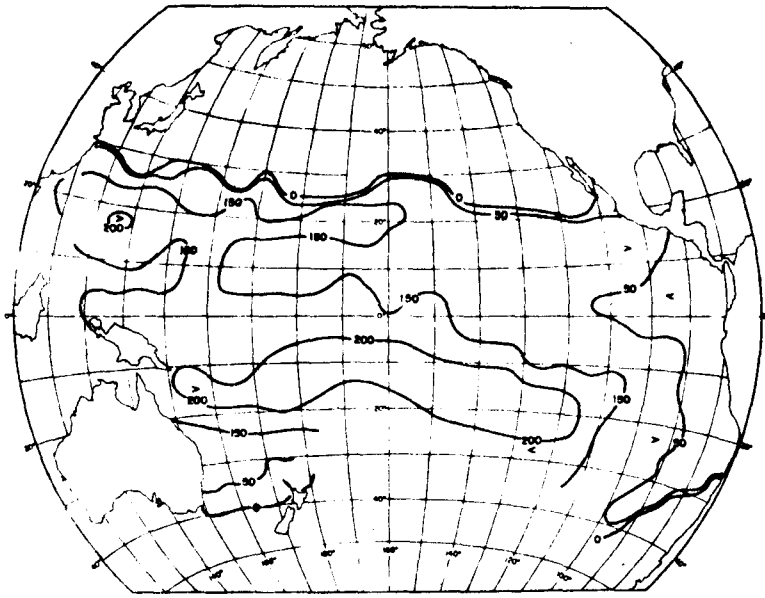


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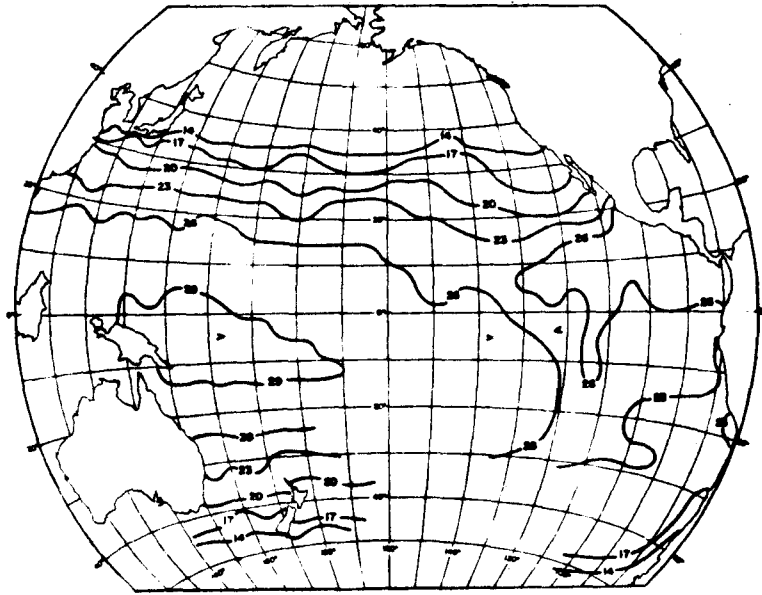


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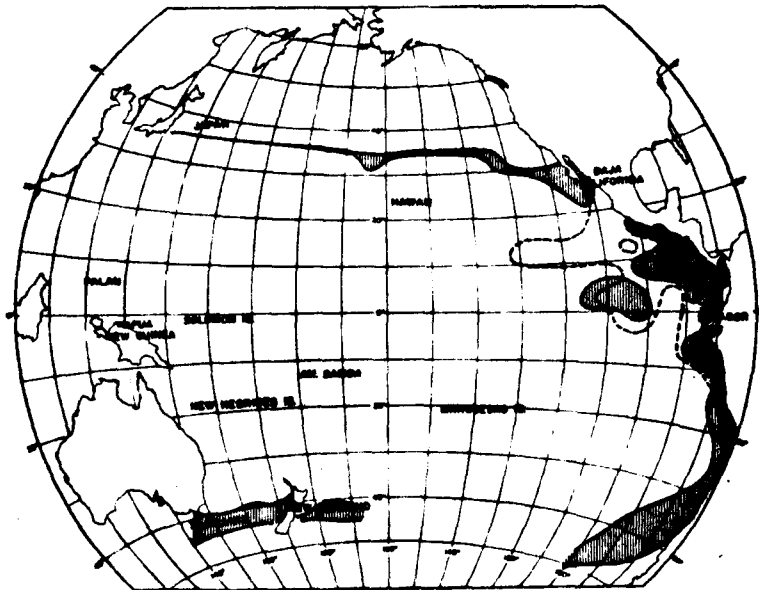
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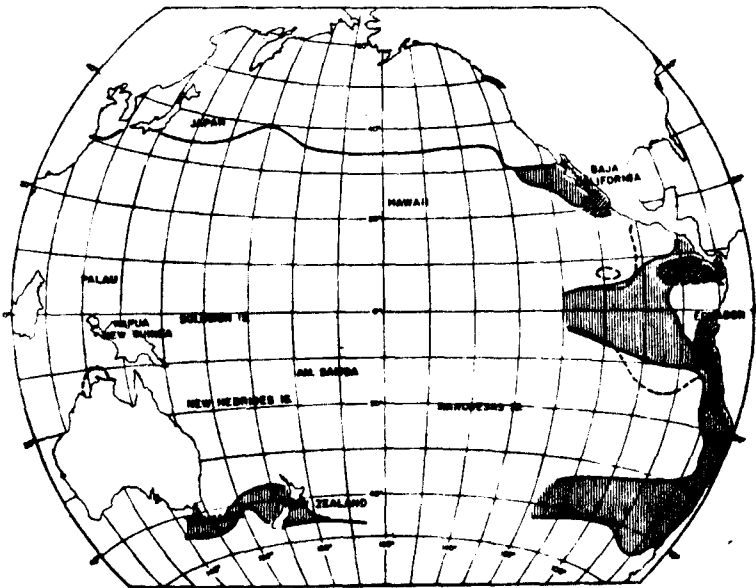
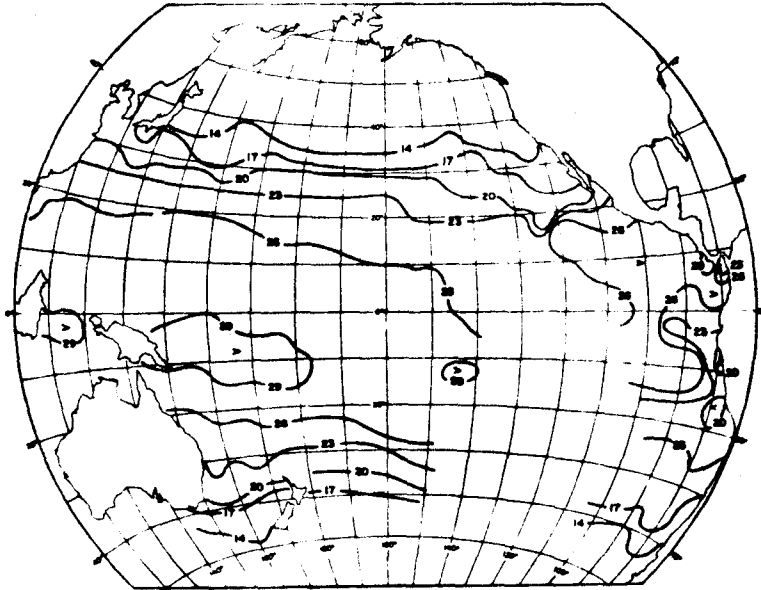
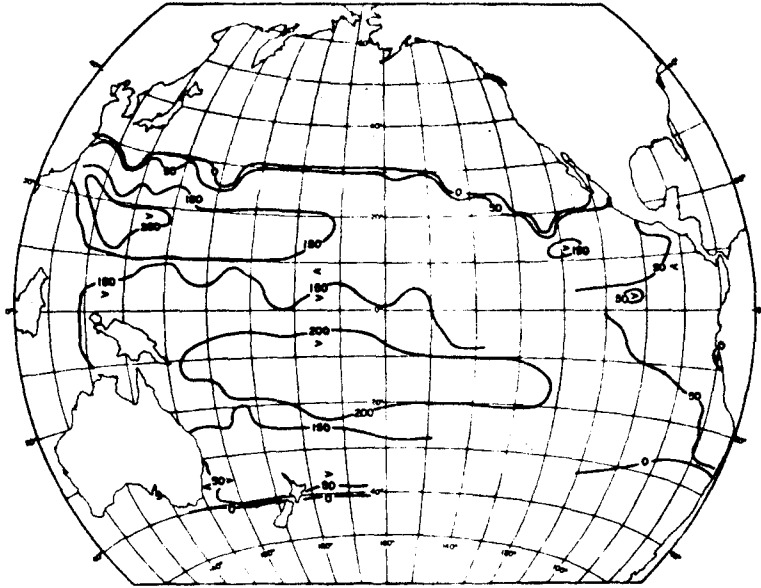
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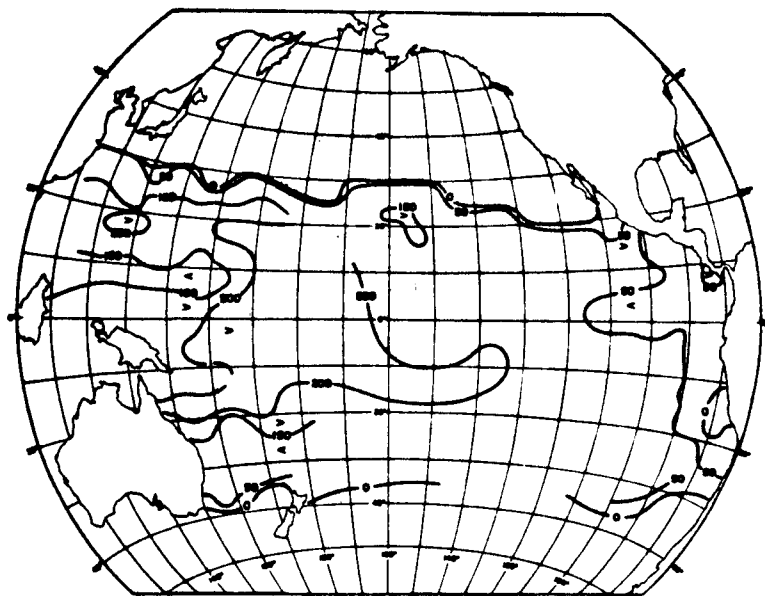
