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STOCK STRUCTURE OF SWORDFISH IN THE PACIFIC

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1. SUMMARY

At this time, the best scientific evidence indicates that there are four stocks of swordfish in the Pacific with centers in the northwest, northeast, southwest and southeast. Analyses of previously hypothesized stock structures using genetic data presented herein indicate that those hypotheses are not to be preferred to the four-stock structure of Alvarado Bremer *et al.* (2006). The IATTC is continuing investigations of stock structure in of swordfish in the Pacific, and stock assessments for eastern Pacific swordfish stocks.

2. STOCK STRUCTURE

2.1. Analyses of fisheries data

Information used by fisheries scientists to define the boundaries of stocks of fish include data on relative abundance, size and spawning condition of individual fish, distribution of larval fish, genetics, and movements as determined from tagging. The boundaries determined from this basic research (Brown *et al.* 1985) may then be employed in studies that estimate the status of a stock with respect to conservation and management objectives (Hinton and Deriso 1998). Hinton and Deriso (1998) reviewed and discussed various definitions and applications of the term stock in fisheries research and management:

> "The least useful definition of stock, from a management or conservation point of view, is "the part of a fish population which is under consideration from the viewpoint of actual or potential utilization" (Ricker 1975). For example, strictly interpreted this definition may exclude those portions of populations which contribute to the presence and level of the stock, *i.e.* the stock may consist only of juveniles whose existence derives from the reproductive success of those surviving utilization, but the survivors are not considered part of the stock. The environment and fishing in any part of the range of a fish population affects the subsequent abundance and distribution of the species throughout its range, giving this narrowly constricted definition little value within our current framework of knowledge in oceanography and fisheries science. Application to management or conservation questions requires that a stock be a "self-sustaining component of a particular species" (Sinclair 1988). So defined, a stock has biological and genetic significance (Sinclair 1988), which provides the basis of measures (Brown *et al.* 1985) commonly used to differentiate among stocks. However, "in all cases some indications of significant degree of physical separation at spawning is required to support biological bases for separate stocks" (Brown *et al.* 1985). To the extent that relative abundance data accurately depicts the spatial and temporal distribution of a stock, the stock is a function of nature and not an abstraction (Sinclair 1988).

A number of stock structure hypotheses have been used or advanced for analysis of status of swordfish stocks in the Pacific Ocean. Sakagawa and Bell (1980), and more recently Bartoo and Coan (1988) using data through 1980, each included an EPO stock in their three-stock hypotheses (Figures 1 and 2). These analyses bounded the distribution of swordfish stocks using estimates of relative abundance based on annual nominal catch-per-unit-of-effort (CPUNE). The ability of such annualized data to accurately

reflect the spatial and temporal distribution of stocks, which may exhibit migratory behavior (Yabe, Ueyanagi *et al.* 1959; Sosa-Nishizaki and Shimizu 1991), is doubtful (Hinton and Deriso 1998).

Nakano (1994) used standardized catch rates (CPUSE) and yet another three-stock model (Figure 3), with the caveat that "even if there is only one southern stock, division of the South Pacific into smaller regions will serve to monitor local depletion …," to evaluate the condition of swordfish stock status in the Pacific.

A four-stock hypothesis (Figure 4) based on CPUNE data with monthly resolution was advanced by Sosa-Nishizaki (1990) and Sosa-Nishizaki and Shimizu (1991). They reported on some evidence of differences in spawning activity in the four regions, and specific evidence of larval swordfish in the north-and southwest Pacific. But at the core of their determination were the independent seasonal trends in the extensions of local relative abundance about centers of high abundance, with the result that their definition of stock was in essence that of Ricker (1975) noted above. Noting the need for increased biological information, Sosa-Nishizaki (1990) concluded:

 "I think that these four different areas can represent different stocks, not in the complete biological sense, but as fishery management units. In other words, the stocks thus agreed upon were in the sense of defining a manageable resource not to define the borderline of movements of individuals, nor do stocks intend to be referred to [as] isolated genetic units, as was stated for the management of Atlantic swordfish populations (Miyake and Rey 1989)."

Sosa-Nishizaki and Shimizu (1991) went on to describe the areas as unit stocks for assessment and management. Such initial stock structure hypotheses may provide a sound basis for further research (Brown *et al.* 1987).

