

Reproductive dynamics of striped marlin (*Kajikia audax*) in the central North Pacific

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ABSTRACT

Context. Within the western and central North Pacific Ocean stock of striped marlin (*Kajikia audax*), reproductive information is lacking for the central North Pacific. **Aims.** To derive estimates of sex-specific functional maturity ogives, eye-to-fork length at 50% maturity, reproductive phase composition, spawning season and sex ratios by sampling the Hawaii-based pelagic longline fishery. **Methods.** Gonad histology was exclusively used to confirm sex and estimate all reproductive life history traits. **Key results.** Females spawn in May–July; males are capable of spawning year-round. Best length at 50% maturity estimates were based on datasets restricted to the female spawning season (eye–fork length for females 152.2 cm and for males 109.0 cm). Length distributions and sex ratios are seasonally dynamic around Hawaii and differ from those in other Pacific regions.

Conclusions. Length-at-maturity estimates for the central North Pacific are lower than all sex-specific estimates reported from other Pacific regions. **Implications.** The new maturity estimates will improve determinations of stock resilience and productivity in upcoming international assessments.

Keywords: billfish, central North Pacific, functional maturity ogive, gonad histology, Hawaii-based pelagic longline fishery, length at maturity, length distribution, sex ratio, spawning season, stock mixing, striped marlin.

Introduction

Striped marlin, *Kajikia audax* (Perciformes: Istiophoridae), is a large epipelagic predator inhabiting tropical to seasonally warm temperate waters of the Pacific and Indian oceans (Howard and Ueyanagi 1965; Parin 1968). Commercial high-seas pelagic longline fisheries are the primary sources of striped marlin catch in the Pacific Ocean, along with a variety of secondary contributing fisheries (commercial coastal drift net, purse seine, harpoon, handline and recreational troll).

Within the North Pacific, striped marlin is caught primarily as bycatch in the commercial pelagic longline fisheries of several nations (Japan, Taiwan, South Korea and Mexico), including the USA (Hawaii and California). The central North Pacific waters surrounding the Hawaiian Archipelago have among the highest relative densities of striped marlin catch (Lien *et al.* 2014). Within the central North Pacific, striped marlin is caught year-round by the Hawaii-based pelagic longline fishery (HPLF) and Hawaii coastal troll recreational fishery, although catch typically declines precipitously during the summer months of July–September (Royce 1957; Strasberg 1970). Although not a target of longline fisheries, bycatch of striped marlin is retained for sale as fresh or frozen fish and, in Hawaii, it is the primary billfish species sold locally for raw fish consumption (Hawaii Seafood Council 2015). However, longline bycatch and spawning biomass of striped marlin in the western-central North Pacific Ocean (WCNPO) has declined since 1990, precipitating recent efforts to assess this stock (Piner *et al.* 2013; International Scientific Committee for Tuna and Tuna-Like Species in the North Pacific 2019, 2023).

Currently three Pacific stocks of striped marlin are generally recognised, namely, an expansive WCNPO stock that includes Taiwan, Japan, Hawaii and California, an eastern Pacific Ocean (EPO) stock that extends along the Pacific coast and offshore waters of Mexico south along Central America to Ecuador and Peru, and a south-western Pacific

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Ocean (SWPO) stock that includes Australia and New Zealand (Purcell and Edmands 2011; Mamoozadeh *et al.* 2020). A recent international stock assessment of North Pacific striped marlin (International Scientific Committee for Tuna and Tuna-Like Species in the North Pacific 2023) recognised two separate stocks consisting of the WCNPO stock managed under the authority of the Western and Central Pacific Fisheries Commission and the EPO stock managed exclusively by the Inter-American Tropical Tuna Commission. Recent research (Evans *et al.* 2021; Martinez 2021; Lam *et al.* 2022) provides genetic evidence for the co-occurrence of SWPO and WCNPO fish in the central North Pacific fishing grounds of the HPLF. Martinez (2021) reported that the majority of fish sampled from the HPLF in 2019–2020 were of WCNPO stock origin during boreal winter–spring (January–February, June, December), whereas the SWPO stock dominated during boreal summer–autumn (July–November). Lam *et al.* (2022) reported the occurrence of SWPO fish (35%) during June–August 2017 from fish landed in Honolulu by HPLF vessels. However, because of the difficulties in objectively differentiating stock origin within the available fisheries assessment data, recent and past assessments for the WCNPO region proceeded under the assumption of a single management unit stock (International Scientific Committee for Tuna and Tuna-Like Species in the North Pacific 2019, 2023).

The most recent international stock assessment of the WCNPO management area concluded that the stock was very likely to be overfished and likely to be subject to overfishing relative to 20% spawning stock biomass-based reference points (International Scientific Committee for Tuna and Tuna-Like Species in the North Pacific 2023). Recovery of the WCNPO striped marlin stock has been hindered by below-average recruitment since the 1990s (Piner *et al.* 2013; International Scientific Committee for Tuna and Tuna-Like Species in the North Pacific 2019; Brodziak and Sculley 2020). The resilience of a stock to recover from excess fishing depends on its reproductive potential, namely the annual fluctuation in a stock's production of offspring that successfully recruit to the fishery (Trippel 1999). One measure of stock resilience is determined by modelling the steepness of the stock–recruitment relationship. Model simulations to determine the probable distribution of stock–recruitment steepness for WCNPO striped marlin found that several life history characteristics, particularly female reproductive maturity, have an important influence on steepness (Brodziak *et al.* 2015).

No peer-reviewed published studies on reproductive maturity exist for the central North Pacific. Currently, reproductive maturity information for the WCNPO management area is based on a study that sampled the western North Pacific tuna longline fishery off Taiwan (Chang *et al.* 2018). The western boundary location of the Chang *et al.* (2018) study belies the extensive spatial void in sampling across the WCNPO and lack of current understanding of reproductive biology within a substantial portion of the management area.

On the basis of at-sea gonad sampling of striped marlin captured in the central North Pacific by the HPLF and exclusive use of gonad histology, we provide first-time estimates of maturity ogives and length (eye–fork length, EFL) at median (50%) reproductive maturity (L_{EF50}) for females and males. Because these new reproductive parameters, specifically for females, are expected to be applied in future stock assessments, our focus is to provide estimates of functional maturity rather than physiological maturity. Functional maturity infers the capacity to spawn during the sample-collection season (vitellogenesis in females), whereas physiological maturity begins with the initial onset of hormone-induced reproductive development (appearance of cortical alveoli) that may or may not lead to spawning during the sampling season (Pacicco *et al.* 2023; Reed *et al.* 2023). These latter studies caution the use of physiological-maturity estimates as they can provide lower (less conservative) L_{50} estimates than does functional maturity. Functional maturity-based estimates, not estimates based on physiological maturity, are the standard used in large pelagic fish assessments such as for yellowfin tuna (International Committee for the Conservation of Atlantic Tuna 2019) and striped marlin (International Scientific Committee for Tuna and Tuna-Like Species in the North Pacific 2019) to determine biomass status and develop projections of future stock biomass.

Owing to the mounting evidence of SWPO stock mixing with the WCNPO stock over the HPLF grounds (Evans *et al.* 2021; Martinez 2021; Lam *et al.* 2022), we assume only one WCNPO stock spawns in the central North Pacific and that spawning occurs during the boreal spring–summer as reported by Chang *et al.* (2018) for the WCNPO stock in the western North Pacific off Taiwan. Furthermore, reproductive-maturity studies of the SWPO stock of striped marlin reported that spawning occurred between ~18 and 32°S latitude during October–January, a temporal offset of ~6 months from the WCNPO stock (Kopf *et al.* 2012; Farley *et al.* 2021). Given these assumptions and previous findings, we assume the presence of two stocks with only one spawning stock (WCNPO) in central North Pacific waters. Our approach in the estimation of functional-maturity ogives and L_{EF50} included analyses based on datasets restricted to the female spawning season as well as alternative analyses based on datasets excluding regenerating (EXREG) phase fish (mature but reproductively dormant) from the spawning season data to account for the possibility of SWPO stock mixing in the WCNPO region (i.e. Lam *et al.* 2022). We also present new information on sex-specific monthly reproductive composition, spawning season, length distributions by sex and season and observed sex ratios.

Materials and methods

Sample collection

Gonad samples were obtained onboard HPLF vessels during fishing trips targeting bigeye tuna and swordfish in the

central North Pacific. Contracted fishery observers trained and monitored by the National Marine Fisheries Service, Pacific Islands Regional Office in Honolulu, Hawaii, conducted all sampling at sea. Observers were requested to sample a maximum of 10 fish per trip and to randomly sample across the available length range. Gonad sampling involved the excision of a 1.5- × 2.5-cm section from the middle portion of either lobe of the testis or ovary that included a portion of the gonad wall. Excised gonads were preserved at sea in individual 100-mL plastic bottles containing the histological preservative Shandon Glyo-Fixx RTU (ThermoScientific). When this preservative was not available, samples were stored frozen at sea. Each sampled fish was measured for eye-fork length (EFL; posterior margin of the orbit to the centre tip of the caudal fin) to the nearest centimetre. Other recorded data associated with each sampled fish included capture date and location (latitude and longitude).

The collection period ranged from March 2008 through July 2012 and included gonad samples collected from 399 HPLF vessel trips. Observers sampled across a range of sizes during each trip and across all calendar months. The capture locations of sampled fish of both sexes over the 4-year sampling period are bounded between 5 and 40°N latitude and 135°W and 180° longitude (Fig. 1). Areas of concentrated sampling primarily align with waters immediately north of the Hawaiian Archipelago from north of the north-western

Hawaiian Islands (NWHI) eastward above to and past the main Hawaiian Islands (MHI). A smaller concentration of samples occurred in an area south-west of the MHI and east of Johnston Atoll between 10 and 20°N latitude and 160 and 170°W longitude (Fig. 1). These sampling areas coincide with the spatial distribution of catch and effort conducted by the HPLF fleet during 2008–2013 (Tagami and Wang 2015).

Sample preparation

In the laboratory, gonad samples were prepared for histology. Fresh samples preserved at sea (females $n = 286$, males $n = 279$) were cross-sectioned, a subsample containing the gonad wall was removed, placed in histology cassettes and stored in a container of fresh Shandon Glyo-Fixx RTU (Thermo Scientific) preservative. Frozen samples (females $n = 305$, males $n = 215$) were similarly subsampled on thawing, placed in histology cassettes and fixed in a container of 10% neutrally buffered formalin. Preservation method for a small portion of the histology samples (females $n = 7$, males $n = 36$) was not recorded. Transverse sections of all gonad samples were placed with their transverse sides facing the front and back of the histology cassette prior to histology. Histological preparation of each gonad consisted of three sequential 5-µm-thick cross-sections mounted and sealed on a microscope slide, all stained and counterstained with haematoxylin and eosin respectively. Histology was performed by the Histology Core facility of the John A. Burns School of Medicine, University of Hawaii, Manoa. The exclusive use of histology preparations in this study was essential because this methodology provides the most definitive and accurate means to distinguish between reproductively immature (virgin) and reproductively quiescent (regenerating phase) mature fish of either sex (Luers *et al.* 2018).

Histological examination

All gonad histology slide preparations were examined with a compound microscope over a range of magnifications (40–600 \times). Each slide was evaluated microscopically to identify sex and document all developmental stages of oogenesis or spermatogenesis present. Other ovarian features recorded included relative ovarian wall thickness and the presence of vascularised connective tissue, lamellae, atretic oocytes and residual hydrated oocytes. For females only, the visual quality of an individual histology slide, in terms of ability to assign reproductive phase, was categorised as either distinct, adequate or marginal. In testes, lobules were examined to identify spermatogonia (SA) and spermatogenic stages (spermatocytes, SC, and spermatids, ST) present within cysts, the condition of the germinal epithelium (continuous or discontinuous), the presence or absence of spermatozoa (SZ) in the lumen of lobules and sperm ducts, and the cross-sectional shape of the sperm duct.