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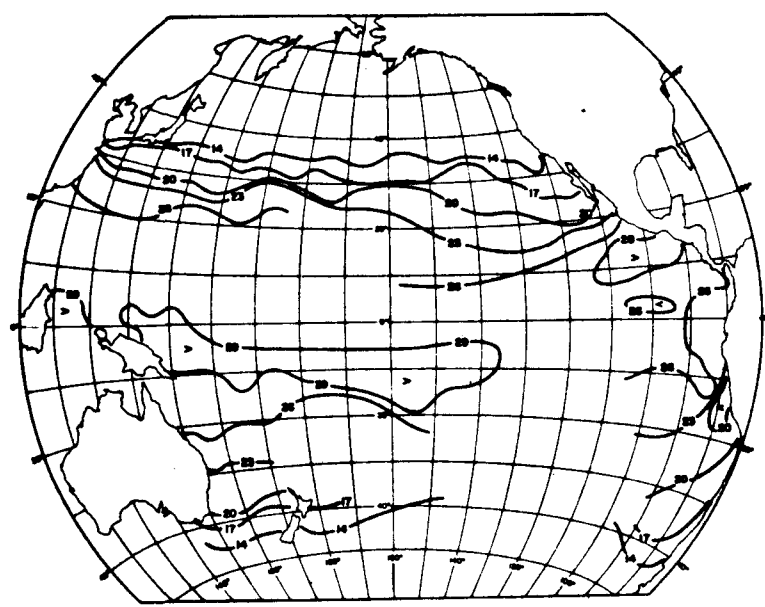


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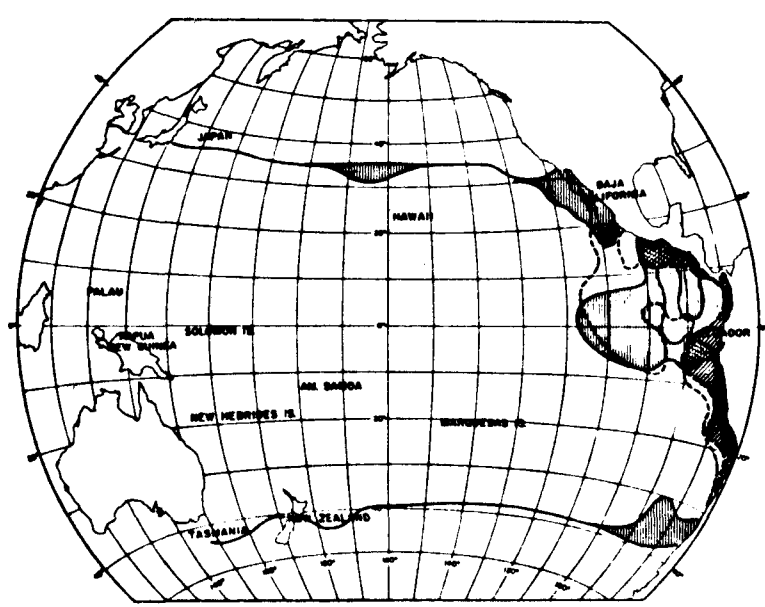
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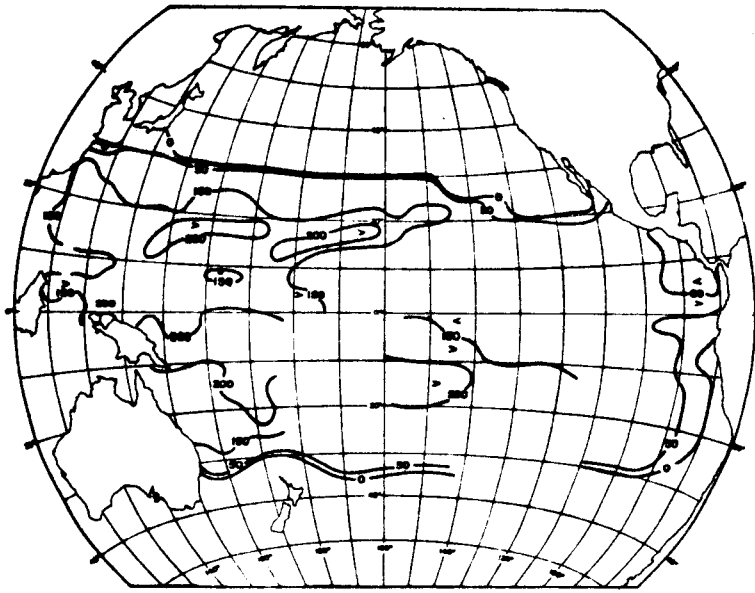


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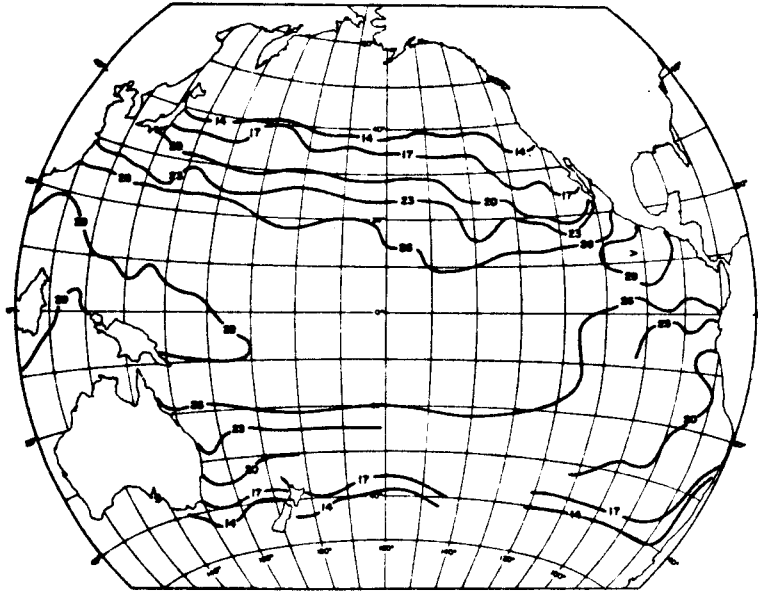


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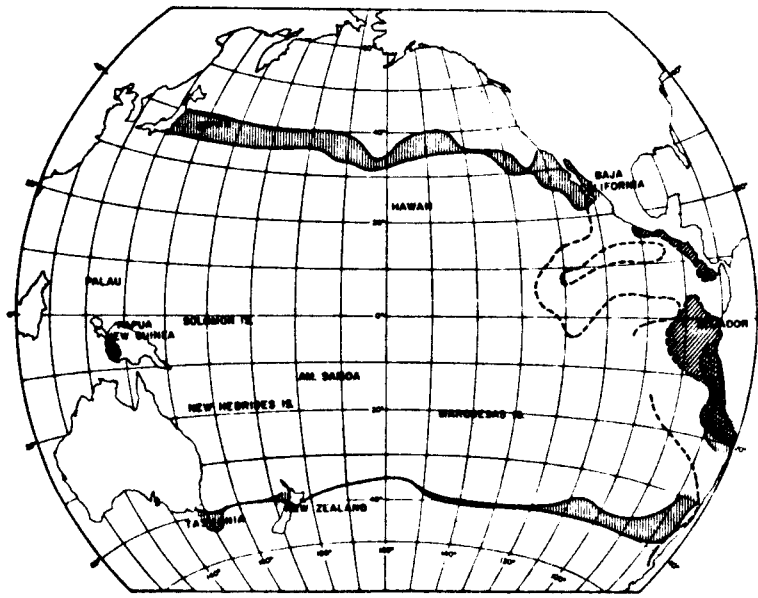