With the compilation of available data, review and work of Sosa-Nishizaki and Shimizu (1991), the question of stock structure of swordfish in the western Pacific was presenting a consistent picture using fisheries data, however the structure in the eastern Pacific remained unclear. Proposals advanced had included both one and two stocks, and distribution boundaries remained undefined.

Hinton and Deriso (1994) presented an analyses of stock structure and status using standardized catch rates (CPUSE) from the region east of 150°W; information on spatial/temporal size frequency distributions; and distribution of gonad index values. Their analyses were conducted at a bi-monthly period by 2° latitude by 5° longitude grid. They showed a clear separation of mature individuals in spawning condition in regions suitable for spawning in the north and south areas. Based principally on the continuous clear separation in all seasons of the populations and spawning, the analysis of changes in distributions of length frequency distributions over space in time, and the coincident seasonal latitudinal movements in both north and south, they found that there were two stocks of swordfish in the eastern Pacific Ocean, one in the northeast and one in the southeast, suggesting a boundary at 5°S. The use of finer-scale and additional data, and use of standardized catch rates, were identified as the likely reasons for the differences between their results and those of Sosa-Nishizaki and Shimizu (1991).

Hinton (2003), using general linear models, obtained standardized catch rates "to investigate and document the stock structure of the swordfish (*Xiphius gladius*) resources of the eastern Pacific Ocean [EPO]." The region was divided into five areas (Figure 5) which corresponded well with the oceanic provinces in region, and within each area the annual trends in relative abundance, size frequency, spatial/temporal distributions of abundance, and stock status were examined. There were significant differences among the trends of abundance in the areas. Hinton (2003) reported that the trends in CPUSE for the northern region (N of 10°N) and the equatorial region (5°S to 10°N) were not significantly different ($P = 0.564$), while there was a significant difference ($P = 0.036$) between the trends of annual abundance in the equatorial region and the southern region (S of 5°S). Hinton (2003) subsequently compared the trend in the southern region to that in the region between 5°S and the equator and found them to be significantly different ($P = 0.017$).

2.2. Analyses of genetic data

Studies of swordfish genetics in the Atlantic Ocean and the Mediterranean Sea using mitochondrial DNA indicate distinct stocks in these oceans, and also differentiation between swordfish in the Atlantic and the Pacific (discussion in Hinton and Deriso, 1998). Since the publication of Hinton and Deriso (1998), the analysis of stock structure in Pacific swordfish has continued, primarily with genetic studies combined with the fisheries oceanography studies of Hinton and Deriso (1998) and Hinton (2003), as well as without. Alvarado Bremer *et al.* (2004) reviewed the published genetic studies of swordfish populations in the Pacific Ocean. They noted that in general, levels of population structuring in the Pacific Ocean are extremely low, compared to other basins, with two studies reporting significant heterogeneity in the Pacific, while four others found no significant differences. The contrasting views and hypotheses of population structure derived from different kinds of data were given. It was concluded that additional analyses with larger samples sizes and additional genetic markers were needed to resolve the population structure of swordfish in the Pacific Ocean. Finally, Alvarado Bremer *et al.* (2006) published findings on stock structure indicating that there are significant genetic differences between stocks of the north and south eastern Pacific Ocean (east of 150°W), Hawaii, and Australia (southwest Pacific). Details on these genetic studies, their interpretation, and notes on the ease with which they may be easily be misunderstood by those not familiar with or closely reading the genetic procedures being utilized, are provided.

2.2.1. Alvarado-Bremer *et al.* (2004 and 2006)

At the meeting of the Swordfish Working Group of the Interim Scientific Committee (ISC) for Tunas and Tuna-like Species (ISC-04), the then current status of results from genetic studies was presented by Alvarado-Bremer *et al.* (2004). Briefly, they reported the findings of studies of mtDNA, which differentiated Japan and Australia, but did not differentiate stocks within the EPO, as follows:

> "Globally, analyses of mitochondrial DNA data have shown inter-oceanic population differentiation in swordfish populations (Alvarado Bremer *et al.* 1995; 1996; Kotoulas *et al.* 1995; Rosel and Block 1996; Chow *et al.* 1997; Greig 2000; Chow *et al.* 2000). Population studies within the Pacific Ocean have employed a variety of techniques to survey variation contained in the mitochondrial genome, including an RFLP analysis of the entire mtDNA molecule (Grijalva-Chon *et al.* 1994), PCR-RFLP of the D-loop fragment (Chow *et al.* 1997l Chow and Takeyama 2000), and direct sequencing of the D-Loop region (Rosel and Block 1996). Specifically, all these studies failed to reveal differences among populations within the EPO. Recently, Reeb *et al.* (2000), analyzed D-loop sequence data from samples collected on a larger geographical scale across the Pacific Ocean, and described significant differences between samples from the NW Pacific (Japan) and Australia (pooled NW and NE Australian samples). Concordant with previous studies, no differences among samples from the EPO were found."