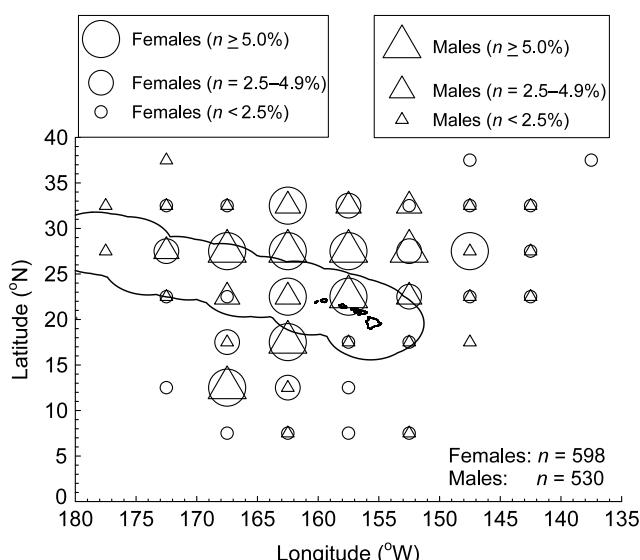


Fig. 1. Central North Pacific capture locations of histology-confirmed female ($n = 598$) and male ($n = 530$) striped marlin sampled by NOAA domestic fishery observers onboard longline fishery vessels of the Hawaii-based pelagic longline fleet during March 2008 to July 2012. Sampling locations are spatially aggregated into 5-degree squares in latitude and longitude to protect the confidentiality of fishery data. The outlines of the main Hawaiian Islands and the 200-nautical mile (~370-km) US exclusive economic zone (EEZ) boundary associated with the Hawaiian Archipelago are plotted for perspective.

Previous billfish reproductive studies have used a variety of reproductive terminology and maturity criteria. In this study, we have adopted the standard terminology of Brown-Peterson *et al.* (2011) to guide in the classification of reproductive phases or subphases for females and males. Spawning season was delineated by the start and end dates when actively spawning subphase females were observed.

Statistical analysis

All data recorded from the microscopic evaluation of prepared gonad histology slides were digitised for statistical analysis. Data included sex, reproductive phase, oogenesis or spermatogenesis developmental stages present, observations on additional gonadal structures present and preservation method. Histology data for each gonad were linked to the observer collection data of the field-sampled fish that included sample identification number, capture date, location (latitude and longitude) and length (EFL).

Logistic regression, which is the appropriate form of generalised linear model for a binary response variable such as maturity state, was used to estimate the intercept (eye-fork length at median (50%) maturity, L_{EF50}) and the slope of the logistic maturity ogive (β_1), where the probability that a fish is mature (p) is a function of its length (EFL), as follows:

$$p = \frac{1}{1 + \exp(-\beta_1 EFL - L_{EF50})} \quad (1)$$

In this context, fish length was a continuous predictor and month was a factor variable. Ogive parameters were determined using a robust logistic regression approach based on a broad class of robust ‘maximum likelihood type-estimates’ (M-estimates) for which the objective function to be minimised is a sample average¹ (Huber 1981; Cantoni and Ronchetti 2001). We used a robust regression approach to reduce the impact of biological outliers on parameter estimates. This was undertaken to account for the potential impacts of including some striped marlin samples that originated in the SWPO (e.g. Lam *et al.* 2022) or the EPO stocks. The robust regression models were fitted using the Huber M-estimator (i.e. `glmrob()` in R package ‘robustbase’, ver. 0.93-9, see <https://cran.r-project.org/package=robustbase>; Huber 1981) with a tuning constant of $k = 1.345\sigma$, where σ was the standard deviation of the errors for each fitted model and dataset. This choice of tuning constant provided an ~95% coverage for the case of normally distributed errors, while also providing robustness by down-weighting outliers. We also fit logistic regressions by using a maximum-likelihood approach with least squares for comparison. The logistic regression models were fitted in the R language (ver. 4.1.0, R Foundation for Statistical

Computing, Vienna, Austria, see <https://www.r-project.org/>) by using the `glmrob()` (Cantoni 2004) and `glm()` functions to compute the M-estimates and maximum-likelihood estimates of the maturity-ogive parameters respectively.

Two working hypotheses about striped marlin maturation by sex as a function of fish length were examined using logistic regression models. These were as follows: (1) fish maturity is solely a function of fish length (Model 1); and (2) fish maturity is a function of both fish length and the month sampled (Model 2). Thus, Model 2 included an additional seasonal effect on observed maturity state. Differences in the goodness of fits of Models 1 and 2 were evaluated using Wald’s robust test; results indicated whether Model 1 would be rejected in favour of Model 2 (or not) at the 5% significance level. Sex-specific maturity ogives were determined on the basis of the total sample size, sample size during the female defined spawning season and total and spawning season samples that exclude regenerating (EXREG) or dormant phase fish. M-estimates of the median (50%) length at maturity (L_{EF50}), the 95th percentile of length at maturity (L_{EF95}), the slope of the maturity ogive (β_1) and their standard errors were calculated using the `dose.p()` function in the R package ‘robustbase’ (ver. 0.93-9; Todorov and Filzmoser 2009). Maximum likelihood estimates of all the latter parameters were calculated using the `dose.p()` function in the R package ‘MASS’ (ver. 7.3-53.1, see <https://CRAN.R-project.org/package=MASS>).

Plots of length density distribution of all sampled fish were produced to examine whether sex-specific length distributions differed by maturity status, season, and presence or exclusion of regenerating phase fish. Each length density was calculated using 10 000 non-parametric bootstrap replicates and fitted using the function `density()` in the R language. Empirical comparisons of mean lengths by sampling group were considered similar if there was some overlap in their 95% confidence intervals. We note that the calculated standard errors of the mean lengths could be underestimated if some cluster sampling occurred and reduced the effective sample size of the length-composition datasets.

Ethics statement

Gonad samples were collected from striped marlin caught by Hawaii-based longline vessels under federal permit to conduct commercial fishing for pelagic species on the high-seas around Hawaii. Expired striped marlin individuals were first retrieved from the gear and processed by vessel crew members, gonad samples were then extracted by an onboard fishery observer, and the remaining carcass was stored on ice for commercial sale on return to port in Honolulu.

¹For data \mathbf{x} and parameter vector $\boldsymbol{\theta}$ an M-estimator minimises an objective function $\sum_{i=1}^n g(x_i, \boldsymbol{\theta})$ for a function $g(x_i, \boldsymbol{\theta})$ selected to be robust to outlier data points.

Results

Histological evaluation of samples

Ovary and testis samples were collected during March 2008–July 2012 across all calendar year months. The spatial distribution of our sample collection by sex (Fig. 1) overlapped the reported spatial distribution of effort across the HPLF grounds (Tagami and Wang 2015). Histological determination of sex, reproductive phase or subphase and assignment of maturity status were successfully conducted on 1128 gonad histology samples that constituted 598 females and 530 males over a length range of 87–192 and 93–193 cm EFL respectively.

Visual clarity of ovarian histological preparations was conducted on 563 of the 598 females examined. Results indicated that for mature females, similar proportions among the categories of visual clarity (distinct, adequate or marginal) occurred regardless of the preservation method. However, among immature females, frozen samples later preserved in formalin yielded smaller proportions of samples categorised as visually distinct and higher proportions of samples categorised as adequate and marginal than did samples after immediate Glyo-Fixx preservation at sea (Supplementary Table S1).

Microscopic images that characterise the reproductive phases or subphases and structural features in females and males are respectively shown in Fig. 2a–h and 3a–g. Microscopic observations showed instances where gonadal structures or intracellular features differed from those set forth in Brown-Peterson *et al.* (2011). On the basis of these differences, several modifications to the set of histological criteria associated with female and male reproductive phases or subphases and maturity status were made to the classification scheme of Brown-Peterson *et al.* (2011) (see Table 1). We observed the co-occurrence of secondary vitellogenic oocytes (Vtg2) and tertiary vitellogenic oocytes (Vtg3) with more advanced-stage oocytes (migratory nucleus through hydration) within the same ovary. On the basis of this observation and the probable accelerated pace of vitellogenesis within striped marlin females inhabiting subtropical epipelagic waters, we used the presence of Vtg2 oocytes (rather than Vtg3-stage oocytes) as the minimal threshold for attainment to the female spawning capable phase and functional maturity. Hence, females undergoing vitellogenesis were assigned as reproductively immature if Vtg1 oocytes were the most advanced oocytes present. The occurrence of residual hydrated oocytes (as noted in Kopf *et al.* 2012) provided an additional histological feature unique to the regenerating phase, to distinguish these mature reproductively dormant individuals from immature phase virgin females.

A recent refinement of the sex-specific histological criteria for reproductive development and terminology has been provided in Lowerre-Barbieri *et al.* (2023). The latter publication proposed a more conservative criteria for classifying females

as spawning capable and also proposed limits to the reproductive phases included in length-at-maturity estimation (immature and spawning phases only). Use of these revised criteria was not adopted in the present study because this would have substantially reduced the sample size used to estimate L_{EF50} .

Histological observations of spawning capable ovaries showed that primary oocytes co-occurred with advanced oocyte stages (migratory nucleus through hydration); the latter two oocyte stages occasionally co-occurred with post-ovulatory follicles in actively spawning subphase ovaries. These observations support earlier findings (Kopf *et al.* 2012; Chang *et al.* 2018) that females are asynchronous batch spawners with indeterminate fecundity.

For males, we modified the criteria of the developing phase proposed by Brown-Peterson *et al.* (2011) to include conditions where spermatozoa (SZ) are present in the lumen of lobules but absent from sperm ducts. Males were assigned to the spawning capable phase when SZ were observed within both the lumen of lobules and sperm ducts.

Spawning season and regenerating phase composition

The timing of spawning and reproductive development differed by sex. The spawning season occurred during May–July; most spawning females occurred in May ($n = 23$), with the remainder occurring in June ($n = 14$) and July ($n = 4$). Actively spawning subphase females comprised 18% (41 of 227 sampled fish) of all females sampled during the spawning season. Immature- and mature-stage females constituted respectively 36 and 64% of the total females ($n = 227$) sampled during the spawning season. During the August–April non-spawning season, immature and mature females contributed respectively 84 and 16% of the total females ($n = 371$) sampled (Fig. 4a).

The female immature (virgin) phase was the single overall dominant phase (58%) among the four female reproductive phases (and three subphases) in each calendar month except June. The female subphases of early and late developing were minor overall components (5 and 3% respectively), with peak occurrence in the 1–2 months preceding the spawning season. The occurrence of spawning capable females began in March, 2 months prior to the start of the spawning season and ceased by August. Regressing females were infrequent (3%) and occurred only during the spawning season and into August. Regenerating females were the phase with the second-highest (16%) occurrence among the four female reproductive phases and three subphases, albeit having a lower occurrence than did the predominant immature virgin phase females. Regenerating phase females occurred in all months and comprised 32 and 80% of all mature females within and outside the spawning season respectively.

