Reproductive Characteristics of Longtailed Red Snapper (Onaga, *Etelis coruscans)* in the Main Hawaiian Islands

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Executive Summary

The reproductive characteristics of the longtail snapper, *Etelis coruscans* — known locally in Hawaii as "onaga," — was last assessed in 1989; therefore, updated information is needed for improving its stock assessment and management in the bottomfish fishery of the main Hawaiian Islands (MHI). Specimens were collected during research cruises and either donated by individual fishers or purchased from markets during 2007–2008 and 2012–2017. These samples were supplemented with additional monthly samples beginning in April 2019. In this study we provide a length distribution of samples used for analyses, describe an allometric length-weight relationship (b = 2.81), updated length-at-maturity (L_{50}) estimates using six different combinations of data, and estimated the spawning season in the MHI. Females (N = 285) ranged in size from 21.2 to 96.0 cm fork length (FL) with a mean of 58.0 cm and a median of 60.0 cm FL. Of the six types of length-at-maturity combinations estimated, a functional maturity criterion using fish captured during the spawning season was deemed the most accurate despite having the lowest sample size (N = 107). This resulted in a L_{50} estimate of 62.2 cm FL (95% CI, 59.3–65.1), compared to previous estimates of 66.3 cm FL in the MHI and 67.1 cm FL in Okinawa. The functional maturity method had the lowest sample size but was the most comparable to published estimates based on histological methodology. Alternatively, our L_{50} estimate using the physiological maturity method within the spawning season was 54.7 cm FL (95% CI, 51.8–57.6 cm), with a L_{95} of 68.2 cm FL (95% CI, 65.34–71.06 cm). This L_{95} value is similar to a previous L_{50} estimate and may be an appropriate surrogate value in situations when sampling is unable to collect obviously mature females in the spawning–capable phase or at locations where the spawning period is unknown. Data collected to date shows that the *E. coruscans* progresses in oocyte development during January–April, and clearly spawning–capable females occur during September–December. The largest proportion of regressed females occur in December, most likely indicating the end of the spawning period. The addition of more spawning–capable females during the presumed spawning season in future sampling efforts would help to increase the robustness of our functionally mature length-at-maturity estimates and more accurately define the spawning period.

Introduction

Throughout the Indo-Pacific, deep-water eteline (Lutjanidae: subfamily Etelinae) snappers are an important component of small-scale commercial fisheries and increasingly support island artisanal fisheries (Dalzell 1996; Newman et al. 2016; Williams et al. 2017). In general, deep-water fishes are known to have greater longevity, slower growth, and later maturation than shallower–dwelling species and congeners (Koslow et al. 2000; Cailliet and Andrews 2008; Norse et al. 2012). There is growing literature on the life-history characteristics of tropical eteline snappers across their range that indicate low productivity and high vulnerability to overexploitation as a consequence of these characteristics (Haight et al. 1993; Koslow et al. 2000; Newman et al. 2016). Region-specific and species-specific biological and fisheries information is still lacking for stock assessments of many deep-water snappers (Newman et al. 2016; Newman et al. 2018). More specifically, necessary reproductive biology information, such as spawning season and length– and age–at–maturity for these species is limited (Stearns 1992; Newman et al. 2016). In addition to existing life history information, timely comparisons of historical estimates of parameters are needed for assessing stock health and future sustainability.

In Hawaii, the "Deep 7" are a complex of six eteline snappers and one grouper that is managed according to the Western Pacific Regional Fishery Management Council's (WPRFMC) Hawaii Fishery Ecosystem Plan for the Hawaiian Archipelago (Western Pacific Regional Fishery Management Council 2009). The Hawaiian bottomfish fishery began at the turn of the century with native Hawaiian fishers using deep-set handlines from small boats or canoes (Haight et al. 1993a; Langseth et al. 2018). The end of World War II led to the modern-day commercial Hawaiian Deep 7 bottomfish fishery, which had a recorded annual catch limit of 490,000 lb for the 2015–2016 calendar year (Langseth et al. 2018). In 2012, the fishery was worth US$2.35 million dollars at an annual catch limit of 346,000 lb in the main Hawaiian Islands (MHI) (Brodziak et al. 2014), indicating that the fishery revenue increased in recent years. Historically, limited quantitative biological information has been available for the Hawaii bottomfish fishery due to the difficulty in obtaining these high-cost specimens (DeMartini 2016).

The deep-water longtail snapper *Etelis coruscans* — known as "onaga" in Hawaii — occurs across the tropical and subtropical Indo-Pacific (Randall 1978). Of the Hawaii Deep 7, *E. coruscans* is the second most common species by landings but the most valuable in terms of price per pound (Langseth et al. 2018). They occupy the deepest water-column depth range among the Hawaiian eteline snappers, ranging from 210 to 300 m; adults show a preference for associating with greatly sloping hard substrates (Misa et al. 2013). Aspects of habitat (Misa et al. 2013; Moore et al. 2016; Oyafuso et al. 2017), diet (Haight et al. 1993b), genetics (Andrews et al. 2014; Loeun et al. 2014), movement behavior (Okuyama et al. 2019), and larval development (Leis and Lee 1994) have also been documented for this species. Like several other species of etelines, *E. coruscans* is described as long-lived, slow-growing, and late to mature (Uehara et al. 2018; Uehara et al. 2020; Andrews 2020). Across regions, growth and longevity have been documented in New Caledonia, Okinawa, and Hawaii (Williams et al. 2013; Uehara et al. 2020; Andrews et al. 2020). Reproductive characteristics for *E. coruscans* in the MHI were first described by Everson et al. (1989) and included estimates of size at first maturity, median length at maturity, and a spawning season of June to November. In Okinawa, *E. coruscans* displayed similar lengths-at-maturity and a slightly extended spawning season of May to November, compared to the Everson et al. (1989) findings for the MHI (Uehara et al. 2018). However,

information on the length-at-maturity relationship and the spawning season used for *E. coruscans* in the Hawaiian bottomfish fishery assessments is more than 30 years old and needs to be updated. In addition to providing contemporary information for stock assessments, this updated information will allow for a direct species-specific and regional comparison with the best available data to date.

One of the most important aspects of fish reproductive biology that is essential for sustainable fisheries management is the length at which 50% of females become sexually mature (median length–at–maturity, L_{50}). Accurate estimates of L_{50} allow stock assessment scientists to evaluate the spawning stock biomass for potential effects of fishing mortality on a population (Polovina 1987). Traditionally, size-at-maturity is estimated using the known spawning period and histological techniques to assess functional maturity, which is commonly described as the reproductive state of female fish with vitellogenic oocytes capable of spawning within the given year (West 1990; Brown-Peterson et al. 2011). This method of estimation for L_{50} is widely used in fisheries research because of its accuracy and ability to easily identify mature, spawning individuals (Hunter and Macewicz 1985; DeMartini 2016). However, when spawning–capable females are difficult to obtain because of restrictions to sampling effort, fishery dynamics, and cost constraints, maturity may still be estimated using an alternative approach based on physiological maturity. Physiological maturity, the point at which fish become physically mature and incapable of reverting back to immaturity, is defined as the gonadotropin-dependent phase of ovarian development first indicated by cortical alveolar oocytes (Wallace and Selman 1981; Brown-Peterson et al. 2011). This appearance of cortical alveolar oocytes has been used previously to define secondary growth (Murua and Saborido-Rey 2003; Luckenbach et al. 2008; Lowerre-Barbieri et al. 2011) but may need further study before it is used as a surrogate for functional maturity.