Alvarado-Bremer *et al.* (2004) went on to summarize information from nDNA and allozyme studies, and presented the following table of comparative results. They also explained why such differences among the results of the studies could likely be expected to be seen, given the nature of the various methods used and sample sizes involved.

Source	Data type	Approach - Locus	Regions compared	Interpretation	Comments
Grijalva-Chon *et al.* 1994	mtDNA	RFLP entire molecule	Central Pacific (Hawaii) and EPO (Mexico), Western (Japan and China Sea)	No differences	
Grijalva-Chon *et al.* 1996	Allozymes	26 allozymes/4 polymorphic	Central Pacific (Hawaii) and EPO (Mexico)	Significant differences	Freq. Differences for ODH*, PROT-2* and PROT-3*

Rosel and Block 1996	mtDNA	Sequence/D-loop	EPO (Mexico, Chile), Central Pacific (Hawaii), NW Pacific (Japan, Taiwan)	No differences	Significant differences against Atlantic and Med. samples
Reeb *et al.* 2000	mtDNA	Sequence/D-loop	NW Pacific (Japan), C. Pacific (Hawaii), EPO (California/Mexico, Ecuador), S.W. Pacific (Australia)		See note 2 [Alvarado Bremer *et al. 2004*]
Chow *et al.* 1997	mtDNA	PCR-RFLP/D-loop	NW Pacific (Japan), C. Pac.(Hawaii), EPO (Mexico, Ecuador and Peru), SWPO (New Zealand).	No differences	Significant differences against Atlantic and Med. samples
Chow and Takeyama (2000)	MtDNA nDNA	PCR-RFLP/D-loop and Calmodulin intron 4 (CaM)	NW Pacific (Japan) and EPO (Peru)	No differences	
Alvarado Bremer *et al.* 2001	MtDNA nDNA	Sequencing/D-loop Sequencing/LdhA	Hawaii, Mexico, Peru, Ecuador, Australia	D-loop data/Significant *ldh*-A incipient differentiation between EPO and 3 Hawaiian samples	D-loop difference vs. Australian sample [see note 2: Alvarado Bremer *et al. 2004*]. *ldh*-A: Larger samples required

Since the first report presented by Alvarado-Bremer *et al.* (2004), results of ongoing research on stock structure of Pacific swordfish using genetic techniques has been published (Alvarado-Bremer *et al.* 2006). The study used significantly more genetic samples than any others known for swordfish. The results were consistent with a number of the previous studies, but it added detailed information and resolved conflicts, which was not possible from the techniques or sample sizes previously used. A summary of their findings is presented as follows:

"DNA sequence polymorphisms contained in intron 6 of the lactate dehydrogenase-A (*ldh*-A) gene were used to examine the genetic population structure of Pacific swordfish (*Xiphius gladius*). Seven alleles defined by five polymorphic sites were identified among 305 swordfish. Comparisons of allele frequency were conducted for 11 samples, including Chile (multiple years), Ecuador (multiple years), Mexico, Hawaii (multiple years), eastern Australia, and western Australia. Although there was evidence of genic differentiation, global differentiation was low (F_{st} =0.001). To increase the power of the tests of differentiation, samples within each region were pooled into four regional samples. No deviations from Hardy-Weinberg equilibrium were observed, and the global fixation index increased more than ten-fold (F_{st}=0.013). Global exact tests of genic and genotypic differentiation were significant, and so were the pair-wise comparisons between the south-eastern Pacific Ocean (SEPO) sample from Chile, and all other regions. In addition, the north-eastern Pacific Ocean (NEPO; Ecuador to Mexico) was different from the north-central Pacific Ocean (NCPO; Hawaii), which in turn was different from the south-western Pacific Ocean (SWPO; pooled eastern and western Australia). These results may have important implications towards the fishery management of Pacific swordfish, particularly because of the heterogeneity observed between SEPO and NEPO."

