

Comparative biology of key inter-reefal serranid species on the Great Barrier Reef

Project Milestone Report

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Acronyms Used In This Report

APE	Average percent error
ELF	Effets of Line Fishing (Experiment)
FL	Fork length
GBR	Great Barrier Reef
GBRWHA	Great Barrier Reef World Heritage Area
GSI	Gonadosomatic Index
IAPE	Index of average percent error
TACC	Total allowable commercial catch
TL	Total length
VBGT	von Bertalanffy Growth Function
W	Weight

Introduction

The sub-family Epinephelinae (Family: Serranidae) is comprised of a diverse group of fishes, including 15 genera and 159 species. These species are widely distributed throughout the world and form important components of commercial, recreational and artisanal fisheries within coastal areas in tropical and subtropical waters. Commonly referred to as groupers, species can range in size from large Queensland grouper (*Epinephelus lanceolatus*), which grow to 270 cm and over 400 kg, to small *Cephalopholis* species, which only grow to 20 cm (Randall *et al.* 1997). Due to over-fishing in some regions, there is concern about the status of a number of larger grouper species caught in tropical and temperate fisheries (Morris *et al.* 2000). However, grouper species remain important economic components of tropical coral reef fisheries. Within Southeast Asia, the development of the live reef fish trade has led to increased catches of tropical coral reef grouper, with some species being highly desirable as live food fish (Sadovy *et al.* 2003). Coral reef fisheries are typically diverse multi-species, multi-gear fisheries with a large number of fish from different families and genera included in the catch. It is therefore likely that a number of grouper species will be represented in the catch of these fisheries. Groupers are generally considered to be susceptible to fishing pressures due to their extended longevity, mating and reproductive biology (Sadovy, 1996; Pears *et al.* 2006). Basic information including life history parameters for grouper species are needed to make decisions about the management needs for fisheries, and the status of species within these fisheries. Life history characteristics of coral reef fishes vary among families and also between species within families (Sale, 2002; Gust *et al.* 2002). This variability in life history traits will have an influence on the response of species to fishing pressure. Due to the diversity of this group of fishes, these species also offer a wealth of comparative data.

Otolith based age estimates exist for some species within the genera *Epinephelus*, *Plectropomus*, *Mycteroperca* and *Cephalopholis*. Age estimates in excess of twenty years (Manickchand-Heileman and Phillip, 2000; Bullock *et al.* 1992) and as high as forty years (Manooch and Mason, 1987; Pears *et al.* 2006) have been reported for *Epinephelus* species. Species within this genus generally have been reported to have slow growth rates and low estimates of natural mortality. In contrast, the genus *Cephalopholis* includes some of the smallest species of grouper (<30 cm) and one of the longest lived of any of the grouper species (*C. cyanostigma* – 46 years) (data from Mosse, 2002 used in this study). Other estimates of maximum age for *Cephalopholis* species range from eleven years for *C. boenak* (Chan and Sadovy, 2002) to 25 years for *C. fulva* (de Araujo and Martins, 2006). *Mycteroperca* species are distributed throughout the subtropical and tropical regions of the Atlantic and Eastern Pacific Oceans. Age estimates for these species ranged from thirteen years (*M. phenax*, Matherson *et al.* 1986) to 41 years (*M. interstitialis*, Manickchand-Heileman and Phillip, 2000). Species within the genus *Plectropomus* have become an important component of the live reef fish trade in Southeast Asia (Mapstone *et al.* 1996). Due to the commercial importance of these species they are probably the most well studied of all the groupers. In the Australasian region, estimates of age, growth and mortality exist for *Plectropomus leopardus*, *P. maculatus* and *P. areolatus* collected from coral reefs in northeast Australia (Williams *et al.* 2008; Ferreira and Russ, 1994). The estimates of maximum age and growth are more moderate than those reported for some *Epinephelus*, *Cephalopholis* and *Mycteroperca* species.

When considering comparative life history data there is a great deal of information which can be collected from studies of the reproductive patterns of fish species. The reproductive development of epinephelinae groupers is complex. It includes fish which are gonochoristic and protogynous hermaphrodites. The incidence of gonochorism, where fish function as either a male or female throughout their lives, is rare with only two species, *E. striatus* and *Mycteroperca rosacea*, diagnosed as functionally gonochoric (Sadovy and Colin, 1995;

Erisman *et al.* 2008). Most grouper species are protogynous hermaphrodites (Heemstra and Randell, 1993). In this instance reproductive development involves a sequential change from female to male. Protogyny is further divided into monandry (males are derived exclusively from mature females) and diandry (males develop from mature females or directly from the juvenile female phase). Two characteristics expected with monandric protogyny are a length frequency, which includes predominantly larger males, and a female biased sex ratio in the catch, though it is not necessarily the case that these characteristics will be present in all cases (Adams, 2000). Though grouper are predominantly monandric protogynous hermaphrodites, recent studies have reported species which are diandric protogynous hermaphrodites (Chan and Sadovy, 2002; Adams, 2003). Understanding the complex reproductive development of grouper species has important implications for fishery management.

Within the Coral Sea and Great Barrier Reef (GBR) region there are more than forty species of grouper, representing eight genus; *Epinephelus* (23), *Plectropomus* (5), *Cephalopholis* (11), *Variola* (2), *Anyperodon* (1), *Aethaloperca* (1) and *Cromileptes* (1). A number of the larger and mid-sized grouper are taken as part of the multi-sector reef line fishery which operates within the Great Barrier Reef World Heritage Area (GBRWHA). Groupers make up more than 53% of the catch within the commercial fleet; more than 26% of the recreational; and more than 32% of the charter fishing catch (Simpfendorfer *et al.* 2007). Coral trout (*Plectropomus leopardus*), a medium sized grouper, is the primary target species of the fishery and is taken by commercial fishers under a species specific Total Allowable Commercial Catch (TACC), primarily to fulfil the demand for live reef fish in southeast Asia. All other harvested grouper species along with the majority of other fish species are included in a combined 'other species' TACC. Size limits apply to all sectors of the fishery, and bag limits apply to recreational fishers. Some species of grouper are totally protected from harvest, including *Epinephelus lanceolatus*, *Epinephelus tukula* and *Cromileptes altivelis*. The majority of the catch is taken within the Great Barrier Reef Marine Park (GBRMP). This is a multiple-use marine park with some areas closed to any form of fishing.

