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Comparative age-specific demography of four commercially important deep-water snappers: implication for fishery management of a long-lived lutjanid

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Abstract

Lutjanid snappers belonging to the subfamilies Apsilinae and Etelinae are commercially valuable components of tropical deep-water fisheries throughout much of the Indo-Pacific region. Based on age assessment using sagittal otoliths, the age-specific demographic characteristics of four deep-water snappers, *Etelis coruscans*, *Paracaesio caerulea*, *Pristipomoides filamentosus* and *Pristipomoides sieboldii*, in the Okinawa Islands, southwestern Japan, were examined, and the results were discussed for fishery management. Age validation using edge-type analysis demonstrated that opaque zones in all species were formed once per year and were considered valid annual growth increments. The von Bertalanffy growth equations were also determined for each species. These snappers are long-lived (>50 years for *E. coruscans* and *P. caerulea* and >30 years for the two species of *Pristipomoides*) and relatively slow-growing. The age of acquiring sexual maturity in females was relatively later in *E. coruscans*, *P. caerulea* and *P. filamentosus* than in *P. sieboldii*. The results revealed differences in the biological traits among these four species; *E. coruscans* and *P. caerulea* with long life spans and late maturation are particularly more vulnerable to fishing impact than the two *Pristipomoides* species. Therefore, further approaches to decrease and control fishing intensity, such as networking of marine-protected areas and regulation to control the numbers of boats and/or the total allowable catch, are necessary for the management of the stock of these species, especially for *E. coruscans* and *P. caerulea*.

KEYWORDS
age and growth, deep-water snapper, fishery management, longevity, maturity schedule, Okinawa Islands

1 | INTRODUCTION

The lutjanids of the subfamilies Apsilinae and Etelinae, commonly known as snappers, are commercially valuable fish living at depths ranging from shallow-reef-associated habitats to ~550 m of oceanic island and continental habitats in subtropical and tropical waters of both the Atlantic and Indo-Pacific regions (Allen, 1985; Anderson, 2003; Anderson & Allen, 2001; Nelson, 2006; Polovina &

Ralston, 1987). In the Okinawan waters of northwestern Pacific, the lutjanid snappers of both subfamilies, locally known in the Okinawa Islands as "machi," comprise at least 17 species (Sata, 1991) and support regional deep-water fishery. Of these species, *Etelis coruscans*, *Paracaesio caerulea*, *Pristipomoides filamentosus* and *Pristipomoides sieboldii* are important commercial target species, accounting for 90% of deep-water snapper catches (Catch Statistics of Okinawa Prefectural Fisheries Research and Extension Center).

A recent IUCN Red List of these four snappers has included them in the "least concern" category or "data-deficient" category (Acero, 2010; Russell *et al*., 2016a,b,c). Nonetheless, these four species are often highly exploited as esteemed seafood and preferred fishery targets, and indicators, such as catch rates and catch per unit of effort, suggest that these snappers may be overfished throughout much of the Indo-Pacific region (Brodziak *et al*., 2011; Friedlander *et al*., 2014; Fry *et al*., 2006; Grandcourt, 2003; Uehara *et al*., 2017a,b). For example, the Hawaiian populations of deep-water snappers, including *E. coruscans*, *P. filamentosus* and *P. sieboldii*, and groupers have been overfished and are managed by marine-protected areas (MPAs) and total allowable catch (TAC) regulations (Friedlander *et al*., 2014; Sackett *et al*., 2014). In Japan, 50 important species, including four deep-water snappers, have been assessed by the Japan Fisheries Research and Education Agency. The main aim of this assessment is to estimate the acceptable biological catch (ABC) for the following year and to provide indicators of the stock statuses (high, middle or low) as well as trends (increase, constant or decrease) (Ichinokawa *et al*., 2017). Stock assessments are updated every year and are available at http://abchan.fra.go.jp in Japanese. The Ryukyu Archipelago populations of these four snappers show no sign of a significant turnaround in the stock biomass because the current stock status of the four deep-water snapper is at a low level (Shimose *et al*., 2019). Thus, there are increasing concerns about the stock status of the Okinawan populations of these four species.

Biological research on tropical deep-water fishes has been generally limited to a few studies in geographically restricted areas, often focusing on a few species and specific biological traits (Newman *et al*., 2016). Three of these four species of deep-water snappers, *E. coruscans*, *P. filamentosus* and *P. sieboldii*, have been well studied in the Seychelles (Hardman-Mountford *et al*., 1997; Mees, 1993; Mees & Rousseau, 1997; Pilling *et al*., 2000), the Hawaiian and Mariana Archipelagos (*e.g*., DeMartini, 2016; Everson *et al*., 1989; Luers *et al*., 2017; Williams & Lowe, 1997), the South Pacific Ocean (Fry *et al*., 2006; Loeun *et al*., 2014; Williams *et al*., 2013, 2015) and Japanese waters (*e.g*., Ebisawa *et al*., 2010; Okuyama *et al*., 2019; Tokyo Fisheries Experimental Station, 1974; Uehara *et al*., 2018a). In addition to biological traits, fisheries, stock assessment & effectiveness of deep-water MPAs for *E. coruscans*, *P. caerulea*, *P. filamentosus* and *P. sieboldii* have been well reported in the Seychelles (Grandcourt, 1994, 2003; Mees, 1993; Mees & Rousseau, 1997), the Hawaiian and Mariana Archipelagos (*e.g*., Moore *et al*., 2013; Polovina, 1987; Sackett *et al*., 2014; Zeller *et al*., 2008), the South Pacific Ocean (Langi, 1990; Williams *et al*., 2013, 2015) and Japanese waters (Tokyo Fisheries Experimental Station, 1974; Uehara *et al*., 2012, 2013, 2015, 2017a,b,c, 2018b).

In these studies, several techniques have been used to determine the age of *E. coruscans*, *P. caerulea*, *P. filamentosus* and *P. sieboldii*, but there have been limited attempts at age validation (Andrews *et al*., 2012; Pilling *et al*., 2000; Ralston & Miyamoto, 1983). In fisheries science, age is the most influential of biological variables (Campana, 2001). Accurate and reliable age determination is essential for the derivation of growth and mortality rates and for the estimation

of age-structured population analysis from a fished stock (Beverton & Holt, 1957; Campana, 2001). Errors in age determination can result in ambiguous demographic parameters and provide misleading impressions of the production potential of fish stocks (Newman *et al*., 2000). It is usually stated that deep-water fish otoliths do not form sufficiently clear growth increments to enable their routine use for age estimation. Many age and growth studies of deep-water snappers have not used sagittal otoliths to age the fish (*e.g*., Hardman-Mountford *et al*., 1997; Mees & Rousseau, 1997) and/or have not been directly validated (*e.g*., Fry *et al*., 2006; Williams *et al*., 2013, 2015). Currently, annual formation of increments has been demonstrated for some deep-water snappers (Newman & Dunk, 2003; Pilling *et al*., 2000). Age validation in deep-water snappers has been further advanced by bomb radiocarbon and radiometric dating of otoliths (Andrews *et al*., 2011, 2012). Nonetheless, there is a lack of reliable information on the longevity, growth parameters according to sex and maturity schedule for these four snappers, despite their ecological and commercial importance, and it is necessary to evaluate these demographic parameters.

The primary objectives of the present study were to (a) validate the annual periodicity of growth rings on sectioned otoliths using edge-type analysis, which can be a useful alternative to marginal increment analysis (MIA) (Newman & Dunk, 2003) and is inexpensive and logistically simple (Piddocke *et al*., 2015); (b) to determine the longevity, sex-specific growth and maturity schedule of *E. coruscans*, *P. caerulea*, *P. filamentosus* and *P. sieboldii*; and to (c) comment on the implications of this new information for fishery management of deep-water snappers.

