Sexual maturity, sex ratio, and size composition of swordfish, *Xiphias gladius*, caught by the Hawaii-based pelagic longline fishery

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Abstract.–Swordfish (*Xiphias gladius*) caught by the Hawaii-based pelagic longline fishery during March 1994–June 1997 were examined at sea by observers of the National Marine Fisheries Service, Southwest Region. Observers provided unbiased size and sex composition data for 4.8% of the swordfish catch and 4.9% of the effort in number of hooks of the fishery during the 40-mo. period. Observers measured body lengths for more than 8600 swordfish brought aboard participating vessels; sex, based on macroscopic appearance of gonads, was identified aboard ship for 77% of measured fish. Sex identifications were later verified (0.5% error rate) and gonadal developmental stage described for 1336 fish whose sex was identified in the field. Logistic regression was used to estimate sex-specific, median body size at sexual maturity (L_{50}) by using microscopic morphological evidence for gonadal development. L_{50} was 102 cm ±2.5 (95% CI) cm eye-to-fork length (EFL) and 144 ±2.8 cm EFL for males (*n*=506) and females (*n*=822), respectively. Sex ratios were an increasing power function between 100 and 220 cm, and nearly all fish >220 cm EFL were females. Sex composition and body size varied temporally and spatially, especially the latter. Relatively more males were caught south of 27°N; females dominated catches north of 27°N. Small-bodied fish of both sexes prevailed year-round below 22°N. A greater percentage of large-bodied (>156-cm [males], >172-cm [females] EFL) fish were caught north of 35°N during the late summer–early winter. The latter observations are consistent with several nonmutually exclusive hypotheses of migration energetics and body muscle heat conservation, both of which are discussed.

Rapid expansion of the Hawaii-based pelagic longline fishery for swordfish (*Xiphias gladius*) during the late 1980s and early 1990s has generated a need for an explicit management plan and assessment of swordfish stocks in the Pacific. Assessments for swordfish might be improved by using size- or age-structured, rather than surplus production, models for several reasons. Size- and age-structured models are less dependent on effort statistics (Gulland and Rosenberg, 1992) and in the Pacific as in the Atlantic, adequate effort statistics are largely unavailable for pelagic longline catches. Effort data are further complicated by geographically separated fisheries that differentially target swordfish or other pelagic fishes and by multiple jurisdictions with varying data collection standards. In the Atlantic these difficulties might be overcome by using nonequilibrium production models and virtual population analyses (ICCAT, 1997).

Estimates of body size and age at sexual maturity are of fundamental importance for the determination of fishery management thresholds based on size- and age-structured stock assessments. In particular, determination of the spawning potential ratio (SPR: Goodyear, 1993) depends on size at maturity. Sex-specific size composition data are also needed to stratify catch and effort statistics, thereby reducing the variances of CPUE estimates.

Information on reproductive biology is inadequate for swordfish in the Pacific. Nakamura et al. (1951) were the first to infer spawning seasonality in the western Pacific based on net collections of swordfish larvae. Yabe et al. (1959) further described swordfish eggs and larvae and used plots of gonad weight versus body length for fish on spawning grounds to approximate body size at sexual maturity for female swordfish in the western Pacific. Kume and Joseph (1969) estimated body size at sexual maturity for female swordfish in the eastern Pacific, and Sosa-Nishizaki (1990) estimated body size at sexual maturity for female swordfish throughout the North Pacific. Uchiyama and Shomura (1974) estimated total fecundities for eight fish and provided anecdotal evidence of swordfish spawning near the Hawaiian Archipelago. Adult-size swordfish caught in the eastern North Pacific were described by Weber and Goldberg (1986) as reproductively inactive during late August–November. Hinton and Deriso's (1998) more recent evaluation of swordfish gonadal index data from the Japanese longline fishery, however, has documented the seasonal presence of reproductively active swordfish near Baja California during May–August. Although largely nonexistent for the Pacific, reproductive and related growth parameters have recently been estimated for swordfish in the Northwest Atlantic (Arocha et al., 1994; Arocha and Lee, 1995, 1996; Ehrhardt et al., 1996; Arocha, 1997).

Catch and effort data for swordfish in Pacific fisheries have been summarized by Miyabe and Bayliff (1987) and Nakano and Bayliff (1992) and reviewed

by Sosa-Nishizaki (1990) and Sosa-Nishizaki and Shimizu (1991). DiNardo and Kwok (1998) have provided a preliminary description of catch statistics and the body size and sex composition of swordfish caught by the Hawaii-based longline fishery in the central North Pacific.

Our study had several complementary objectives, and the ultimate goal of providing accurate and precise information for stock assessments of Pacific swordfish. In our study, we estimated size at sexual maturity for swordfish captured by the Hawaii-based pelagic longline fishery in the central North Pacific. Because the growth rates of adult male and female swordfish differ in the Pacific (Uchiyama et al., 1998), as elsewhere (Ehrhardt et al., 1996), size at maturity was characterized separately for males and females. We classified maturity on the basis of histological analyses of gonads subsampled from a larger sample of field-sexed fish and used this maturity classification as the basis for our estimates of size at maturity. The latter are compared with a complementary characterization of reproductive activity using gonad indices (Hinton et al., 1997). Data on body size (length), date, and location of capture of swordfish in the parent sample of field-sexed fish were used to provide preliminary descriptions of temporal and spatial patterns of size- and sex-specific catch. These patterns of sex and size composition identified factors that could be used for stratifying catch and effort data for the Hawaii-based longline fishery, thereby reducing the variance of population parameter estimates based on logbook records used in future stock assessments. Finally, we interpreted spatial and temporal variations in catch in terms of possibly different migratory behaviors by swordfish of different body sizes and sexes.

Methods and materials

Shipboard collections and measurements

About 90% of the swordfish analyzed were caught by commercial vessels fishing pelagic longlines in the central North Pacific from March 1994 to June 1997. Most (65%: Ito and Machado, 1996,[1] 1997,[2] 1999[3]) swordfish were caught on trips on which swordfish were targeted. Another 34% were caught on "mixed sets" (both tuna and swordfish

targeted), and the remaining 1% on "tuna sets" (Boggs and Ito, 1993; He et al., 1997). The remaining 10% of swordfish examined were caught on swordfish research cruises of the NOAA ship *Townsend Cromwell* during 1992–97 in the region of the commercial fishery.

Commercial fishermen dressed all swordfish as the fish were brought aboard ship; observers noted that about 10% were alive and 90% moribund or dead upon retrieval. Viability of fish when sampled is important for interpreting the quality of histological specimens. Observers (NMFS SWR) were assigned to participating longline vessels according to a stratified random design based on vessel size (effort). Observers recorded eye-to-fork length (EFL, cm) for most swordfish caught. For most swordfish that were measured, sex was identified on the basis of macroscopic appearance of the gonads, and, for a random subsample of sexed fish, a gonad tissue sample (2 cm³, including gonad wall) was collected from the middle of either gonad lobe and immediately fixed in 10% buffered formalin. Swordfish gonad samples were collected during most months of four consecutive years (172 trips sampled during March 1994–June 1997), complemented by specimens collected by research cruises in April–May of 1992 and 1993, September 1996, and March–April 1997. Specimens examined histologically thus spanned several annual cycles; overall 81% of the fish examined were collected during March–July spawning periods (Fig. 1). Fish were sampled throughout the spatial range of the longline fishery during March 1994–June 1997, mostly between lat. 17–41°N and long. 141–180°W (Fig. 2).