With this analysis, the findings of the fisheries oceanography and catch rate analysis of Hinton and Deriso (1998) was supported with differentiated stocks within the north and south eastern Pacific Ocean, and as well with a differentiation of a northern eastern Pacific stock from a "Hawaiian" stock, and the southeastern from a southwestern stock, resulting in a fisheries and genetically supported four-stock

structure for swordfish in the Pacific (Figure 6). Since the preliminary results were first available (2004-2005), stock assessments in the eastern Pacific have been conducted as if on two closed populations separated at 5°S and from more westerly stocks at 150°W (e.g. Hinton and Maunder 2005; Hinton and Maunder 2007).

Hinton and Alvarado (2007) presented an updated review of the stock structure of swordfish in the Pacific to the swordfish working group of the ISC in March 2007. Subsequent discussion on the use of genetic data for estimation of stock structure in swordfish in the Pacific focused on two items: (1) that F_{ST} values smaller than 0.02, as in Alvarado Bremer *et al.* (2006) are not sufficiently large to resolve stock structure, (2) the use of a single locus by Alvarado Bremer *et al.* (2006).

The following paragraphs address the concerns noted as discussion above, with a particular focus on presenting a review of the meaning of the Waples (1998) study, on which the comments related to (1) above were based, followed by a review of Alvarado Bremer *et al.* (2006) given Waples (1998). In addition, we have examined and evaluated the stock structure hypotheses assumed or advanced by other studies by restructuring the genetic data and conducting stock structure analyses for those hypotheses. The results of these analyses are presented.

2.2.2. Can small F_{st} values (<0.02) be biologically meaningful?

The parameter F_{ST} is a measure of the proportion of total gene diversity that is allocated among populations. Accordingly, F_{ST} values can range from zero, when there is no differentiation among populations; to unity, when there is complete fixation for different alleles in reproductively isolated populations. Because of strong active and passive dispersal capabilities, marine fishes tend to have small (0.02) median F_{ST} estimates (Ward *et al.* 1994; Waples 1998). Such small F_{ST} values can result from random sampling error (noise) or have biological meaning (signal), and it is important to partition the relative contribution of each component. Waples (1998) provided guidelines to determine the relative importance of noise-to-signal associated with such weak signals of differentiation.. He explained that the relative contribution of intra-locus sampling to the signal to noise ratio can be estimated from 1/(2S), where S is sample size. For a sample of S = 25 individuals this proportion is 0.02, a value identical to the median F_{ST} estimate for marine fishes (0.02), whereas this proportion is substantially smaller than the median values for freshwater (0.14) and anadromous (0.08) fishes. A misinterpretation that can, and does, often emerge from this comparison is to conclude that F_{ST} estimates smaller than 0.02 are not biologically meaningful. If the noise and the signal have the same magnitude, then when the difference of these values is made to obtain an unbiased estimate, the resulting F_{ST} would not be different from zero. However, as Waples explains, the relative importance of intra-locus sampling error tends to asymptotically decline when estimating F_{ST} as sample size increases. Accordingly, Waples stressed the importance of utilizing larger sample sizes when comparing genetic variation in marine fishes. The correct question for Alvarado Bremer *et al.* (2006) was not whether F_{ST} was greater than 0.02, but whether the sample size used was large enough to reduce the intra-locus sampling error (noise) to detect genetic signal.

Alvarado Bremer *et al.* (2006) presented results from 305 swordfish sampled from various localities in the Pacific and obtained a statistically significant F_{ST} value of 0.013. This result was primarily driven by heterogeneity in distribution of *ldh*-A alleles in the southeast Pacific Ocean compared to other three areas (northeast, southwest, and the northwestern-central Pacific Ocean). The amount of noise for this sample size would be 0.001, or less than 8% of the signal, implying that intra-locus sampling error does not play an important role in explaining the reported value of F_{ST}. It should be noted that further samples have been obtained, and as well that analyses continue on previously obtained, but unanalyzed samples, which will increase the sample size and coverage of the study. As well, funding has been sought to automate the analysis of a suite of exon-primed-amplified-introns (see below) to allow more precise estimation of stock structure of swordfish in the Pacific.