2 | MATERIALS AND METHODS

2.1 | Collection and preparation of sample

From May 2001 to January 2015, 1796 deep-water snappers were collected from Okinawan waters (Table 1). Of these, 1316 fishes (*E. coruscans*, $n = 410$; *P. caerulea*, $n = 329$; *P. filamentosus*, $n = 245$; *P. sieboldii*, $n = 332$) were obtained at the fish markets of Tomari Uoichiba Limited Liability Partnership and the Itoman Fishery Cooperative Association. These specimens were caught by commercial fishermen using line-based fishing gears (vertical longline and trotline). The remaining 480 specimens (*E. coruscans*, $n = 364$; *P. caerulea*, $n = 16$; *P. filamentosus*, $n = 58$; *P. sieboldii*, $n = 42$) were collected using trotline aboard the Okinawa Prefectural Government's research vessel *Tonanmaru* (176 tonnes) from August 2006 to October 2014. The fishing grounds for these four snappers were in south Ryukyu, middle Ryukyu and the slope and margin of the continental shelf, including the Senkaku Islands (Uehara *et al*., 2018a). For all fresh specimens, fork length (FL) and body weight were measured to the nearest 1 mm and 1 g, respectively. Sagittal otoliths were extracted from 774 *E. coruscans*, 344 *P. caerulea*, 303 *P. filamentosus* and 374 *P. sieboldii*; cleaned; and dried for otolith processing.

TABLE 1 Summary of deep-water snapper specimens examined in the present study

Species	Fishing area	Sampling period	Number of specimens	Range of FL (cm)
Etelis coruscans	South and middle Ryukyu	May 2001–August 2014	742	18.1–88.2
	Continental shelf	February 2012–April 2014	32	28.4–75.7
Paracaesio caerulea	South and middle Ryukyu	April 2004–August 2014	280	15.7–52.7
	Continental shelf	December 2010–April 2014	65	22.4–48.7
Pristipomoides filamentosus	South and middle Ryukyu	October 2006–January 2015	235	26.6–75.1
	Continental shelf	October 2011–April 2014	68	21.9–70.5
Pristipomoides sieboldii	South and middle Ryukyu	October 2006–August 2014	250	18.1–45.5
	Continental shelf	August 2008–August 2013	124	20.4–45.9

Note. FL, fork length.

2.2 | Age determination

The right sagittal otoliths were used for age determination; nonetheless, if they were damaged during extraction from the fish or the sectioning process, the left sagittal otolith was used. Sagittal otoliths were weighted to the nearest 0.001 g, unless broken. Otolith weight was presented as the average of a pair of otoliths or as the values from a single intact otolith. Sagittal otoliths were embedded in epoxy resin and sectioned transversely through the focus at a thickness of ~450 μm using a Buehler Isomet low-speed saw (ISOMET, Buehler, Lake Bluff, IL, USA). Sections were then mounted on a glass slide using Eukitt mounting medium (O. Kindler, Freiburg, Germany).

Sectioned otoliths (*E. coruscans*, n = 749; *P. caerulea*, n = 342; *P. filamentosus*, n = 303; *P. sieboldii*, n = 374) were examined under a binocular microscope (SMZ800, Nikon Instech Co., Ltd., Minato-ku, Tokyo, Japan) using transmitted light. Alternating translucent and opaque zones were visible; thus, it was assumed that one pair of translucent and opaque zones was laid down each year as on an annulus. The number of opaque zones was counted along a consistent axis near the sulcus on at least two occasions with an interval of >2 months between counts and without knowledge of the details of the specimens (month of collection, body size and sex). Otolith pictures were recorded at the first observation using a Nikon DS-Ri1 camera with NIS-Elements D (version 4.10) software for Windows (Figure 1). A second observation was performed by the same reader Masato Uehara (M. U.) based on the otolith picture without the knowledge of the previous data. If the two counts coincided, the reading was accepted; if they differed, the otolith was read once or twice more, and any two coinciding counts were accepted. The precision of the otolith zone counts for these fish was quantified by the average percent error (APE) (Beamish & Fournier, 1981) and the C.V. (Chang, 1982).

Two established validation methods were used to test the assumption that the increments in growth were annuli (*e.g.*, Choat & Axe, 1996; Manickchand-Heileman & Phillip, 2000; Newman & Dunk, 2003; Pears *et al.*, 2006). First, edge-type analysis was conducted (Manickchand-Heileman & Phillip, 2000; Newman & Dunk, 2003; Pears *et al.*, 2006). The outer margin of each otolith section was determined to be translucent or opaque. It was difficult to determine the edge type in some otoliths (n = 598) because the number of uncertain edge types increased
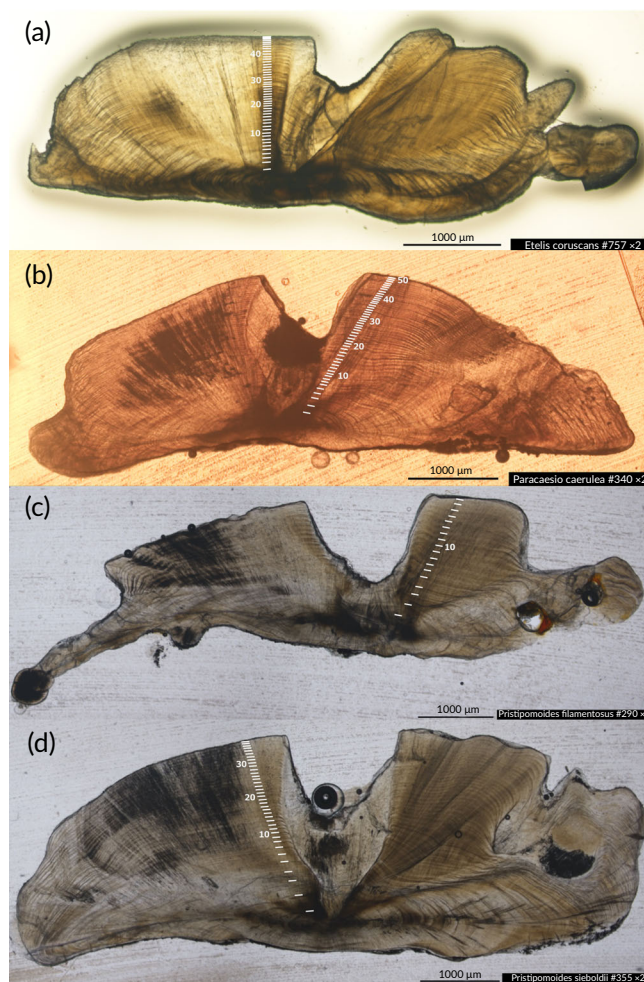