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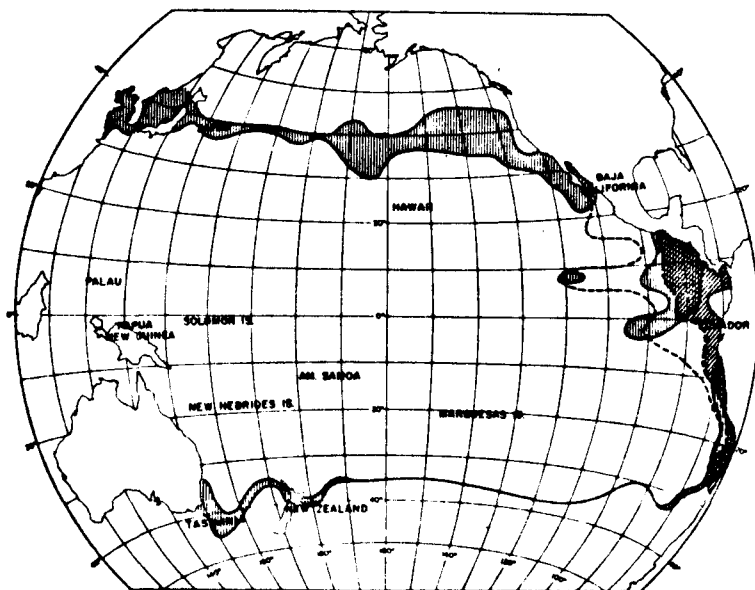
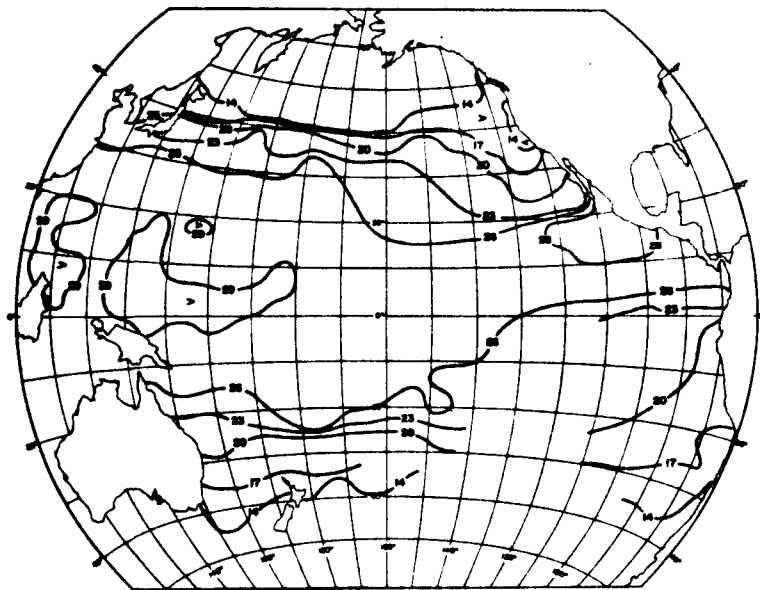
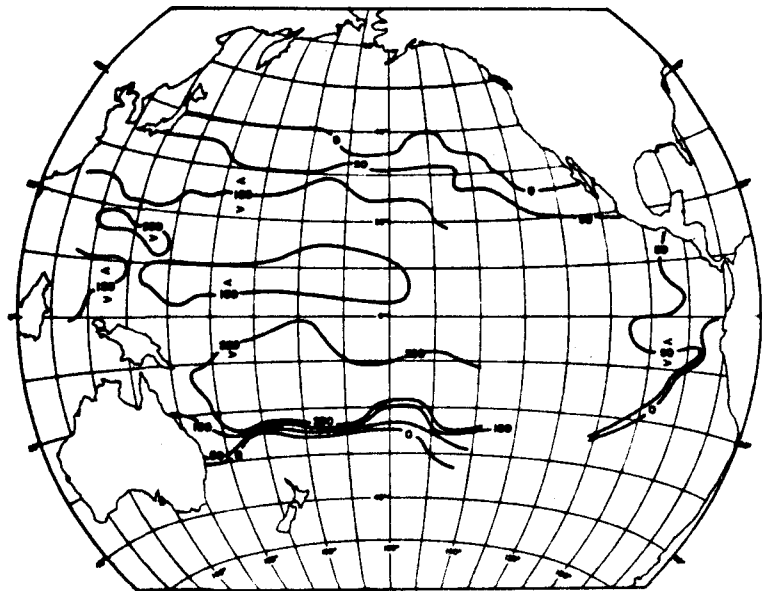
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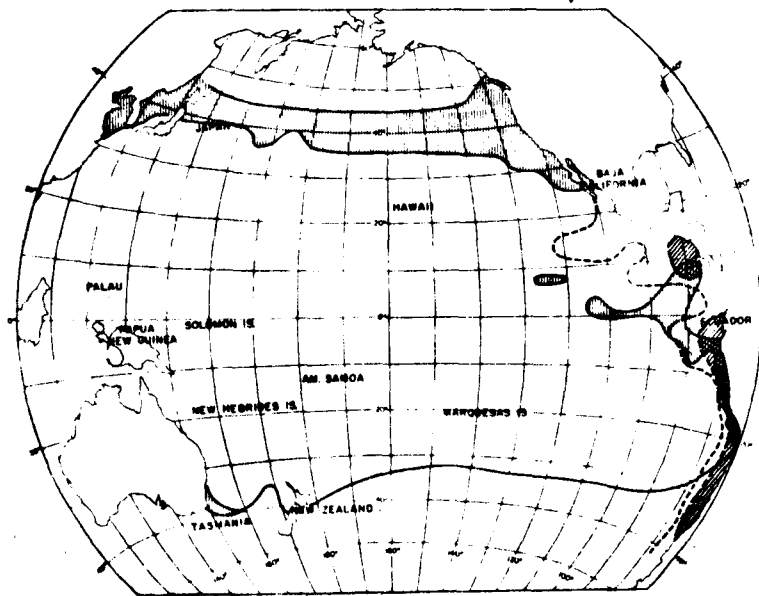
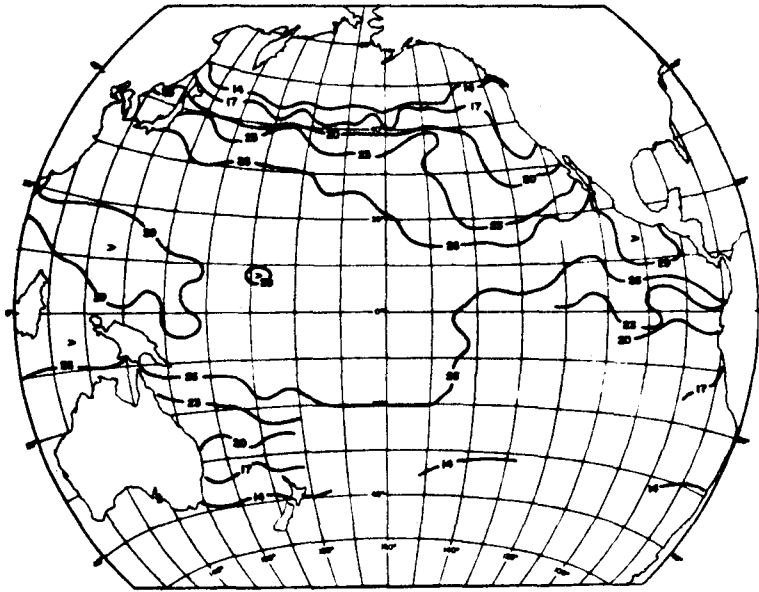
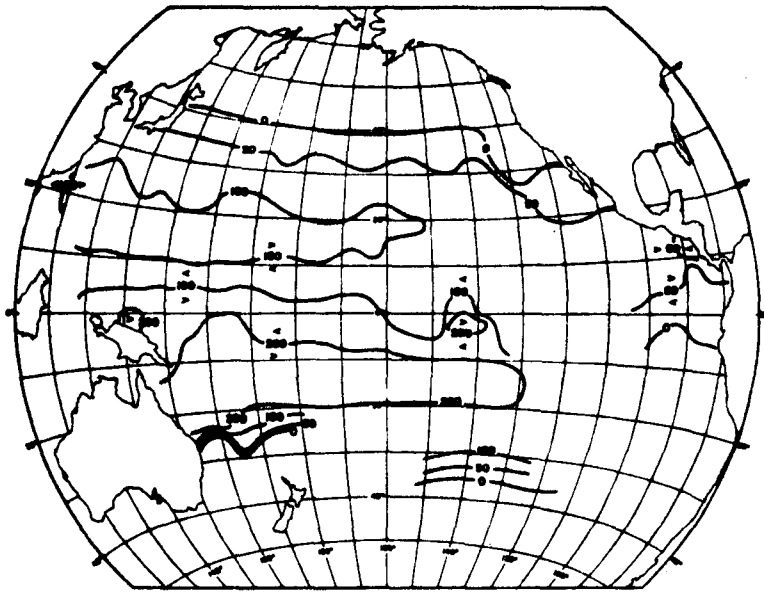


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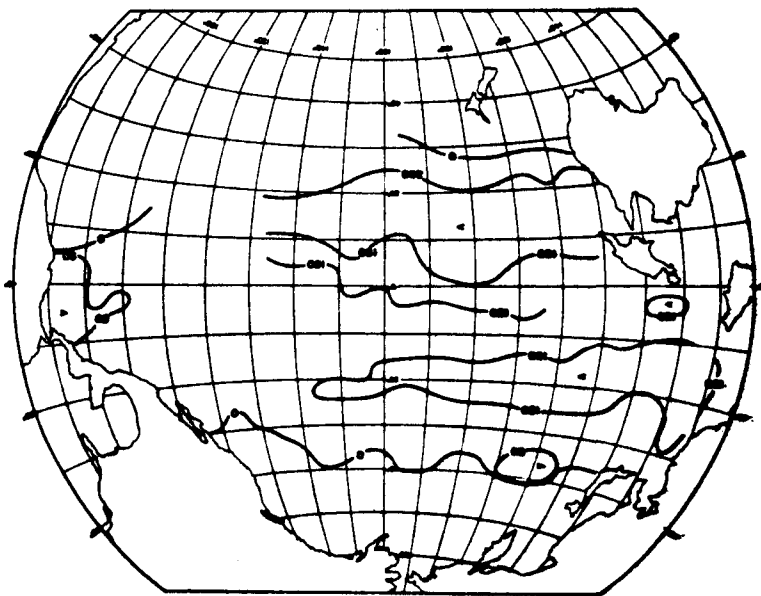
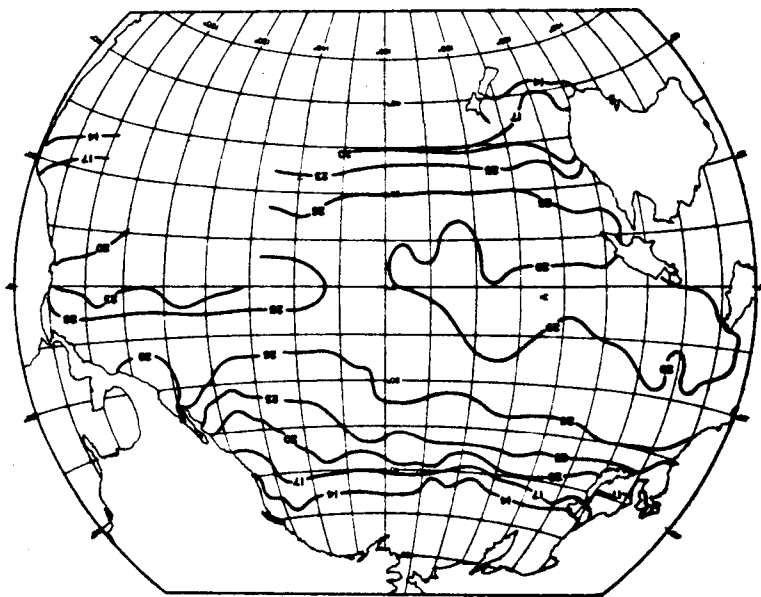