The ecological value of grouper species to reef communities and economic value to fisheries within the GBR make further studies of the life history characteristics important. The diversity and complex life histories of species offer the potential to further understand the impacts of fisheries in coral reef communities. The aim of this study was to investigate the biological characteristics including length, age, growth, mortality and reproduction for a suite of epinepheline serranids representing five genera.

Methodology

Sample collection

Biological samples and associated catch information were collected from 11,369 individual Epinephelinae serranids representing 26 species within five genera, from the GBR, Australia ([Table 1](#)). The majority of samples were collected from reefs in four regions of the GBR (Lizard Island, Townsville, Mackay and Storm Cay) over eleven years from 1995 to 2005 as part of research surveys associated with the Effects of Line Fishing (ELF) experiment (Mapstone *et al.* 1996) ([Figure 1](#)). Fish were collected during the ELF surveys using standardised hook and line gear, which was similar to gear used by the commercial fishing fleet. Structured sampling was undertaken in such a way that it matched closely with the operations of commercial fishing vessels but remained comparable between reefs and between years. In addition to the ELF samples which were aggregated by region, by year and by zone, fish were collected opportunistically from the catch of commercial line fishing vessels and during fisheries-independent sampling trips using hand spears and hook-and-line gear. These samples were collected to supplement ELF samples to provide better estimates of biological parameters and greater temporal resolution. For each species, all samples were pooled to estimate biological parameters. However, fishery-independent (non-ELF) samples were removed from length based catch curves and age based catch curves which were used for estimates of mortality. In some instances species identification was problematic given the similarity in appearance of some groupers; in these cases species have been grouped together ([Table 1](#)). Samples that have been included in these species groups were not included in any further analysis.

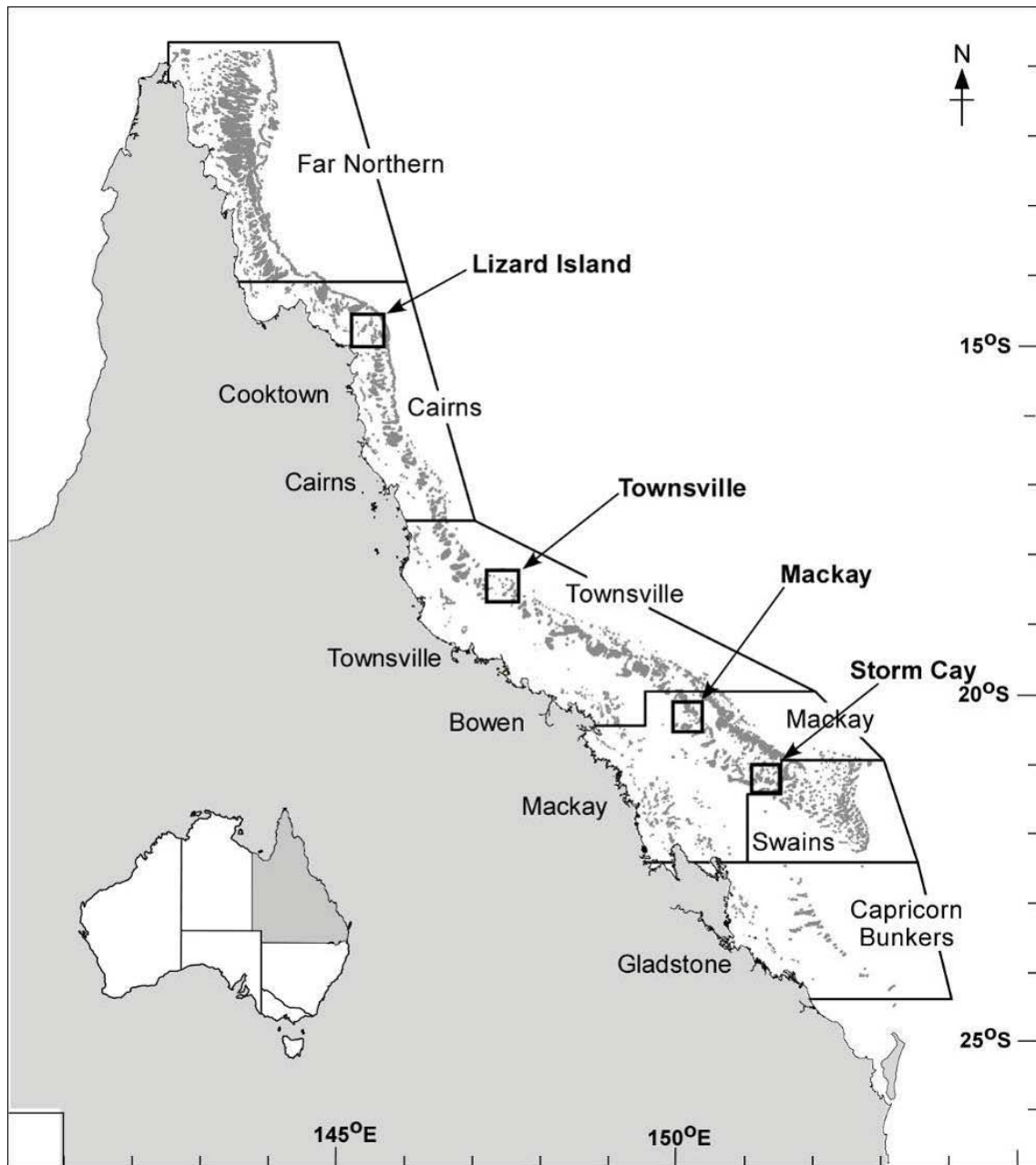


Figure 1: Map of the Great Barrier Reef World Heritage Area, showing reefs sampled for each of four regions (Lizard Island, Townsville, Mackay, Storm Cay – indicated by small squares) as part of the Effects of Line Fishing experiment.

Table 1: Numbers of Epinephinae grouper species collected from Great Barrier Reef waters, including ELF and non-ELF samples. Symbol (†) indicates a species group.