During spring 1997, SWR observers collected whole ovaries of approximately 100 swordfish as they were being dressed aboard ship. For each pair of ovaries, a fresh tissue specimen was collected and fixed for later histological evaluation of developmental stage (as described below), and the remainder of the ovaries were frozen for weighing ashore. The latter samples were used in analyses of gonad indices.
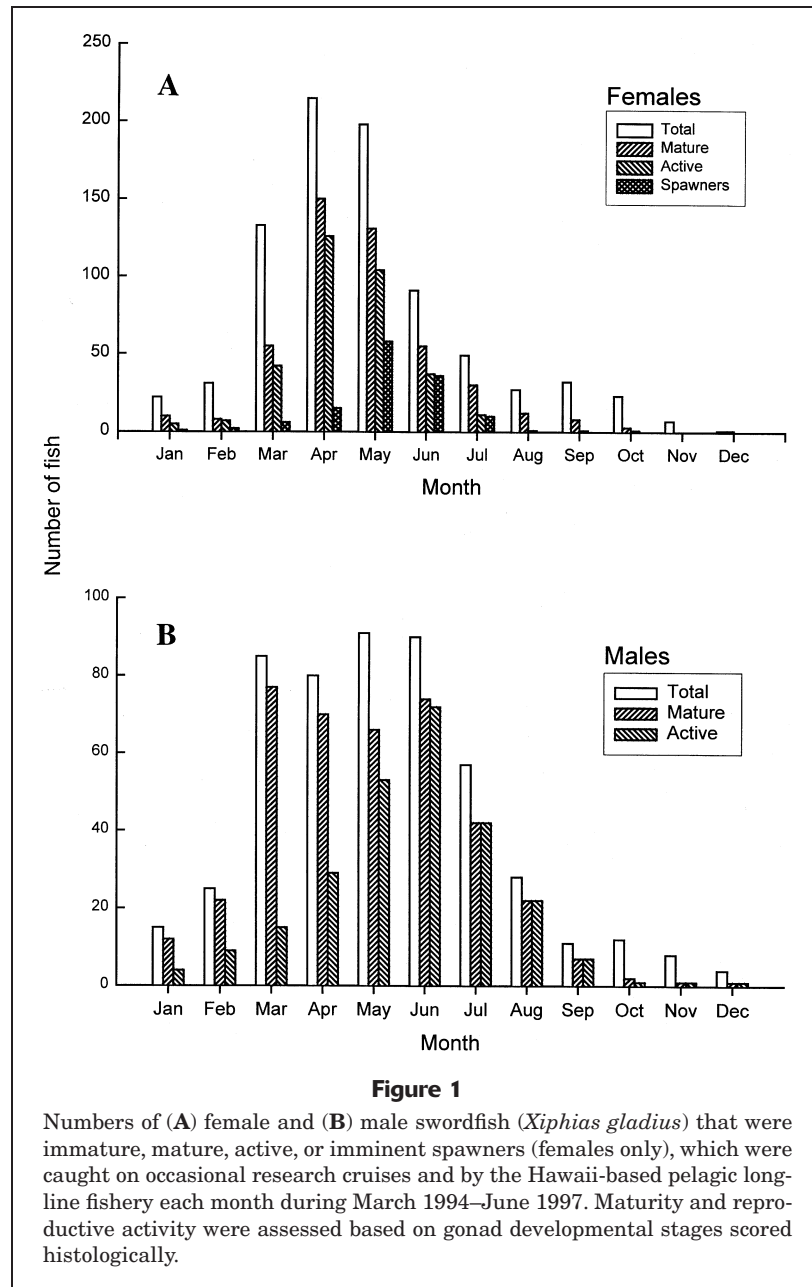
Laboratory processing

Field-classified sex was verified and reproductive condition evaluated based on gonadal developmental stage determined by microscopic examination of histological preparations and oocyte size frequencies. Fixed gonad specimens were stored for at least 60 days before oocytes were measured or a subsample was prepared for histological analyses. A single series of sequential, histological sections (6 μm thick) (2–8: mode=3[ovaries], mode=4[testes]) was cut and stained with Harris's hematoxylin, followed by eosin counterstain (Hunter and Macewicz, 1985). Slide sections were examined with a compound microscope at 60–300× and developmental stage categorized following the stage criteria of Murphy and Taylor (1990). For females, the following characteristics were noted for the largest size mode of oocytes present: presence and relative quantity of eosinophilic yolk, partly to moderately yolked oocytes, and fully yolked oocytes. If oocytes were fully yolked, we further noted the presence of hydrating or hydrated oocytes (HYDs), postovulatory follicles (POFs), and fully

[1] Ito, R. Y., and W. A. Machado. 1996. Annual report of the Hawaii-based longline fishery for 1995. Southwest Fish. Sci. Cent. Admin. Rep. H-96-12, Honolulu Laboratory, Southwest Fish. Sci. Cent., Natl. Mar. Fish. Serv., NOAA, Honolulu, HI 96822-2396, 45 p.

[2] Ito, R. Y., and W. A. Machado. 1997. Annual report of the Hawaii-based longline fishery for 1996. Southwest Fish. Sci. Cent., Admin. Rep. H-97-12, Honolulu Laboratory, Southwest Fish. Sci. Cent., Natl. Mar. Fish. Serv., NOAA, Honolulu, HI 96822-2396, 48 p.

[3] Ito, R. Y., and W. A. Machado. 1999. Annual report of the Hawaii-based longline fishery for 1998. Southwest Fish. Sci. Cent. Admin. Rep. H-99-06, Honolulu laboratory, Southwest Fish. Sci. Cent., Natl. Mar. Fish. Serv., NOAA, Honolulu, HI 96822-2396, 62 p.
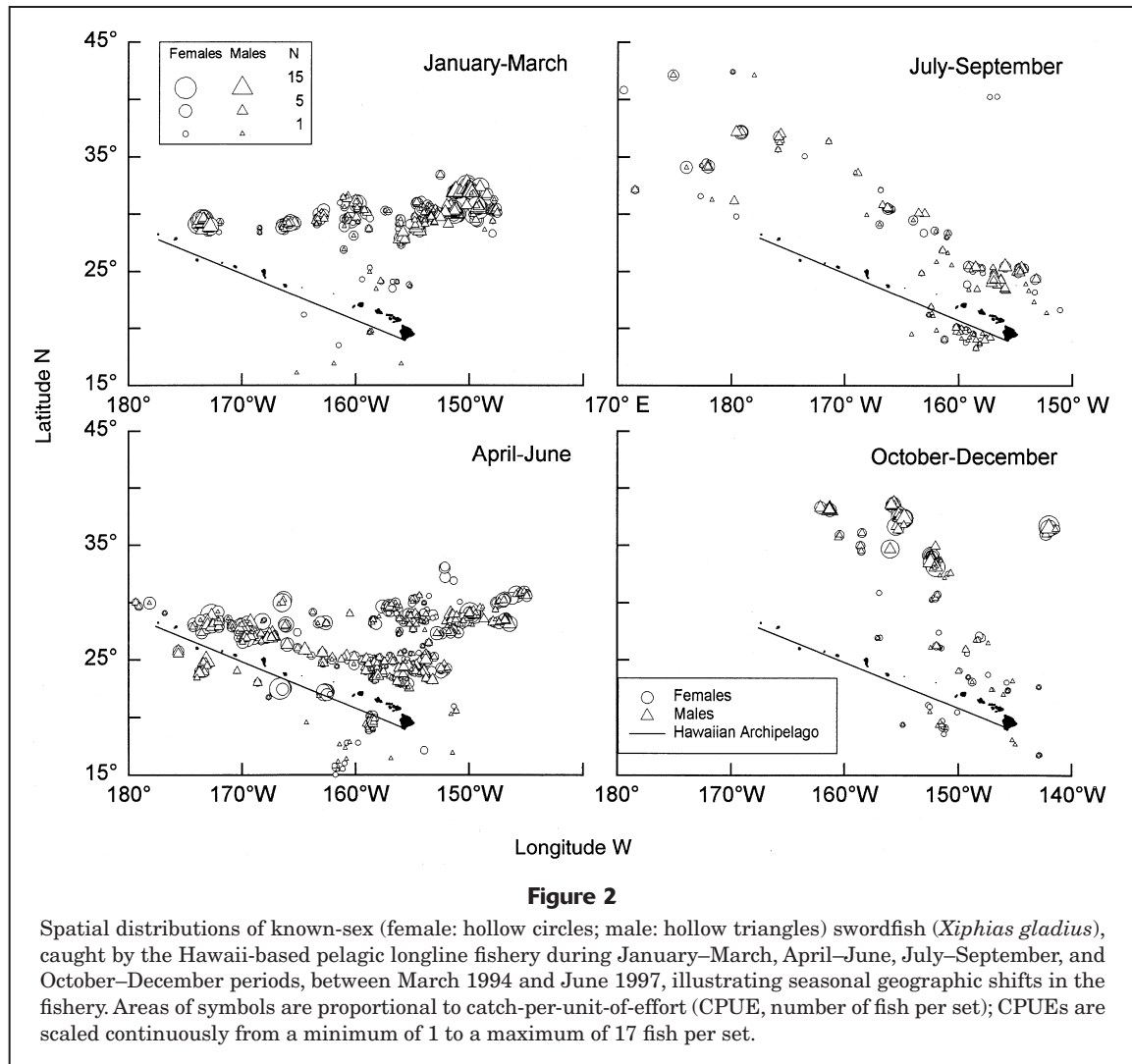
Figure 1

Numbers of (**A**) female and (**B**) male swordfish (*Xiphias gladius*) that were immature, mature, active, or imminent spawners (females only), which were caught on occasional research cruises and by the Hawaii-based pelagic long-line fishery each month during March 1994–June 1997. Maturity and reproductive activity were assessed based on gonad developmental stages scored histologically.

yolked oocytes undergoing α-, or β- and later atresia (Table 1). Female individuals were designated as "immature" if their most advanced oocytes were unyolked or only partly to moderately yolked without substantial atresia, or as "mature" if their most advanced oocytes were fully yolked with or without atresia ("active-mature") or if their most advanced oocytes were less than fully yolked but with alpha or beta atretic stages present. Developmental stages were further described according to the diameters of the largest size class mode of oocytes present. Among mature females, fish were deemed "ripening mature" if fully yolked but lacking HYDs or POFs, "ripe mature" (imminent spawners) if POFs or HYDs were present, or "resting mature" if a majority of yolked oocytes were atretic.