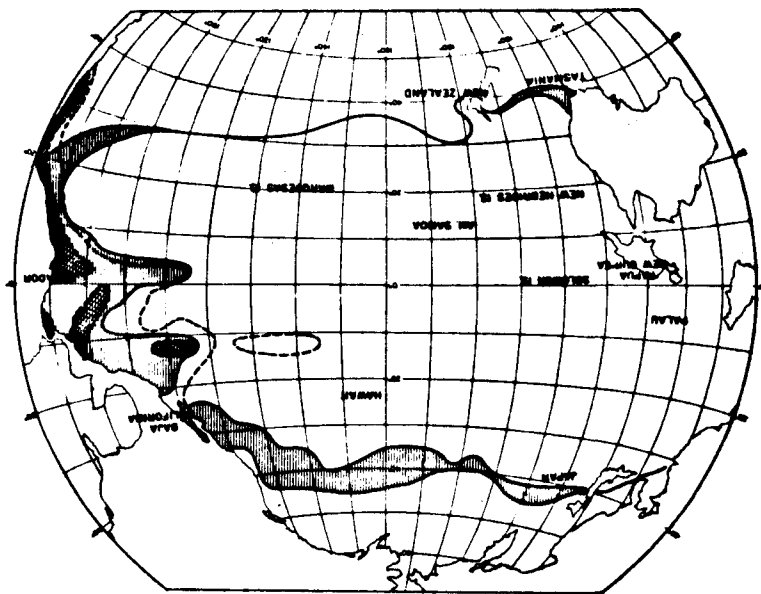
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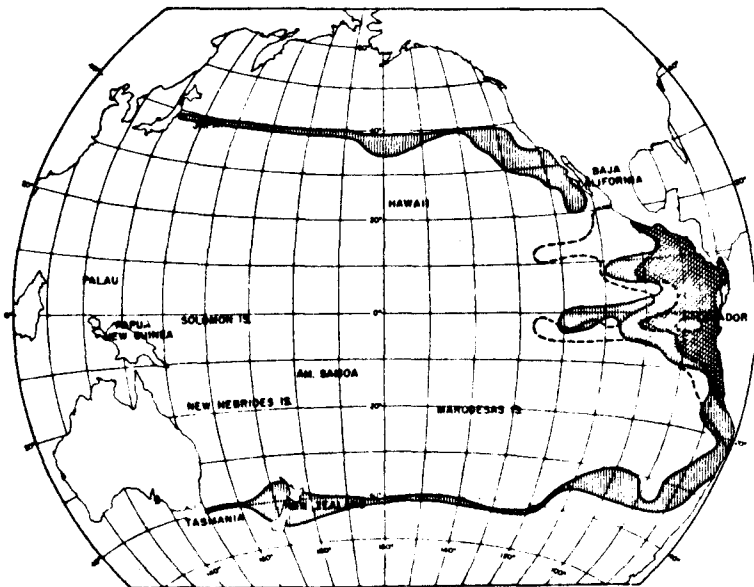
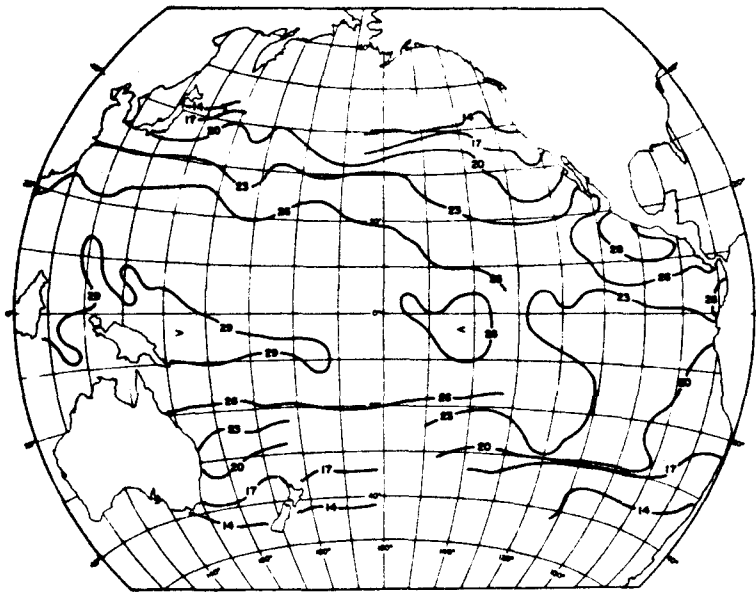
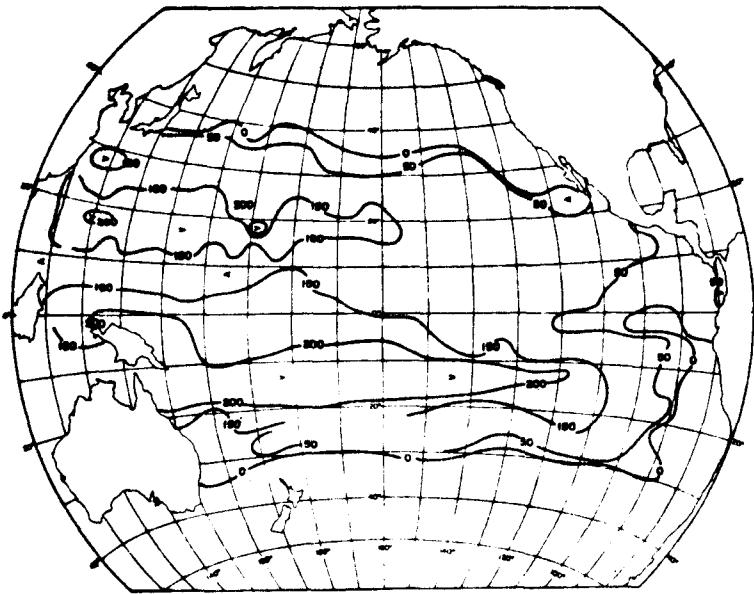






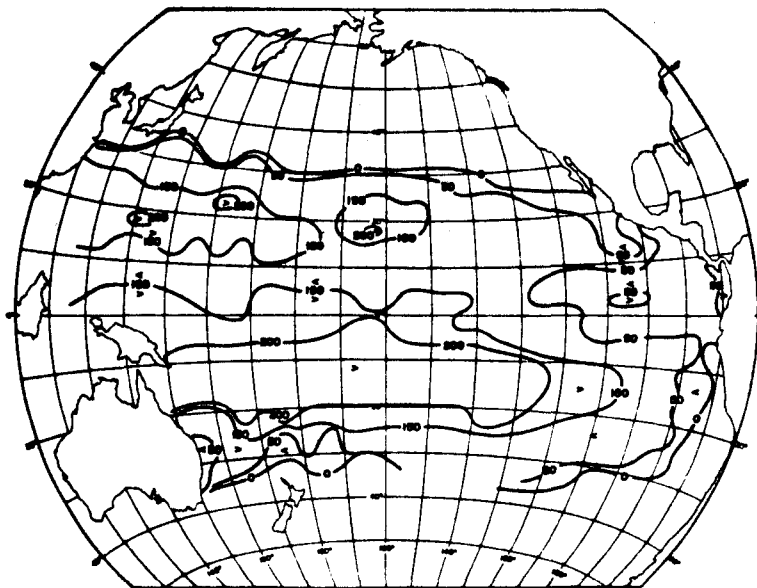
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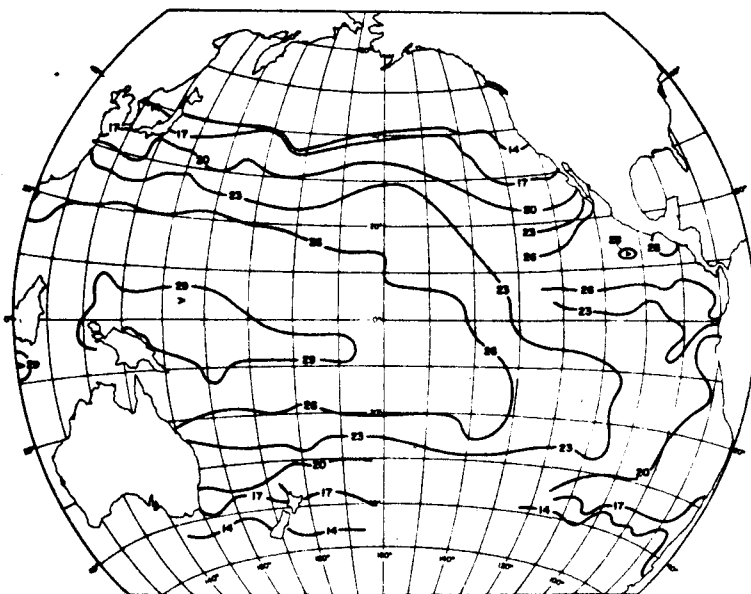


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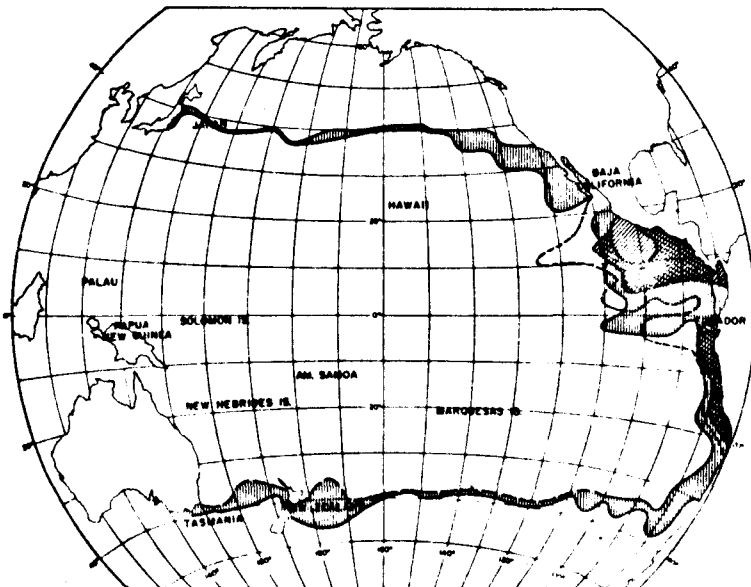