Common Name	Species	ELF samples	Non-ELF samples	Grand Total
Bommie rockcod	<i>Cephalopholis cyanostigma</i>	4,276	438	4,714
Footballer Cod	<i>Epinephelus fasciatus</i>	1,334	220	1,554
Mori rock cod	<i>Epinephelus ongus</i>	1,034	119	1,153
Wire netting cod†	(<i>Epinephelus merra</i> , <i>E. hexagonatus</i> , <i>E. quoyanus</i> , <i>E. macrospilos</i> , <i>E. spilotoceps</i>)	584	12	596
Flowery cod	<i>Epinephelus fuscoguttatus</i>	424	153	577
Camouflage cod	<i>Epinephelus polyphekadion</i>	344	136	480
Long-fin rockcod	<i>Epinephelus quoyanus</i>	282	65	347
Peacock rockcod	<i>Cephalopholis argus</i>	260	245	505
Coronation trout	<i>Variola louti</i>	167	51	218
Blue maori cod	<i>Epinephelus cyanopodus</i>	113	8	121
Trout cod	<i>Epinephelus maculatus</i>	113	65	178
White-lined rockcod	<i>Anyperodon leucogrammicus</i>	102	67	169
Lyretail trout	<i>Variola albimarginata</i>	80	3	83
Coral cod	<i>Cephalopholis miniata</i>	71	37	108
Honey-comb cod	<i>Epinephelus merra</i>	43	37	43
Chocolate cod	<i>Cephalopholis boenak</i>	34	26	60
Estuary Cod†	(<i>Epinephelus malabaricus</i> , <i>E. coioides</i>)	49	49	98
Redmouth rockcod	<i>Aethaloperca rogaa</i>	15	37	52
Flagtail rockcod	<i>Cephalopholis urodeta</i>	12	114	126
Blacksaddle rockcod	<i>Epinephelus howlandi</i>	11	5	16
Coral rockcod	<i>Epinephelus corallicola</i>	9	4	13
Six spot rockcod	<i>Cephalopholis sexmaculata</i>	6	8	14
Hexagon rockcod	<i>Epinephelus hexagonatus</i>	5	5	10
Tomato rockcod	<i>Cephalopholis sonnerati</i>	3	3	6
Greasy rockcod	<i>Epinephelus tauvina</i>	2	13	15
Snubnose rockcod	<i>Epinephelus macrospilos</i>	2		2
Dottailed rockcod	<i>Cephalopholis microprion</i>	1	24	25
Four saddle rockcod	<i>Epinephelus spilotoceps</i>	1	48	49
Total		9,377	1,992	11,369

Sample processing

For samples, total length (*TL*) or, in the case of *Variola* species, fork length (*FL*) was measured to the nearest millimetre. Whole wet weight (*W*) was measured to the nearest 10 g for a smaller subsample of fish. Sagittal otoliths were removed, cleaned of any residual material, and stored dry in paper envelopes. Age estimates were derived from thin (~400 µm) transverse sections of sagittal otoliths. Whole otoliths were not used as they were judged as unreadable for all species and more accurate estimates could be determined from thin sections, particularly for long lived species (Newman *et al.* 2000). Each otolith was embedded in a resin block before being cut using an Isomet[®] low speed saw fitted with two diamond blades separated by a thin spacer. The use of two blades allowed thin sections to be achieved with a single cut through the nucleus of the otolith. The thin sections were mounted on glass slides under a cover slip. Once mounted they were viewed using transmitted or reflected light, depending on the protocols established for a particular species. Alternating opaque and translucent bands were present on all otoliths, and these bands were considered to represent one year of growth. Each non-marginal opaque band was counted along an axis as close as possible to the sulcus. Otoliths were read multiple times (at least twice) by an experienced reader at low (40x) to medium (100x) magnification depending on the species. Repeated counts which matched were included as the final age estimate. Where repeated (>3) estimates did not match but were within acceptable limits (IAPE ≤10 %), the median age was taken as the final age. This approach was considered appropriate given that it was likely some species would be long lived and there is the potential that it would be difficult to reach agreement between reads for older fish (Marriott and Mapstone, 2006). An index of average percent error (APE) (Beamish and Fournier, 1981) was calculated for each species to assess the precision of age estimates. Validation of the annual formation of opaque and translucent bands on otoliths has been completed for a number of grouper (Pears *et al.* 2006; Pears *unpub. data*). It was assumed that the consistent pattern of banding observed was annual for all species, including those which had not been formally validated.

Gonads from fish were either removed at sea and stored in 10% phosphate buffered formalin, or immediately frozen whole for processing back in the laboratory where they were removed, thawed and similarly preserved in formalin. After fixation, each pair of ovaries or testes was dried of excess fixative, and gonad weight was measured to the nearest 0.01 g. Where only one gonad lobe was available due to damage during processing, gonad weight was estimated by multiplying the mass of the single complete lobe by two. It was assumed that this provided a reasonably accurate measure of gonad weight, as the two gonad lobes are generally equal in size for other groupers (Adams, 2003). Histological sections were taken from all gonads following the procedures outlined by Adams (2003). All sex assignment and maturity staging was completed using histological sections of gonads under a high power microscope. The stage of ovary development was based on the most advanced non-atretic cell type present (West, 1990). Additional features used in histological staging included the presence of brown bodies, atretic oocytes, vascularisation, and the relative thickness of the gonad wall, all of which may indicate prior spawning (Sadovy and Shapiro, 1987). Ovaries and testes were classified into developmental stages adapted from Ferreira (1995) and Adams (2003). Females were classified into five stages: Immature, Resting, Ripe, Running Ripe and Spent. Males were classified into three stages: Resting, Ripe and Spent. The reproductive information was matched with age, length and month of capture.

Length and age frequency and sex ratio

Length and age frequency distributions were constructed separately for each species with more than twenty records and only including samples collected during the ELF experiment. The 90th percentiles of length (L_{90}) and age (A_{90}) for each species was also calculated for these species as a proxy for longevity. The number of samples, length and age range was provided for all species where data was available. ELF data was used to calculate sex ratios as the data had been collected using standardised gear and techniques. Only mature individuals were used to determine sex ratio for species for which reproductive data was available. The operational sex ratio was calculated as the number of mature females to mature males. These sex ratios were compared with an expected ratio of 1:1 using a χ^2 goodness-of-fit test.