For males sampled during the female spawning season ($n = 228$), immature- and mature-status individuals

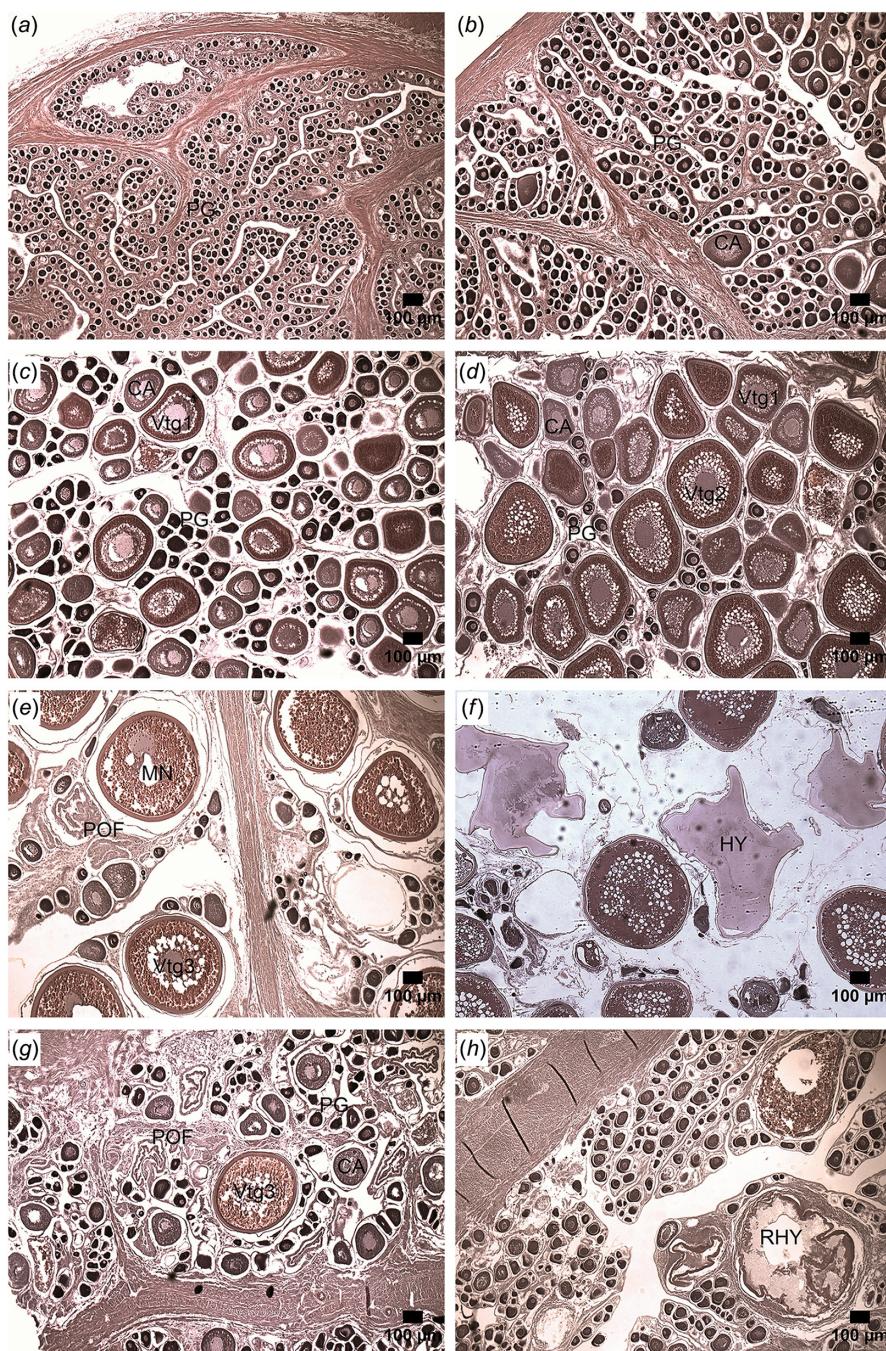


Fig. 2. Striped marlin reproductive phases and subphases observed among ovaries throughout the course of development. (a) A virgin (immature phase) juvenile with only primary-growth (PG) oocytes present. (b) An immature (early developing subphase) female with primarily PG and some cortical alveoli (CA) present. (c) An immature (late developing subphase) female with PG, CA and primary vitellogenic (Vtg1) oocytes present. (d) A mature (spawning capable phase) female with PG, CA, Vtg1 and secondary vitellogenic (Vtg2) oocytes present. (e) A mature (actively spawning subphase) female with tertiary vitellogenic (Vtg3) oocytes, migratory nucleus (MN) oocytes and post-ovulatory follicles (POFs) present. (f) A mature (actively spawning subphase) female with hydrated (HY) oocytes present. (g) A mature (regressing phase) female with predominantly PG, CA and degraded POFs; rarity or absence of viable vitellogenic and more advanced stage oocytes. (h) A mature reproductively dormant (regenerating phase) female with a residual hydrated (RHY) oocyte and atretic yolked oocyte present that indicates that this fish had undergone a previous spawning event.

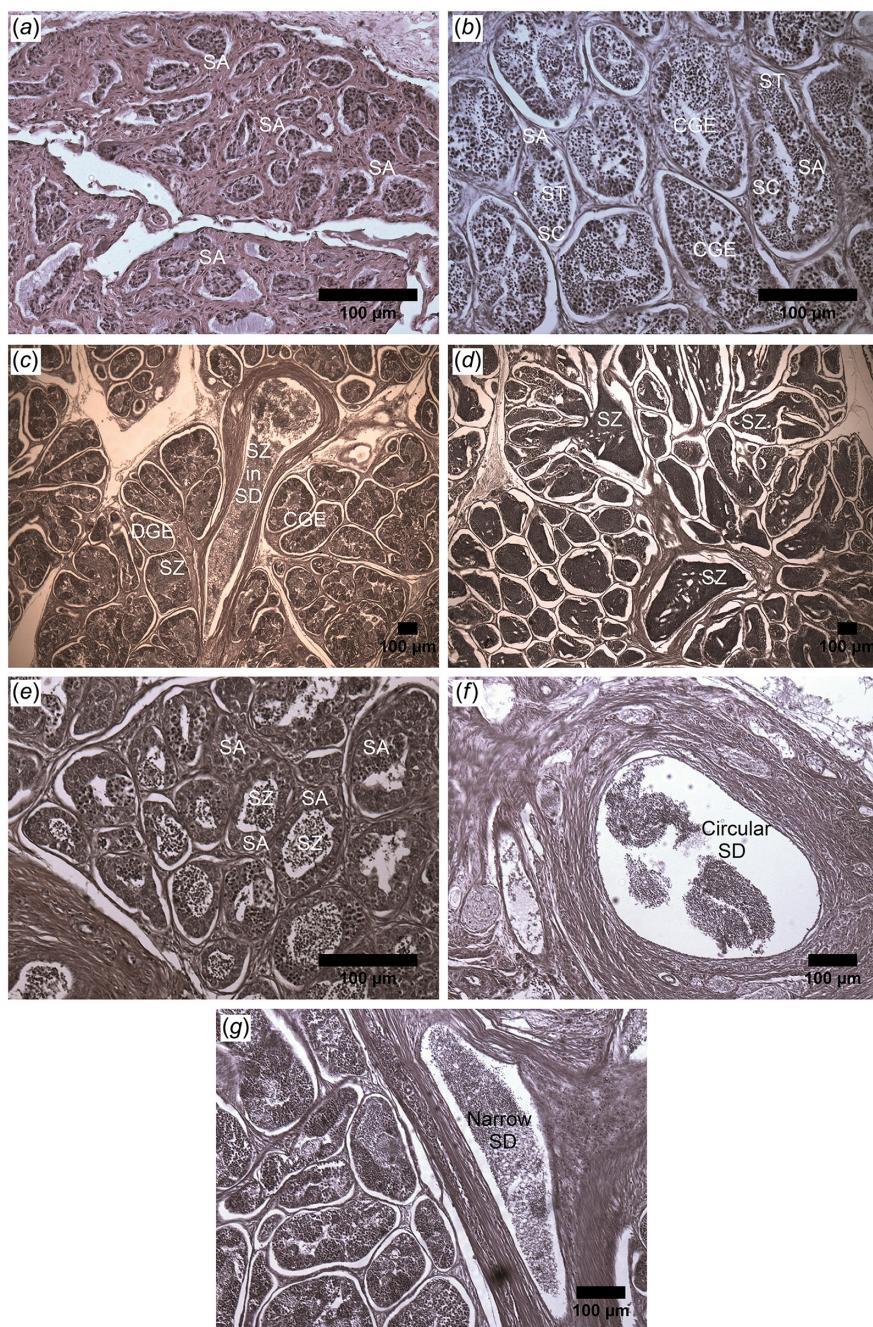


Fig. 3. Striped marlin reproductive phases observed among testes throughout the course of development. (a) Virgin (immature phase) male with no spermatogenic activity present and only spermatogonia (SA) present in lobules. (b) An immature (developing phase) male with spermatogenesis present, lobules display continuous germinal epithelium (CGE) with cysts present containing SA, spermatocytes (SC) and spermatozoa (ST), but no spermatozoa (SZ) present in lumen of lobules. (c) A mature (spawning capable phase) male with SZ present in lumen of lobules, lobules with CGE and discontinuous germinal epithelium (DGE) and sperm duct (SD) densely packed with SZ. (d) A mature (regressing phase) male with no active spermatogenesis present, lobules filled only with SZ. (e) A mature reproductively dormant (regenerating phase) male with residual SZ present in lumen of lobules, SA lining the lobular lumen but without the presence of spermatogenesis. (f) An open-shaped SD of a spawning capable male filled with SZ. (g) Example of a spawning capable male displaying a narrow-shaped SD similarly filled with SZ. Note that the SD shown in (c) is a combination of an open shape (f) on one end and the remainder being narrow (g) in shape.

comprised 9 and 91% respectively, whereas males sampled ($n = 302$) in the female non-spawning season consisted of 18% immature and 82% mature males. Mature-status males dominated (>73%) in samples collected across all calendar year months (Fig. 4b). Immature (virgin) phase males occurred in most months, but were overall the least frequent (5%) of the five male reproductive phases. Developing phase males were encountered across most months, although they were a minor overall phase component (9%) that peaked (>14%) in January–March. Spawning capable males were overall the most prevalent (61%) of the five male reproductive phases.

Spawning capable males occurred year round and were the dominant reproductive phase prior to (January–April), during (May–July) and after (August and October) the female spawning season. Regressing phase males were also present during most months, but were a minor overall phase component (7%), reaching a monthly maximum occurrence (23%) in July. Regenerating phase males accounted for the second-highest total phase component (18%), although having a lower occurrence than for the dominant spawning capable phase males. Within and outside the female spawning season, regenerating males comprised respectively 14 and 27% of all

Table 1. Sex-specific striped marlin reproductive classification based on microscopic descriptions of gonad histology preparations on the basis of the criteria of Brown-Peterson *et al.* (2011).

Sample size (n)	Sex	Maturity status	Reproductive phase or subphase	Phase or subphase description	Histological features
345	Female	Immature	Immature phase	Virgin, never spawned	Only oogonia and PG oocytes present. No atresia or muscle bundles. Thin ovarian wall and little space between oocytes.
30	Female	Immature	Early developing subphase	Ovaries beginning to develop, but not ready to spawn	PG and CA oocytes only.
19	Female	Immature	Late developing subphase	Ovaries beginning to develop, but not ready to spawn	PG, CA and Vtg1 oocytes present. No evidence of POFs or either Vtg2 or Vtg3 oocytes. Some atresia can be present.
50	Female	Mature	Spawning capable phase	Fish are developmentally and physiologically able to spawn in this cycle	Vtg2 or Vtg3 oocytes or both present or POFs present in batch spawners. Atresia of vitellogenic and/or hydrated oocytes may be present. Early stages of OM can be present.
41	Female	Mature	Actively spawning subphase	Fish are developmentally and physiologically able to spawn in this cycle	Oocytes undergoing early to late GVM, GVBD, hydration or ovulation.
20	Female	Mature	Regressing phase	Cessation of spawning	Atresia (any stage) and POFs present. Some CA and/or vitellogenic (Vtg1, Vtg2) oocytes present.
93	Female	Mature	Regenerating phase	Sexually mature, reproductively inactive	Only oogonia and PG oocytes present. Muscle bundles, enlarged blood vessels, thick ovarian wall and/or gamma/delta atresia or old, degenerating POFs, residual hydrated oocytes or both maybe present.
27	Male	Immature	Immature phase	Virgin; never spawned	Only Sa1, Sa2 or both present; no lumen in lobules.
47	Male	Immature	Developing phase	Testes beginning to grow and develop	Spermatocysts evident along lobules. Sa1, Sa2, Sc1, Sc2, St and Sz can be present in spermatocysts. Sz may be present in lumen of lobules but not in sperm ducts. GE continuous throughout.
322	Male	Mature	Spawning capable phase	Fish are developmentally and physiologically able to spawn in this cycle	Sz present in both lumen of lobules and sperm ducts. All stages of spermatogenesis (Sa2, Sc, St, Sz) can be present. Spermatocysts throughout testes, active spermatogenesis. GE can be continuous or discontinuous.
38	Male	Mature	Regressing phase	Cessation of spawning	Volume of Sz present in lumen of lobules and in sperm ducts range from engorged to residual. Widely scattered spermatocysts near periphery containing Sc, St, Sz typically not present. Little to no active spermatogenesis. Spermatogonial proliferation and regeneration of GE not common in periphery of testes.
96	Male	Mature	Regenerating phase	Sexually mature, reproductively inactive	No spermatocysts. Lumen of lobule often nonexistent. Proliferation of spermatogonia throughout testes. GE continuous throughout. Small amount of residual Sz occasionally present in lumen of lobules and in sperm duct.