Oocyte diameters were measured by using formalin-fixed whole oocytes or oocyte cross sections on histological slides. For formalin-fixed specimens, diameters of 25 of the largest oocytes were measured with a dissecting microscope (random axis, 25–50×). The median of 25 random diameters provides a cost-efficient estimator of average maximum oocyte size for multiple-spawning fishes (Lau and DeMartini, 1994); swordfish are multiple-spawners (Uchiyama and Shomura, 1974; Arocha, 1997). Histological slides were prepared for a random subset of these specimens; diameters of oocyte cross sections on slides were measured at 60–300× and for each fish ovary examined, maximum and minimum diameters were averaged for 5–10 of the largest oocyte sections present

Figure 2

Spatial distributions of known-sex (female: hollow circles; male: hollow triangles) swordfish (*Xiphias gladius*), caught by the Hawaii-based pelagic longline fishery during January–March, April–June, July–September, and October–December periods, between March 1994 and June 1997, illustrating seasonal geographic shifts in the fishery. Areas of symbols are proportional to catch-per-unit-of-effort (CPUE, number of fish per set); CPUEs are scaled continuously from a minimum of 1 to a maximum of 17 fish per set.

that included a central nucleus and were spherical (least deformed by processing), so that the coefficient of variation (CV) of the diameter estimate was <10%. Diameters measured for a subset of matched (formalin-fixed, histology) specimens were used to convert between the two types of measurements.

The gonadal development of males was classified by using the criteria of Grier (1981) as specified for billfish by de Sylva and Breder (1997). Males were scored as "immature" if spermatogenesis (meiosis) was absent or, when occurring, if ripe (fully tailed) spermatozoa were restricted to crypts and lobules (tubules) of testes. Males were deemed mature only if ripe sperm were present in spermatic ducts, as well as in crypts and lobules, or as spent or resting if they had developed lobules but no spermatogenesis present (Table 1).

Sex was histologically verified for 506 males and 830 females. The sex of only 23 swordfish (8 males: 70–153 cm EFL, March–December; 15 females: 98–212 cm EFL, April–December) was misclassified from gross visual inspection

of gonads by observers aboard commercial longliners. Misclassification error was unrelated to true sex ($\chi^2=0.02$; df=1; $P=0.9$), and appeared unrelated to fish size or period of capture, although the data were too few to formally evaluate size and period effects. Because the misclassification rate was so low (0.5%), we ignored it in further analyses of the sex composition of swordfish catch where field-sexed fish were used.

For ovary specimens collected in spring 1997, frozen specimens were thawed overnight in a refrigerator. Each lobe of bilobed ovaries was weighed damp; accuracy was 1 g (if total ovary weight ≤500 g) or 20 g (if >500 g). Seven of 95 females caught during the spring 1997 spawning period lacked weights for one ovary lobe; total ovary weights of these fish were estimated by using the relationship between both ovaries (total gonad weight, GW) and right (RO) and left (LO) ovary weights (in g): $GW = 1.807RO$, and $GW = 2.170LO + 133.6$ (both $r^2>0.98$; $n=88$). Right ovaries of the swordfish examined were 28% heavier than left ovaries (matched-pair t-test; $t=6.9$; $n=88$).

Table 1

Histological criteria for classification of gonadal developmental stages and maturation in male and female swordfish, *Xiphias gladius*, caught in the central North Pacific during the period April 1992–June 1997. Maturity stages are based on the criteria of Murphy and Taylor (1990). Median observed oocyte diameters are for 10% formalin-fixed (sea water) specimens.

Maturity stage by sex		Histological appearance of the most advanced gamete stage present in gonads
Females		
1	vestigial	Primitive oogonia only; 80 μm
2	developing	Primary oocytes (basophilic) only present; 133 μm
3	maturing	Early vitellogenesis; beginnings of nucleus breakdown and development of fat inclusions; no chorionic membrane (zona pellucida); 211 μm
4	ripening	Oocytes well-yolked (completely eosinophilic); nuclear membrane indistinct; prominent chorionic membrane, with fat inclusions distributed throughout cytoplasm; 547 μm
5	spawning	Migratory (eccentric) nucleus, hydrating or hydrated oocytes present; 1012 μm
6	recently spawned	Postovulatory follicles present; 1197 μm
7	spent or resting	A majority of classes 4–5 yolked oocytes present undergoing α- β-, or later atresia; 201 μm
Males		
1	undeveloped	Spermatocytes only present; spermatogenesis (meiosis) lacking
2–3	maturing	Spermatogenesis present; some to many ripe (fully tailed) spermatozoa present in crypts and lobules (tubules), but none in spermatic ducts
4	ripe	Ripe sperm present in spermatic ducts as well as crypts and lobules; relatively little spermatogenic activity
5	spent	Developed lobules containing few remaining sperm

Statistical analyses

We estimated body length at median sexual maturity (L_{50}) for males and females separately using nonlinear regression. A derivative-free maximum likelihood method (Proc NLIN; SAS, 1989) was used to fit percentage maturity by 5-cm length class to the two-parameter logistic model,

$$P_x = 100 \,/\, (1+\exp^{(a-bEFL)}),$$

where P = percentage mature at length x; and
L_{50} = $(-a/b)$.

Sex ratios (females/total) also were related to 5-cm length class by using nonlinear regression. Regressions were weighted by the square root of the number of fish examined in each length class. Ninety-five percent confidence intervals on L_{50}'s were calculated by using SAS Proc PROBIT. Logistic regression (STATISTIX, vers. 4.1; Analytical Software, 1994) was used to relate ovarian developmental stage to oocyte diameter and to predict reproductive readiness with gonad weight plus body size. Contingency chi-square and unbalanced fixed-factor ANOVAs (Zar, 1984; SAS, 1989) were used to compare sex ratios and the relative body size compositions of swordfish catches, pooled by 1° lat. by 1° long. bins, during spawning (March–July) and nonspawning (August–February; see "Results" section) periods. Least-squares regression was used to regress median body length versus latitude after body length distributions were made linear by rank transformation. Analyses of sex ratios and size composition were limited to observer-sampled trips and should be considered a first approximation of patterns for the total Hawaii-based longline catches of swordfish during March 1994–June 1997. Significance was based on an alpha level of 0.05.

Results

Sex and maturity composition of sampled fish

During the 40-mo. sampling period, an estimated 142,000 swordfish were caught by the Hawaii-based pelagic longline fishery (2.26 million hooks: Ito and Machado, 1996,[1] 1997,[2] 1999[3]). Data for the 6639 field-sexed fish examined herein thus represent about 4.8% of the commercial landings of swordfish, with the samples reflecting about 4.9% of the total longline effort (2.26 million out of 45.7 million hooks) expended during the period. The sex ratio (females as fraction of total) of the field-sexed commercial catch was 0.533 (SE=0.006; $P<0.001$). About 64% of the 1336 swordfish examined histologically were sexually mature (stages ≥4, Table 1). The two sexes differed in maturity composition based on histological classification (χ^2=67.4; $P<0.001$): 78% of 506 confirmed males but only 56% of 828 confirmed females were mature.

About 73% of 463 mature females were reproductively active (stages 4–6; including 28% stages 5–6 imminent spawners) and 27% were spent or resting (stage 7, Table 1). Of a total 130 spawning females, 33 had ovaries containing oocytes that were hydrating or hydrated, indicating imminent spawning. The ovaries of 122 fish contained POFs, suggesting ovulation within several days prior to capture. The exact age of POFs was inestimable because the likely temperature-dependent (Fitzhugh and Hettler, 1995) degradation rate of swordfish POFs is unknown and because gonad samples were collected from fish that had been hooked for differing lengths of time at varying water temperatures. Twenty-five of the 130 fish had ovaries containing both unovulated, hydrated oocytes and POFs from a previous spawning (Fig. 3, A and B). Of a total 395 mature (stage ≥4) males, 65% were reproductively active (stage 4) and 35% were spent or resting (stage 5, Table 1).

Oocyte size and developmental stage

Ovarian developmental stage was closely related to diameter of the largest size class mode of oocytes present in ovaries. The diameters of formalin-fixed whole oocytes (OD, in µm) and oocyte cross sections (XS, in eyepiece units [epu], where 1 epu=0.1544 µm) on histological slides were best related by the linear regression

$$OD = 11.9 + 6.320XS \qquad (r^2=0.948, n=182, P<0.001).$$

With logistic regression, ovarian development as an indicator of reproductive activity (where active=stages 4–6; inactive=stages 1–3, 7) was predicted with 97.5% accuracy for 828 fish collected during both spawning and nonspawning periods. The predictive relationship was

$$\ln(p/(1-p)) = -6.318 + 0.0180OD,$$

where OD = whole oocyte diameter (in µm); and
$\quad p$ = the probability of active stages 4–6.

The threshold ($p=0.5$) for stages 4–6 is predicted at a whole oocyte diameter of 351 µm. Oocyte size distributions are related graphically to ovarian stages in Figure 4. Median oocyte diameters for the respective stages are listed in Table 1.

Body lengths at sexual maturity

Estimates of L_{50} with all females were indistinguishable (<1 cm different: G-test; P=0.3) from those where females were used that had been caught during the 5-mo. (March–July) spawning periods when reproductively active females (stages 4–6) were present. L_{50} estimates for males were improved if immature (most likely less-than-year-old) fish, many of which were available only during nonspawning periods, were included. We therefore felt it preferable to describe L_{50}'s using all gonad sample fish collected year-round.