Length-weight relationship length and age frequency distributions

The relationship between TL or FL depending on the species and W was described using a power function,

$$W = a \times FL^b$$

where a is the coefficient of the power function and b is the exponent. This relationship was plotted. Length-weight relationships were determined to be either isometric ($b \approx 3$) or allometric when compared between species. For those fish with allometric growth, if the estimate of b was greater than 3, allometric growth was positive and if the estimate of b was less than 3, allometric growth was negative.

Growth

The von Bertalanffy growth function (VBGF) was fitted by nonlinear least-squares regression of FL on age for each species with twenty or more matching length and age records. The form of the VBGF used to model length-at-age data was,

$$L_t = L_\infty \left(1 - e^{-K(t-t_0)}\right)$$

where L_t is the length at age t , L_∞ is the mean asymptotic fork length, K is the growth coefficient or rate at which L_∞ is approached, t is the age of the fish and t_0 is the age at which the fish have a theoretical length of zero. The growth curves were grouped by genus and plotted for each species.

Mortality

Age-based catch curves (Ricker, 1975) were used to estimate the instantaneous rate of total mortality (Z). Only those samples collected during the ELF experiment for species with more than twenty records were included. The number of fish in each age class was log transformed and regressed against the corresponding age, and the descending slope provided an estimate of Z . Regressions were fitted from the first age class that was fully selected by the sampling gear through to the oldest age class that was preceded by no more than two consecutive zero frequencies. For three species there are alternative estimates of mortality. The first estimate, (a) includes all data. Alternative estimates were given using natural breaks in the age distribution for *E. fuscoguttatus* (b), *E. polyphkadion* (b) and *C. cyanostigma* (b and c).

Spawning seasonality and size and age at sex change

Reproductive information for each individual species was combined spatially and temporally. The spawning season was examined using samples collected in different months throughout the year. A gonadosomatic index ($GSI = \text{gonad weight} / W \times 100$) was calculated for each sample, which provided a relative measure of reproductive stage. Measurements of W were not always available. Consequently, W was estimated for some samples using the species-specific length-weight relationship. It was assumed that estimates of W would suffice for use in estimating GSI because only the temporal patterns in GSI, rather than the absolute values of GSI, were required to determine the spawning season. The proportions of mature female and mature male reproductive stages in each month were plotted throughout the year, and the degree of spawning activity occurring in each month for each species.

Where sample sizes were large enough, and males were present in the catch, a logistic function was fitted to the proportion of males (relative to females) in each length and age class. This allowed an estimate of the size and age of sex change. The logistic equation used was:

$$P_s = \left(1 + e^{-\ln 19(s-s_{50})/(s_{95}-s_{50})}\right)^{-1}$$

Where P_s is the proportion of males in age or 10 mm length class s , and s_{50} and s_{95} are the age and length at which 50% and 95% of the population are males. While transitional and bisexual fish were not included in the analysis the presence of these fish provide additional evidence of the size and age at sex change.

Results

Length and age frequency and sex ratio

The length modes were not consistent across species ([Figure 2](#)). In those genera with more than one species there was some variability in the range of sizes between species. The largest length modes were 495 mm for *E. polyphkadion* and 485 mm for *E. fuscoguttatus* ([Figure 2](#)). There were a greater number of larger *E. fuscoguttatus*, leading to a long tail in the length distribution. The majority of fish were smaller to mid sized species, with only three species having a modal length above 400 mm ([Figure 2](#)). However, eight species had L_{90} values greater than 400 mm ([Table 2](#)). Of all the grouper sampled during the ELF project the largest was *E. fuscoguttatus* (950 mm) and the smallest *E. fasciatus* (132 mm). Of all the species with plotted size ranges, *C. boenak* had the smallest modal size (195 mm).

Age frequencies varied among species. *E. cyanopodus*, *E. maculatus* and *V. louti* had maximum ages less than ten years. These three species were not the smallest sampled. The modal age of all *Cephalopholis* species was greater than ten years. These three species also had the highest values for A_{90} (>20 years). Age estimates of more than forty years were recorded for three species, *E. fuscoguttatus* (42 years), *E. polyphkadion* (44 years) and *C. cyanostigma* (46 years). These older species include the two largest species and one of the smallest species sampled. The age distributions of *E. fuscoguttatus* and *E. polyphkadion* were not normally distributed and included small numbers of samples in age classes from ten years until around forty years ([Figure 3](#)).

A number of species had female biased sex ratios ([Table 2](#)). *E. maculatus*, a mid-sized grouper, had the highest female bias of all the species (17.5:1). The largest species, *E. fuscoguttatus* had the next largest female biases (13.45:1). Generally the smaller sized species ($L_{90} < 400$) were more likely to have a male bias in the sex ratio ([Table 3](#)). Three species, *A. leucogrammicus* ($\chi^2 = 0.676$, $p = 0.41$), *V. albimarginata* ($\chi^2 = 3.5$, $p = 0.061$) and *C. argus* ($\chi^2 = 0.605$, $p = 0.437$), had sex ratios which were not significantly different from 1:1.

Table 2: Sample size for each length and age frequency plot including only data collected as part of the ELF project. Included are the 90th percentiles of length (L_{90}) and age (A_{90}) for each species. Number of mature males and females and an estimate of the operation sex ratio (mature females to mature males). Note, an asterisk (*) indicates sex ratios which were not significantly different from 1:1 (mature females to mature males).