FIGURE 1 Transverse sections of sagittal otolith with annuli indicated by white bars. (a) *Etelis coruscans*, 49-year-old male [74.7 cm fork length (FL)]; (b) *Paracaesio caerulea*, 50-year-old male (50.5 cm FL); (c) *Pristipomoides filamentosus*, 18-year-old female (59.0 cm FL); and (d) *Pristipomoides sieboldii*, 38-year-old female (42.6 cm FL)

with the number of increments (Pears *et al.*, 2006). For that reason, any two coinciding edge types (n = 1140) were accepted. The monthly frequency of opaque margins was compared with a uniform distribution
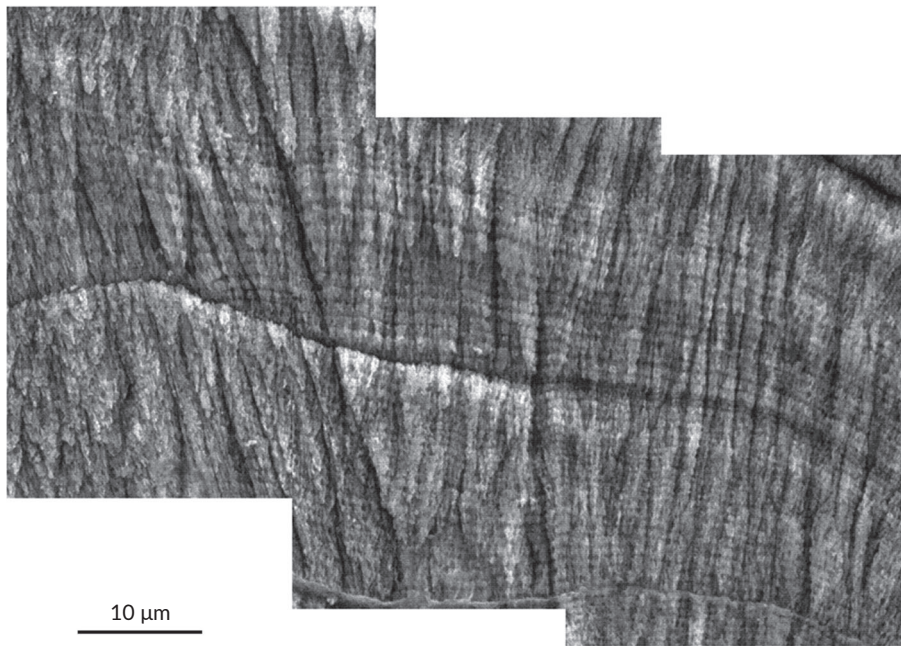
FIGURE 2 Scanning electron microscopy image of a sagittal otolith from *Etelis coruscans* [1395-day-old female, 37 cm fork length (FL)]

10 μm

using the χ^2 goodness-of-fit test for circular distribution (Zar, 1984). Second, the relationship between otolith weight and number of increments was examined using correlation analysis (Choat & Axe, 1996). A strong correlation between otolith weight and number of increments was expected if otoliths accreted calcium carbonate throughout the life of the fish. On the assumption that the opaque zones were annual rings, the age of each individual in years was considered as the number of opaque zones counted.

For 25 specimens of *E. coruscans* and 2 of *P. caerulea*, the microstructure was also examined using a scanning electron microscope (S3000N, Hitachi High-Tech Corp., Minato-ku, Tokyo, Japan) (Figure 2). The sections for examining the microstructure were ground with waterproof silicon carbide paper (FEPA P#2400, Struers, Ballerup, Copenhagen, Denmark) and polished with a polishing cloth (DP-Nap, Struers, Ballerup, Copenhagen, Denmark) and 3 μm alumina paste (AP-D Powder, Struers, Ballerup, Copenhagen, Denmark) using a grinding and polishing machine (RotoPol-35/PdM-Force-20, Struers, Ballerup, Copenhagen, Denmark). The polished sections were etched for ~10 s with 1%–2% hydrochloric acid. After etching, the sections were gently washed in water, dried, coated with metal using Ion Sputter (E-1010, Hitachi High-Tech Corp., Minato-ku, Tokyo, Japan) and viewed using a scanning electron microscope at various magnifications (×1000–3000). A microincrement was considered a daily increment, and its method of counting was done as described previously (Ebisawa & Maeda, 2006).

2.3 | Growth analysis and age at sexual maturity

Sex-specific growth patterns were modelled by fitting the von Bertalanffy growth equation (von Bertalanffy, 1938) to the length-at-age data using non-linear regression with KaleidaGraph (version 3.5J) software for Windows:

$$L_t = L_\infty \{1 - \exp[-K(t - t_0)]\},$$

where L_t is the FL of fish at age t, L_∞ is the mean asymptotic FL, K is the growth coefficient and t_0 is the theoretical age at which FL = 0. Growth parameters between sexes were compared statistically by a likelihood ratio test (Kimura, 1980) using the fishmethods package of the R language (http://cran.r-project.org).

The spawning season was estimated to occur from May to November for *E. coruscans*, from April to September for *P. caerulea* and from March to October for *P. filamentosus* and *P. sieboldii* (Uehara *et al*., 2018a). The age at 50% female maturity (A_{50}) was estimated by examining the specimens obtained during the spawning season for each species and by a generalized linear model with a binomial error structure and a logit-link function using the FSA package of R language (http://cran.r-project.org). The histological data for 707 specimens (*E. coruscans*, n = 299; *P. caerulea*, n = 95; *P. filamentosus*, n = 101; *P. sieboldii*, n = 212) were quoted from Uehara *et al*. (2018a). A_{50} was defined as the age at which 50% of all individuals had reached sexual maturity. C.I. at the 95% level for A_{50} was derived by bootstrap resampling with replacement through 1000 iterations.

3 | RESULTS

3.1 | Condition of otolith edges

Of the sectioned otoliths observed (Figure 1), 96.2%–99.5% had visible increments, and these were used for age determination of the four species (Table 2). Age estimates by three counts or less were consistent for 69.9%–88.2% of the sectioned otoliths (Table 2). APE and mean C.V. ranged from 10.7% to 21.6% and from 14.0% to 28.6%, respectively

TABLE 2   Number of samples, statistics and parameters to indicate accuracy and validity of age assessment

Contents	Etelis coruscans	Paracaesio caerulea	Pristipomoides filamentosus	Pristipomoides sieboldii
Age determination				
N_0: number of sectioned otoliths observed[a]	749	342	303	374
N_1: number of ages determined[a]	745	329	296	368
N_1/N_0 (%)	99.5	96.2	97.7	98.4
N_2: the first two counts coincided	102	29	54	59
N_3: two out of three counts coincided	555	214	153	214
N_4: two out of four counts coincided	88	86	89	94
N_2/N_1 (%)	13.7	8.8	18.2	16.0
N_3/N_1 (%)	74.5	65.0	51.7	58.2
N_4/N_1 (%)	11.8	26.1	30.1	25.5
Average percent error	10.7	21.6	17.1	12.7
Mean c.v.	14.0	28.6	22.7	16.8
Annual cycle of increment formation				
Goodness-of-fit test for circular distributions χ^2	167.4 ($P < 0.001$)	38.4 ($P < 0.001$)	46.2 ($P < 0.001$)	30.8 ($P < 0.001$)
Linear relationship between otolith weight (OW, g) and presumed age (age, year); Age = aOW + b				
a	151.62	283.55	81.77	104.09
b	−3.16	−8.49	−3.59	−3.17
r^2	0.803	0.892	0.841	0.831
P	<0.001	<0.001	<0.001	<0.001
n	681	156	188	179

[a]The microstructure excludes 25 *E. coruscans* and 2 *P. caerulea*.