Sample size (n) associated with each sex-specific reproductive phase is in left column followed by sex, reproductive phase or subphase, maturity status, phase or subphase description, and histological features, including modifications (in italic) to the Brown-Peterson *et al.* (2011) classification. GE, germinal epithelium; GVBD, germinal vesicle breakdown; GVM, germinal vesicle migration; OM, oocyte maturation; PG, primary growth; POF, postovulatory follicle; Sc, spermatocyte; Sa1, primary spermatogonia; Sa2, secondary spermatogonia; St, spermatid; Sz, spermatozoa; Vtg1, primary vitellogenic; Vtg2, secondary vitellogenic; Vtg3, tertiary vitellogenic.

mature males. The monthly contribution of the male regenerating phase peaked during August–December (29–63%), exceeding the male spawning capable phase during the months of September and November–December.

Within the female spawning season, samples of both sexes were most concentrated within the area bounded by 15–35°N, 150–175°W (Fig. 5a); primarily north of the Main Hawaiian Islands (MHI) and the north-western Hawaiian Islands

(NWHI). The sampling locations of spawning capable phase males during the female spawning season overlapped the spatial distribution of actively spawning subphase females (Fig. 5b). Spawning in both sexes was most concentrated immediately north of the MHI and NWHI, particularly in the areas bounded by 25–30°N, 145–175°W and 20–35°N, 155–160°W. Low numbers of spawning capable males were more widely dispersed in longitude than were their female

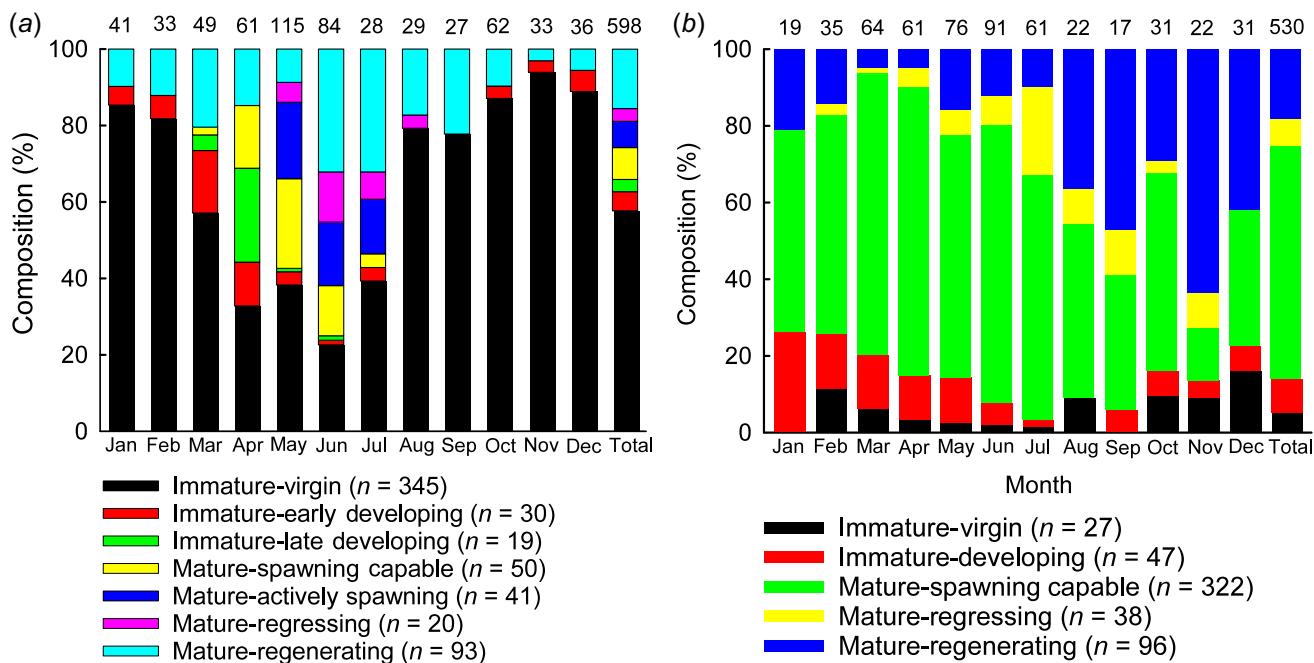


Fig. 4. Monthly composition of striped marlin reproductive phases or subphases for (a) females and (b) males on the basis of all ovary ($n = 598$) and testes ($n = 530$) samples for which reproductive phase or subphase could be histologically determined. Cumulative overall composition of reproductive phases and subphases in each graph is displayed over the label 'Total' on the rightmost side of the x-axis.

counterparts extending westward to 180° longitude and eastward to 140°W. A separate smaller concentration (primarily males) occurred south-west of the MHI between 15 and 20°N and 160 and 170°W. Actively spawning females were not captured above 35°N and below 15°N latitude; overall sampling effort in these areas were low.

Length at maturity

Logistic regression analyses were based on the robust M-estimation approach that down-weighted the influence of outliers in the observed maturity-at-length datasets. The best-fitting maturity ogive for the total female sample was based on the robust GLM Model 2 (including month as a factor variable) logistic regression, where using Model 2 significantly improved the fit to the data (Table 2, robust Wald test, $P < 0.001$). In contrast, Model 1 provided the best fit for the spawning season female sample as Model 2 did not improve the fit (Table 2, Supplementary Fig. S1 and S2; robust Wald test, $P = 0.75$). The best estimate of female L_{EF50} (152.2 ± 1.8 cm) was based on the spawning season (May–July) compared with the L_{EF50} (161.0 ± 4.0 cm) estimate based on the total female dataset. EXREG female L_{EF50} estimates based on the total (165.2 ± 1.1 cm) and spawning season (153.6 ± 1.9 cm) were best fit using Model 1 (Table S2, Fig. S3 and S4; robust Wald test, $P = 0.88$). The resultant ogive and L_{EF50} based on the spawning season EXREG female dataset differed little and did not improve our estimates based on the dataset that included all females sampled during the spawning season

(Fig. 6). Results of additional logistic regression-model runs for all females and EXREG-sampled females, respectively including spawning v. non-spawning season, are given in Tables S2–S6.

For males, the best-fit maturity ogives were all based on robust GLM Model 1 logistic regressions. Male L_{EF50} estimates based on the spawning season dataset (109.0 ± 10.0 cm) provided a better fit than did the total male (119.6 ± 2.6 cm) dataset (Table 2, robust Wald-test P -values to reject Model 1 were $P = 0.07$ and $P = 0.71$). EXREG male L_{EF50} estimates, based on total and spawning season only datasets, were 120.9 ± 2.8 and 109.8 ± 10.3 cm EFL respectively (Table S2, robust Wald-test P -values to reject Model 1 were $P = 0.45$ and $P = 0.08$). Similar to females, best L_{EF50} estimates of total and EXREG males (109.0 ± 10.0 and 109.8 ± 10.3 cm EFL respectively) were achieved using the dataset restricted to the female spawning season. The EXREG male ogive and L_{EF50} estimate differed little and did not improve our L_{EF50} estimate (109.0 cm EFL) based on the dataset of total males sampled within the female spawning season (Fig. 6).

Median lengths (female = 167 cm EFL and male = 155 cm EFL) of actively spawning subphase females and spawning capable phase males during the spawning season exceeded their respective L_{EF50} estimates, particularly among males. The forementioned sex-specific median lengths coincided more closely with their respective L_{EF95} estimates (Tables 2, female $L_{EF95} = 166.6$ cm; male $L_{EF95} = 155.2$ cm).

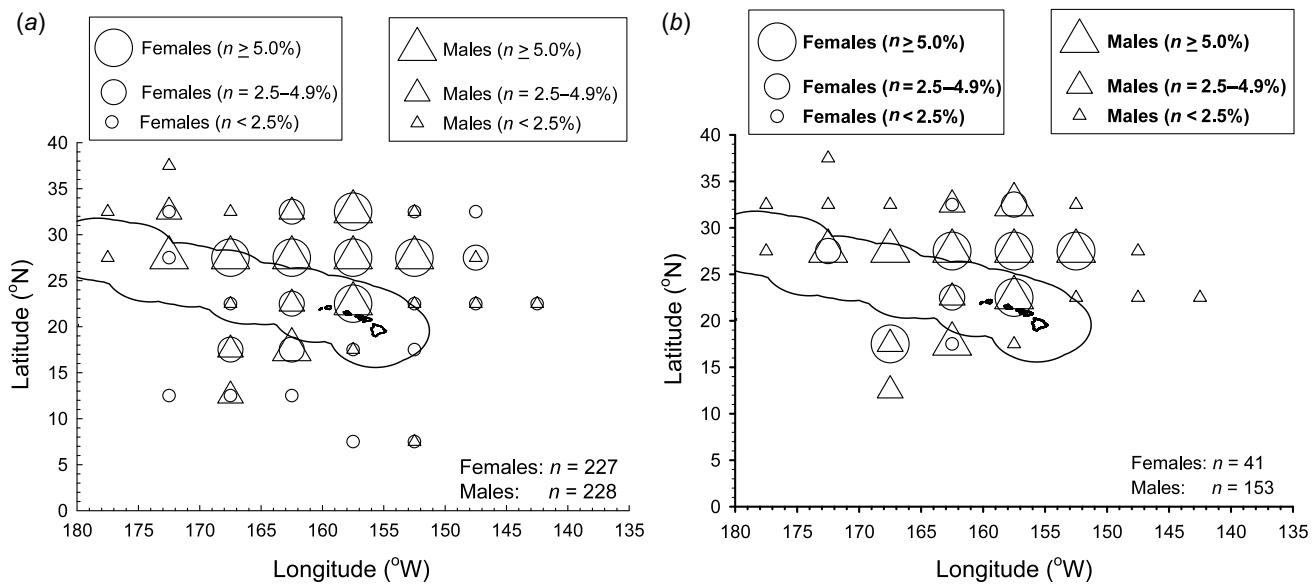


Fig. 5. Central North Pacific locations of striped marlin gonads collected by NOAA domestic fishery observers onboard longline fishery vessels of the Hawaii-based pelagic longline fleet during the female spawning season (May–July) over the years 2008–2012. (a) Spatial distribution and relative abundance of gonad histology-confirmed females ($n = 227$) and males ($n = 228$) and (b) actively spawning subphase females ($n = 41$) and spawning capable phase males ($n = 153$). Sampling locations are spatially aggregated into 5° squares in latitude and longitude to protect the confidentiality of fishery data. The outlines of the main Hawaiian Islands and the 200-nautical mile (~370-km) US exclusive economic zone (EEZ) boundary associated with the Hawaiian Archipelago are plotted for perspective.

Table 2. Summary of striped marlin female and male maturity-ogive results based on robust logistic regression analysis on total (January–December) and spawning season (May–July) female and male samples respectively.