Genus/species	Length			Age			Sex		
	N	Range (mm)	L_{90}	N	Range (years)	A_{90}	Mature Male	Mature Female	Sex ratio
Epinephelus									
<i>E. fuscoguttatus</i>	424	(250-950)	740	290	(1-42)	22	11	148	13.45
<i>E. polyphkadion</i>	343	(220-691)	565	221	(2-44)	27	33	95	2.88
<i>E. ongus</i>	1032	(198-460)	385	818	(3-30)	18	479	117	0.24
<i>E. fasciatus</i>	1330	(132-440)	300	1005	(1-21)	14	271	158	0.58
<i>E. quoyanus</i>	282	(212-390)	342	194	(2-14)	8	78	10	0.13
<i>E. maculatus</i>	113	(226-448)	401	48	(1-7)	4	2	35	17.50
<i>E. cyanopodus</i>	111	(236-548)	471	38	(1-4)	3			
<i>E. merra</i>	43	(190-310)	253						
<i>E. microspilus</i>	1	365							
<i>E. hexagonatus</i>	5	(230-413)							
<i>E. tauvina</i>	2	(456-486)							
<i>E. corallicola</i>	9	(264-590)							
<i>E. howlandi</i>	9	(270 -479)							
Anyperodon									
<i>A. leucogrammicus</i>	101	(310-555)	493	75	(2-27)	16	21	16	0.76 *
Aethaloperca									
<i>A. roгаа</i>	15	(250-470)		6	(13-18)				
Variola									
<i>V. louti</i>	166	(195-516)	459	59	(1-7)	5	14	60	4.29
<i>V. albimarginata</i>	74	(221-377)	326	55	(3-12)	8	35	21	0.60 *
Cephalopholis									
<i>C. argus</i>	256	(176-485)	421	158	(3-39)	25	37	44	1.19 *
<i>C. miniata</i>	71	(250-475)	412	33	(6-30)	28			
<i>C. boenak</i>	34	(149-234)	214	4	(8-18)				
<i>C. microprion</i>	1	153							
<i>C. cyanostigma</i>	4275	(171-428)	289	2634	(5-46)	28	423	250	0.59
<i>C. urodeta</i>	12	(204-250)							
<i>C. sexmaculata</i>	6	(309-432)							
<i>C. sonnerati</i>	2	(167-390)							

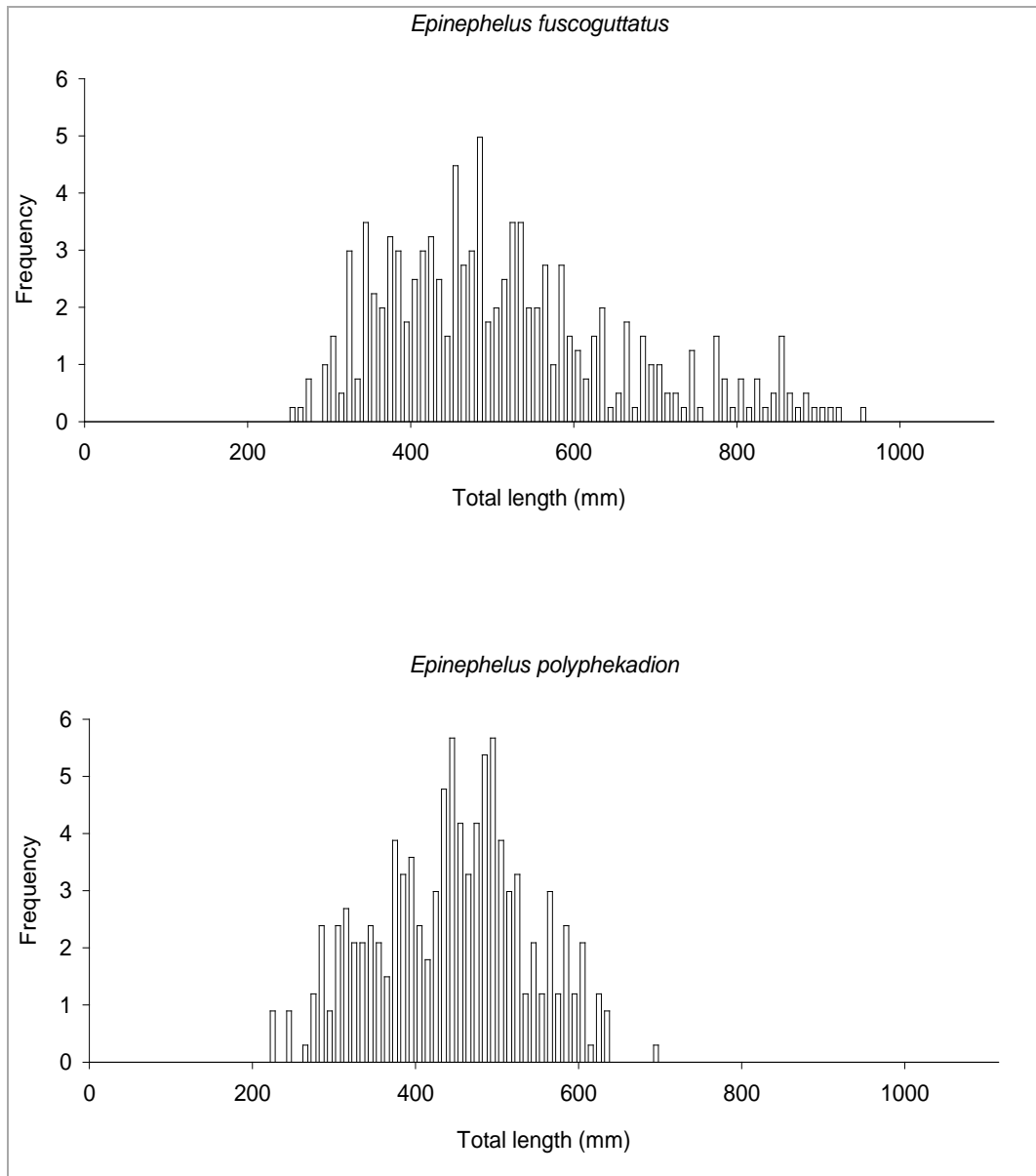


Figure 2 (continues to pages 12-14): Length frequency distributions for 15 Epinephelinae grouper species in 10 mm bins.