The purpose of this study is to update the reproductive characteristics of female *E. coruscans* from the MHI. Specifically, we seek to re-estimate the L_{50} and spawning period of females using the most current data available. Due to the difficulty in obtaining spawning–capable females, we provide additional estimates of L_{50} ogives that are based on reproductive phase, maturity classification (functional or physiological), and inclusion of fish that were captured year-round or only during the spawning period. Finally, we discuss the appropriateness of a physiological maturity classification when a functional classification is unobtainable.

Methods

Sample collection

Female *E. coruscans* were opportunistically sampled during 2007–2008 and 2012–2017 (Table 1). In an effort to produce comprehensive and updated species-specific reproductive information on females, additional samples were targeted for collection from April 2019 to February 2020 in collaboration with fishers and their partners on Maui (Table 1). Samples were also collected from other projects in 2019, including a fishery-independent cruise SE-19-04 in the Main Hawaiian Islands aboard the NOAA Ship *Oscar Elton Sette* in June and the annual BFISH (Bottomfish Fishery Independent Survey) survey in August and September. Fishery-dependent and -independent collection methods used hook-and-line with electric and hydraulic handline gurdies to fish at depths between 100 m and 300 m. Samples were collected at various locations among the MHI, including the islands of Oahu, Maui, Molokai, Kauai and Niihau.

Once caught, fish were placed on ice for 4–24 hrs prior to being processed. A general location, date, vessel, species, and species identification number were recorded for each fish. Biological data were recorded for each fish, including fork length (*FL*, 0.1 cm), weight (*W*, 0.01 kg), and gonad weight (*GW*, 0.01 g). Macroscopic sex identification and a gross macroscopic assessment of maturity (immature, mature) were recorded. A 1.0-cm section, taken from the mid-section of the right gonad, was preserved in a 10% neutral buffered formalin solution for histological verification of sex and reproductive phase at a later date. During the 2019–2020 collection period, gonads were periodically shipped to the laboratory overnight on ice thereby increasing the time on ice to 48 hrs in some cases. However, all specimens were considered to be in good condition upon arrival at the lab, with negligible tissue degradation, and 1-cm sections were immediately preserved for subsequent histological processing.

Table 1. Total number of female onaga (*E. coruscans*) specimens collected from the main Hawaiian Islands by year and month verified with histological analysis. Shaded columns indicate additional sampling that began in April 2019.

Month	*2007*	*2008*	*2012*	*2013*	*2014*	*2015*	*2016*	*2017*	*2019*	*2020*	Total
Jan		3				1	4			**12**	***20***
Feb		18				3				**19**	***40***
Mar		48				2					***50***
Apr		3		2					**13**		***18***
May						2					***2***
Jun									**7**		***7***
Jul			5						**1**		***6***
Aug				6			1		**12**		***19***
Sep					3		2	5	**10**		***20***
Oct	2		13	1	4	7	6		**22**		***55***
Nov	5				1	3			**14**		***23***
Dec	4				2	1			**18**		***25***
Total	11	72	18	9	10	19	13	5	**97**	**31**	***285***

Reproductive biology

Females were chosen for histological analysis of ovarian tissue for validation of the recorded macroscopic sex and maturity and to identify reproductive phase. Formalin-fixed tissue was dehydrated in a series of graded alcohols, cleared in xylene and embedded in paraffin wax following standard histological protocols. Embedded tissue was sectioned transversely at 6 µm, mounted on slides and stained with hematoxylin and eosin. Histology slides were viewed with a compound microscope between magnifications 10–40× for determination of reproductive phase and maturity following Brown-Peterson et al (2011). Female fish were considered functionally mature when ovaries contained vitellogenic oocytes (Brown-Peterson et al. 2011; Lowerre-Barbieri et al. 2011) or physiologically mature when cortical alveolar (CA) oocytes were present (Brown-Peterson et al. 2011). Due to the scarcity of vitellogenic oocytes present in our samples and the large proportion of female *E. coruscans* in a reproductively inactive state across a wide range of sizes, reliance on secondary characteristics and CA oocytes to determine sexual maturity was necessary. However, since the regenerating reproductive phase lacks CA oocytes, secondary characteristics to distinguish between immature and mature but regenerating individuals included the presence of greater spacing among ovarian cells, developed interstitial tissue, capillaries around primary growth oocytes, the presence of atretic yolked-oocytes, and muscle bundles (Brown-Peterson et al. 2011). Reproductive phase was determined by the most advanced oocyte stage present (Table 2) and therefore used for the length–at–maturity analyses.

Determination of maturity ogives

Six different combinations of female reproductive phases and spawning periods were assessed in accordance with our definitions of functional and physiological maturity to estimate length-specific sexual maturity using a logistic curve.

1) Functionally mature individuals caught during the spawning period included the developing, spawning-capable, and regressing reproductive phases. Functionally immature individuals are defined as those in the immature and early developing reproductive phases.
2) Physiologically mature individuals caught during the spawning period included the early developing, developing, spawning-capable, and regressing reproductive phases. Physiologically immature individuals included only the immature reproductive phase.
3) A hybrid approach for functionally mature individuals caught during the spawning period was used to increase sample numbers. Functionally mature individuals included the developing, spawning-capable, regressing, and regenerating reproductive phases. Functionally immature individuals are in the immature and early developing reproductive phases.
4) A hybrid approach for physiologically mature individuals caught during the spawning period included the early developing, developing, spawning-capable, regressing, and regenerating reproductive phases. Physiologically immature individuals included only the immature reproductive phase.
5) Functionally mature individuals captured during all months of the year included the developing, spawning-capable, regressing, and regenerating reproductive phases. Functionally immature individuals captured during all months of the year included the immature and early developing reproductive phases.
6) Physiologically mature individuals captured during all months of the year included the early developing, developing, spawning-capable, regressing and regenerating reproductive phases. Physiologically immature individuals captured during all months of the year included only the immature reproductive phase.

Due to our ongoing sampling and the current lack of specimens from summer months, we defined the beginning of the spawning period as June based on a previous study (Everson et al. 1989). The end of the spawning season was based on the last month (December) during which we identified spawning-capable females.

Table 2. Histological classification of ovarian development for onaga (*E. coruscans*) from the main Hawaiian Islands. Terminology follows Brown-Peterson et al. (2011). Oocyte stage abbreviations: CA = cortical alveolar; GVBD = Germinal Vesicle Breakdown; GVM = G erminal Vesicle Migration; OM = oocyte maturation; and PG = primary growth; POF = Postovulatory complex; Vtg1 = Primary vitellogenic; Vtg2 = secondary vitellogenic; Vtg3 = tertiary vitellogenic oocytes.