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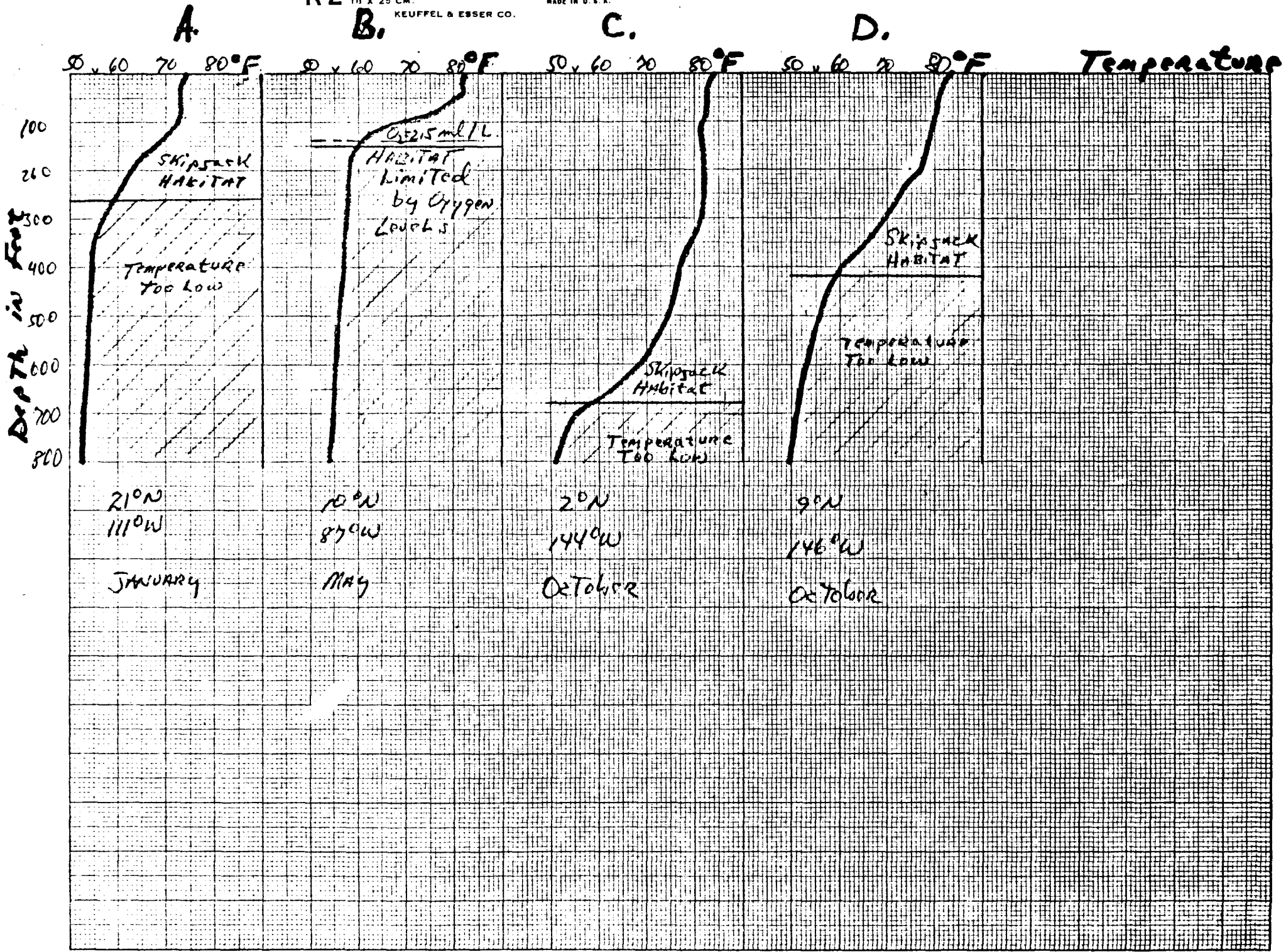


TABLE 1. Morphological characteristics of selected scombrids and their variations compared to corresponding variations in size and preferred habitat, where known. (Shank & Pirago, in press)

Species or groups	Red muscle Configuration	Complete dorsal aorta	Developed Heat exchanger(s)	Lateral cutaneous arteries and veins (each side)	Preferred temperature range if known	Habitat and relative size