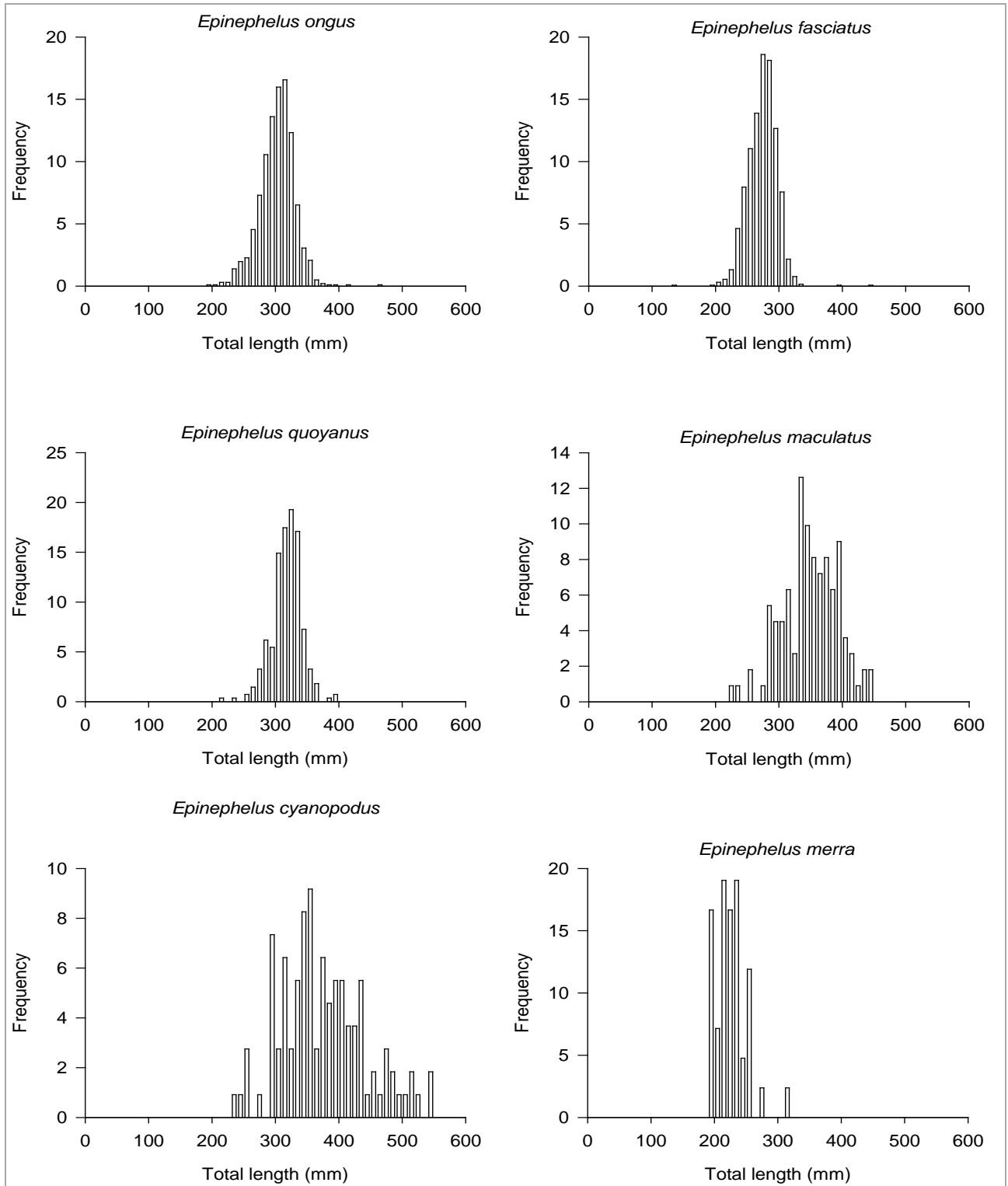


Figure 2 (continued).