Phase	Histological Description
Immature	PG and oogonia dominate. PG are densely packed and highly organized. Chromatin nucleolar stages more common than perinucleolar stages of PG. Thin gonad wall and no atresia present. Few blood vessels present. No evidence of prior spawning.
Early developing Subphase	Only PG and CA oocytes present.
Developing	PG, CA, and early stage vitellogenic oocytes (Vtg1 and Vtg2). No evidence of prior spawning such as POF or muscle bundles, some oocyte atresia may be present.
Spawning–capable	Late stage vitellogenic oocytes (Vtg3) but all stages of vitellogenesis present (Vtg3, Vtg2, and Vtg1). Atresia of vitellogenic oocytes and blood vessels prominent. POF may be present.
Actively Spawning Subphase	Presence of GVM, GVBD, and/or hydrated oocytes and general internal ovarian structure disorganization. All stages of vitellogenesis present (Vtg1, Vtg2, and Vtg3). POF and atretic oocytes may be present.
Regressing	PG dominate, blood vessels prominent, and internal structure of ovary is disorganized. Evidence of recent spawning indicated by POFs, muscle bundles, thick gonad wall or atretic vitellogenic oocytes. Some CA and vitellogenic oocytes (Vtg1, Vtg2, and Vtg3) may be present.
Regenerating	PG and oogonia dominate. Perinucleolar stage PG oocytes common. Thick gonad wall with evidence of prior spawning indicated by presence of intra-lamellar muscle bundles and/or spaces, obvious blood vessels, gamma

Phase	Histological Description
	or delta atresia, interstitial tissue, capillaries around primary growth oocytes, and degenerating post ovulatory follicles may be present. Internal ovarian structure more organized than in Regressing phase.

Data analysis

The relationship between *W* and *FL* was estimated for female *E. coruscans* from the MHI using a power function:

$$W = aFL^b,$$

where *W* is in g, *FL* is in cm,

and

$\log W = \log a + b \log FL$,

where *a* is the scaling coefficient of the power function and *b* is the exponent describing the change in FL relative to weight. Length and weight data were log-transformed to satisfy assumptions of linearity. Ordinary least squares regression was used to evaluate the L-W relation.

Estimates of L_{50} and L_{95} (length at 95% maturity) were evaluated by plotting the proportional frequencies of mature and immature individuals by 5-cm length class across all samples. The selection of samples as immature and mature was based on either functional or physiological maturity categorization in a generalized linear model (GLM) using R ver. 4.0.2 (Core Team R 2020). A two-parameter logistic curve was fit to the proportional frequencies:

$$p = \frac{1}{1+e^{-a(L-L_{50})}},$$

where *p* is the estimated percent of mature individuals at a given length (L), L_{50} is as previously defined, and L_{95} is the length at 95% maturity (Chen and Paloheimo 1994). Ninety-five percent confidence intervals for each parameter were derived by bootstrapping using random sampling with replacement for 2000 iterations.

A proportional frequency of female reproductive phases was plotted by collection month to provide more information on seasonal changes in reproductive status. A gonadosomatic index (GSI) was calculated using all physiologically mature individuals as $GSI = \frac{GW}{(W-GW)} X\ 100$

Spawning seasonality was described using temporal trends in GSI values by plotting mean GSIs across months. A monthly grand mean GSI that was ≥ 0.63 was used to flag reproductively active fish, together with whether a fish was in the spawning–capable phase or not.

Results

Length and weight summary

A total of 293 female *E. coruscans* were collected from October 2007 to February 2020 from various fishing locations across the MHI (Table 1). The length distribution of 283 females ranged from 21.2 to 96.0 cm FL with a mean of 58.0 cm FL and median of 60.0 cm *FL* (Figure 1A). The length-weight relationship for 282 females was $W = 0.00003298 * FL^{2.81}$; $r^2 = 0.99$ (95% CI of slope 2.778–2.841, 95% CI of intercept 0.00002907 to 0.00003737). The confidence interval for the slope fell within accepted bounds for allometric growth. The W–L relationship was highly significant ($P < 0.0001$) (Figure 2).

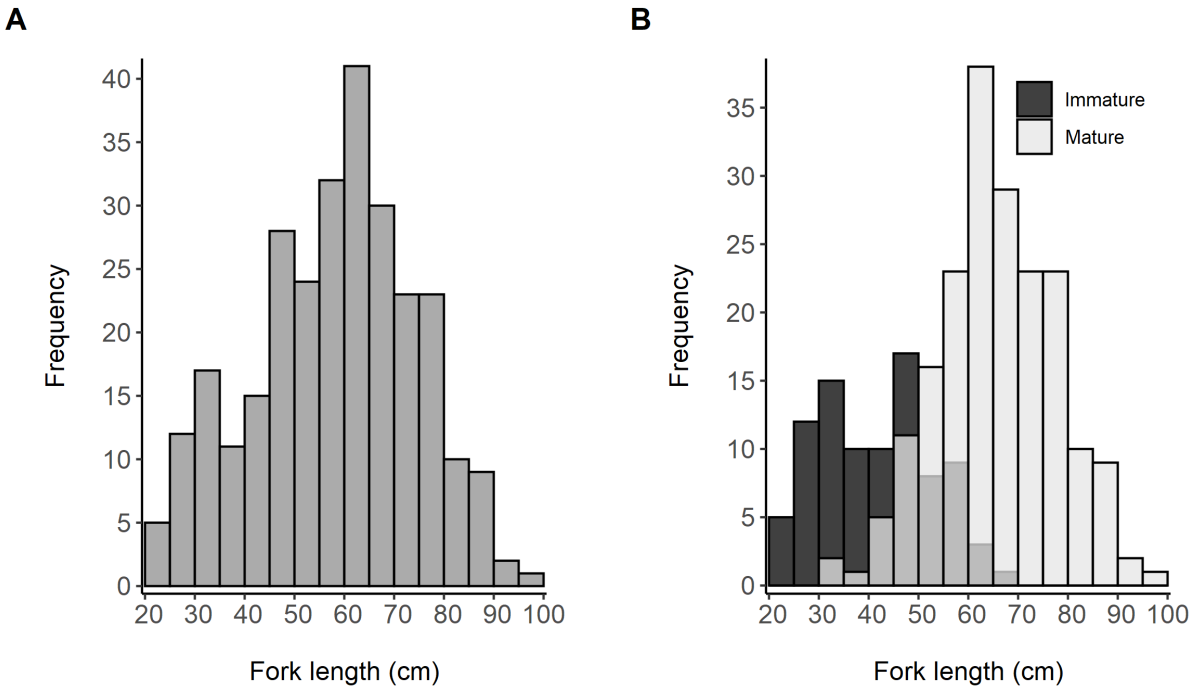

Figure 1. Length frequency distribution of sampled female onaga (*E. coruscans*) collected from October 2007 to February 2020, main Hawaiian Islands. A) Length frequency distribution for all years, N = 283; B) Length frequency distribution (5 cm size bins) of physiologically mature (N = 193) and immature individuals (N = 90). The overlap of immature and mature individual sizes are in light grey, immature females in black, and mature females in white.