2.2.3. Comparing the F_{st} Values of alternative hypotheses of population structure in Pacific swordfish

We compared the F_{ST} obtained by Alvarado Bremer *et al.* (2006) with alternative models of population structure for Pacific swordfish, by pooling the *ldh*-A allele frequency data for the four regions characterized in that study (southeast, northeast, southwest, and northwestern-central Pacific Ocean) to correspond to alternative models of stock structure (see Table below). Estimates of F_{ST} were in all cases lower when samples were pooled to correspond with the three alternative models than when they were kept separate. In particular, no signal of differentiation was obtained with the alternative two-stock, north and south Pacific model of Nakano (1994), and virtually none was seen with the three-stock hypothesis derived by Bartoo and Coan (1988). The three stock model of Nakano (1994) explained nearly as much of the overall variability as the four-stock model, but this model was out of Hardy-Weinberg Equilibrium (HWE) for the southeastern Pacific stock, which indicates that this three-stock model includes inappropriate pooling of multiple, identifiable stock regions in the south Pacific.

Stock Hypothesis	Source / Basis	F_{ST}	HWE*
3-stock: NW, SW, & EPO	Bartoo and Coan (1988) (Figure 2)	0.0085	No for EPO ($P = 0.0002$)
3-stock: N, SW & SE boundary at 10°N	Nakano (1994) (Figure 3)	0.0111	No for SEPO ($P = 0.0002$)
2-Stock alternative: N & S, boundary 10°N	Nakano (1994) (Figure 3)	-0.0009	N/A
4-stock, NW, SW, NE, & SE	Sosa-Nishizaki and Shimizu (1991); Alvarado Bremer *et al.* (2006)	0.0130	Yes

*HWE: Hardy-Weinberg Equilibrium

2.2.4. Additional potential biases associated with F_{st} estimates

The F_{ST} estimate for Pacific swordfish presented by Alvarado Bremer *et al.* (2006) was derived from a single locus (*ldh*-A), and thus the relative proportion of inter-locus sampling error cannot be estimated. This is a major limitation of that study, and one stressed by the authors, who recognized the need to characterize additional nuclear loci, preferentially exon-primed-amplified-introns. The preference to use exon-primed-amplified-introns over microsatellite data stems from the evidence that in highly migratory fishes, the signal of genetic differentiation is substantially smaller with microsatellites than with other loci; perhaps as the result of noise associated with large population sizes and the high mutation rate of tandemly repeated di- and/or tetra-nucleotides (O'Reilly *et al.* 2004). A reduced inter-population signal obtained with microsatellites compared with the relatively stronger signal obtained with mtDNA has been documented for the inter-ocean comparisons of Atlantic and Indo-Pacific blue marlin (Buonaccorsi *et al.* 1999), and similar results have been presented in Atlantic and Mediterranean swordfish, where the signal of differentiation with microsatellites is substantially lower than that obtained: unlike the higher differentiation signals which are found, as in this study, with such as *ldh*A, Calmodulin and mtDNA control region data.

3. OVERALL SUMMARY

At this time the best scientific data indicates that there are four stocks of swordfish in the Pacific Ocean. This finding is consistent in both studies of fisheries and with genetic analyses, including a study that employed the largest number of samples known for a stock structure study of swordfish, which study also allowed comparison with and showed consistency among previously conducted, lower-sample size, genetic-based analyses using a number of approaches. The stocks of swordfish in the Pacific are centered in the northwest, northeast, southwest and southeast. In the previous analyses of stock status in the eastern Pacific Ocean, the IATTC has regularly conducted research and analyses of the stock structure and status of swordfish stocks in the Pacific Ocean, with emphasis on the eastern Pacific, and this research is continuing. Results of additional genetic analyses are expected in the near future. The current best data

would suggest that separate analyses for east and western stocks should be conducted, and would also suggest that conservation recommendations be developed based on these individual regional units.