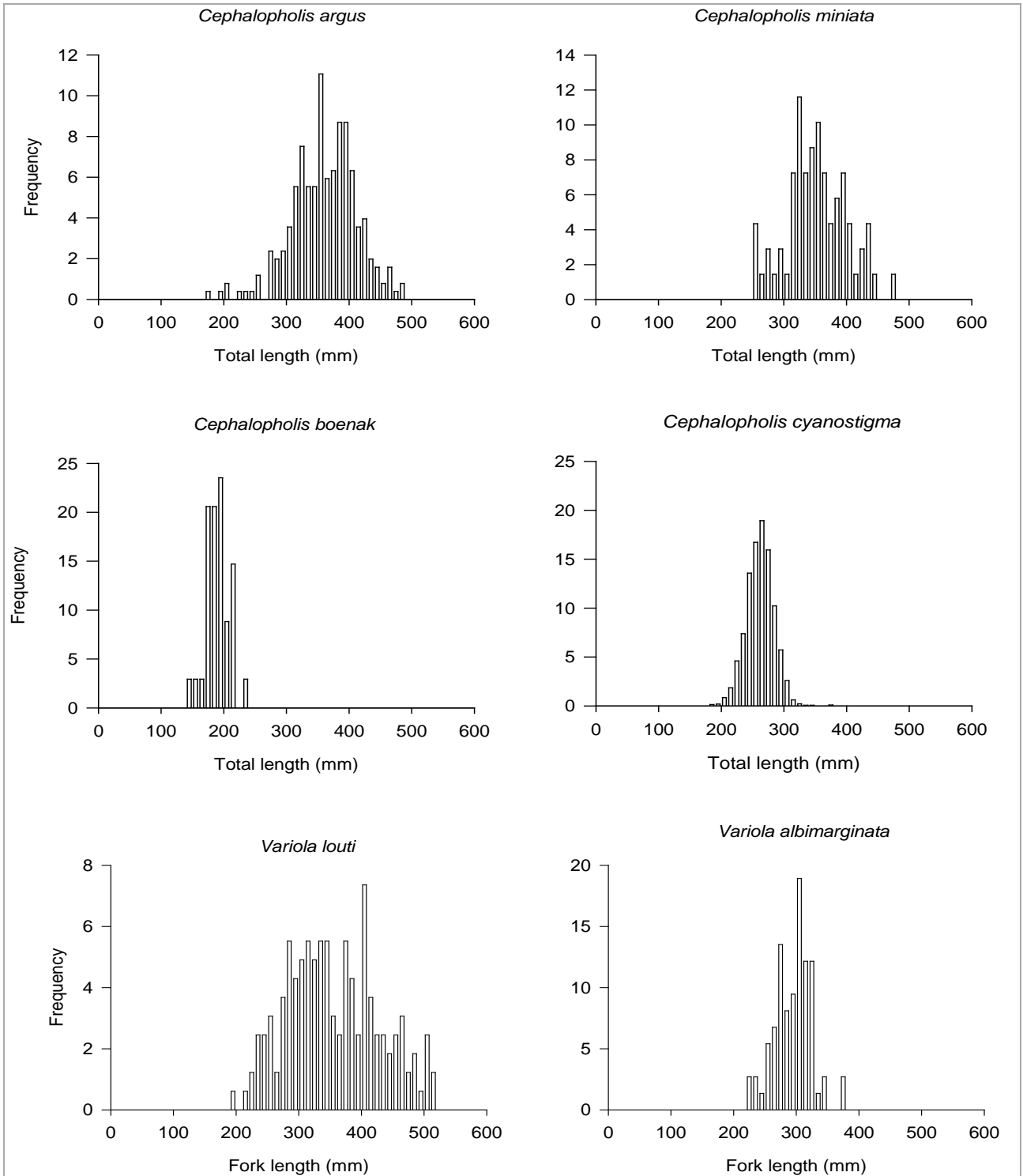


Figure 2 (continued).

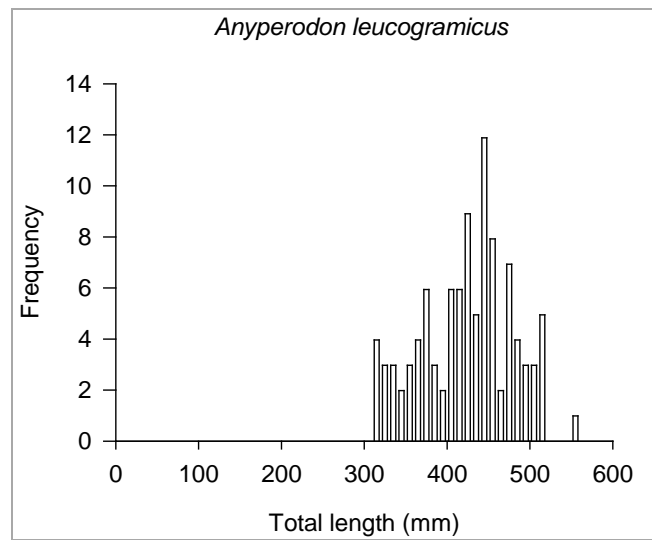


Figure 2 (continued).

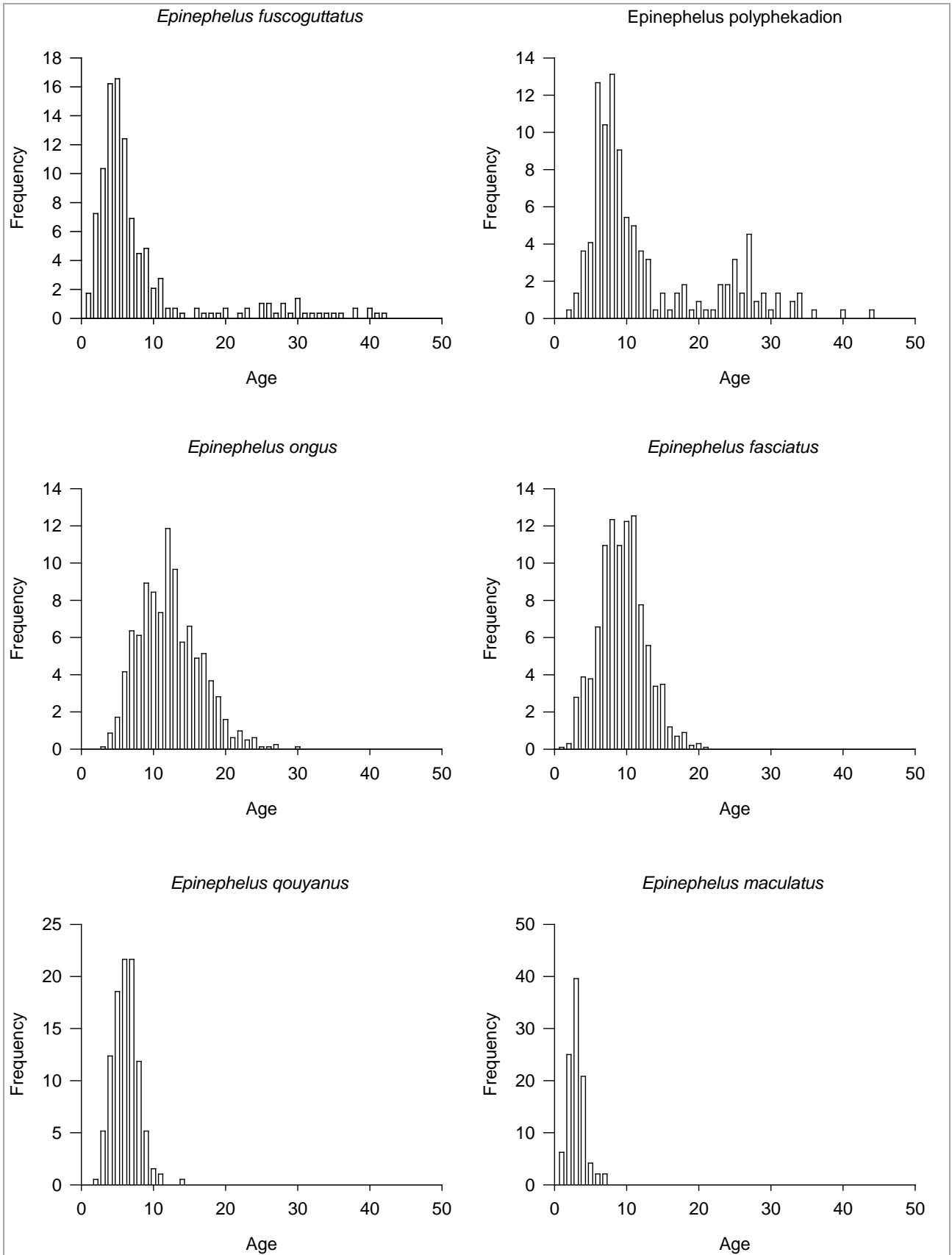


Figure 3 (continues to pages 16-17): Age frequency distributions for 13 Epinephelinae grouper species.