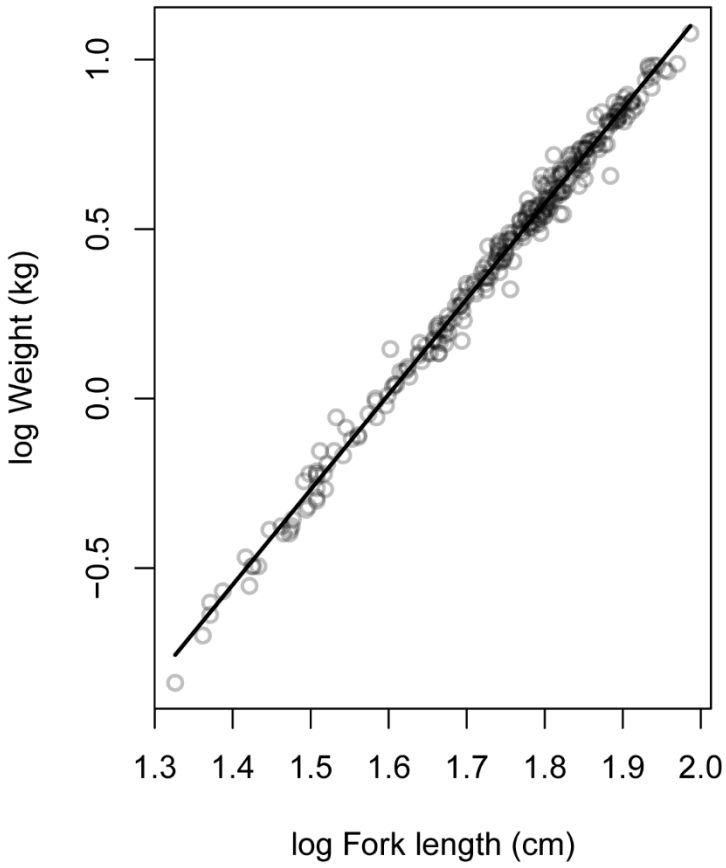

Figure 2. Linear model of FL-W relationship double log-transformed with a best fit line superimposed. The allometric growth relationship of female E. coruscans is W = 0.00003298 * FL2.81; r2 = 0.99, n= 282.

Female reproductive characteristics

We used GSI as one method to determine the spawning season for the MHI based on 193 physiologically mature females. The monthly mean GSI values indicate two peaks, a small one in spring and a larger one in the fall (Figure 3). The initial peak may be evidence of oocyte development while preparing to spawn later in the year. A pronounced drop in monthly mean GSI is indicated in the summer months of May–July; however, this also corresponds with our fewest monthly specimen numbers and should be interpreted with caution (Figure 3).

A total of 285 fish were used for histological reproductive analyses. This species was found to have asynchronous oocyte development, which is typical of a batch spawner. The numbers of fish and proportions of females at each reproductive phase during each month are provided in Table 3. Immature fish (N = 95) were present from February to November, and only immatures were collected in June. However, the specimen numbers during the summer months (May to July) were quite low due to the difficulty in obtaining fish during this time; thus the June sample size was relatively small (N = 7). The winter months to early spring (January to April)

had the highest proportions of early developing individuals (N = 63), but this phase also occurred in small proportions during the second half of the year (August to December). The relatively high percentage of early developing females we found during March and April may help explain the increase in GSI during those spring months (Table 3). Few fish with vitellogenic oocytes were encountered at any size or at any time (N = 32). Relatively few developing females (N = 11) were recorded from February to April and October to November. Spawning–capable females were only found during the months of September to December (N = 21) and only one individual was observed to be actively spawning in September 2019. Regressing females (N = 7) were observed October to December, indicating the end of the spawning season. Regenerating females were the second most abundant reproductive phase (N = 87) and they were present during all months except May and June. Our updated characterization of the spawning period based on the occurrence of spawning–capable females and a seasonal increase in mean GSI indicates that the spawning season is September through December for the MHI. However, due to the lack of mature fish samples from May through August, we define the spawning season for purposes of calculating L_{50} and L_{95} as June through December based on a combination of our data and previous reports (Everson et al. 1989) for the species.

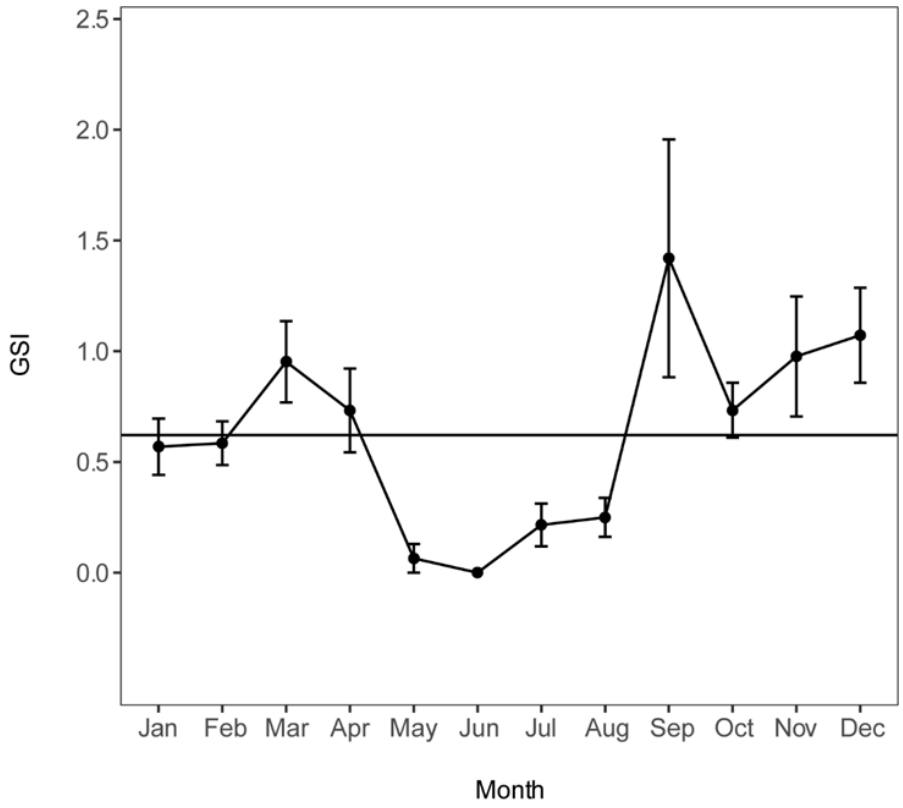

Figure 3. Spawning seasonality of main Hawaiian Islands female onaga (*E. coruscans*). Monthly mean (±SE) gonadosomatic indices (GSI). Plots are restricted to all physiologically mature individuals (N = 193). Numbers of fish are indicated adjacent to each monthly mean. Black horizontal line in indicates the grand mean GSI (0.6305) across all months.