L_{50}'s were 102.0 ± 2.5 (95% CI) cm EFL for males ($r^2=0.98$; $n=506$) and 143.6 ± 2.8 cm EFL for females ($r^2=0.97$; $n=816$; Fig. 5). Fits to the logistic model were as follows:

Males: $\quad \% \, Mature = 100/(1 + e^{(14.4011 - 0.1412EFL)})$
Females: $\% \, Mature = 100/(1 + e^{(14.8569 - 0.1034EFL)})$.

Females attained ≥95% sexual maturity at 173 cm EFL. The corresponding value for males was 123 cm EFL. The smallest reproductively active female whose ovaries contained hydrated oocytes or postovultory follicles was 134 cm EFL. Sample sizes ranged from 2 to 45 fish of each sex per 5-cm EFL class; only 6 out of 36 and 12 out of 31 classes contained <10 fish for females and males, respectively. Median sample sizes were 22 (for females) and 17 (for males) for each 5-cm class (Fig. 5).

Indices of spawning readiness

Reproductive readiness (verified by histological staging of ovaries) of female swordfish in the Hawaii-based fishery could be predicted by logistic regressions with body size (length, weight) and ovary weight (or with length- or weight-based gonad indices). Although the spawning activity of female swordfish was predictable from body size and ovary weight alone, the accuracy of prediction was improved if a measure of ovary maturation (such as size of the largest oocytes present) was included. Overall, about 96% of 95 females (range 8–295 kg, 76–247 cm EFL; Table 2A) were correctly classified (with reference to histological stages 4–6) as either reproductively active (1) or not (0) by the logistic regression

$$\ln(p/(1-p)) = \ln(RW) + \ln(GW) + \ln(EV),$$

where RW = round weight in kg;
$\quad GW$ = gonad weight in g; and
$\quad EV$ = oocyte volume in mm³ = $4/3\pi r^3$; and
$\quad r$ = diameter/2 (Table 2A).

The fit of this model was similar to those where oocyte volume plus any of several length- or weight-based gonad indices were used. Among the latter, the index, $GI(2') = [\ln(GW)/\ln(RW)]$, was best (90% accurate), and overall classification accuracy increased to 97% if oocyte volume was added to the model (Table 2B). The index, $GI(2) = [\ln(GW)/\ln(EFL)]$ of Hinton et al. (1997), plus oocyte volume, showed comparable accuracy (94%; Table 2C), and retained 87% accuracy even if oocyte volume was excluded (Table 2D). The latter length-based gonad index itself (Table 2D) should have the widest applicability, despite some loss in predictive power because an oocyte volume term is lacking, because data on swordfish body lengths and gonad weights are often available but body weight and egg size data are not. We also provide (Table 3) several key regressions of swordfish length-on-length and weight-on-length, summarized from Uchiyama et al. (1999), to enable conversions between the different index-based predictors of reproductive readiness.

Temporal and spatial spawning patterns

Swordfish caught by the Hawaii-based longline fishery during March 1994–June 1997 included both reproductively inactive and active adult fish, in addition to imma-
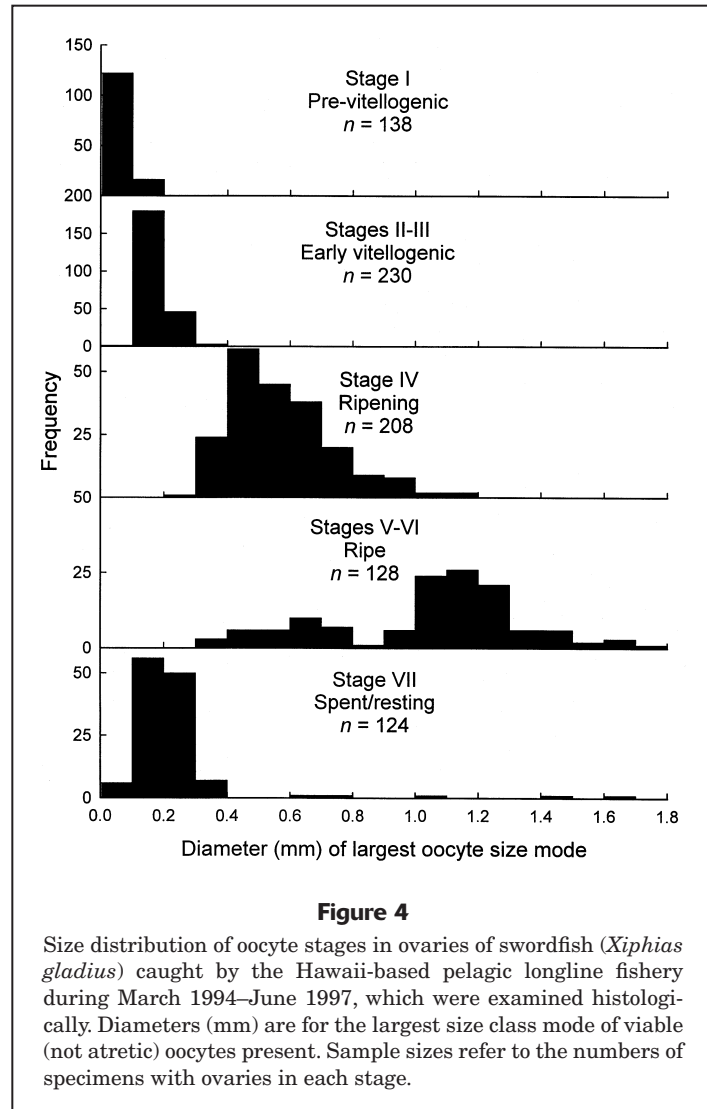
Figure 3

Histological sections of the ovaries of imminently spawning swordfish (*Xiphias gladius*) illustrating (**A**) hydrated oocytes (hyd; stage 5) and (**B**) postovulatory follicles (pof; stage 6). Several other developmental stages of oocytes are also present, including primitive oogonia (pog; stage 1); previtellogenic oocytes (poc; stage 2); early vitellogenic (evo: stage 3) and vitellogenic (vo; stage 4) oocytes; and atretic oocytes (atret; stage 7; an α-atretic, vitellogenic oocyte indicated by arrow in 3A).

ture, mostly female fish. Reproductively active females (stages 4–6) were caught primarily during spring (Fig. 6). Ninety-eight percent of all imminently spawning females were caught during March–July periods, and 73% were caught during May–June (Fig. 6). POFs and hydrated oocytes often co-occurred in ovaries (in 25 out of 33 cases;

Figure 4

Size distribution of oocyte stages in ovaries of swordfish (*Xiphias gladius*) caught by the Hawaii-based pelagic longline fishery during March 1994–June 1997, which were examined histologically. Diameters (mm) are for the largest size class mode of viable (not atretic) oocytes present. Sample sizes refer to the numbers of specimens with ovaries in each stage.

χ^2=23.1; df=1; P<0.001). The relative numbers of active females and imminent spawners were independent of moon phase (Table 4), although indicating no lunar spawning periodicity. Eighty-two percent of all reproductively active (stage 4) males were caught during March–July. Many imminently spawning females were caught within several hundred km of the Hawaiian Archipelago (Fig. 6), not far beyond the borders of the 75- and 50-mile closures to pelagic longlining in the main Hawaiian and Northwestern Hawaiian Islands, respectively.
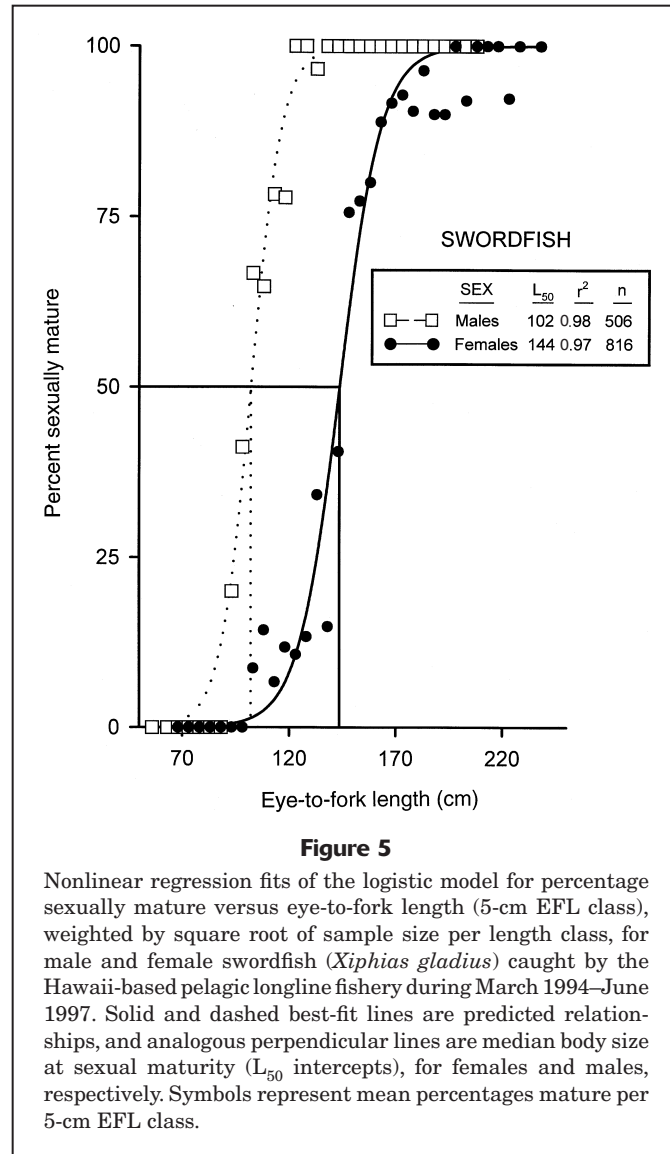
Size, sex, and maturity composition of catches