(Table 2). The edge types of 19.9%–38.8% of the sectioned otoliths were uncertain. Edge-type analysis revealed an annual periodicity of increment formation with significant differences among the monthly changes of opaque margin for all four species (Table 2). Increment formation occurred from April to October in *E. coruscans*, from March to September in *P. caerulea*, from March to October in *P. filamentosus* and
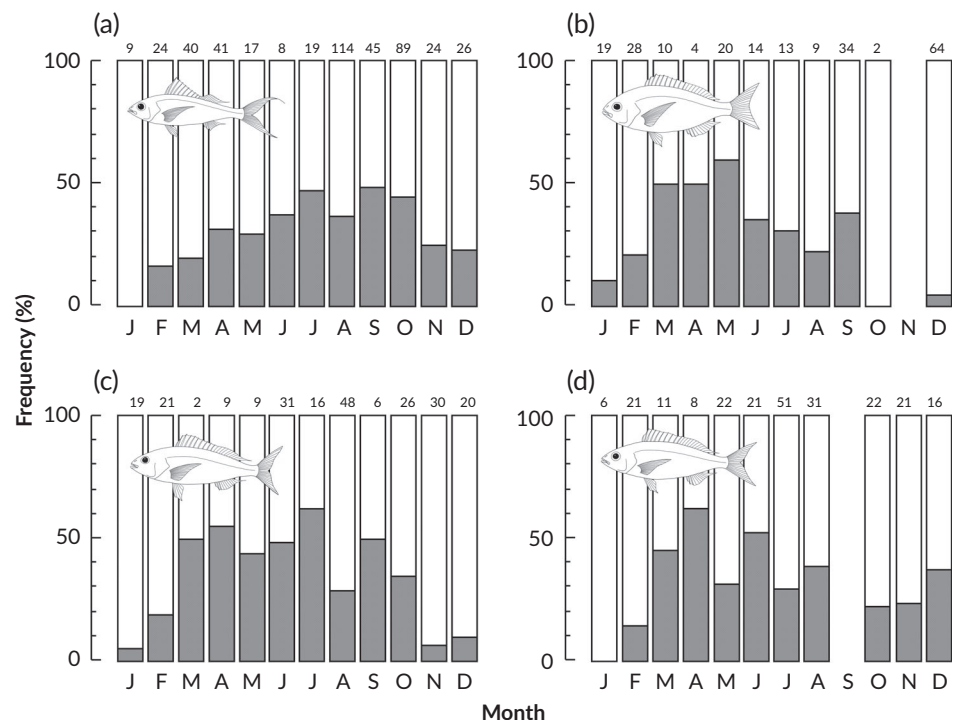

FIGURE 3   Edge-type analysis of sectioned otoliths of (a) *Etelis coruscans*, (b) *Paracaesio caerulea*, (c) *Pristipomoides filamentosus* and (d) *Pristipomoides sieboldii* showing the percentage of otolith edge condition (*white bars*: translucent; *grey bars*: opaque). Numbers on bars indicate sample size
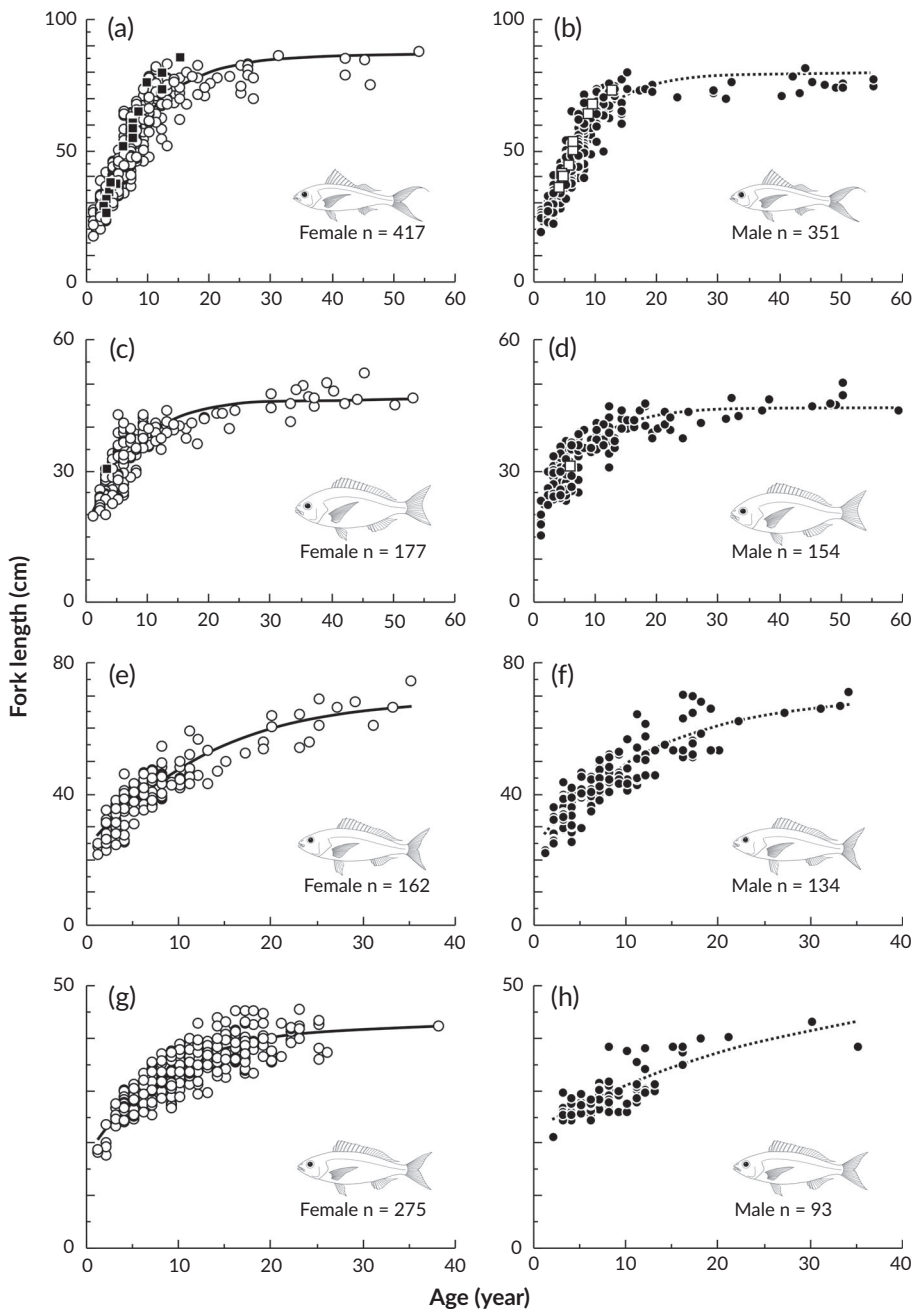
FIGURE 4 Von Bertalanffy growth curves fitted for observed fork length and female age (*open circles, bold lines*) and male age (*filled circles, dotted lines*) of (a, b) *Etelis coruscans*, (c, d) *Paracaesio caerulea*, (e, f) *Pristipomoides filamentosus* and (g, h) *Pristipomoides sieboldii*. *Open* and *filled squares* indicate the age estimated by daily increment analysis

from March to December in *P. sieboldii* (Figure 3). There were significant positive correlations between otolith weight and presumed age in all four species (Table 2). These results strongly indicated that the age determination of the four species performed in this study was effective.

3.2 | Age and growth

Growth curves for all four species are shown in Figure 4, and their equations provided good fits to length-at-age data (Table 3). A likelihood ratio test indicated that there was a significant difference (*E. coruscans*, χ^2 = 18.61, *df* = 3, *P* < 0.001; *P. sieboldii*, χ^2 = 56.27, *df* = 3, *P* < 0.001) between the von Bertalanffy growth equations

calculated for females and males of *E. coruscans* and *P. sieboldii*. In *P. caerulea* and *P. filamentosus*, the equations showed no significant differences between the sexes (*P. caerulea*, χ^2 = 6.07, *df* = 3, *P* = 0.108; *P. filamentosus*, χ^2 = 5.86, *df* = 3, *P* = 0.119).