Table 3. Monthly percentages of female fish in each reproductive phase. Six reproductive phases were identified during the sampling period of October 2007 to February 2020.

Month	Total (N)	Immature	Developing (Early)	Developing	Spawning –capable	Actively Spawning	Regressing	Regenerating
Jan	20	*0*	*60*	*0*	*0*	*0*	*0*	*40*
Feb	40	*13*	*48*	*5*	*0*	*0*	*0*	*35*
Mar	50	*46*	*20*	*6*	*0*	*0*	*0*	*28*
Apr	18	*17*	*39*	*6*	*0*	*0*	*0*	*39*
May	2	*100*	*0*	*0*	*0*	*0*	*0*	*0*
Jun	7	*100*	*0*	*0*	*0*	*0*	*0*	*0*
Jul	6	*17*	*0*	*0*	*0*	*0*	*0*	*83*
Aug	19	*58*	*26*	*5*	*0*	*0*	*0*	*11*
Sep	20	*55*	*0*	*5*	*15*	*5*	*0*	*20*
Oct	55	*38*	*11*	*2*	*18*	*0*	*4*	*27*
Nov	23	*48*	*4*	*9*	*9*	*0*	*4*	*26*
Dec	25	*0*	*12*	*0*	*20*	*0*	*20*	*48*
Total (N)	**285**	**95**	**63**	**11**	**20**	**1**	**7**	**87**

Size at Maturity

The size range of physiologically immature females was 21.2–66.6 cm FL and for physiologically mature females was 32.2–96.0 cm FL (Figure 1B). A total 107 specimens (33 mature, 77 immature) were used to estimate L_{50} and L_{95} during the spawning season (June to December) for the functional maturity calculations. The L_{50} and L_{95} estimates for functional maturity and spawning season were 62.2 cm (95% CI, 59.3–65.1 cm) and 80.9 cm FL (95% CI, 78.0–83.8 cm; Figure 4A), respectively. Individuals determined to be physiologically mature during the spawning period (Figure 3B) included 58 immature fish and 49 mature fish, for a total 107 specimens. The L_{50} and L_{95} estimates for physiological maturity and spawning season were 54.7 cm (95% CI, 51.8–57.6 cm) and 68.2 cm FL (95% CI, 65.3–71.1 cm; Figure 3B), respectively. Functionally mature individuals using the hybrid method during the spawning period (Figure 3C) included 74 immature fish and 79 mature fish, for a total 153 specimens. The L_{50} and L_{95} estimates of functional maturity using the hybrid method during the spawning period were 53.0 cm (95% CI, 50.80–55.20 cm) and 83.5 cm FL (95% CI, 81.30–85.70 cm; Figure 3C),

respectively. Physiologically mature individuals using the hybrid method during the spawning period included 58 immature fish and 96 mature fish, for a total 153 specimens. The L_{50} estimate using the hybrid method for physiologically mature individuals during the spawning period is 48.3 cm (95% CI, 46.10–50.50 cm) and that for L_{95} was 68.7 cm FL (95% CI, 66.50–70.90 cm; Figure 3D). Functionally mature individuals using data from all months included 164 immature and 119 mature individuals, for a total 283 specimens. For functionally mature individuals across all months, the L_{50} estimate was 60.0 cm (95% CI, 58.09–61.91 cm) and the L_{95} estimate was 122.0 cm FL (95% CI,120.09 –123.91 cm; Figure 3E). Physiologically mature individuals across all months included 90 immature 193 mature individuals, totaling 283 fish. For physiologically mature individuals across all months, the L_{50} estimate was 46.8 cm (95% CI, 44.89 –48.71 cm) and the L_{95} estimate was 64.4 cm FL (95% CI, 62.49–66.31 cm; Figure 3F). Table 4 summarizes our L_{50} and L_{95} estimates for each method used to determine maturity and compares them to estimates from previous studies.

Thirty-two regenerating females fell within a size range of 44–60 cm. These females are within a size range encompassing the length-at-50% maturities found in this analysis, and as a result we further assessed their secondary histological characteristics to verify their maturity designation. Of these, 10 or 31.25%, were determined “likely” to be mature opposed to 73.3% determined “definite” matures. This observation highlights the difficulty in determining maturity of recruit spawners.