Model name	β_1	β_1 (s.d.)	β_1 (cv)	P-value	Test statistic	d.f.	Pr > ChiSq	n	L_{EF50}	L_{EF50} s.d.	L_{EF95}	L_{EF95} s.d.
♀M1.Total	0.165	0.017	10%	<0.001	9.80	596	<0.001	598	161.0	0.8	178.9	1.9
♀M2.Total	0.166	0.019	11%	<0.001	59.68	585	<0.001	598	159.0	4.0	176.7	4.6
♀M1.SS	0.204	0.034	17%	<0.001	5.97	225	<0.001	227	152.2	1.8	166.6	2.2
♀M2.SS	0.197	0.033	17%	<0.001	0.57	223	0.754	227	153.4	2.2	168.3	2.6
♂M1.Total	0.091	0.011	12%	<0.001	8.16	528	<0.001	530	119.6	2.6	152.2	2.8
♂M2.Total	0.088	0.012	13%	<0.001	8.07	517	0.707	530	126.1	7.9	159.5	8.6
♂M1.SS	0.064	0.019	29%	<0.001	3.43	226	<0.001	228	109.0	10.0	155.2	5.9
♂M2.SS	0.065	0.019	29%	<0.001	5.28	224	0.071	228	121.3	8.9	166.4	8.6

Model names 'M1' have eye-fork length (EFL) as the predictor, whereas 'M2' uses EFL and month as predictors. All model runs include regenerating phase females and males. Parameter values of best-fit model for each sample category are displayed in bold. β_1 , slope of the maturity ogive; cv, coefficient of variation; d.f., degrees of freedom; L_{EF50} , length at median (50%) maturity; L_{EF95} , length at 95% maturity; n, sample size; s.d., standard deviation; ♀, females; ♂, males; SS, female spawning season (May–July).

Length distribution

The length density distribution among total females displayed a gradual increase, with length culminating in a single major mode centred at ~165 cm EFL, followed by a rapid decline beyond 170 cm EFL (Fig. 7a). When partitioned by maturity status, total immature females (Fig. 7b) displayed a more bimodal distribution, with a minor and major mode centred at ~115 and ~145 cm EFL respectively. Total mature females displayed a distinctly smaller length range composed of a single narrow mode centred at ~165 cm EFL (Fig. 7c).

Length density distributions of total and immature females during the spawning season (Fig. 7d, e respectively) were both bimodal, although the corresponding lengths of their major and minor modes were transposed from one another. Mature spawning season females displayed a distinctly different distribution with a narrow major mode (Fig. 7f). In the non-spawning season, total females and immature females displayed similar bimodal distributions (Fig. 7g, h respectively), whereas the distribution of non-spawning season mature females was restricted to a single major mode (Fig. 7i). Within both the spawning (Fig. 7e, f) and

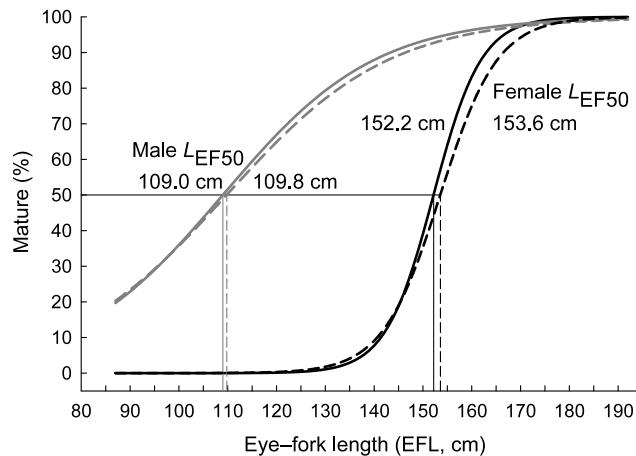


Fig. 6. Striped marlin maturity ogives derived for females and males on the basis of all ovary and testes samples collected during the spawning-season (May–July) interval including (solid line) and excluding (dashed line) regenerating phase fish for which a length measurement (posterior margin of the orbit to the centre tip of the caudal fin, EFL) was available and reproductive phase or subphase could be histologically determined. Dashed horizontal and vertical lines converge on the point for each ogive that corresponds to length at 50% maturity.

non-spawning seasons (**Fig. 7h, i**) seasons, immature v. mature females displayed distinctly different length distributions. Among immature females, length distributions differed between the spawning and non-spawning seasons (**Fig. 7e, h**), whereas mature females showed little seasonal difference (**Fig. 7f, i**).

Length density distributions of EXREG females (Fig. S5a–i) differed from their respective female counterparts (**Fig. 7a–i**) only among mature females. Mature EXREG females exhibited a broader major mode and the presence of a minor mode was centred at ~185 cm EFL (Fig. S5c, f, i) in comparison to their mature female counterparts (**Fig. 7c, f, i**).

Total males (**Fig. 8a**) exhibited a broad major-length mode composed of two adjacent peaks at ~145 and ~155 cm EFL, distinct from that of total females (**Fig. 7a**). Total immature males displayed a bimodal length distribution, with major modes centred at ~115 and ~155 cm EFL (**Fig. 8b**), whereas the distribution of total mature males (**Fig. 8c**) closely coincided with total males (**Fig. 8a**). Both total immature and total mature males showed major and minor modes that differed from those of their respective female counterparts (**Fig. 7b, c**). During the spawning season, the male length distribution of both total males and mature males were similar with a major mode centred at ~160 cm; however, this mode appeared diminished in the distribution of immature

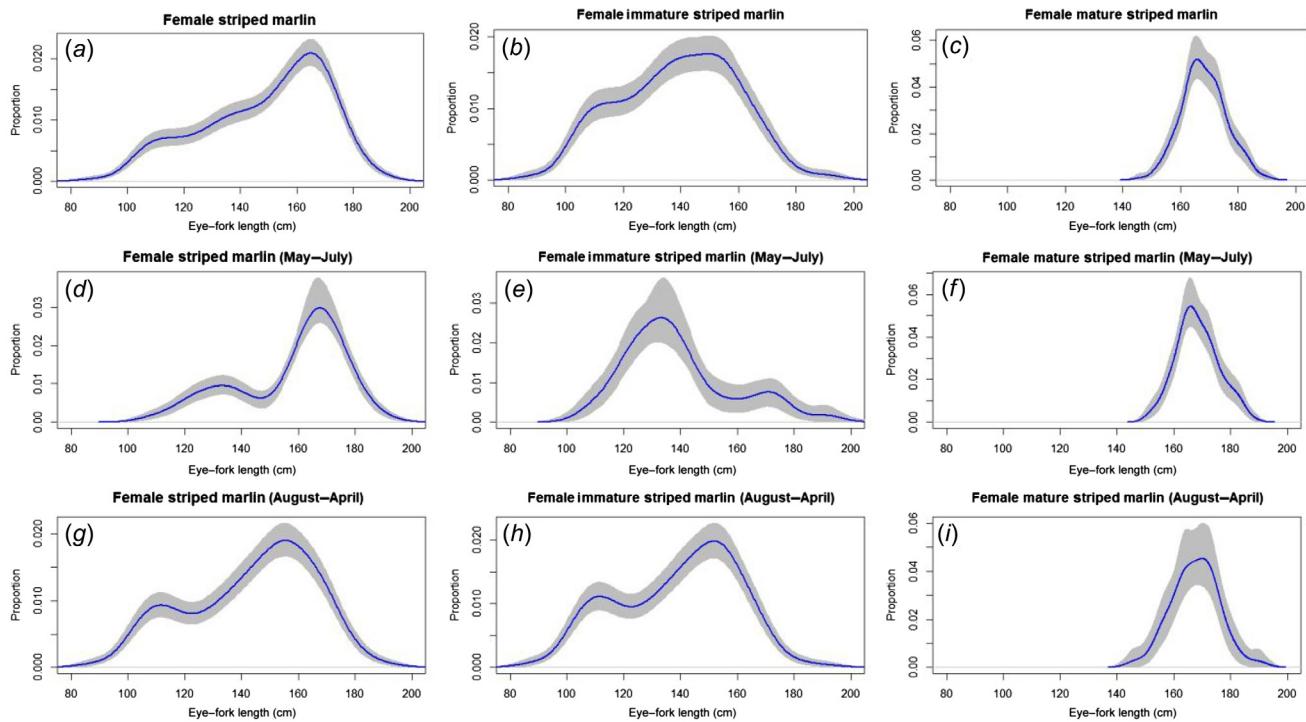


Fig. 7. Female length density-distribution plots of striped marlin lengths (eye-fork length, cm) measured and sampled for subsequent gonad histology by domestic longline observers onboard vessels of the Hawaii-based pelagic longline fleet fishing in the central North Pacific. Plots displayed are based on sampled females (including regenerating phase females) that represent (a) total females ($n = 598$), (b) total immature females ($n = 394$), (c) total mature females ($n = 204$), (d) spawning season females ($n = 227$), (e) spawning season immature females ($n = 82$), (f) spawning season mature females ($n = 145$), (g) non-spawning season females ($n = 371$), (h) non-spawning season immature females ($n = 312$), (i) non-spawning season mature females ($n = 59$).

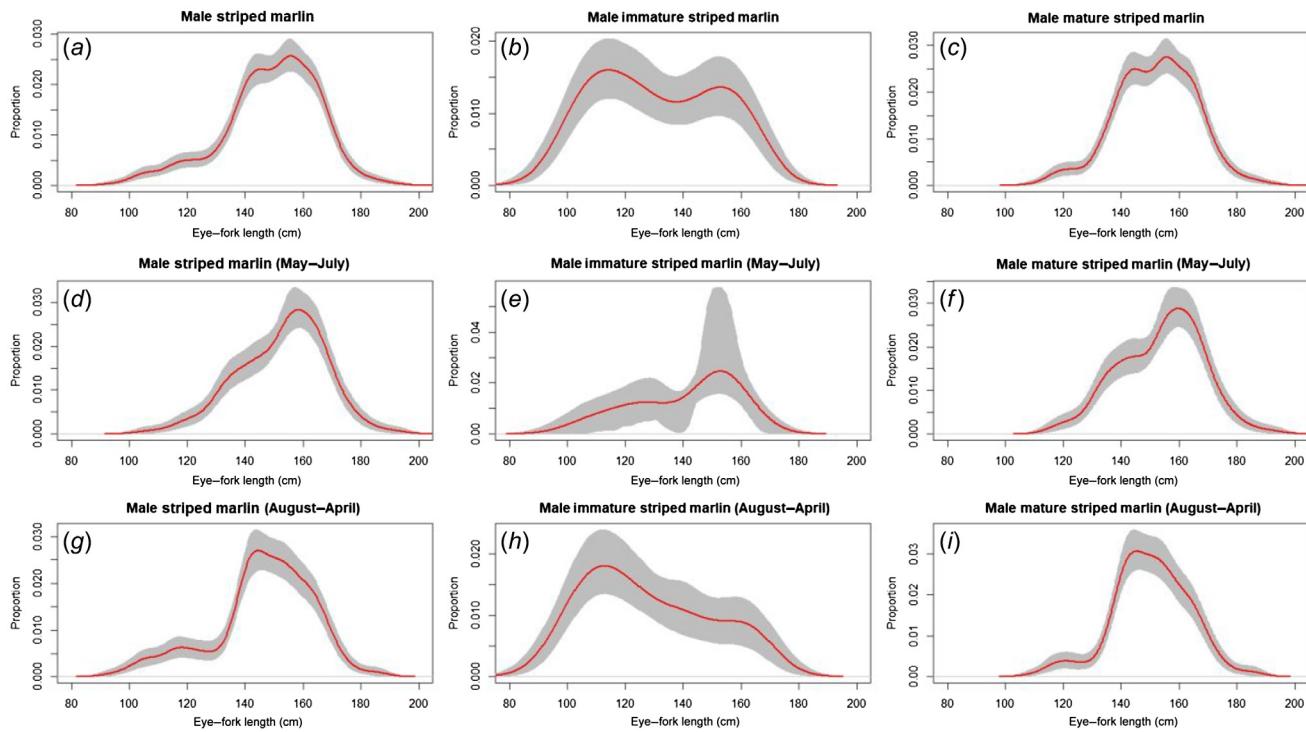


Fig. 8. Male length density-distribution plots of striped marlin lengths (eye-fork length, cm) measured and sampled for subsequent gonad histology by domestic longline observers onboard vessels of the Hawaii-based pelagic longline fleet fishing in the central North Pacific. Plots displayed are based on sampled males (including regenerating phase males) that represent (a) total males ($n = 530$), (b) total immature males ($n = 74$), (c) total mature males ($n = 456$), (d) spawning season males ($n = 228$), (e) spawning season immature males ($n = 20$), (f) spawning season mature males ($n = 208$), (g) non-spawning season males ($n = 302$), (h) non-spawning season immature males ($n = 54$), (i) non-spawning season mature males ($n = 248$).

males (Fig. 8d–f). These latter spawning season distribution patterns differed from those displayed by their female counterparts (Fig. 7d–f). In the non-spawning season, the major and minor modes for total and mature males appeared similar, with the major mode being centred at ~145 cm EFL, whereas immature males displayed a distinctly different distribution (Fig. 8g–i). The major length modes among non-spawning season males were aligned at smaller lengths than those of their respective female counterparts (Fig. 7g–i). Among males, seasonal length distributions varied among mature males (Fig. 8f, i) whereas seasonal differences were more pronounced among immature males (Fig. 8e, h).