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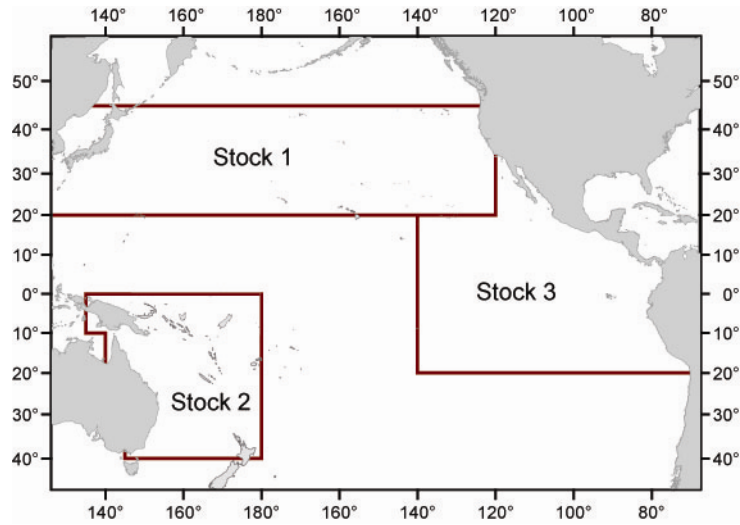
FIGURE 1. Three-stock structure of swordfish used for stock assessment by Sakagawa and Bell (1980).
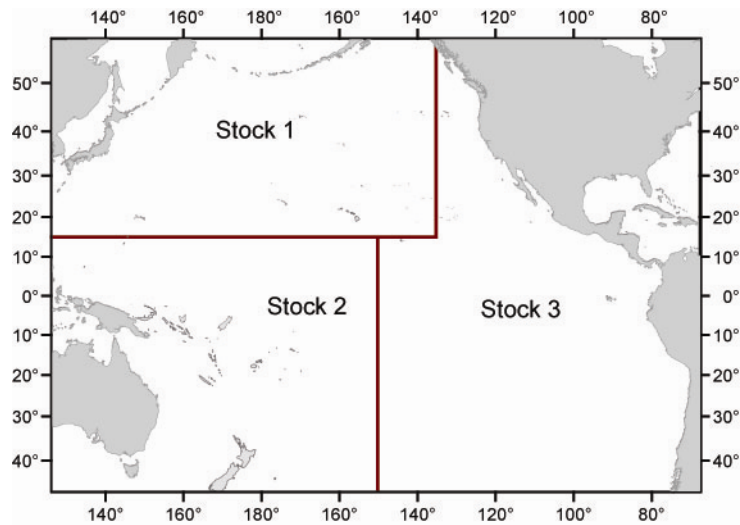

FIGURE 2. Three-stock structure of swordfish used for stock assessment by Bartoo and Coan (1988).
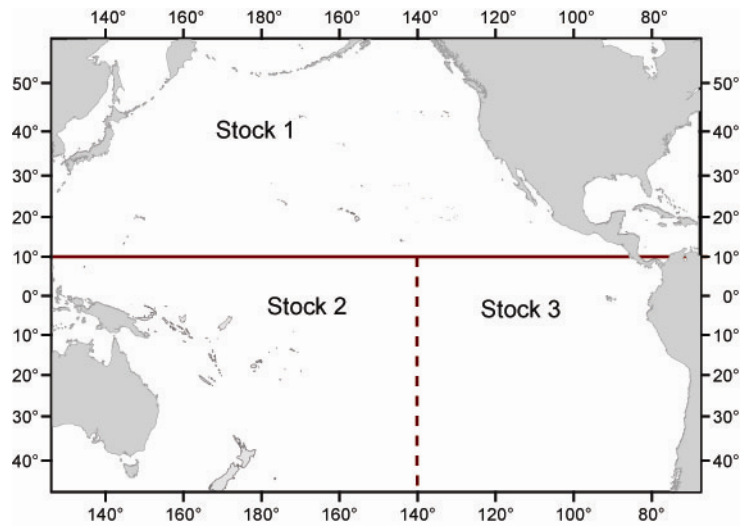
FIGURE 3. Three-stock structure used for stock assessment by Nakano (1994; Figure 3). Two-stock alternative had north and south stocks, only.
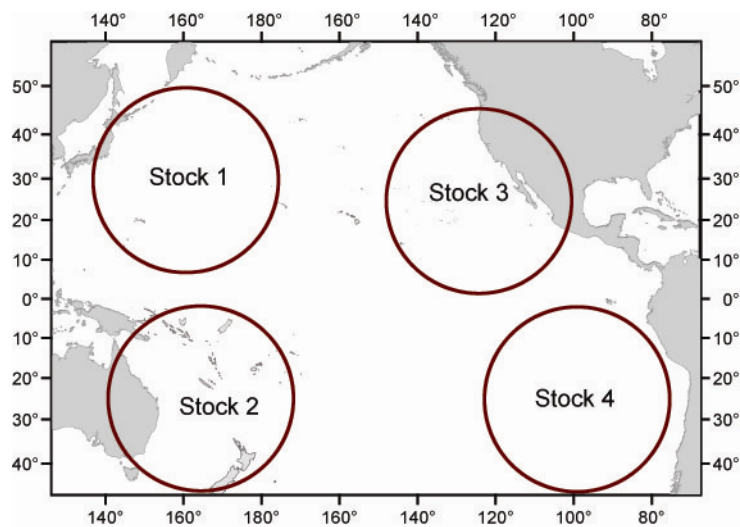