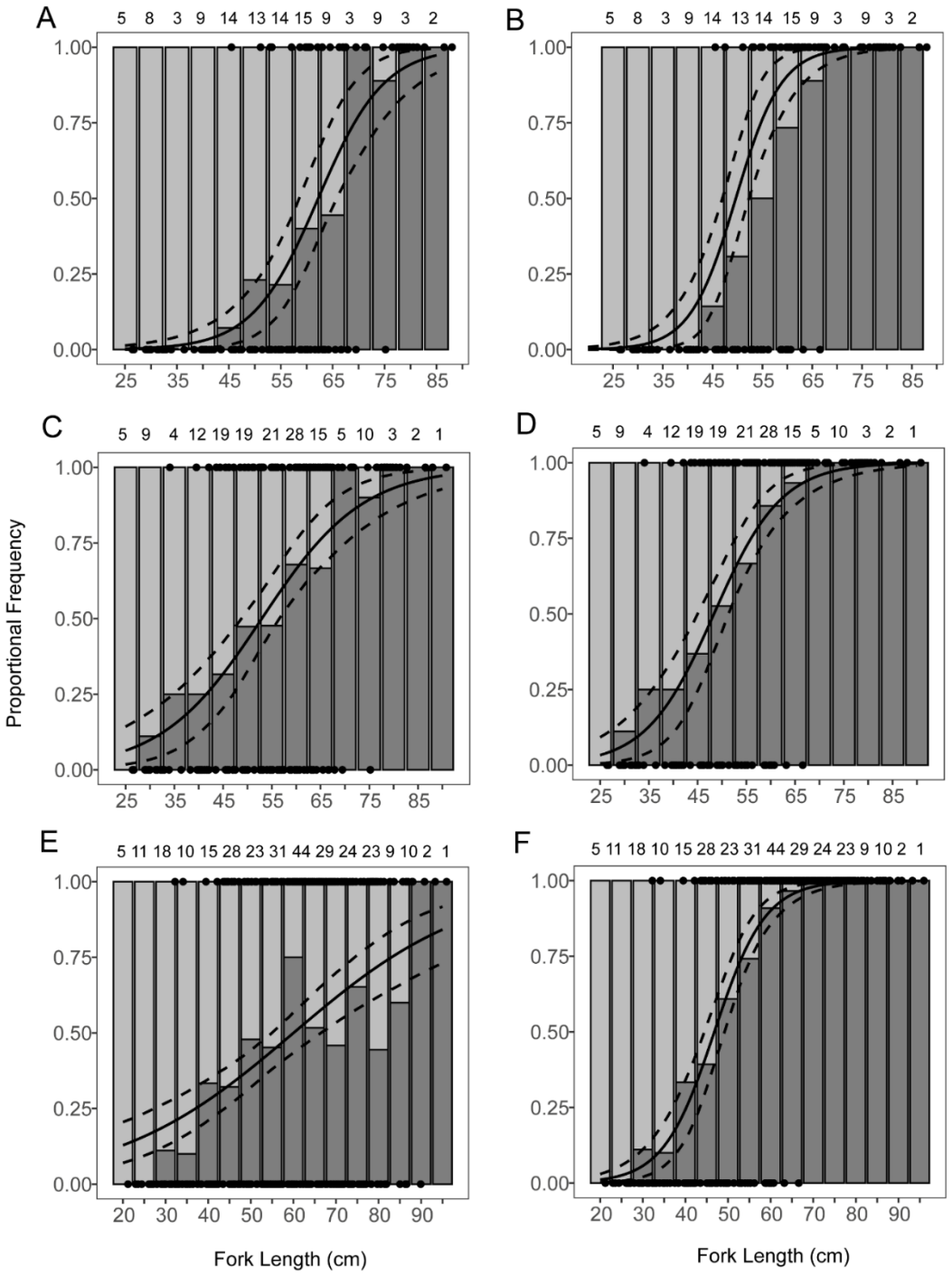

Figure 4. . Fitted logistic regression for the proportion of mature female E. coruscans and proportional frequency of immature (light grey) and mature (dark grey) by 5-cm length bins. Maturity classification is based on the histological criteria, functional vs. physiological maturity determination, and in- vs exclusion of spawning period. A) Functional maturity and spawning period; B) Physiological maturity and spawning period; C) Functional hybrid and spawning period; D) Physiological hybrid and spawning period; E) Functional maturity and all months; and F) Physiological maturity and all months. Note different x-axis values for E) and F).

Table 4. Summary of reproductive characteristics for female E. coruscans, including previous studies. Lmax, observed maximum length, Lf length at first maturity, L50 length at 50% maturity, L95 length at 95% maturity. Immature and mature indicates histological phases used for each maturity designation, with sample numbers in parentheses. Note the spawning period for the present study is estimated as 7 months based on a combination of our histological data and previous literature reports.

Region	L_{max} (FL cm)	L_f (FL cm)	L_{50} (FL cm)	L_{95} (FL cm)	Total *N*	Type of L_{50}	Immature (*N*)	Mature (*N*)	Spawning period	Citation
Hawaii (present)	88.0	45.5	62.2	80.9	***107***	***Functional maturity + Spawning period***	*Immature, Early developing* ***(74)***	***Developing, Spawning Capable, Regressing (33)***	7 months (June–Dec.)	1
Hawaii (present)	88.0	45.5	54.7	68.2	***107***	***Physiological maturity + Spawning period***	*Immature* ***(58)***	***Early Developing, Developing, Spawning Capable, Regressing (49)***	7 months (June–Dec.)	1
Hawaii (present)	90.8	32.2	53.0	83.5	***153***	***Functional hybrid + Spawning period***	*Immature, Early developing* ***(74)***	***Developing, Spawning Capable, Regressing, Regenerating (79)***	7 months (June–Dec.)	1
Hawaii (present)	90.8	32.2	48.3	68.7	***153***	***Physiological hybrid + Spawning period***	*Immature* ***(58)***	***Early Developing, Developing, Spawning Capable, Regressing, Regenerating (96)***	7 months (June–Dec.)	1
Hawaii (present)	96.0	32.2	60.0	122	***283***	***Functional maturity + All months***	*Immature, Early developing* ***(164)***	***Developing, Spawning Capable, Regressing, Regenerating (119)***	NA	1
Hawaii (present)	96.0	32.2	46.8	64.4	***283***	***Physiological maturity + All months***	*Immature* ***(90)***	***Early Developing, Developing, Spawning Capable, Regressing, Regenerating (193)***	NA	1
Okinawa (2018)	88.2	61.2	67.1	NA	***324***	***Functional maturity + Spawning period***	*Immature, Early developing* ***(?)***	***Developing, Spawning Capable, Regressing (?)***	7 months (May–Nov.)	2
Hawaii (1989)	95.0	52.2	66.3	NA	***95***	***Functional maturity + Spawning period***	*Immature, Early developing* ***(?)***	***Developing, Spawning Capable, Regressing (?)***	6 months (June–Nov.)	3

(1) Present research; (2) Uehara et al. (2018); (3) Everson et al. (1989).

Discussion

This analysis—an excerpt of an on-going study of MHI female *E. coruscans* reproductive characteristics—provides updated specimen length distributions for this study, a length-weight relationship that was within the normal bounds of allometric growth, and L_{50} and L_{95} estimates using six different data combinations based on different maturity criteria. Additionally, we include an estimate of spawning seasonality thus far, which is consistent with other published observations. The current data set consists of 293 female *E. coruscans*, of which 285 fish were used for reproductive analyses. Recent monthly sampling efforts nearly doubled the previous sample size over the last 10 months. However, the number of individuals in the spawning capable reproductive phase for this data set still remains relatively small (N = 21) during the informative months of September through December and nonexistent during the putative June through August early portion of the spawning period. Spawning capable individuals caught during the spawning season are commonly used by fisheries scientists to estimate L_{50}; however, because of the few specimens bearing vitellogenic oocytes, alternative approaches for estimating length-at-maturity were explored to develop a robust parameter and are the best available data to date.

Prior to the start of this project there was only one published estimate of L_{50} and spawning period for *E. coruscans* in the MHI (Everson et al. 1989). Published estimates of female L_{50} include 66.3 cm FL from the MHI (Everson et al. 1989) and 67.1 cm FL from Okinawa, Japan (Uehara et al. 2018). Our results indicate a slightly smaller L_{50} (62.2 cm FL) for the MHI when using similar classifications and data inputs (functionally mature females caught during the spawning season; Table 4, Figure 4A). Our results will be further strengthened with an increase in the number of spawning capable females from May through December 2020. Everson et al. (1989) indicated a spawning period from June to November which corresponds closely to the spawning period reported in 2018 for Okinawa (May to November). Our preliminary spawning period for females in MHI covers the same general time span but is slightly shorter (4 vs. 6 months) and extends into December. This shortened preliminary spawning period may be a result of insufficient sampling of larger individuals (> 65 cm FL) in the summer months due to the fishery switching from bottomfish to the more lucrative pelagic species (e.g., tuna). Both previously published studies based their estimates of length at maturity on fish that were caught during the spawning season and were observed to be functionally mature, i.e., individuals with ovaries containing vitellogenic oocytes. In order to appropriately examine temporal and spatial variability in reproductive characteristics of this species, both recent information and methodologically similar estimates are needed.