The size and sex composition of swordfish catches were related (Table 5; Fig. 7). Most (0.55) of the swordfish caught that were <140 cm were male, most (0.64) of those >150 cm were female, whereas the sex ratio (females/total) of fish between 140 and 150 cm EFL was indistinguishable from 0.5 (Fig. 8). Sex ratios fluctuated around 0.5 without pattern at lengths <100 cm, were an increasing power function of fish length between 100 and 220 cm (proportion female=0.0018$EFL^{1.1418}$; r^2=0.87; n=24 5-cm classes; P<0.001) and were consistently >0.9 at lengths >220 cm EFL (Fig. 7). Overall, males represented about 39.5% of the March 1994–June 1997 observer-sampled swordfish catch by weight. The female catch by weight was 60.5%.

The maturity composition of swordfish catches differed between the sexes. During March 1994–June 1997, mature fish represented about 56% and 77% of the sampled female catch in terms of numbers and weight, respectively. Mature fish comprised 88% (numbers) and 96% (weight) of the sampled male catch. Overall, 71% and 85% of the total sampled catch (both sexes) were mature by numbers and weight, respectively.

Both the sex and size composition of swordfish catches varied spatially (Fig. 9; Table 6). Latitude had a stronger influence on sex ratio and size composition than did longitude (Table 6, A and B). A large majority (61%) of all swordfish caught south of 27°N were males. The body size (hence sex) of swordfish caught might vary with depth and time

Figure 5

Nonlinear regression fits of the logistic model for percentage sexually mature versus eye-to-fork length (5-cm EFL class), weighted by square root of sample size per length class, for male and female swordfish (*Xiphias gladius*) caught by the Hawaii-based pelagic longline fishery during March 1994–June 1997. Solid and dashed best-fit lines are predicted relationships, and analogous perpendicular lines are median body size at sexual maturity (L_{50} intercepts), for females and males, respectively. Symbols represent mean percentages mature per 5-cm EFL class.

of day fished, and relatively more "tuna sets" (deep, daytime soak) are made during the peak summertime tuna season, particularly at latitudes at and below the Hawaiian Archipelago (He et al., 1997). We therefore reevaluated the sex composition of swordfish catches south and north of 27°N using only the fish caught on sets on which swordfish were targeted (He et al., 1997). A total of 5547 fish were caught on swordfish sets, representing 84% of all swordfish present in the parent sample. The male proportion of 585 swordfish caught on swordfish sets south of 27°N was the same (61%) as for all observer-sampled sets. Proportions of females in catches at and north of 27°N also were the same (56%) for total and swordfish-targeted sets.

Sex and size composition of the swordfish catch varied with season (Table 6A). Small-bodied males and females dominated lower-latitude catches during spawning as well as nonspawning periods (Table 6B). Overall, about 64% by numbers and 65% by weight of all swordfish were caught during March–July spawning periods.

Several interesting spatial patterns were apparent in the size composition data. Relatively greater numbers of "small-bodied" (<25th length percentile; females: <126 cm; males: <118 cm EFL) swordfish were caught south of 22°N (Table 6B). Relatively greater numbers of "large-bodied" (>75th percentile; females: >172 cm; males: >156 cm EFL) fish were caught north of 35°N (Table 6C). Median body sizes of swordfish caught increased with latitude (regressions of ranked median EFL on 1° bins, r^2>0.8 for each sex, n=21, P<0.001) with the proportions of catch that were small-bodied (and mostly male) greater south of about 22°N (Fig. 9).

Discussion

Sex-specific sizes at maturity

Effects of methods Ninety-five percent confidence intervals on our estimates of median body size (L_{50}) at sexual

Table 2

Summary results of logistic regressions predicting reproductive activity (histological stages 4–6) versus inactivity (stages 1–3, 7; see Table 1) based on (**A**) round weight (RW), gonad weight (GW), plus egg volume (EV); (**B**) a weight-based gonad index [GI(2')] plus EV; (**C**) a length- based gonad index [GI(2)] plus EV; or (**D**) GI(2) alone; for female swordfish, *Xiphias gladius,* sampled from the Hawaii-based pelagic longline fishery during May–June of 1997.

A $\ln(p/(1-p)) = \ln(RW) + \ln(GW) + \ln(EV)$

Predictor variables	Coefficient	Standard error	P-value
ln(RW)	−10.740	3.437	0.0018
ln(GW)	4.228	1.899	0.0260
ln(EV)	2.073	0.610	0.0007

Classification table			Proportion correctly classified		
	Predictions		0	1	overall
Actual	0	1	0.900	0.973	0.958
0	18	2			
1	2	73			

B $\ln(p/(1-p)) = GI(2') + \ln(EV)$, where $GI(2') = [\ln(GW)/\ln(RW)]$

Predictor variables	Coefficient	Standard error	P-value
GI (2')	−21.464	5.176	0.0001
ln(EV)	2.822	0.610	0.0001

Classification table			Proportion correctly classified		
	Predictions		0	1	overall
Actual	0	1	0.850	1.000	0.968
0	17	3			
1	0	75			

C $\ln(p/(1-p)) = GI(2) + \ln(EV)$, where $GI(2) = [\ln(GW)/(\ln(EFL)]$

Predictor variables	Coefficient	Standard error	P-value
GI (2)	−15.916	3.847	0.0001
ln(EV)	1.934	0.444	0.0001

Classification table			Proportion correctly classified		
	Predictions		0	1	overall
Actual	0	1	0.700	1.000	0.937
0	14	6			
1	0	75			

D $\ln(p/(1-p)) = GI(2)$

Predictor variables	Coefficient	Standard error	P-value
GI (2)	20.559	4.823	0.0001
Intercept	−24.968	6.008	0.0001

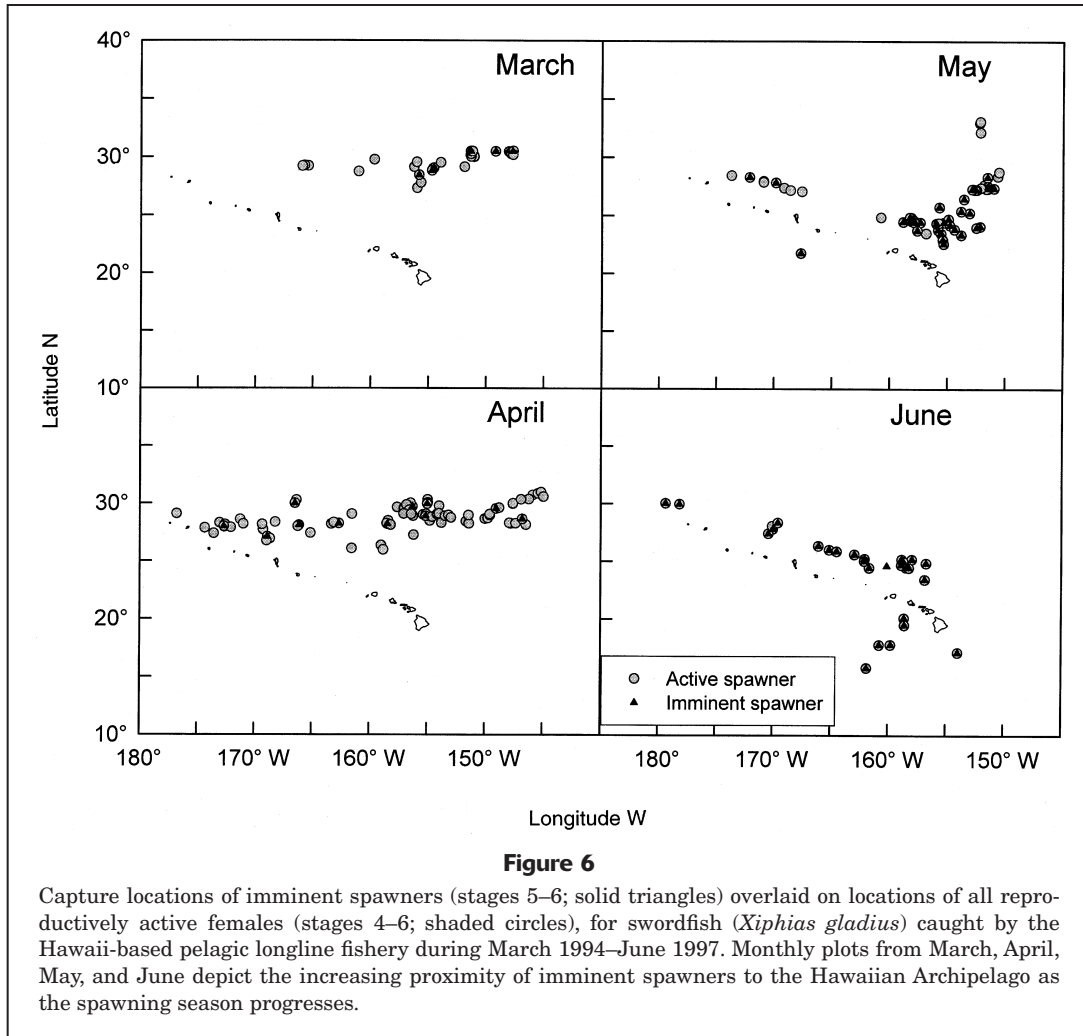| Classification table			Proportion correctly classified		
	Predictions		0	1	overall
Actual	0	1	0.650	0.933	0.874
0	13	7			
1	5	70			

Table 3

Predictive equations and summary statistics for best-fit regressions relating various body length and weight metrics for swordfish, *Xiphias gladius*, in the central North Pacific. Source: Uchiyama et al. (1999). Eye-to-fork length (EFL) and lower jaw-to-fork length (LJFL) are cm; and round weight (RW) and dressed weight[1] (DW) are kg. Sample size (*n*) is number of fish (sexes pooled). All equations are significant at $P<0.001$.