FIGURE 4. Four-stock structure for Pacific swordfish advanced by Sosa-Nishizaki (1990) and Sosa-Nishizaki and Shimizu (1991).
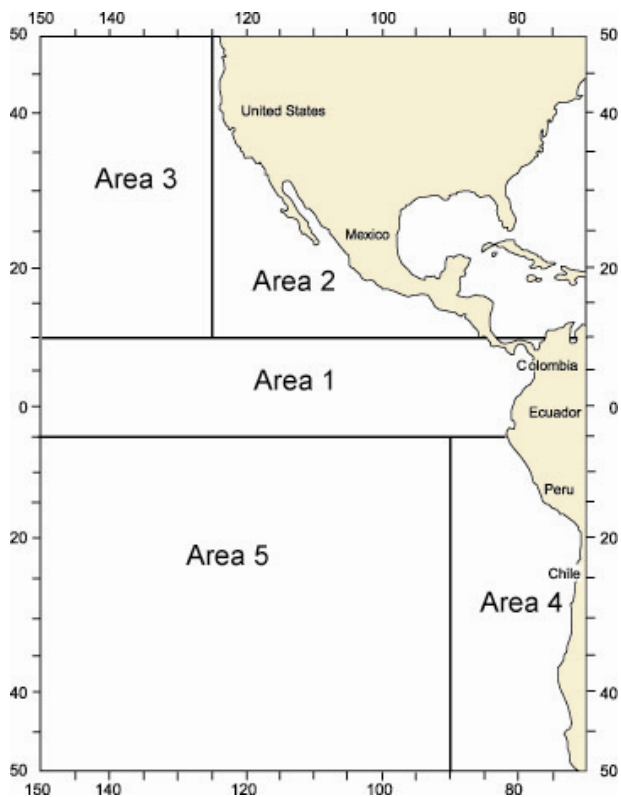
FIGURE 5. Five-area stratification used for analysis of stock structure of swordfish in the eastern Pacific Ocean (Hinton 2003, Figure 2).
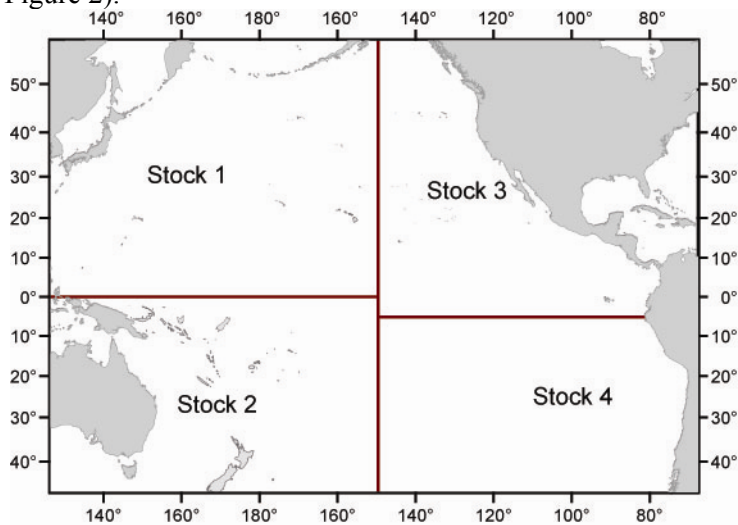

FIGURE 6. Eastern Pacific stock structure from Hinton and Deriso (1998) and Hinton (2003), with western stock structure from a multiple of authors, including Sosa-Nishizaki and Shimizu (1991), Reeb *et al.* (2000), and Alvarado Bremer *et al.* (2006).