Length density distributions of EXREG males (Fig. S6a–i) differed from their respective non-EXREG male counterparts (Fig. 8a–i) in the length alignment of the major mode. In the non-spawning season, EXREG males (Fig. S6g) and mature males (Fig. S6i) had a major mode centred at ~155–160 cm EFL, whereas the major mode of their male counterparts was centred at ~145 cm EFL (Fig. 8g, i). Length distributions of EXREG immature males (Fig. S6b, e, h) and their respective immature male counterparts (Fig. 8b, e, h) remained identical because all regenerating phase males were mature.

Total mean length of each sex was identical (149 cm EFL); however, females were significantly larger than males when

compared by maturity status, spawning season and combinations of these two factors, except during the non-spawning season and among immature fish during the spawning season (Table 3). The largest mean length for both sexes occurred among mature fish during the spawning season. For each sex, mature fish were slightly larger in the spawning than non-spawning season. However, mature females were significantly larger than mature males within and outside the spawning season. Smallest female mean length occurred among immature females both within and outside the spawning season, whereas the smallest male mean length was among immature males in the non-spawning season. Mean lengths of EXREG females were comparable to those of their non-EXREG counterparts, except in three categories (total sample, spawning season and non-spawning season) where the means of EXREG females were ~3 cm lower. Mean length differences between EXREG males and their non-EXREG counterparts were within 1 cm (Table 3).

Sex ratio

The total sex ratio (females:(females + males)) based on all histology samples analysed ($n = 1128$) was 0.53. The seasonal total sex ratio was at parity (0.50) and increased (0.55) during

Table 3. Sex-specific striped marlin length-distribution statistics by sample category.

Item	Females				Males			
	n	Mean	s.d.	s.e.m.	n	Mean	s.d.	s.e.m.
Category (total)								
Total sample	598	148.9	22.1	0.9	530	149.0	16.6	0.7
Immature	394	138.9	20.5	1.0	74	131.2	21.2	2.5
Mature	204	168.1	7.7	0.5	456	151.9	13.8	0.6
Spawning season	227	157.7	19.1	1.3	228	152.7	15.0	1.0
Non-spawning season	371	143.5	22.0	1.1	302	146.3	17.3	1.0
Immature × spawning season	82	138.9	19.0	2.1	20	140.5	17.7	4.0
Mature × spawning season	145	168.4	7.5	0.6	208	153.8	14.3	1.0
Immature × non-spawning season	312	138.9	20.8	1.2	54	127.8	21.5	2.9
Mature × non-spawning season	59	167.5	8.3	1.1	248	150.3	13.2	0.8
Category (EXREG)								
Total sample	505	145.4	22.1	1.0	434	148.8	17.4	0.8
Immature	394	138.9	20.5	1.0	74	131.2	21.2	2.5
Mature	111	168.3	7.6	0.7	360	152.4	14.0	0.7
Spawning season	181	155.0	20.2	1.5	199	152.2	14.9	1.1
Non-spawning season	324	140.0	21.3	1.2	235	145.8	18.8	1.2
Immature × spawning season	82	138.9	19.0	2.1	20	140.5	17.7	4.0
Mature × spawning season	99	168.3	7.4	0.7	179	153.5	14.0	1.0
Immature × non-spawning season	312	138.9	20.8	1.2	54	127.8	21.5	2.9
Mature × non-spawning season	12	168.3	8.9	2.6	181	151.2	14.0	1.0

Separate statistics by category are shown for 'total' samples and samples excluding regenerating (EXREG) phase fish. Mean is eye-to-fork length (EFL, cm). n, sample size; s.d., standard deviation; s.e.m., standard error of the mean.

the May–July spawning and August–April non-spawning seasons respectively. By size, total and seasonal sex ratios among the lower (≤ 135 cm EFL) and upper (≥ 160 cm EFL) portions of the total sample length distribution remained predominantly female. However, within the mid-range interval (135–160 cm EFL) of this length distribution, the total and seasonal sex ratios favoured males (Fig. 9).

During the spawning season, the sample sex ratio was predominantly male (0.15–0.45) over the mid-range (135–160 cm EFL) length interval. This mid-range dominance of males consisted primarily of mature (92%) rather than immature males (8%), whereas among females, immature (57%) rather than mature (43%) females were more prevalent. Among the mature reproductive phases, the regenerating phase within the mid-range lengths constituted only 12 and 4% of mature males and females respectively.

In the non-spawning season, the sample sex ratio dominance of males over mid-range lengths declined (0.40–0.65). However, mature males (92%) continued to dominate over immature males (8%) within mid-range lengths, whereas the presence of mature females among all females declined abruptly to 8%. Among mature fish, the regenerating phase within the mid-range lengths rose to 33 and 87% for males and females respectively.

Discussion

Length at maturity

Results of this study provide the first sex-specific histology-derived maturity ogives and L_{EF50} estimates for striped marlin sampled from the central North Pacific. In this study, our 2008–2012 gonad sampling preceded the current accumulation of evidence for stock intermingling within the HPLF fishing grounds (Evans *et al.* 2021; Martinez 2021; Lam *et al.* 2022). Because DNA tissue sampling was not conducted concurrently during gonad collections, an alternate approach was applied to minimise the influence of SWPO stock fish being potentially present in our gonad collections. Sex-specific maturity ogives and L_{EF50} estimates were based on the following two biological assertions: (1) during the central North Pacific spawning season, only the WCNPO stock undergoes spawning on the sampled HPLF fishing grounds, and (2) any mature SWPO females present on the HPLF fishing grounds during the spawning season are reproductively dormant (regenerating phase) because the SWPO spawning season in the South Pacific is offset by ~6 months from the central North Pacific (Kopf *et al.* 2012).

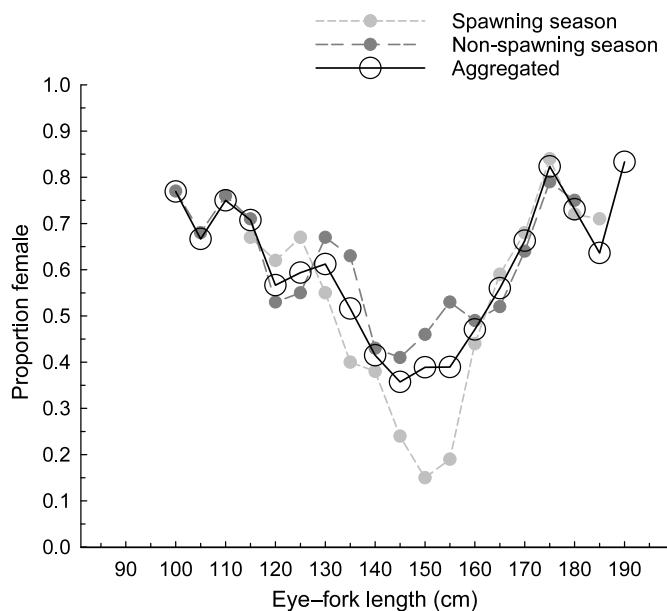


Fig. 9. Length distribution of striped marlin sex ratios (females:(females + males)) based only on histology-confirmed females and males sampled in the study. Plots of sex ratio are shown in relation to length for all months combined (black line), months of the spawning season (May–July) (light grey line) and non-spawning season (August–April) (dark grey line). Sex ratios are binned into 5-cm length intervals; intervals with sample sizes <5 have been excluded.

Estimates of L_{EF50} based on data restricted to the spawning season were similar and not significantly different within each sex whether regenerating phase fish were included or excluded from the analysis. The largest sex-specific L_{EF50} differences occurred when data combined from all sampled months was analysed, typically yielding L_{EF50} estimates 7–12 cm higher than the spawning season estimates. Furthermore, sex-specific maturation estimates based on samples collected over all months do not provide a means to minimise potential biases owing to either mixed-stock samples or cumulative growth realised by mature fish sampled during the middle or late portion of the extensive (9-month) non-spawning season. This latter factor is particularly applicable to striped marlin, which undergo extremely rapid early growth (Kopf *et al.* 2011; Farley *et al.* 2021). Rapid growth and the co-occurrence of immature and mature fish are important reasons why analysis based on spawning season rather than total samples is considered a more accurate approach to length-at-maturity estimation for billfish (Arocha and Barrios 2009). In the case of the central North Pacific, we conclude that our estimates of maturity ogives and L_{EF50} restricted to spawning season samples provided a data-based approach best suited to minimise the specific biases posed by the potential presence of some samples of SWPO fish and the rapid early growth of striped marlin.

Our histology-based sample sizes used to determine sex-specific maturity ogives and L_{EF50} estimates were equivalent

to sample sizes of previous histology-based maturity studies (Table 4) conducted in the western North Pacific off Taiwan (female $n = 228$) by Chang *et al.* (2018), in the eastern North Pacific off Cabo San Lucas, Mexico (female $n = 78$; male $n = 202$) by Sevilla-Rodriguez (2013), and in the western South Pacific (female $n = 186$; male $n = 212$) by Kopf *et al.* (2012). This similarity was true despite using HPLF samples that were restricted to the female spawning season.

Our central North Pacific L_{EF50} estimates (female $L_{EF50} = 152.2$ cm; male $L_{EF50} = 109.0$ cm) were lower for both sexes than were those from other regional Pacific studies based on gonad histology (Table 4). Kopf *et al.* (2012) derived sex-specific L_{EF50} estimates (originally based on lower-jaw fork length, L_{LJ50}) equivalent in EFL to 178.4 and 142.9 cm for females and males respectively, on the basis of longline sampling in the western South Pacific. Farley *et al.* (2021) re-evaluated histology preparations, female maturity criteria, and data analysis used by Kopf *et al.* (2012) to obtain a revised female L_{LJ50} estimate equivalent to ~184 cm EFL. Sevilla-Rodriguez (2013) sampled the sportfishing fleet off Cabo San Lucas, Baja California Sur, Mexico, and reported L_{LJ50} estimates equivalent in EFL to 166.5 and 158.6 cm for females and males respectively. For the western North Pacific area around Taiwan, Chang *et al.* (2018) reported a female L_{EF50} of 180.8 cm but no estimate of male L_{EF50} . These higher female L_{EF50} estimates derived from other regional Pacific studies are not the result of differing histology-based maturity criteria because all used a similar minimum threshold (presence of vitellogenic oocytes) to denote mature females. Except for the L_{EF50} estimate of females off Mexico (Sevilla-Rodriguez 2013), the higher L_{EF50} values of western North and South Pacific females align with those rarely caught HPLF fish at the uppermost limit of the reported length distribution (Sculley 2019). We also note that for male L_{EF50} values, our estimate was considerably less than that derived by Kopf *et al.* (2012) and Sevilla-Rodriguez (2013). Thus, both sexes exhibited the lowest median size at maturity compared with all other Pacific stock regions (Table 4).