Model	Equation	SE *b*	SE *a*	*n*	r^2
$EFL = a + b \times LJFL$	$EFL = -6.543 + 0.927 \times LJFL$	0.006	0.849	179	0.992
$LJFL = a + b \times EFL$	$LJFL = 8.009 + 1.071 \times EFL$	0.007	0.865	179	0.992
$RW = a \times EFL^b$	$RW = 1.299 \times 10^{-5} \times EFL^{3.074}$	0.041	3.010×10^{-6}	166	0.967
$DW = a \times RW^b$	$DW = 0.646 \times RW^{1.032}$	0.051	0.016	73	0.987

[1] Dressed weight is defined as round (total) weight minus the head, entrails, vertical and pectoral fins, and with caudal fin (including caudal peduncle and keel) removed by a cut make between the 22nd and 23rd vertebrae (Uchiyama et al., 1999).

maturity were within ±2–3% of their respective estimate and provide reasonably precise input parameters for stock assessment. Occasional estimates of less-than-complete maturity in some larger length classes of females (Fig. 5)

likely reflect chance indetection of relatively rare, large atretic oocytes in the ovaries of inactive but mature females. Such may be expected when only a single region of ovary is examined histologically. We feel that the evalu-

Figure 6

Capture locations of imminent spawners (stages 5–6; solid triangles) overlaid on locations of all reproductively active females (stages 4–6; shaded circles), for swordfish (*Xiphias gladius*) caught by the Hawaii-based pelagic longline fishery during March 1994–June 1997. Monthly plots from March, April, May, and June depict the increasing proximity of imminent spawners to the Hawaiian Archipelago as the spawning season progresses.

ation of greater numbers of females by using only a single ovary section offsets the rare failure to detect maturity in mature but inactive females.

Histological examination of gonadal developmental stage is the most accurate and expensive method of characterizing sexual maturity, and cost-effective alternatives are desirable (West, 1990). Gonad indices (GIs) represent one such general (West, 1990) and specific (Hinton et al., 1997) option. Our findings indicate that swordfish body weight plus ovary weight together can predict reproductive activity with >90% accuracy in swordfish caught by the Hawaii-based fishery. Our observations support the conclusion of Hinton et al. (1997) that GIs can provide useful proxies of reproductive activity in swordfish. We reiterate, however, that GIs alone are limited to detection of reproductive activity (Hinton et al., 1997); without ancillary data such as gonad development or oocyte size, GIs are often not reliable measures to distinguish reproductively inactive but mature females from immature females during the nonspawning season (West, 1990; Mejuto and Garcia, 1997). GIs are most often used for determining spawning seasons; if nonspawning season fish are to be included in a

Table 4

Results of 2×3 χ^2 test comparing relative frequency with which imminently spawning (stages 5–6) female swordfish, *Xiphias gladius*, were caught, among all reproductively active females (stages 4-6) caught during new, quarter, and full moon periods by the Hawaii-based pelagic longline fishery during March 1994–June 1997. χ^2 = 3.28, df = 2, P = 0.20.

Period	Active	Spawning	Both
New	34	27(44%)	61
Quarter	76	39(34%)	115
Full	74	59(44%)	133
All	184	125	309

size-at-maturity evaluation, a relatively inexpensive alternative to histological staging (such as oocyte size) should be used for deducing maturation stages. Oocyte size can provide an accurate proxy for gonadal developmental stage

Table 5

Monthly sex ratios (females/total), effort (positive swordfish sets), and summary statistics for body sizes of female and male swordfish, *Xiphias gladius,* used to describe sex and size composition of catch. n = number of fish in sample. EFL = eye-to-fork length (cm).

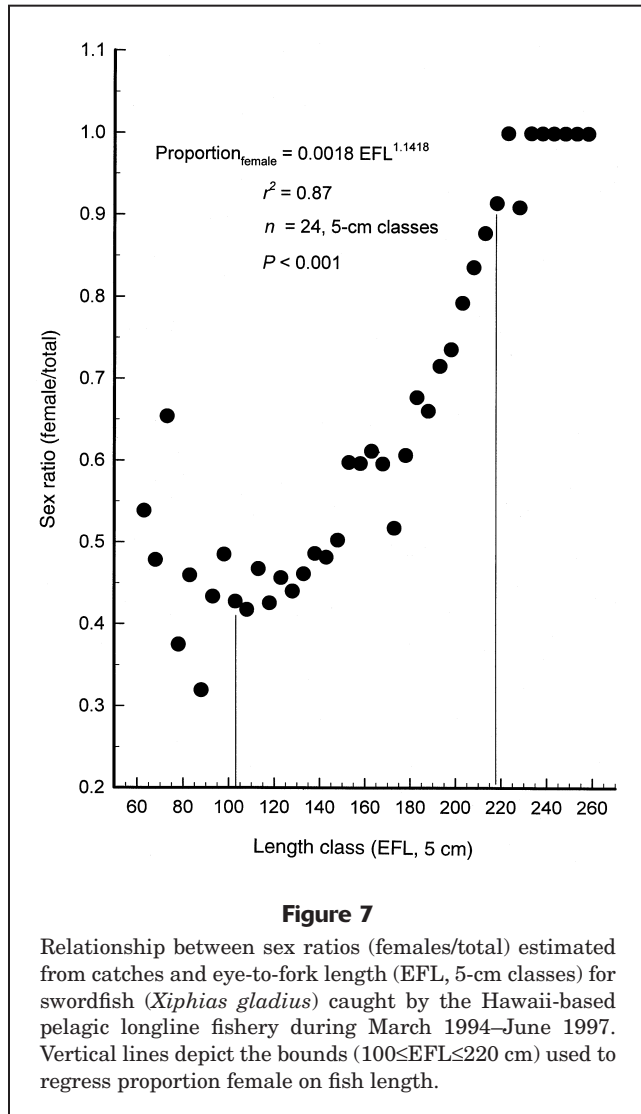| Month	Sex	n	Sex ratio	Trips (sets)	25th percentile	Median EFL	75th percentile
Jan	F	182	0.56	3 (35)	132	153	176
	M	142		3 (32)	125	144	163
Feb	F	334	0.56	9 (66)	129	148	165
	M	264		11 (60)	125	141	159
Mar	F	883	0.55	13 (161)	129	151	175
	M	723		13 (165)	121	136	159
Apr	F	746	0.58	15 (170)	128	150	175
	M	531		17 (164)	118	134	152
May	F	359	0.51	14 (110)	120	151	181
	M	340		14 (108)	115	129	148
Jun	F	183	0.44	12 (71)	118	148	171
	M	237		14 (83)	118	139	160
Jul	F	174	0.46	11 (51)	118	152	178
	M	204		10 (60)	114	135	157
Aug	F	39	0.39	4 (17)	106	136	152
	M	62		7 (29)	102	125	151
Sep	F	41	0.53	6 (24)	93	105	122
	M	36		6 (21)	68	102	126
Oct	F	159	0.45	11 (50)	120	140	155
	M	193		10 (50)	119	138	164
Nov	F	283	0.56	6 (49)	124	151	167
	M	218		5 (47)	108	133	152
Dec	F	156	0.51	7 (36)	136	159	180
	M	150		6 (39)	121	140	160
All	F	3539	0.533	111 (840)	126	149	172
	M	3100		116 (858)	118	136	156

in swordfish (Taylor and Murphy, 1992; Arocha and Lee, 1995; our study). Gonad weights scaled for body length (because body lengths, not weights, are typically collected for swordfish at sea) deserve further evaluation as predictors of spawning readiness, particularly because our findings for swordfish in the central North Pacific are so similar to those of Hinton et al. (1997) for Atlantic swordfish.