Age estimates ranged from 1 to 55 years for *E. coruscans*, from 1 to 59 years for *P. caerulea*, from 1 to 35 years for *P. filamentosus* and from 1 to 38 years for *P. sieboldii* (Figure 4). The observed maximum ages for both sexes were similar in these four species (Table 3). Age estimates based on total counts of microincrements ranged from 954 to 5439 days for 25 *E. coruscans*, with the smallest (27.0 cm FL) an estimated 1045 days and the largest (86.3 cm FL) an estimated 5439 days, and the smallest (30.7 cm FL) an estimated 1156 days and the largest (31.3 cm FL) an estimated 2095 days for *P. caerulea*

TABLE 3 Parameters of the von Bertalanffy growth equation for four deep-water snappers

Species/location	Sex	L_∞	K	t_0	r^2	A_{max}	L_{max}	References
Etelis coruscans								
Okinawa Islands	Female	86.2 (1.6)[a]	0.122 (0.007)[a]	−0.848 (0.186)[a]	0.850	54	88.2	Present study
	Male	79.2 (2.0)[a]	0.140 (0.010)[a]	−0.723 (0.267)[a]	0.873	55	82.5	Present study
	Combined	82.1 (1.0)[a]	0.133 (0.005)[a]	−0.738 (0.132)[a]	0.857	55	88.2	Present study
	Combined	–	–	–	–	55	–	Ebisawa et al. (2010)
Mariana Archipelago	Combined	109.1	0.12	−1.19	–	8.7	96.0	Ralston & Williams (1988)
Papua New Guinea	Combined	72.9[b] (79.2)[c]	0.27	–	0.98	20	77.0[b] (83.6)[c]	Fry et al. (2006)
New Caledonia	Combined	99.4	0.14	−0.93	–	18	90.0	Williams et al. (2013)
South Pacific Ocean	Combined	–	–	–	–	40	90.0	Williams et al. (2015)
Paracaesio caerulea								
Okinawa Islands	Female	46.3 (0.9)[a]	0.133 (0.013)[a]	−3.332 (0.599)[a]	0.772	53	52.7	Present study
	Male	44.6 (1.2)[a]	0.134 (0.019)[a]	−3.648 (0.891)[a]	0.781	59	50.5	Present study
	Combined	45.4 (0.6)[a]	0.133 (0.010)[a]	−3.510 (0.448)[a]	0.772	59	52.7	Present study
Izu Islands	Combined	88.3	0.078	−1.972	–	6	60.0	Tokyo Fisheries Experimental Station (1974)
Pristipomoides filamentosus								
Okinawa Islands	Female	70.4 (3.4)[a]	0.080 (0.013)[a]	−5.217 (0.904)[a]	0.790	34	71.5	Present study
	Male	70.8 (4.8)[a]	0.072 (0.017)[a]	−5.612 (1.323)[a]	0.829	35	75.1	Present study
	Combined	70.3 (2.3)[a]	0.078 (0.008)[a]	−5.279 (0.642)[a]	0.806	35	75.1	Present study
Hawaiian Archipelago	Combined	78.0	0.146	−1.670	–	16.6	68.7	Ralston & Miyamoto (1983)
	Combined	97.1	0.31	0.02	–	5	–	Uchiyama & Tagami (1984)
	Combined	–	–	–	–	6.1	72.0	Radtke (1987)
	Combined	70.4	0.25	−0.22	–	–	68.7	DeMartini et al. (1994)
	Combined	78.0[d]	0.21	–	–	–	25.0	Moffitt & Parrish (1996)
	Combined	67.5	0.242	−0.29	–	43	76.8	Andrews et al. (2012)
Mariana Archipelago	Combined	58.4	0.29	−0.54	–	6.0	64.0	Ralston & Williams (1988)
Papua New Guinea	Combined	41.2[b] (46.0)[c]	0.34	–	0.62	12	50.0[b] (55.8)[c]	Fry et al. (2006)
South Pacific Ocean	Combined	–	–	–	–	64	78.0	Williams et al. (2015)
Seychelles	Female	77.6[e]	0.36	0.06	–	–	–	Hardman-Mountford et al. (1997)
	Male	85.8[e]	0.33	−0.16	–	–	–	
	Combined	75.8	0.244	−0.26	–	–	–	Mees & Rousseau (1997)
	Combined	62.3	0.11	–	–	30	73.0	Pilling et al. (2000)

TABLE 3 (Continued)

Species/location	Sex	L_∞	K	t_0	A_{max}	L_{max}	r^2	References
Pristipomoides sieboldii								
Okinawa Islands	Female	42.5 (0.9)[a]	0.115 (0.013)[a]	−4.553 (0.765)[a]	38	45.9	0.737	Present study
	Male	51.7 (10.0)[a]	0.035 (0.022)[a]	−16.281 (5.384)[a]	35	43.4	0.656	
	Combined	44.4 (1.3)[a]	0.087 (0.011)[a]	−6.332 (0.941)[a]	38	45.9	0.723	
Mariana Archipelago	Combined	44.1	0.351	−0.33	4.4	–	–	Ralston & Williams (1988)

Note. L_∞, K, t_0, A_{max} and L_{max} are the asymptotic fork length (FL), the growth coefficient, the theoretical age at which FL = 0, the observed maximum age and the observed maximum FL, respectively.
[a]Standard error.
[b]Standard length.
[c]Length reported as standard length was converted to FL using a conversion factor of Uehara et al. (2018a).
[d]Using the values of L_∞ calculated by Ralston and Miyamoto (1983).
[e]Using the values of L_∞ calculated by Mees (1993).

(Figure 4). Age distributions did not differ significantly between the sexes in *E. coruscans*, *P. caerulea* and *P. filamentosus* (Wilcoxon rank-sum test; *E. coruscans*, $W = 74{,}074$, $P = 0.770$; *P. caerulea*, $W = 13{,}086$, $P = 0.530$; *P. filamentosus*, $W = 11{,}306$, $P = 0.536$), whereas there was a significant difference between the sexes in *P. sieboldii* ($W = 17{,}466$, $P < 0.001$) (Figure 5).

3.3 | Age at maturity

The observed smallest (youngest) females with mature gonads in the four species were 2–7 years old (Figure 6). The A_{50} values of females were 11.3 (C.I.: 10.5–12.7) years in *E. coruscans*, 7.0 (6.2–8.0) years in *P. caerulea* and 4.9 (4.0–5.8) years in *P. filamentosus*. The A_{50} value of female of *P. sieboldii* was already observable in the first year. Age at female maturity was modelled for *P. sieboldii* based on only two specimens in the first two age groups, and therefore, the maturity schedule should be interpreted cautiously.

4 | DISCUSSION

4.1 | Age validation and longevity

The ages of specimens were estimated using sectioned sagittal otoliths (Figure 1), which is widely used in the ageing structure for lutjanids (*e.g.*, Newman & Dunk, 2002, 2003; Piddocke, 2015; Pilling *et al.*, 2000; Taylor *et al.*, 2018). A high percentage (96.2%–99.5%) of visible opaque zones and acceptable APE values (10.7%–21.6%) were encountered compared with previous studies (Table 2). In a review, Campana (2001) reported that most age and growth studies (241 of 372 reports, 65%) did not provide estimates of the precision of ageing and that APE and C.V. were widely used and were statistically sound measures of the precision of ageing. Age and growth studies of lutjanid fish in the Indo-West Pacific region provided indices of the precision of ageing for only nine species, with APE values ranging from 0.7% to 18.1% (Table 4). The APE values were generally consistent with these data (Table 4). For moderately and extremely long-lived fishes with otoliths that are relatively difficult to read, APE values of up to 5% are considered acceptable (Allman *et al.*, 2005; Fry & Milton, 2009; Marriott & Mapstone, 2006; Newman & Dunk, 2003). Thus, the precision of age determination in the present study is considered acceptable, given the difficulty in their ageing.