Regional differences in female L_{EF50} estimates between the western and central Pacific are not without precedence for other billfish species. In the central North Pacific, female swordfish is also smaller at L_{EF50} (143.7 cm; DeMartini *et al.* 2000) than in the western North Pacific off Taiwan (150.7 cm EFL; Wang *et al.* 2003) and western South Pacific off eastern Australia (161.5 cm EFL; Farley *et al.* 2016). These studies also shared similar ovarian histology-based criteria and the differences are not the result of methodological differences. These earlier maturation rates in the central North Pacific indicate a level of plasticity in billfish reproductive life history, and although the factors that influence earlier maturation remain unknown, regional differences in oceanographic characteristics have been suggested as influencing differences in the life-history characteristics of striped marlin (Lam *et al.* 2022).

Table 4. Chronological listing of previous published striped marlin reproductive studies conducted in the Pacific Ocean that determined length at 50% maturity (L_{EF50}) or spawning season.

Pacific Ocean region	L_{EF50} (cm)	L_{EF50} gonad samples (n)	Spawning season	Spawning season (n)	Method used	Reference
Western NP	NR		May–June	104 total larvae ^A	Larval captures by 1.4- and 2.0-m diameter plankton net tows	Ueyanagi (1964)
Western-central SP	NR		October–January	104 total larvae ^A	Larval captures by 1.4- and 2.0-m diameter plankton net tows	Ueyanagi (1964)
Eastern NP	NR		May–June	46 ovaries	GSI \geq 3.0	Kume and Joseph (1969)
Eastern SP	NR		November–December	19 ovaries	GSI \geq 3.0	Kume and Joseph (1969)
Western SP	NR		November–December	26 ovaries	GSI $>$ 5.0	Hanamoto (1977)
Western-central NP	NR		Primarily April–June	674 larvae	Larval captures by 1.4- and 2.0-m diameter plankton net tows	Nishikawa <i>et al.</i> (1985)
Western-central SP	NR		Primarily October–December	149 larvae	Larval captures by 1.4- and 2.0-m diameter plankton net tows	Nishikawa <i>et al.</i> (1985)
Eastern NP, off Gulf of California, Mexico	NR		June–September, November	68 larvae	Surface larval captures by 0.6-m diameter plankton net tows	Gonzalez-Armas <i>et al.</i> (1999)
Eastern NP, off coastal Mexico	NR		May–December	75 ‘mature’ ovaries	Gonad histology	Gonzalez-Armas <i>et al.</i> (2006)
Eastern NP, off coastal Mexico	NR		June–September, November	76 larvae	Surface larval captures by 0.6-m diameter plankton net tows	Gonzalez-Armas <i>et al.</i> (2006)
Central NP, Kona coast, Hawaii Island	NR		May	7 larvae	Surface larval captures by 1.8 m wide Issac-Kidd trawl	Hyde <i>et al.</i> (2006)
Western SP	♀ 178.4	♀ 186	♀ October–January	17 ‘actively spawning’ ovaries	Gonad histology	Kopf <i>et al.</i> (2012)
Western SP	♂ 142.9	♂ 212	♂ September–March	67 ‘actively spawning’ testes	Gonad histology	Kopf <i>et al.</i> (2012)
Eastern NP, Mexico	♀ 166.5	♀ 78	♀ April–September	♀ NR	Gonad histology; IGS	Sevilla-Rodriguez (2013)
Eastern NP, Mexico	♂ 158.6	♂ 202	♂ Year-round	♂ NR	Gonad histology; IGS	Sevilla-Rodriguez (2013)
Western NP, Taiwan	♀ 180.8	♀ 228	♀ April–August	♀ NR	Gonad histology, GSI	Chang <i>et al.</i> (2018)
Western SP	♀ ~184	♀ 150	♀ October–January	24 ‘spawning capable’ and ‘actively spawning’ ovaries	Gonad histology	Farley <i>et al.</i> (2021)
Central NP	♀ 152.2	♀ 227	♀ May–July	41 ‘actively spawning subphase’ ovaries	Gonad histology	Present study
Central NP	♂ 109.0	♂ 228	♂ Year-round	322 ‘spawning capable phase’ testes	Gonad histology	Present study

Successful larval-capture studies were also included in the determination of spawning season. Sample size (n) associated with the determination of eye-fork length at 50% maturity (L_{EF50}) and the determination of the spawning season appear in columns immediately to the right of the latter two life-history traits. NP, North Pacific; SP, South Pacific; EFL, eye-fork length; ♀, female; ♂, male; NR, not reported; GSI, gonad somatic index (gonad weight \div length³ \times 10⁴); IGS, *indice gonadosomatico* (gonadosomatic index; gonad weight \div (body weight – gonad weight) \times 100).

^AWestern NP and Western-central SP counts are combined.

However, for males of striped marlin, the evaluation of reported regional differences in L_{EF50} estimates are confounded by different male maturity criteria used among studies. The histological basis for distinguishing mature from immature males in the present study was primarily the presence of spermatozoa in the lumen of lobules and sperm ducts, a criterion used in tropical tuna (Schaefer 2001) and swordfish (DeMartini *et al.* 2000) maturation studies. The study of Kopf *et al.* (2012) used additional maturity criteria that included the proportion of SZ within lobules (mature: >75% full) and sperm-duct morphology (mature if ducts are circular in cross-section; immature if narrow or convoluted). These two additional male-maturity criteria applied in the study of Kopf *et al.* (2012) were considered too arbitrary and were not used in our study. Inclusion of the sperm duct-morphology criterion by Kopf *et al.* (2012) was originally used to help assess maturity in skipjack tuna (Ratty *et al.* 1990). However, we observed SZ present within sperm-duct cross-sections ranging from circular to narrowly elliptical to convoluted in shape and therefore also excluded this criterion. The male histology criteria applied in the study of Sevilla-Rodriguez (2013) deemed maturity on the basis of the clustering of enlarged lobules around the main sperm duct and not on either the proportion of SZ within lobules or sperm-duct morphology (Kopf *et al.* 2012), and did not explicitly state whether the occurrence of SZ in sperm ducts was a criterion. Without histology-based standard criteria to distinguish immature from mature males, the validity of current regional disparities in male L_{EF50} estimates remains unresolved.

The lack of standard histology-based criteria to assess male maturity status for billfish species in general has persisted since the histological descriptions of testes development in Atlantic istiophorid species by de Sylva and Breder (1997). The latter study reported the year-round presence of SZ in both the lobules and sperm ducts of small males of Atlantic billfish species. These small males also displayed active spermatogenesis, but were considered not in ripe spawning condition. de Sylva and Breder (1997) considered attainment of maturity to occur in the successive reproductive phase where SZ fills both lobules and sperm ducts and active spermatogenesis is low or has ceased. However, in the reproductive classification presented in Brown-Peterson *et al.* (2011), the latter male-maturity threshold of de Sylva and Breder (1997) would correspond to either the regressing phase or the advanced subphase of spawning capable males. Resolution of the divergent thresholds of maturity attainment in males requires future agreement and adoption of standard methodology either through acceptance of an existing suite of histological criteria applicable to all teleost males (i.e. Brown-Peterson *et al.* 2011; Lowerre-Barbieri *et al.* 2023) or criteria specifically developed for billfish species.

The disparity between sex-specific L_{EF50} values (female $L_{EF50} = 152.2$ cm >> male $L_{EF50} = 109.0$) observed in this study has also been found in the western South Pacific (Kopf *et al.* 2012), but not in the eastern North Pacific

(Sevilla-Rodriguez 2013). Similar patterns of substantially higher female L_{EF50} than male L_{EF50} have been documented among other billfishes. Estimates of female L_{EF50} of ≥40 cm compared with male counterparts have been reported for swordfish in the central North Pacific (DeMartini *et al.* 2000) and in the south-western Indian Ocean (Poisson and Fauvel 2009). Sun *et al.* (2009) also reported a wide sex-specific disparity among blue marlin in the western North Pacific. In the case of striped marlin, the disparity in L_{EF50} between sexes also manifests in sex-specific differences in age at median (50%) maturity (A_{EF50}).

An averaged von Bertalanffy growth model for the central North Pacific, based on fin spine annuli counts and tag-recapture length data, provided A_{EF50} estimates of ~0.5 and ~2.5 years for male and female striped marlin respectively (Fitchett 2019). This latter sex-pooled growth model yields age estimates of the observed spawning season length modes (at ~135 and ~160–170 cm EFL) to be ~1.5 and ~2.5 years respectively. Among both sexes and particularly immature fish, our length density distributions showed that the smallest length mode (~115 cm EFL) appears during the non-spawning season; this is interpreted as the recruitment cohort of young-of-year (YOY) fish into the HPLF. The length mode at ~135 cm EFL in the following spawning season is attributed to successive growth of YOY fish, which attained Age 1 year by the spawning season, in contrast to the estimate of Age ~1.5 years by Fitchett (2019). Age interpretation of the other spawning season length mode (at ~160–170 cm EFL) observed in our study for both female and male length density distributions is confounded by the subsequent decline in annual growth beyond Age 2 years and the potential presence of SWPO-stock fish whose ages would be offset by ~0.5 year compared with WCNPO fish. Nevertheless, the rapid attainment in length by Age 1 year among striped marlin ranks, along with blue marlin, as the fastest absolute growth rates in length recorded for teleost species (Prince *et al.* 1991; Kopf *et al.* 2011).

In other Pacific regions, age and growth analyses based on enumeration of otolith daily growth increments and fin spine annuli indicate that western South Pacific fish also have fast regional growth rates (Kopf *et al.* 2011), with males and females attaining L_{J50} by 1.0 and 2.15 years respectively. Growth rates slower than those in the western South Pacific and central North Pacific have been reported for the western North Pacific off Taiwan (Sun *et al.* 2011) and in the eastern North Pacific off Cabo San Lucas, Mexico (Melo-Barrera *et al.* 2003). These latter growth curves when applied to their respective regional L_{EF50} estimates indicated that females off Taiwan mature no earlier than 4 years, whereas males and females off Mexico mature at ~7 and ~8 years respectively. Confirmation of these regional growth differences and corresponding estimates of A_{EF50} require future efforts to standardise methodologies in fin spine and otolith preparation and annuli and daily growth increment interpretation (Kopf *et al.* 2010).

Length distribution and sex ratio

Spatiotemporal differences in the mean length of HPLF-caught striped marlin by year and quarter-year have previously been reported on the basis of analyses of HPLF observer data (Sculley 2019; Brodziak and Sculley 2022). Fish of mean length of ≥ 150 cm EFL preferentially occur north of Hawaii, in contrast to fish of a smaller mean length (≤ 135 cm EFL) adjacent to or south of the islands. Quarterly analysis of these data showed that larger mean length fish are widely distributed across the Hawaii-based longline fishery during peak spawning (May–June) in the second quarter (April–June). Within a given year, the highest quarterly mean lengths were observed in April–June and the lowest quarterly mean lengths were observed during the first (January–March) and fourth (October–December) quarter. During the first and fourth quarters, smaller mean lengths and the presence of a distinct juvenile length mode (YOY recruits) characterise the HPLF fishing grounds (Sculley 2019). The quarterly length trends are consistent with our seasonal length density-distribution results for females and males. Furthermore, there were notable positive associations observed in 1994–2020 among quarterly mean lengths of striped marlin caught in the HPLF during Quarters 1, 2 and 3 (Brodziak and Sculley 2022). Analyses of annual sex-pooled length-frequency data from the HPLF for the periods 1994–2010 (Courtney 2011), 1995–2017 (Sculley 2019) and 1994–2020 (Brodziak and Sculley 2022) support our assumption that the length characteristics of our samples are consistent with those recorded from the HPLF catch. Our sample mean length (EFL) for both sexes (149 cm) is small compared with either the western North Pacific (females 167 ± 20 cm; males 155 ± 19 cm) reported by Chang *et al.* (2018) or the eastern North Pacific off Cabo San Lucas, Mexico (means only; females 174 cm; males 171–172 cm) reported in Ortega-Garcia *et al.* (2003) and Sevilla-Rodriguez (2013). The combination of higher proportions of small fish, smaller mean length, and rarity of larger fish (≥ 180 cm EFL) distinguishes the overall length composition in the HPLF from other fisheries in the western and eastern North Pacific.