Using physiological maturity to estimate L_{50} in combination with the option of spawning period or inclusion of all months was very informative. Use of physiologically mature individuals captured during the spawning season yielded a 7.5-cm smaller L_{50} vs the functional L_{50} maturity estimate. Interestingly, the physiological L_{95} maturity estimate using fish caught during the spawning period (68.2 cm FL) was the most similar to previously published estimates of L_{50} based on functional maturity. A physiological L_{95} maturity estimate using fish caught during the spawning period therefore might be an appropriate alternative to L_{50} if the numbers of functionally mature individuals are too low to produce a robust estimate. The marker of sexual maturity for physiological maturity is defined as the cortical alveolar (CA) oocyte stage, when

fish move into the gonadotrophin-dependent phase of the reproductive cycle (Brown-Peterson et al. 2011; Lowerre-Barbieri et al. 2011). In warm water marine fish, once CA oocytes have formed they will develop through to vitellogenesis and maturation in the same year (Wright 2007). The appearance of CA oocytes was used to define the secondary growth stage of oocytes in other studies (Murua and Saborido-Rey 2003; S.K. Lowerre-Barbieri et al. 2011; Moncrief et al. 2018); but all of these were based on data for fishes reproducing at more temperate (as opposed to boreal or tropical) temperatures. At least for tropical species like *E. coruscans*, it might be justifiable to use physiologically mature fish in instances where sampling does not produce sufficient specimens of functionally mature individuals to estimate length-at-maturity.

When used with the appropriate assumptions, physiological maturity may be particularly applicable to data-poor species for which a spawning period has not yet been described or in situations where sampling does not include sufficient numbers of spawning–capable specimens (Reed and Taylor 2020). In instances when a small number of reproductively active females are captured, the use of physiologically mature females for estimating maturity ogives increases in importance. For instance, 22% of our samples were determined to be in the early developing sub-phase, with the majority of these individuals found outside of the defined spawning season. It is recognized that the early developing subphase can include recruit–spawners as well as larger and older repeat–spawners (Brown-Peterson et al. 2011). When these individuals are classified as immature, they have the potential to affect the accuracy of the L_{50} estimate (Figure 4A, 4C, 4E). Additionally, we show that functional maturity must be assessed within a spawning period to estimate L_{50} (Figure 4E), whereas physiological maturity may be assessed without the use of a spawning period (Figure 4B, 4D, 4F). This finding is particularly important to the larger knowledge base of fisheries reproductive biology because it could directly affect how we interpret the length-at-maturity for slow growing and late-to-mature fishes. Species with a life history that include reaching large sizes and old ages like *E. coruscans* may be likely to have a higher percentage of early developing females throughout the year. Under the functional maturity criteria, individuals in the early developing reproductive phase would be considered immature. However, the female *E. coruscans* found in the months prior to spawning (January-April) are of size classes greater than the functional L_{50}, indicating that they are unlikely to be immature and very likely to be repeat spawners preparing to spawn in the coming year. If a spawning period is not detectable, then the use of physiological maturity encompassing all months, will provide an accurate representation of length-at-maturity because it is not biased by excluding individuals of large size classes who have not yet developed yolking oocytes typical of the functional maturity classification.

Our analysis provides updated metrics on reproductive characteristics of female *E. coruscans* in the MHI. Additionally, we provide exploratory analysis and discussion of the use of physiological vs. functional maturity to estimate L_{50}. While additional samples will provide further support for our findings, we nonetheless believe that our alternative types of estimation using optional parameters now provide both the best available and sufficient L_{50} and L_{95} inputs for stock assessment scientists and managers.

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Literature Cited

Andrews AH. 2020. Red fish, blue fish, old fish, new fish- onaga can live a half century in the Hawaiian Islands. Lawai'a Mag.:31: 46-51.

Andrews AH, Brodziak J, Demartini EE, Cruz E. 2020. Long-lived life history for onaga *Etelis coruscans* in the Hawaiian Islands. Mar Freshw Res. doi:10.1071/MF20243.

Andrews KR, Moriwake VN, Wilcox C, Grau EG, Kelley C, Pyle RL, Bowen BW. 2014. Phylogeographic analyses of submesophotic snappers *Etelis coruscans* and *Etelis* "marshi" (family lutjanidae) reveal concordant genetic structure across the Hawaiian Archipelago. PLoS One. 9(4). doi:10.1371/journal.pone.0091665.

Brodziak J, Yau A, O'Malley J, Andrews A, Humphreys R, Demartini E, Pan M, Parke M, Fletcher E. 2014. Stock assessment update for the main Hawaiian Islands deep7 bottomfish complex through 2013 with projected annual catch limits through 2016.

Brown-Peterson NJ, Wyanski DM, Saborido-Rey F, Macewicz BJ, Lowerre-Barbieri SK. 2011. A Standardized Terminology for Describing Reproductive Development in Fishes. Mar Coast Fish. 3(1):52–70. doi:10.1080/19425120.2011.555724.

Cailliet G., Andrews AH. 2008. Age-validated longevity of fishes: Its importance for sustainable fisheries. In: K Tsukamoto, T Kawamuraa, T Takeuchi, TD Beard, Jr. MK, editor. Fisheries for global welfare and environment. Tokyo, Japan: 5th World Fisheries Congress 2008, TERRAPUB. p. 103–120.

Chen Y, Paloheimo JE. 1994. Estimating fish length and age at 50% maturity using a logistic type model. Aquat Sci. 56(3):206–219. doi:10.1007/BF00879965.

Core Team R. 2020. A language and environment for statistical computing. https://www.r-project.org/.

Dalzell P. 1996. Catch rates, selectivity and yields of reef fishing. In: IN: Polunin N.V.C. RCM, editor. Reef Fisheries. Chapman & Hall. Springer, Dordrecht. p. 161–192. http://link.springer.com/10.1007/978-94-015-8779-2_7.

DeMartini EE. 2016. Body size at sexual maturity in the eteline snappers *Etelis carbunculus* and *Pristipomoides sieboldii*: subregional comparisons between the main and north-western Hawaiian Islands. Mar Freshw Res.:1178–1186. http://dx.doi.org/10.1071/MF16174.

Everson AR, Williams HA, Ito BM. 1989. Maturation and Reproduction in 2 Hawaiian Eteline Snappers, Uku, Aprion-Virescens, and Onaga, Etelis-Coruscans. Fish Bull. 87(4):877–888.

Haight WR, Parrish JD, Hayes TA. 1993. Feeding Ecology of Deepwater Lutjanid Snappers at Penguin Bank, Hawaii. Trans Am Fish Soc. 122(3):328–347. doi:10.1577/1548-8659(1993)122<0328:feodls>2.3.co;2.

Haight, Kobayashi DR, Kawamoto KE. 1993. Biology and management of deepwater snappers of the Hawaiian Archipelago. Mar Fish Rev. 55(2):20–27.

Hunter JR, Macewicz BJ. 1985. Measurement of spawning frequency in multiple spawning fishes. NOAA Tech Rep NMFS 36.(January 1985):79–94. http://swfsc.noaa.gov/publications/CR/1985/8544.PDF.

Koslow JA, Boehlert GW, Gordon JDM, Haedrich RL, Lorance P, Parin N. 2000. Continental slope and deep-sea fisheries: Implications for a fragile ecosystem. ICES J Mar Sci. 57(3):548–557. doi:10.1006/jmsc.2000.0722.