Our observation of the otolith edge revealed that the opaque zones on the sectioned otoliths were annuli in all four species (Table 2 and Figure 3). Piddocke *et al.* (2015) reviewed the four main approaches used in the validation of lutjanid age: bomb radiocarbon, radiometry, chemical tagging and MIA. Of these four approaches, MIA is inexpensive and logistically simple, and its use for lutjanids will inevitably continue (Piddocke *et al.*, 2015). Where MIA is too irregular to allow measurement, edge-type analysis can be a useful alternative (Newman & Dunk, 2003). The edge-type analysis showed strong

FIGURE 5 Age–frequency distributions for females (*black bars*) and males (*grey bars*) of (a) *Etelis coruscans*, (b) *Paracaesio caerulea*, (c) *Pristipomoides filamentosus* and (d) *Pristipomoides sieboldii*. Age groups are for 1 year
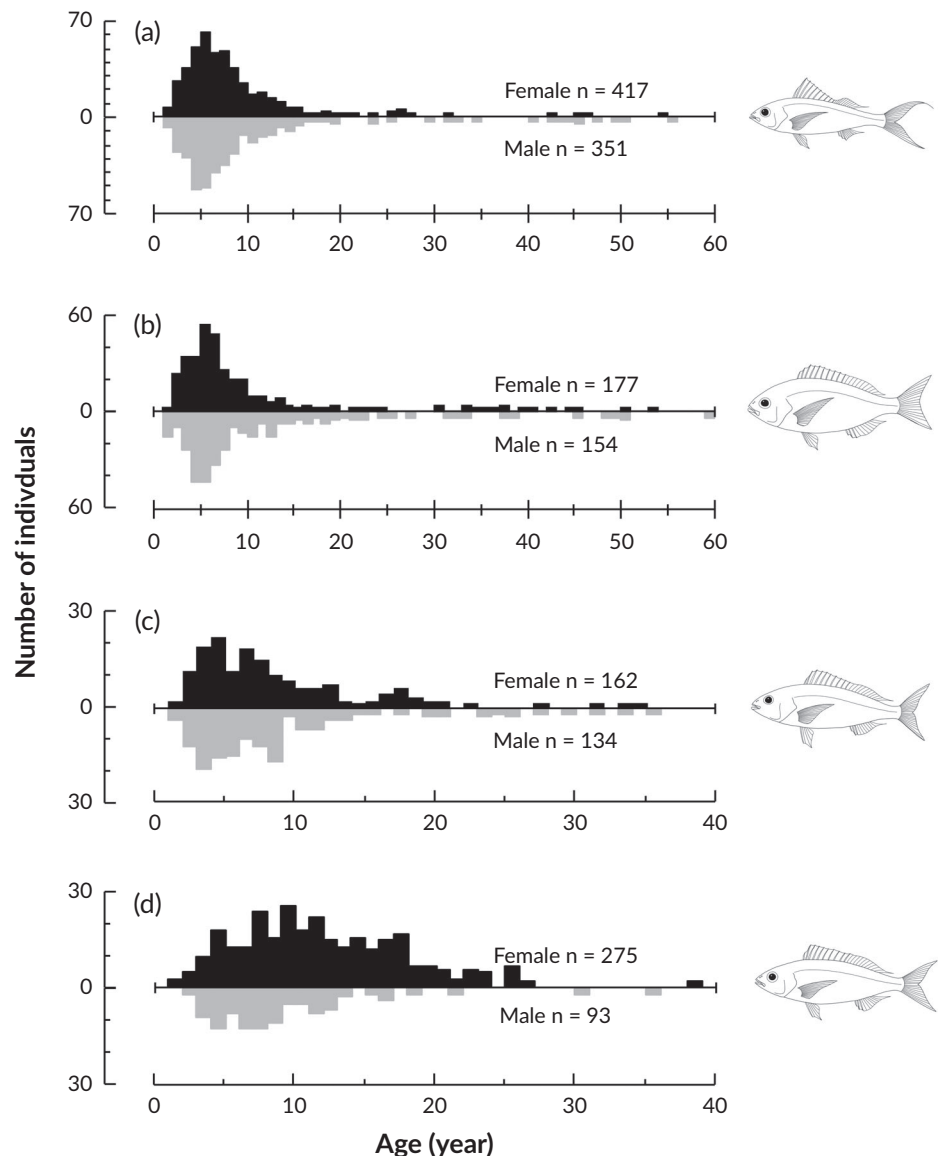
unimodal patterns in all four species (Table 2). Their otoliths also showed positive relationships between the number of opaque zones on the otolith and otolith weight, indicating that otoliths grow throughout the life of individual fish. In addition to these two established methods, the authors' previous tagging experiment indicated that the opaque zones of *P. filamentosus* could be annual rings (Uehara *et al*., 2019). Bomb radiocarbon dating has validated that a single opaque zone is deposited annually in the otoliths of *P. filamentosus* (see Andrews *et al*., 2012). Thus, the ageing assessment provides reliable results that satisfy the three criteria needed to validate the relationship between periodicity of increment formation in otoliths and fish age (Fowler, 1990).

From the observed maximum ages, the estimated longevity exceeded 50 years for *E. coruscans* and *P. caerulea* and 30 years for the two species of *Pristipomoides*. Previous age and growth studies have been reported in all four species (Table 3), but many of these studies did not use sagittal otoliths for ageing, had a small sample size

and/or have not been directly validated. Therefore, comparisons of observed maximum ages are limited when considering lutjanid age validation studies using bomb radiocarbon, radiometry, chemical tagging, edge-type analysis and MIA. The longevity of lutjanids ranges from 20 to 57 years in the large body-size group (≥70 cm) and from 6 to 42 years in the small and medium body-size groups (<70 cm) (Table 4). From another perspective, the longevities and habitats of these lutjanids do not seem to be correlated. The longevity of *P. filamentosus* was estimated as 30 years for the Seychelles population (Pilling *et al*., 2000) and more than 40 years for the Hawaiian population (Andrews *et al*., 2012). According to a preliminary study using bomb radiocarbon (A. H. Andrews, pers. comm.), the longevity of *E. coruscans* was estimated to be more than 50 years. Therefore, the estimated longevities of *E. coruscans* and *P. filamentosus* in the present study were similar to those in other studies. Thus, the validity of the potential longevities for Okinawan deep-water snappers was demonstrated.
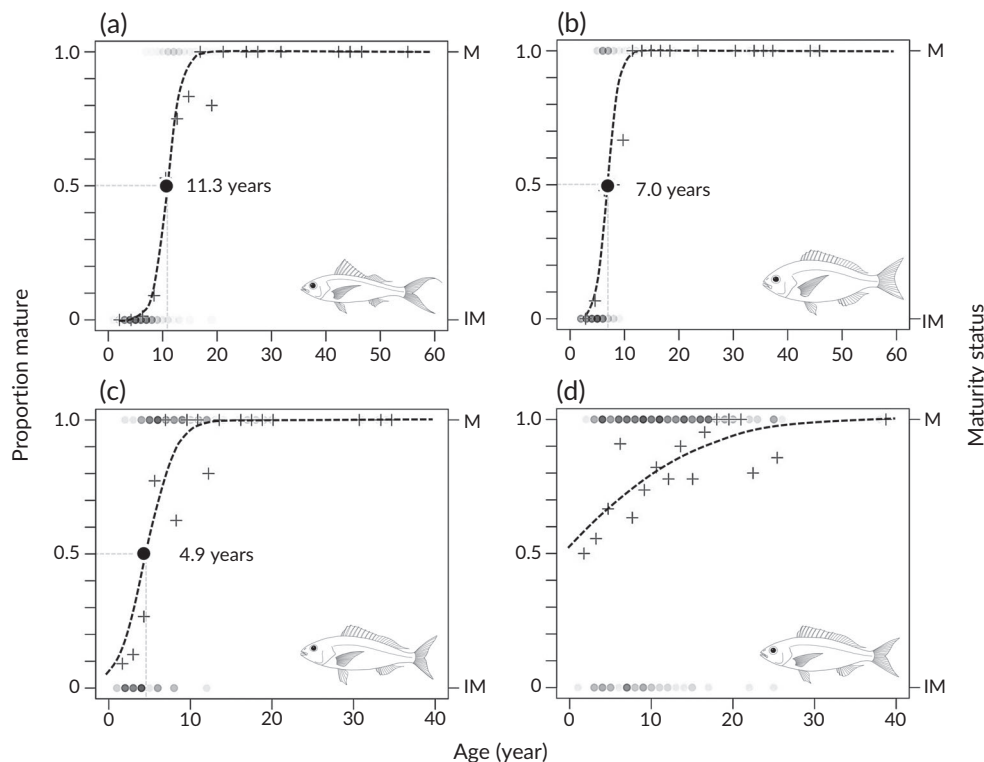
FIGURE 6 Age at maturity of females for (a) *Etelis coruscans*, (b) *Paracaesio caerulea*, (c) *Pristipomoides filamentosus* and (d) *Pristipomoides sieboldii*. Dashed lines represent age at which 50% of the population was mature (A_{50}). *M* and *IM* indicate mature and immature, respectively