The sex-ratio parity observed in the central North Pacific during the spawning season and subsequent increase (to 0.55) during the non-spawning season differs from those in other Pacific regions. In the western North Pacific around Taiwan, Chang *et al.* (2018) reported a low sex ratio (0.37) during their spawning season that increased towards parity (0.49) in the non-spawning season. In the eastern North Pacific, sex ratio data reported by Kume and Joseph (1969) from 1960s catches by the Japan distant-water longline fleet also showed a low sex ratio during the spawning season. A similar observation was reported by Shimose *et al.* (2013) from the near-continental eastern Pacific area off Mexico. However, Sevilla-Rodriguez (2013) found a higher sex ratio (0.58) during the spawning season off Cabo San Lucas, Mexico, whereas males dominated (0.37) during the

non-spawning season. The latter sex-ratio pattern was similarly observed from this same region and fishery by Ortega-Garcia *et al.* (2003). In the longline fishery sampled off eastern Australia, the sex ratio was close to parity during the spawning season, but declined during the non-spawning season (Kopf *et al.* 2012). These observations from other Pacific regions highlight the unique seasonal sex-ratio pattern observed in the central North Pacific.

Fluctuations in sex ratio relative to length is another distinct aspect of spawning observed in the central North Pacific. This specifically refers to the abrupt decline to low spawning season sex ratios only within the mid-range (135–160 cm EFL) interval of the length distribution. When our sex-specific length data are aggregated across all months, this pattern diminishes but remains present within the 140–155 cm EFL interval. This pattern has not been reported from other regional longline fisheries in the western Pacific. Sex ratios favour males of < 165 cm EFL in the western North Pacific (Wang *et al.* 2006; Chang *et al.* 2018) and males of < 197 cm EFL in the western South Pacific (Kopf *et al.* 2012); thereafter, sex ratios increasingly favour females among only the larger length classes in both forementioned regions. Only in the eastern North Pacific (Cabo San Lucas, Mexico) sport-fishery does a similar fluctuation in sex ratio occur within the mid-range (equivalent to ~ 152 –178 cm EFL) of their length distribution (Sevilla-Rodriguez 2013). Additional insight into spawning activity within the central North Pacific lies within the seasonal sex-specific ratio of maturity status associated with the mid-range (135–160 cm EFL) length interval.

In the central North Pacific, immature females and mature males are predominantly represented within the mid-range (135–160 cm EFL) length interval in both the spawning and non-spawning seasons. This result would appear to be due to the large disparity in L_{EF50} between females and males. With YOY recruitment into the HPLF beginning in the fourth quarter (Sculley 2019), immature female recruits do not reach L_{EF50} by the spawning season of the following year, whereas male recruits appear capable of reaching maturation by Age 1 year. However, this explanation is not consistent with spawning season shifts in mid-length range composition, showing an abrupt increase (to 43%) in mature relative to immature females concurrent with a sudden shift to male-dominated sex ratios. An explanation consistent with these latter two observations requires that a seasonal influx of mature fish of both sexes into the HPLF grounds occurs by the start of the spawning season. However, this influx of spawning season mature fish would need to be skewed toward males within the mid-length range, along with a level of influx of mid-length and larger mature females (160–170 cm EFL) to account for their spawning season increase relative to immature females and seasonal increase towards larger mature females. The subsequent post-spawning season departure of these fish from the HPLF would then shift the maturity composition and sex ratios back to non-spawning season levels. If, indeed, seasonal influxes of females and males

account for the observed seasonal changes in the sex ratio-length relation, they would indicate a previously unrealised dynamic complexity within the central North Pacific, which involves sex and length composition, reproductive phases, maturity status, stock mixing and season.

Spawning season

Gonad-based studies (Table 4) have largely defined our current understanding of the temporal extent of the female spawning season, i.e. it primarily occurs within the spring-summer interval in the North and South Pacific where sea-surface temperature is seasonally $\geq 24^{\circ}\text{C}$ (Ueyanagi and Wares 1974; Gonzalez-Armas *et al.* 1999; Bromhead *et al.* 2004). In the western South Pacific, spawning in the Coral Sea area was reported to be during November–December (Hanamoto 1977), whereas Kopf *et al.* (2012) reported a longer duration (October–January) from this area. In the western North Pacific, females are in spawning condition during April to August off Taiwan (Chang *et al.* 2018). In the eastern North Pacific, Kume and Joseph (1969) reported spawning occurring during May–June. However, more recent studies in the eastern North Pacific area off Cabo San Lucas, Mexico (Sevilla-Rodriguez 2013), have shown that spawning spans spring and summer (April–September), whereas Gonzalez-Armas *et al.* (2006) recorded mature (spawning condition) females mainly during July–October (peak spawning in July–August), although a small number was also recorded during May–June and November–December. This temporally extensive spawning season interval (8 months) is unique to the eastern North Pacific and contrasts with the shorter spawning season (3 months) in the central North Pacific, where spawning season declines (July) and ends (by August) during the time interval of peak spawning in the eastern North Pacific.

In contrast to females, the temporal interval of spawning-condition males was year round within the HPLF sampling area. Similar year-round spawning readiness was also observed in catches of males sampled from the sport fishery off Cabo San Lucas, Mexico, by Sevilla-Rodriguez (2013), whereas Kopf *et al.* (2012) reported a less extensive (September–April) interval in the western South Pacific (Table 4). All these studies found temporal overlap in male spawning activity both prior to and beyond their respective female spawning season. The spatial and temporal overlap in the central North Pacific distribution of spawning condition males relative to female spawners may be adaptive in response to (1) low and variable encounter rates owing to the labile occurrence of female spawners across the spawning grounds, (2) the need to compensate for potential shifts in the timing or location of female spawning because of changes in habitat preference or oceanographic conditions, and (3) the need to adapt to encounters with larger females (within and outside the fishing grounds of the HPLF) who may be capable of spawning over a longer time interval.

In contrast to the HPLF in the central North Pacific, large females (≥ 180 cm EFL) constitute a major proportion of spawners in the western North and South Pacific, are more fecund than smaller-sized spawners (Kopf *et al.* 2012; Chang *et al.* 2018) and spawn over a longer time interval (Chang *et al.* 2018). Currently, there is little knowledge of the location of large fish outside of the HPLF grounds. If large fish remain in the greater central North Pacific region, then a more expansive spawning area potentially exists beyond the fishing grounds of the HPLF. Ichthyoplankton sampling of early life stages provides an additional spatial-temporal method to search for and detect spawning events.

Ichthyoplankton surveys provide a sampling approach complementary to gonad sampling, because plankton tows are typically conducted from research vessels in a systematic fishery-independent manner. The most comprehensive surface ichthyoplankton survey of oceanic waters across the western and central Pacific (1956–1981) was conducted by the Japan Far Seas Fisheries Research Laboratory, which included documentation of the spatial-temporal distribution of striped marlin larvae (Nishikawa *et al.* 1985). Within the sampled central North Pacific, striped marlin larvae were concentrated inside the 20–25°N latitude band, with a lesser concentration between 5°N and 15°N latitudes (Nishikawa *et al.* 1985). Most central North Pacific larvae (61%) were captured south of or adjacent to the Hawaiian Archipelago along the 20–25°N latitude band; equatorial waters (0–15°N) accounted for 14% of larvae. Within the vicinity of the main Hawaiian Islands, a previous billfish larval survey found no striped marlin larvae (Matsumoto and Kazama 1974). A later series of surface ichthyoplankton research surveys (1997–2006) targeting billfish early life stages along the Kona Coast of Hawaii Island (R. L. Humphreys Jr, NMFS, unpubl. data) collected several hundred billfish larvae (including egg stages) of swordfish (*Xiphias gladius*), blue marlin (*Makaira nigricans*) and shortbill spearfish (*Tetrapturus angustirostris*). However, only a few ($n = 7$) striped marlin larvae were collected, all from a single survey (May 2005), despite the frequent capture of adults in these coastal waters by sport and local fishers (Hyde *et al.* 2006). Unlike tunas, other billfishes and other large pelagic teleosts, whose early life stages frequent coastal waters adjacent (<15 km) to the Hawaiian Islands (West 2004; Hyde *et al.* 2005; Paine *et al.* 2008), striped marlin spawning activity and early life stages are primarily reported from oceanic waters within the central North Pacific. On the basis of our gonad-sampling and existing larval-catch data, we surmise that the spawning area in the central North Pacific (1) infrequently extends to nearby coastal waters in Hawaii, (2) remains unknown within the north-western Hawaiian Islands protected species zone and open waters <50 nm offshore of the main Hawaiian Islands (as management measures restrict longline fishing in these areas), and (3) is more expansive than the fishing grounds of the HPLF on the basis of reported larval captures in the central North

Pacific out to 180° longitude and into equatorial waters between 0 and 10°N latitudes (Nishikawa *et al.* 1985).

Management implications

Sex-specific L_{EF50} estimates in the central North Pacific were lower than in all other Pacific regions and were also lower than the female L_{EF50} estimate used in the 2019 WCNPO striped marlin stock assessment (177 cm EFL, International Scientific Committee for Tuna and Tuna-Like Species in the North Pacific 2019). The practical impact of reducing the estimated median length at maturity would be to increase the estimated spawning potential of the stock. However, we also found that the median lengths of actively spawning females (167 cm EFL) and spawning capable males (155 cm EFL) exceeded their respective L_{EF50} estimates, particularly males. Furthermore, these latter sex-specific median lengths more closely coincide with their respective spawning-season L_{EF95} estimates (female $L_{EF95} = 166.6$ cm EFL; male $L_{EF95} = 155.2$ cm EFL). As a result, it may be useful to consider L_{EF95} estimates as an alternate length-at-maturity input parameter. This may aid future stock assessments to better account for uncertainty in the WCNPO striped marlin maturity ogive and also to gauge the sensitivity of the assessment model to this parameter.

The scarcity of large striped marlin greater than 180 cm EFL in the HPLF catch is another source of uncertainty when estimating life-history parameters for input into stock assessments. If, indeed, large fish move beyond the reach of the HPLF, this introduces biases in the estimation of age, growth and reproductive parameters restricted to sampling the HPLF portion of the central North Pacific. Additionally, anticipated increases in the spawning season interval and fecundity-length relationships among rarely sampled fish larger than 180 cm EFL would also contribute to bias in estimates of population productivity.

The major uncertainty that also confounds resolution of the aforementioned issues is the need to understand the spatiotemporal dynamics of stock intermingling within the central North Pacific. Currently, our rudimentary understanding of stock mixing within the HPLF catch is based on a handful of synoptic collections restricted to the HPLF grounds. Evidence of stock intermingling currently requires sampling individual fish. Because the determination of stock identity is reliant on molecular methodology (DNA genotyping) and analytics based on population genetics, the interpretation and appropriate application of these results is a challenge for both stock-assessment scientists and fisheries managers. Furthermore, genetic identification of stocks may reflect events occurring on a more evolutionary rather than ecological time scale and may not detect effective stock separation if low levels of gene flow conceal populations that are primarily isolated from each other. These current limitations present difficult challenges for future stock assessment and management efforts. One potential approach

to resolve the current dilemma in estimating the proportion of stock intermingling is to replace current static management boundaries with a more flexible approach. Assessment of areas could be combined across management areas where stock intermingling occurs and the ability to estimate the proportion of fish by stock origin remains intractable (Lam *et al.* 2022). Advancement and support of future stock-assessment efforts across the WCNPO will necessitate future investigations to evaluate the implications of mixed-stock composition and the level of influx and outflux of fish in relation to reproduction and stock origin.

Despite the limitations of our study, the female-maturity ogive and female L_{EF50} determinations have provided crucial biological inputs for ongoing work on the international assessment of the striped marlin stock in the WCNPO (International Scientific Committee for Tuna and Tuna-Like Species in the North Pacific 2023). The results of this stock assessment are important for the future development and implementation of management measures to conserve and rebuild the WCNPO stock of striped marlin (International Scientific Committee for Tuna and Tuna-Like Species in the North Pacific 2023).

Supplementary material

Supplementary material is available online.

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Data availability. The data included in this study are available upon request to the corresponding author.

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