Other maturity estimates　　Prior reported estimates of body size at sexual maturity for female swordfish in the Pacific in general do not agree with ours, but dissimilarities likely reflect the different measures used to gauge sexual maturity used by various researchers. For example, Yabe et al. (1959) concluded, from length distributions and gonad weights, that "most [female] swordfish" in the western Pacific mature sexually between 150 and 170 cm EFL. Kume and Joseph (1969) observed that female swordfish "in spawning condition" (defined as having a greater than defined threshold value of gonad index) were not "regularly encountered" until about 170 cm EFL. Sosa-Nishizaki's (1990, p. 64) estimate of sexual maturity at about 160 cm EFL for "most individuals" was also inferred from a length-based GI. In contrast to

females, ours is the first estimate of any kind for body size at sexual maturity of male swordfish in the Pacific Ocean. Our results overall underscore the importance of sex-specific, histologically validated estimates of median body size at sexual maturity as data for stock assessments.

Our estimates of L_{50} for swordfish caught by the Hawaii-based longline fishery appear comparable (for males) to slightly smaller (females) than estimates for swordfish caught in several regions of the Atlantic. For swordfish from the Straits of Florida, Taylor and Murphy (1992) observed L_{50}'s of 112 and 182 cm lower jaw-to-fork length (LJFL) for males and females, respectively, equivalent to 96 and 161 cm EFL. Arocha and Lee (1996) estimated L_{50}'s of 129 (males) and 179 cm LJFL (females), equivalent to 112 and 158 cm EFL, respectively, for swordfish caught throughout the western Atlantic. We caution that these L_{50} estimates for swordfish in the Atlantic may not be totally comparable to ours because studies might differ in whether estimates apply to fish caught throughout the entire year or during spawning periods only.

Female swordfish in the Mediterranean presently mature at an L_{50} of about 142 cm LJFL (de la Serna et al., 1996),

Figure 7

Relationship between sex ratios (females/total) estimated from catches and eye-to-fork length (EFL, 5-cm classes) for swordfish (*Xiphias gladius*) caught by the Hawaii-based pelagic longline fishery during March 1994–June 1997. Vertical lines depict the bounds ($100 \leq EFL \leq 220$ cm) used to regress proportion female on fish length.

equivalent to an estimated 124 cm EFL, considerably smaller than that documented for females in any other fishery. This estimate by de la Serna et al. (1996) was based on length-based gonad indices that were histologically validated.

For swordfish caught by the Hawaii-based longline fishery, the disparate body lengths at median sexual maturity of males and females are equivalent to a threefold difference between 55 kg RW (40 kg dressed-head off weight, DW) for females and 19 kg RW (14 kg DW) for males. Correponding ratios of female:male body weights at L_{50} for swordfish in the tropical and western North Atlantic are 4.4 (Taylor and Murphy, 1992) and 2.7 (Arocha and Lee, 1996). Details of computation notwithstanding, these disparities in mass clearly represent biologically meaningful differences between the sexes in swordfish. Sexual differences in rates of biomass accrual—likely due to sexually dimorphic growth rates—translate to important differences in the sustainable fisheries yield provided by each sex. With later maturation, the period of rapid prereproductive somatic growth of female swordfish extends several or more years longer than

that of males. Taylor and Murphy (1992) for example estimate ages-at-sexual maturity of swordfish from the Straits of Florida, corresponding to median sizes-at-maturity, as 5.5 yr (for females) and 1.4 yr (for males).

At present our characterization of maturity in North Pacific swordfish is limited to body size. Age-at-maturity estimates must await completion of size-at-age studies being conducted at the Honolulu Laboratory of the National Marine Fisheries Service.
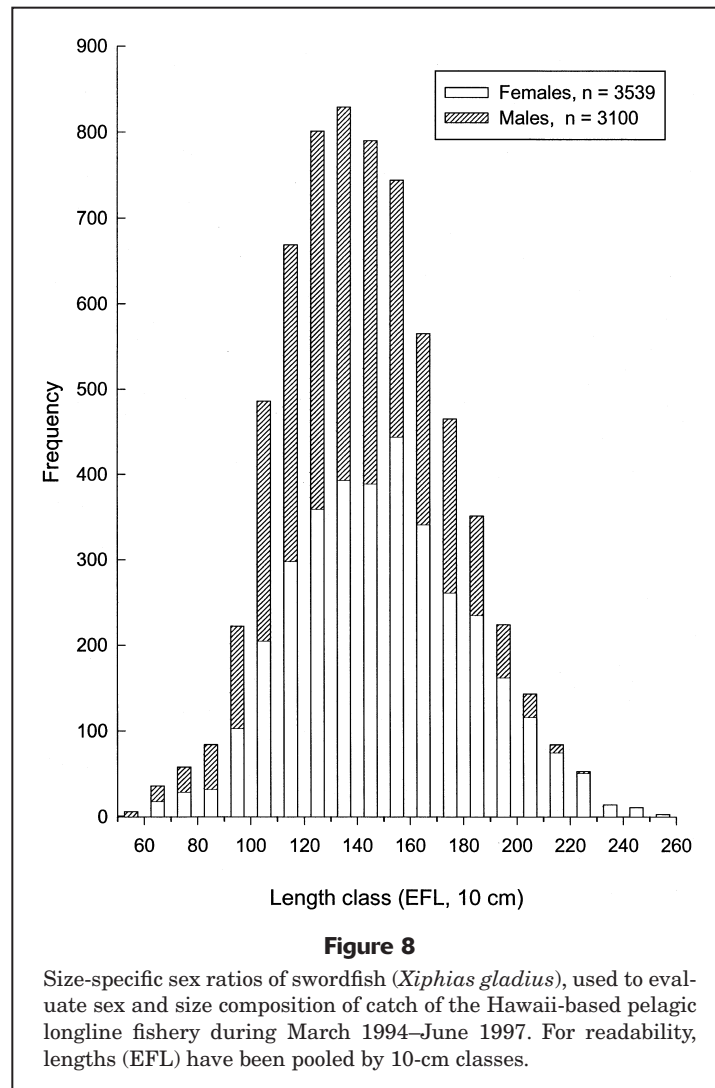
Sex and size composition

Sex ratios of swordfish caught by the Hawaii-based longline fishery vary temporally and spatially. These variations may partly reflect different availabilities or catchabilities resulting from sexual differences in behavior that change seasonally (e.g. during spawning periods). Variations in the sex composition of catches must partly reflect different natural distributions of the sexes. Sex ratios of catches follow recurrent seasonal patterns among years, and spatial differences in the sex composition of catches repeat annually. Neither of these two observations would be likely if, for example, the sex composition of catches represented simple targeting of larger (female) fish by fishermen.

Similarities in sex ratios-at-length between North Atlantic (Stone and Porter, 1997) and central North Pacific swordfish (our study) suggest that size-specific sex ratios of swordfish catches can be predicted with adequate precision from data on the length composition of catches. If true, this could obviate the need for a direct characterization of the sex composition of swordfish catches—a task complicated in fisheries like Hawaii's in which swordfish are landed fully dressed. Sex ratios of swordfish caught by the Hawaii-based fishery are identical for swordfish-targeted and nonswordfish-targeted sets. Estimates of the sex ratio of swordfish catches in the Hawaii-based fishery thus seem robust to the specifics of capture, at least for the period sampled. Further comparisons of sex ratio estimates for catches with different gear types over a longer sampling period would be required to thoroughly evaluate possible sexual differences in catchability and expand inferences on sex ratios beyond catch to stock.

Seasonal patterns Temporal changes in the sex ratios and related size composition of swordfish catches in the Hawaii-based longline fishery resemble those observed for swordfish in other known spawning areas. Taylor and Murphy (1992) observed analogous temporal differences in catches of male and female swordfish in and near the Straits of Florida, where the fraction of males in catches was significantly greater than that of females only during peak (spring–summer) spawning periods. Temporal patterns of changes in sex ratios thus are consistent with sexual differences in migratory and spawning or other reproductive behaviors such as the greater propensity for males to aggregate in group-spawning pelagic species (Hunter and Macewicz, 1986) and other fishes.