Langseth B, Syslo J, Yau A, Kapur M, Brodziak J. 2018. Stock assessment for the main Hawaiian Islands Deep 7 bottomfish complex in 2018, with catch projections through 2022. NOAA Tech Memo NMFS-PIFSC-69.(February):217.

Leis JM, Lee K. 1994. Larval development in the lutjanid subfamily Etelinae (Pisces): The Genera Aphareus, Aprion, Etelis and Pristipomoides. Bull Mar Sci. 55(1):46–125.

Loeun KL, Goldstien S, Gleeson D, Nicol SJ, Bradshaw CJA. 2014. Limited genetic structure among broad-scale regions for two commercially harvested, tropical deep-water snappers in New Caledonia. Fish Sci. 80(1):13–19. doi:10.1007/s12562-013-0673-y.

Lowerre-Barbieri SK, Brown-Peterson NJ, Murua H, Tomkiewicz J, Wyanski DM, Saborido-Rey F. 2011. Emerging issues and methodological advances in fisheries reproductive biology. Mar Coast Fish. 3(1):32–51. doi:10.1080/19425120.2011.555725.

Lowerre-Barbieri SK, Ganias K, Saborido-Rey F, Murua H, Hunter JR. 2011. Reproductive timing in marine fishes: Variability, temporal scales, and methods. Mar Coast Fish. 3(1):71–91. doi:10.1080/19425120.2011.556932.

Luckenbach JA, Iliev DB, Goetz FW, Swanson P. 2008. Identification of differentially expressed ovarian genes during primary and early secondary oocyte growth in coho salmon, Oncorhynchus kisutch. Reprod Biol Endocrinol. 6:1–15. doi:10.1186/1477-7827-6-2.

Misa WFXE, Drazen JC, Kelley CD, Moriwake VN. 2013. Establishing species-habitat associations for 4 eteline snappers with the use of a baited stereo-video camera system. Fish Bull. 111(4):293–308. doi:10.7755/FB.111.4.1.

Moncrief T, Brown-Peterson NJ, Peterson MS. 2018. Age, Growth, and Reproduction of Vermilion Snapper in the North-Central Gulf of Mexico. Trans Am Fish Soc. 147(5):996–1010. doi:10.1002/tafs.10100.

Moore C, Drazen JC, Radford BT, Kelley C, Newman SJ. 2016. Improving essential fish habitat designation to support sustainable ecosystem-based fisheries management. Mar Policy. 69:32–41. doi:10.1016/j.marpol.2016.03.021.

Murua H, Saborido-Rey F. 2003. Female reproductive strategies of marine fish species of the North Atlantic. J Northw Atl Fish Sci. 33:23–31.

Newman SJ, Brown JI, Fairclough D V., Wise BS, Bellchambers LM, Molony BW, Lenanton RCJ, Jackson G, Smith KA, Gaughan DJ, et al. 2018. A risk assessment and prioritisation approach to the selection of indicator species for the assessment of multi-species, multi-gear, multi-sector fishery resources. Mar Policy. 88(November 2017):11–22. doi:10.1016/j.marpol.2017.10.028.

Newman SJ, Williams AJ, Wakefield CB, Nicol SJ, Taylor BM, Malley JMO. 2016. Review of the life history characteristics, ecology and fisheries for deep-water tropical demersal fish in the Indo-Pacific region. Rev Fish Biol Fish. 26(3):537–562. doi:10.1007/s11160-016-9442-1.

Norse EA, Brooke S, Cheung WWL, Clark MR, Ekeland I, Froese R, Gjerde KM, Haedrich RL, Heppell SS, Morato T, et al. 2012. Sustainability of deep-sea fisheries. Mar Policy. 36(2):307–320. doi:10.1016/j.marpol.2011.06.008.

Okuyama J, Shishidou H, Hayashibara T. 2019. Post-release horizontal and vertical behavior and philopatry of deepwater longtail red snapper Etelis coruscans around a bank. Fish Sci. 85(2):361–368. doi:10.1007/s12562-019-01287-2.

Oyafuso ZS, Drazen JC, Moore CH, Franklin EC. 2017. Habitat-based species distribution modelling of the Hawaiian deepwater snapper-grouper complex. Fish Res. 195(June):19–27. doi:10.1016/j.fishres.2017.06.011.

Pacific Islands Fisheries Science Center. 2021. MHI Onaga Reproductive Characteristics. Admin Report, https://www.fisheries.noaa.gov/inport/item/63420.

Polovina JJ. 1987. Assessment and management of deepwater bottom fishes in Hawaii and the Marianas. In: J. J. Polovina and S. Ralston, editor. Tropical snappers and groupers: Biology and fisheries management. Westview Press, Boulder, Colorado. p. 505–532.

Randall JE. 1978. Snappers (Lutjanidae). In: Shore and Reef fish from Hawaii. Vol. 11. p. 10–11.

Reed EM, Taylor B. 2020. Life history of two data-poor but commercially valuable tropical reef fishes, Parupeneus barberinus and Mulloidichthys flavolineatus, from the Saipan fishery, Northern Mariana Islands. Mar Freshw Res. doi:10.1071/MF20049.

Stearns SC. 1992. The evolution of life histories. New York: Oxford Universities Press.

Uehara M, Ebisawa A, Ohta I. 2018. Reproductive traits of deep-sea snappers (Lutjanidae): Implication for Okinawan bottomfish fisheries management. Reg Stud Mar Sci. 17:112–126. doi:10.1016/j.rsma.2017.12.002.

Uehara M, Ebisawa A, Ohta I. 2020. Comparative age-specific demography of four commercially important deep-water snappers: implication for fishery management of a long-lived lutjanid. J Fish Biol.(March). doi:10.1111/jfb.14332.

Wallace RA, Selman K. 1981. Cellular and dynamic aspects of Oocyte growth in Teleosts. Integr Comp Biol. 21(2):325–343. doi:10.1093/icb/21.2.325.

West G. 1990. Methods of assessing ovarian development in fishes: a review. Aust J Mar Freshw Res. 41(2):199–222. doi:10.1071/MF9900199.

Western Pacific Regional Fishery Management Council. 2009. Fishery Ecosystem Plan for the Hawaii Archipelago. http://www.wpcouncil.org/fep/WPRFMC Hawaii FEP (2009-09-21).pdf.

Williams AJ, Loeun K, Nicol SJ, Chavance P, Ducrocq M, Harley SJ, Pilling GM, Allain V, Mellin C, Bradshaw CJA. 2013. Population biology and vulnerability to fishing of deep-water Eteline snappers. J Appl Ichthyol. 29(2):395–403. doi:10.1111/jai.12123.

Williams AJ, Wakefield CB, Newman SJ, Vourey E, Abascal FJ, Halafihi T, Kaltavara J, Nicol SJ. 2017. Oceanic, latitudinal, and sex-specific variation in demography of a tropical deepwater snapper across the indo-pacific region. Front Mar Sci. 4(DEC). doi:10.3389/fmars.2017.00382.

Wright PJ. 2007. Understanding the maturation process for field investigations of fisheries-induced evolution. Mar Ecol Prog Ser. 335:279–283. doi:10.3354/meps335279.