Mackerels	primitive lateral wedge	yes	none	none	temperate or tropical	coastal-zones-neritic small to medium
<u>Sarda</u> spp.	deeply situated lateral wedge	yes	none	none	temperate or tropical	coastal to pelagic medium
<u>Allothunnus</u>	internalized caudally					
<u>Auxis</u> spp.	internalized	yes	central only	one only, complete epaxial portion	tropical	coastal to pelagic small
<u>Euthynnus</u> spp.	internalized with lateral extension	yes	central and one lateral	one only, complete epaxial portion	tropical	coastal to pelagic medium
<u>Katsuwonus pelamis</u>	internalized	yes	central and two lateral	paired, epaxial and hypaxial with lateral heat exchangers	15°C - 29°C	Pelagic migrator medium
<u>Thunnus tonggol</u> <u>T. atlanticus</u>	internalized but contiguous with lateral surface	yes	central and two lateral	paired, epaxial and hypaxial with lateral heat exchangers	25°C to 32°C	neritic-continental shelf medium
<u>T. albacares</u>					23°C to 32°C	pelagic large
<u>T. obesus</u>	internalized and not contiguous with lateral surface	diminished	two lateral	paired as above	11°C to 15°C	deep pelagic large
<u>T. alalunga</u>	deeply internalized and small	no	two lateral	paired and long	14°C to 18°C	pelagic migrator large
<u>T. Thynnus thynnus</u>	deeply internalized and large	no	two lateral	paired and long	5°C to 30°C	pelagic very large
<u>T. Thynnus orientalis</u>					Temperate	migrators large
<u>T. Maccoyii</u>					5°C to 20°C	South Polar Sea - large