4.2 | Age-specific demography

The von Bertalanffy growth equation is frequently used in life-history and fisheries research to determine the relationship between the length or weight of a fish and its age (Ratkowsky, 1986). This equation provided good fits to the data for all four species in the present study (Table 3). The observed maximum lengths (L_{max}) and asymptotic lengths (L_∞) of *E. coruscans* and *P. filamentosus* were greater than those of *P. caerulea* and *P. sieboldii*. Growth was rapid up to 10 years after which it slowed down in *E. coruscans* and *P. caerulea*. Similarly, growth was slow in the two species of *Pristipomoides* (Figure 4). The values of the growth coefficient (*K*) were lower in the two species of *Pristipomoides* than in *E. coruscans* and *P. caerulea* (Table 3). The available studies on age and growth estimated the growth parameters in the four deep-water snappers (Table 3). L_∞ of *E. coruscans* was intermediate to that of the other three populations of the species in the North and South Pacific regions (Fry *et al.*, 2006; Ralston & Williams, 1988; Williams *et al.*, 2013). *K* of the species was also similar to that of the other two populations of the species in the North and South Pacific regions (Ralston & Williams, 1988; Williams *et al.*, 2013). In the Okinawan population of *P. caerulea*, L_∞ was much smaller than that in the population of the Izu Islands, although *K* was higher than that in the population of the Izu Islands (Tokyo Fisheries Experimental Station, 1974). For *P. filamentosus*, L_∞ was intermediate, whereas *K* was somewhat lower in the Indo-Pacific region (Andrews *et al.*, 2012; DeMartini *et al.*, 1994; Fry *et al.*, 2006; Hardman-Mountford *et al.*, 1997; Mees and Rousseau, 1997; Moffitt & Parrish, 1996; Pilling *et al.*, 2000; Radtke, 1987; Ralston & Miyamoto, 1983; Ralston & Williams, 1988; Uchiyama & Tagami, 1984). L_∞ of *P. sieboldii* was similar

to that of the population of the Mariana Archipelago, but *K* was much smaller than that of the Mariana population (Ralston & Williams, 1988). These findings indicate that the regional differences in growth parameters within the same species were found and that Okinawan deep-water snappers grow more slowly than other lutjanid fishes (Manooch, 1987).

The sexual body size dimorphism in Indo-Pacific lutjanid species has various patterns: males are larger than females in some species (Nanami *et al.*, 2010; Newman, 2002; Newman *et al.*, 1996; Taylor *et al.*, 2018) and smaller than females in others (Newman & Dunk, 2002; Shimose & Tachihara, 2005). In some cases, no significant differences in growth are found between the sexes (Newman & Dunk, 2003; Marriott *et al.*, 2007; Piddocke, 2015; Taylor *et al.*, 2018). In the present study, a significant difference was observed between the von Bertalanffy growth equations calculated for both sexes in the case of *E. coruscans* and *P. sieboldii*, whereas the observed maximum lengths for both sexes of *P. sieboldii* were similar (Table 3 and Figure 4); males were larger than females in *P. sieboldii* and smaller than females in *E. coruscans*. Nonetheless, in *P. sieboldii*, age distribution remarkably differed between the sexes (Figure 5). These findings suggest the possibility that the differences in the equations for *P. sieboldii* may be due to the small sample sizes during the young age of males.

Many gonochoristic species in which the sexes differ in growth mate randomly, which suggests that this difference is closely related to the difference in reproductive success between the sexes (Kohda, 2003). In a previous study of *E. coruscans* (see Uehara *et al.*, 2018a) individuals with transitional gonads or nonfunctional intersexes were not observed, and the male gonadosomatic index

TABLE 4   Age validation studies using four main approaches (Piddoche et al., 2015) in the Indo-Pacific lutjanids

Genus/species	Location[a]	Method[b]	Habitat[c]	Size[d]	L_{max}	A_{max}	APE	References
Aprion								
A. virescens	S	EA, MIA	C	L	99.0	27	–	Pilling et al. (2000)
Lutjanus								
L. adetii	GBR	MR	C	S	30.1	24	0.7	Newman et al. (1996)
L. argentimaculatus	NSW	MIA	C	L	101.9	57	1.1	Piddocke (2015)
L. bohar	GBR	EA, MIA, MR	C	L	76.0	56	2.2–4.0	Marriott & Mapstone (2006); Marriott et al. (2007)
	S	EA, MIA, MR	C	L	85.0	55	7.0–12.0	Marriott (2005); Marriott & Mapstone (2006)
L. erythropterus	GBR	MR	C	M	62.4	32	2.9	Cappo et al. (2000); Newman et al. (2000)
	NA	MIA	C	M	46.8[e]	42	1.8–16.2	Fry & Milton (2009)
	EI	MIA	C	M	58.3[e]	40	3.1–18.1	Fry & Milton (2009)
L. kasmira	HA	EA	C	S	33.0[f]	6	–	Morales-Nin & Ralston (1990)
L. malabaricus	GBR	MR	C	L	75.7	20	4.5–5.9	Cappo et al. (2000) and Newman et al. (2000)
	NA	MIA	C	M	68.0[e]	33	2.2–10.7	Fry & Milton (2009)
	EI	MIA	C	L	74.0[e]	48	2.4–4.7	Fry & Milton (2009)
L. fulviflamma	OI	EA	C	S	30.4[e]	24	–	Shimose & Tachihara (2005)
L. fulvus	OI	EA	C	S	33.2	34	0.8	Shimose & Nanami (2014)
L. gibbus	OI	EA	C	M	39.1	24	–	Nanami et al. (2010)
	TI	EA	C	M	49.0	27	–	Taylor et al. (2018)
L. quinquelineatus	GBR	MR	C	S	23.3	31	1.7	Newman et al. (1996)
L. rufolineatus	TI	EA	C	S	27.0	12	–	Taylor et al. (2018)
L. sebae	GBR	MR	C	L	86.0	22	3.6–6.7	Cappo et al. (2000); Newman et al. (2000)
	KC	MIA	C	L	72.8	34	4.7	Newman & Dunk (2002)
Etelis								
E. carbunculus	WA	BR	D	L	93.2[e]	35–39	–	Andrews et al. (2011)
Pristipomoides								
P. filamentosus	S	MIA	D	L	73.0	30	–	Pilling et al. (2000)
	HA	BR	D	L	76.8	43	–	Andrews et al. (2012)
P. multidens	KC	EA	D	L	70.1	30	10.4	Newman & Dunk (2003)