Spatial patterns Arocha and Lee (1995) observed spatial variations, complementary to Taylor and Murphy's (1992)

Figure 8

Size-specific sex ratios of swordfish (*Xiphias gladius*), used to eval-
uate sex and size composition of catch of the Hawaii-based pelagic
longline fishery during March 1994–June 1997. For readability,
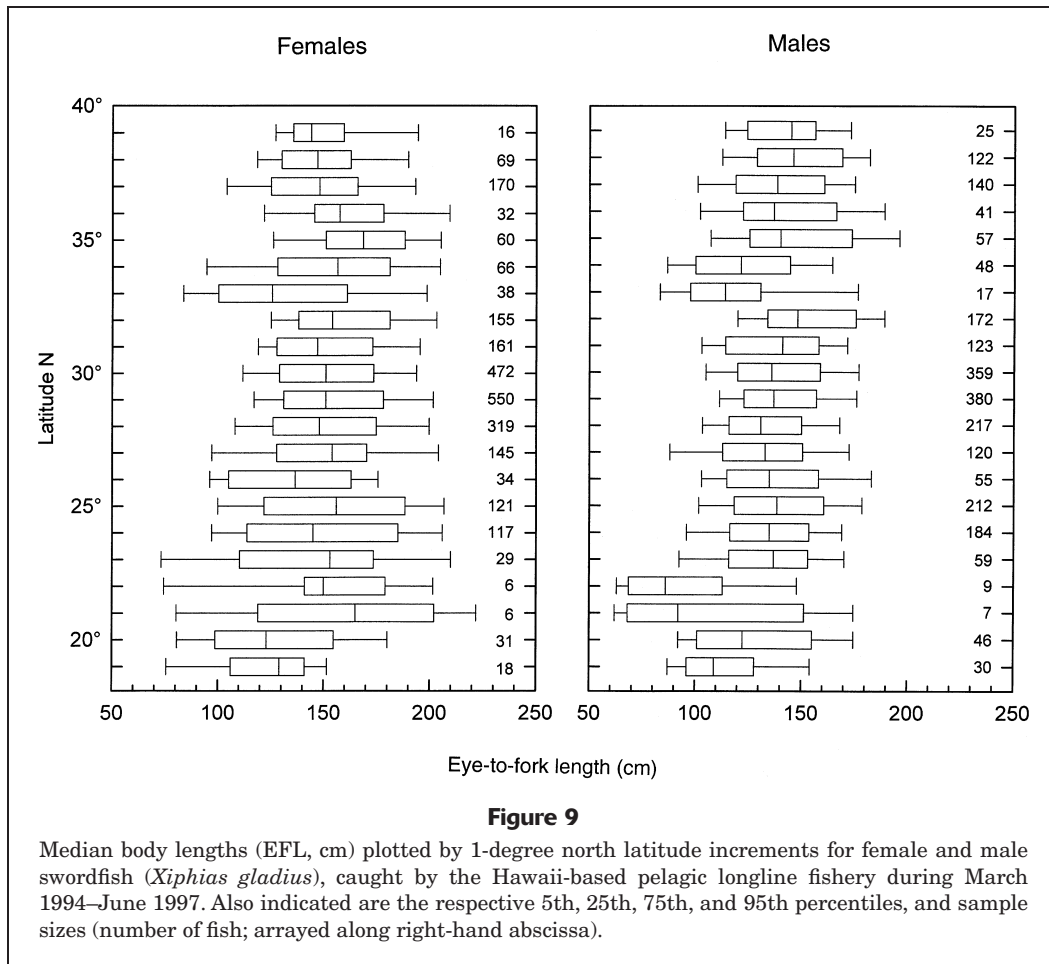lengths (EFL) have been pooled by 10-cm classes.

temporal variations in swordfish sex ratios elsewhere in
the western Atlantic. The sex ratios of adult-size sword-
fish (>125 cm LJFL, but smaller than very large adults
[>195 cm], the size at which the numbers of males dimin-
ish greatly in Atlantic swordfish stocks) are strongly male-
biased only in the subtropical region (19–35°N) in which
most spawning occurs (Arocha et al., 1994; Arocha and
Lee, 1995). Spatial patterns similar to the latter also have
been observed in spawning regions of the tropical western
Atlantic (Mejuto et al., 1998) and western Indian Ocean
(Mejuto et al., 1995).

Spatial differences in the sex and size composition of
swordfish also may be related to sex-specific foraging
migrations. Differences in the sex and size composition of
swordfish catches have been noted by others in western
Atlantic fisheries. Males predominate in catches made at
tropical latitudes but females dominate in waters <18°C
(Beckett, 1974). Most swordfish caught in the western
North Atlantic off New England and the Canadian mari-
time provinces are large female fish (Tibbo et al., 1961).

Distributional ecology and energetics of migration

Limited tag-recapture data[4] suggest that some swordfish
move great distances within the North Pacific. Swordfish
also display marked diel vertical migrations that appear
to vary among fish of different sizes and that inhabit conti-
nental shelf versus open ocean areas (Carey and Robison,
1981; Carey, 1990). As they migrate between warm mixed
layer and cold subthermocline waters, swordfish encoun-
ter changes in water temperature as great as 19° in 2.5 h
(8–27°C: Carey and Robison, 1981). A vascular rete system
enables swordfish to dampen the rate of temperature loss
in swimming muscles on deep dives, and it is likely that
body mass importantly influences this ability (Carey, 1990)
and the metabolic costs of inhabiting cold water masses

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[4] Boggs, C. H. 1998. Unpubl. data. Honolulu Laboratory, South-
west fish. Sci. Cent., Natl. Mar. Fish. Serv., NOAA, Honolulu, HI
96822-2396.

Figure 9

Median body lengths (EFL, cm) plotted by 1-degree north latitude increments for female and male swordfish (*Xiphias gladius*), caught by the Hawaii-based pelagic longline fishery during March 1994–June 1997. Also indicated are the respective 5th, 25th, 75th, and 95th percentiles, and sample sizes (number of fish; arrayed along right-hand abscissa).

(first hypothesized as a "size-temperature mediated physiological mechanism" by Hoey, 1991).

Horizontal movements also incur different energetic costs, as well as other types of costs, for fishes of different body sizes (Roff, 1988). It is plausible that feeding and spawning migrations involve different costs for individual swordfish ranging over the broad spectrum of body sizes (90–210 cm EFL, 13–180 kg; Fig. 8) commonly caught by the Hawaii-based fishery. Because most small swordfish are males and most large swordfish are females, it is further likely that the costs of migration differ between the sexes as well as among fish of varying body sizes that might migrate different distances. The significant relationships observed between latitude and sex ratio and between latitude and body size for swordfish of both sexes in the central North Pacific are consistent with the latter hypothesis.

Recurrent patterns of variation in the sex composition of swordfish catches throughout the world's longline fisheries remain poorly understood. Observed patterns may reflect natural differences in distributions of the sexes, may represent consistent artifacts of different catchabilities of the sexes during spawning periods, or both. A challenging topic for future research will be the evaluation of whether the differences reflect sexually distinct costs versus benefits for vertical or horizontal migration that result from the disparate body masses of males and females.

Implications for stock assessment

It is clear that stratifying swordfish catch statistics by sex could appreciably reduce the variances of catch and effort estimates, and future research should include simulation studies that explore the quantitative effects of sex stratification on stock assessments (Restrepo, 1991). Further, if our observations for swordfish caught by the Hawaii-based longline fishery have identified patterns that are relevant to swordfish caught elsewhere, age-structured stock assessments for swordfish in the Pacific should evaluate explicitly the potentially great importance of temporal and spatial dynamics in the sex and size composition of catches. It will likely be necessary to stratify catches by latitude of capture (and perhaps spawning and nonspawning period), in addition to standardizing CPUE statistics for environmental variables and targeting (e.g. see He et al., 1997; Hinton and Deriso, 1998; Bigelow et al., 1999), in order to reduce the variances of abundance indices used in stock assessments.

Table 6

Results of fixed-factor ANOVAs relating (**A**) sex ratio (females/total) versus period (spawning = Mar–Jul, nonspawning = Aug–Feb), latitude class (North: ≥27°N, South: <27°N) and longitude class (East: ≤160°W, West: >160°W); (**B**) the relative number of fish smaller than the 25th length percentile (RNQ1, see text) versus period and latitude class (Far S: ≤22°N, Other: >22°N); and (**C**) the relative number of fish larger than the 75th percentile (RNQ3, see text) vs sex and latitude class (Far N: ≥35°N, Other: <35°N) on sets with swordfish present, for swordfish, *Xiphias gladius,* caught by the Hawaii-based pelagic longline fishery during March 1994–June 1997. NS terms (e.g. longitude) are unspecified. SS = sum of squares; MS = mean square; LSMEAN = least square mean; SE LSMEAN = Standard error of least square mean.

A Source		df	SS	MS	*F*-value	*Pr>F*
Latitude		1	6.634	6.634	23.13	0.0001
Period × Latitude		2	4.297	2.149	7.49	0.0006

		Sex ratio			
Case	Period × Latitude		LSMEAN	SE LSMEAN	Contrasts
1	Nonspawning	N	0.532	0.012	
2	Nonspawning	S	0.472	0.048	3>1=2=4
3	Spawning	N	0.584	0.009	
4	Spawning	S	0.392	0.016	

B Source		df	SS	MS	*F*-value	*Pr>F*
Period		1	2.634	2.634	10.64	0.0011
Latitude		1	14.179	14.179	57.29	0.0001
Period × Latitude		1	2.009	2.009	8.12	0.0044

		RNQ1			
Case	Period × Latitude		LSMEAN	SE LSMEAN	Contrasts
1	Nonspawning	FarS	0.696	0.073	
2	Nonspawning	Other	0.248	0.011	1>3>2=4
3	Spawning	FarS	0.433	0.043	
4	Spawning	Other	0.230	0.008	

C Source		df	SS	MS	*F*-value	*Pr>F*
Sex		1	0.486	0.486	2.31	0.13
Latitude		1	1.569	1.569	7.47	0.0063
Sex × Latitude		1	1.254	1.254	5.97	0.0146

		RNQ3			
Case	Sex × Latitude		LSMEAN	SE LSMEAN	Contrasts
1	Female	FarN	0.253	0.023	
2	Female	Other	0.248	0.008	3>1=2=4
3	Male	FarN	0.321	0.023	
4	Male	Other	0.232	0.009	

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