Note. L_{max}, A_{max} and APE are the observed maximum length, the observed maximum age and the average percent error (Beamish & Fournier, 1981), respectively.
[a]EI, eastern Indonesia; GBR, Great Barrier Reef; HA, Hawaiian Archipelago; KC, Kimberley coast; NA, northern Australia; NSW, New South Wales; OI, Okinawa Islands; S, Seychelles; TI, Tutuila Island; WA, western Australia.
[b]BR, bomb radiocarbon ageing; EA, edge-type analysis; MIA, marginal increment analysis; MR, mark-recapture.
[c]Habitat was classified according to two divisions following Froese and Pauly (2019) and Shimada (2013) as follows: coastal (C, usually <150 m depth) and deep-water (D, usually ≥150 m depth).
[d]L, large body size (≥70 cm); M, medium body size (<70 cm); S, small body size (<35 cm).
[e]Standard length.
[f]Total length.

values were equivalent to those in fish species that spawn in pairs and/or nonexistent sneakers (Stockley et al., 1997). Female *E. coruscans* have also increased batch fecundity with increasing body length (Uehara & Ebisawa, unpubl. data). As in *E. coruscans*, when females grow larger than males, it may be because females with large body size will gain an advantage in batch fecundity and/or fecundity; this explanation has been theoretically accepted (Kuwamura & Nakashima, 1996; Nakazono & Kuwamura, 1987; Parker, 1992).

In the present study, the A_{50} values for females of three species, excluding *P. sieboldii*, were within a range of 13.2%–20.9% of their observed maximum ages (A_{max}) (Table 3). The available values were equal to or slightly smaller than those for other lutjanids (11.9%–30.4% of A_{max}) (Newman et al., 2001; Newman & Dunk, 2002, 2003; Marriott et al., 2007; Taylor et al., 2018). Okinawan deep-water snappers have a wide range of the A_{50} values. On the contrary, clear results were not obtained for the A_{50} values of the males, except for *P. caerulea*. Nonetheless, the results

showed that males of *P. caerulea* reached sexual maturity before the age of 2 or 3 years, which was earlier than the age of sexual maturity for females. The difference between the sexes in the age of sexual maturity was remarkable especially in *E. coruscans* and *P. caerulea*, although a similar difference has been reported in *Lutjanus bohar*, a coastal lutjanid of large body size, in which the females mature at 9.39 years compared with 1.46 years for males (Marriott *et al.*, 2007). Nonetheless, a similar difference was not observed in *Lutjanus sebae* and *Pristipomoides multidens*, which also belong to the large body-size group (Newman *et al.*, 2001; Newman & Dunk, 2002, 2003). These findings suggest that differences between the sexes in the age of sexual maturity are not associated with the habitat or taxonomic classification of the species.

4.3 | Implications for fishery management

The information presented in this study provides detailed age-based demographic profiles for four Okinawan deep-water snappers that differ markedly in their trait values and life-history patterns. *E. coruscans* is the largest-bodied species, with clear sexual size dimorphism, the latest age of sexual maturation and a long life span. *P. caerulea* is a moderate-bodied species with a moderate age of sexual maturation and a long life span. *P. filamentosus* is a comparatively large-bodied species with a moderate age of sexual maturation and life span. *P. sieboldii* is a moderate-bodied species with a relatively early age of sexual maturation and a moderate life span. Large body size, late maturation and long life span are commonly associated with greater vulnerability to overexploitation (Abesamis *et al.*, 2014; Drazen & Haedrich, 2012; Koslow *et al.*, 2000; Moore & Mace, 1999). The estimated limit values of ABC in 2017 differed among the four species, and the actual catch of *E. coruscans*, *P. caerulea* and *P. filamentosus* in 2017 had ~1.5 times the ABC limit (Shimose *et al.*, 2019). In addition, the current stock status of four deep-water snappers (the Ryukyu Archipelago populations) is at a low level (Shimose *et al.*, 2019). Therefore, it seems that their vulnerability to overexploitation can explain the observed age-based demographic profiles.

The relative abundance of these four snappers in the MPA is influenced by whether protection is year-round or seasonal. Their responses to fishing differ, and the abundance of *E. coruscans* and *P. caerulea* decreased markedly when the ban was lifted (Uehara *et al.*, 2019). Abesamis *et al.* (2014) investigated predicted vulnerability to fishing (Cheung *et al.*, 2005) in 145 species of reef fishes belonging to 10 families. *L. bohar*, which has a large body size, late maturation and a long life span (Marriott *et al.*, 2007), has been placed on the vulnerability index in the "high to very high" category (Abesamis *et al.*, 2014). Therefore, *E. coruscans* and *P. caerulea*, which are similar to *L. bohar* in that they have long life spans and late maturation, are probably more vulnerable to fishing disturbance than the two species of *Pristipomoides*.

In Okinawa, *E. coruscans*, *P. caerulea*, *P. filamentosus* and *P. sieboldii* have been managed using multiple MPAs since 2005. In 2010, local fishermen introduced self-restricting rules on the size limit of catches in the Okinawan waters, with FL < 30 cm for *E. coruscans* and FL < 20 cm for *P. caerulea*, *P. filamentosus* and *P. sieboldii* in all of the MPAs. Although the MPA approach is generally adopted to protect multiple species in fisheries management, year-round closure for a long period is needed for population recovery of deep-water snappers (Friedlander *et al.*, 2014; Sackett *et al.*, 2014; Uehara *et al.*, 2019). Therefore, the current status of the Ryukyu Archipelago or the Okinawan populations of the four deep-water snappers shows no sign of a significant turnaround in the stock biomass (Shimose *et al.*, 2019; Uehara et al., 2017a, 2017b). The maximum sustainable levels of exploitation of the tropical deep-water species are likely to be as low as 5%–10% of biomass, commensurate with levels of natural mortality in many cases of less than ~0.1 (Martin *et al.*, 2014; Newman *et al.*, 2012). In fact, the natural mortality coefficients (M) (Tanaka, 1960) of the four Okinawan deep-water snappers are <0.1, and their harvest rates (catch/biomass) are estimated to exceed 10% of the stock size calculated by virtual population analysis (Uehara *et al.*, unpubl. data). On the contrary, extended periods of high exploitation are also likely to result in decreases in the spawning stock biomass and constriction of the age structure of fish populations (removal of older fish) and thus decrease the number of reproductive events (Newman *et al.*, 2016). Previous studies of the authors specifically demonstrated that spawning-capable individuals of *E. coruscans* are less than 2% of those landed in Okinawan waters (Uehara *et al.*, 2012, 2013, 2015, 2017b,c 2018b). This means that the reproductive potential of the Okinawan population of *E. coruscans* is under worse circumstances (Uehara *et al.*, 2019). These findings indicate that further approaches to decrease and control fishing intensity, such as networking of MPAs and regulation to control the numbers of boats and/or the TAC, will be necessary for the management of the stock of these snapper species, especially for *E. coruscans* and *P. caerulea*, which are particularly vulnerable to fishing impact.

AUTHOR CONTRIBUTIONS

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