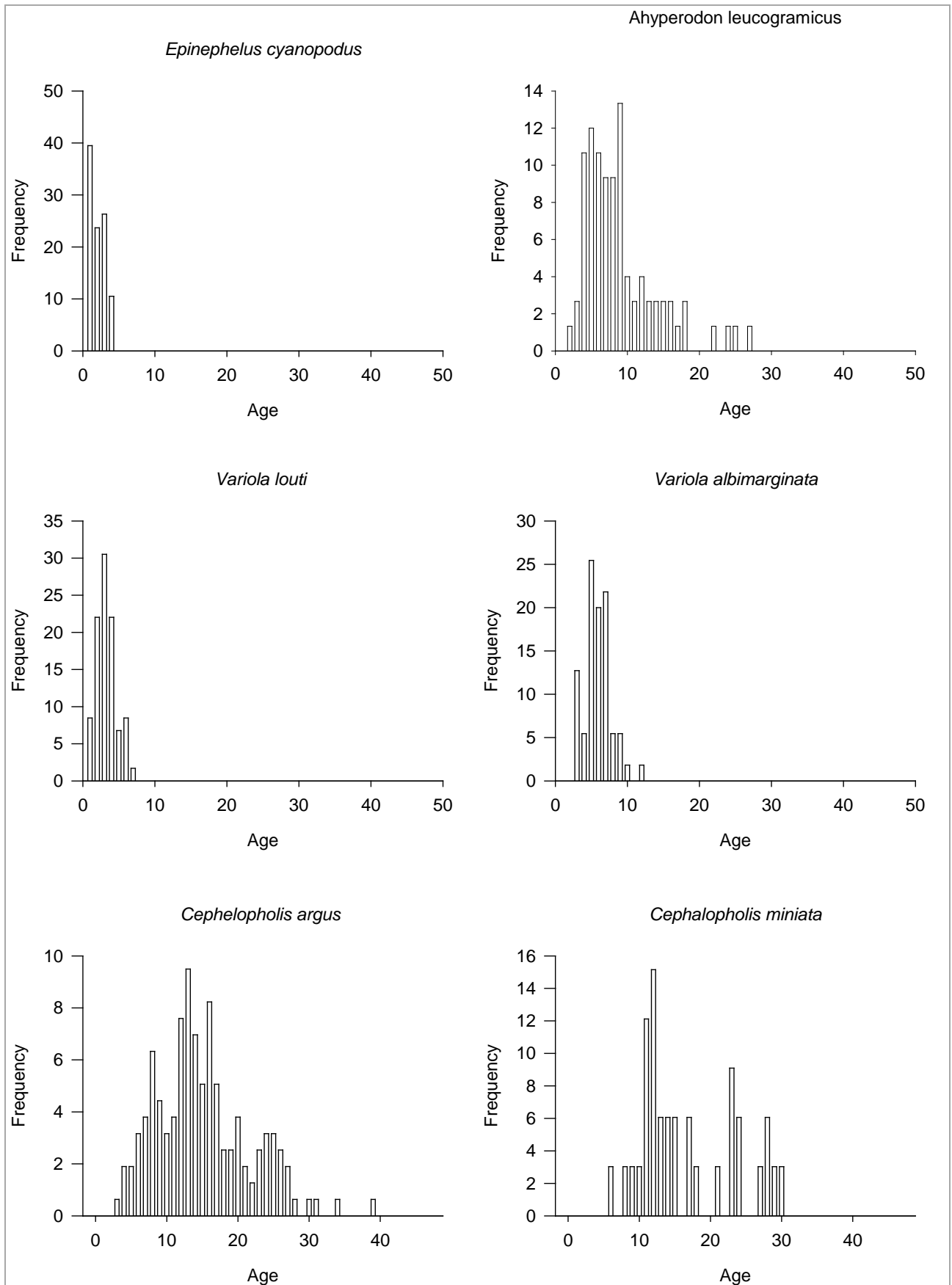


Figure 3 (continued).

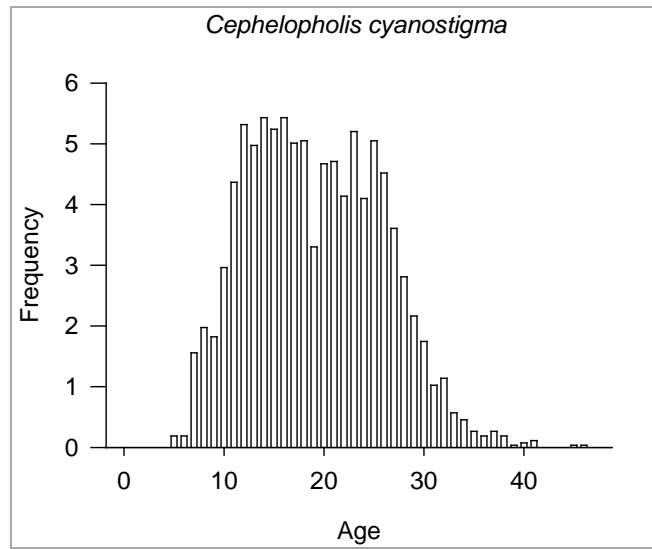


Figure 3 (continued).

Length-weight relationships

The length-weight data was plotted for each species (Figure 4). Length-weight relationships were determined to be isometric ($b \approx 3$), with fish becoming heavier bodied as they grow, for ten species (Table 3). Isometric growth was observed for species within each genus except for *Aethaloperca*. Both positive and negative allometric growth was observed for individual species within the genus *Epinephelus* and *Cephalopholis*. Negative allometric growth was observed for *Aethaloperca rogae*.

Table 3: Length-weight parameter estimates for 18 Epinephelinae species collected from the Great Barrier Reef including all samples. Data and fitted power curves are plotted in Figure 4. Note, the symbol '+' indicates a positive relationship; the symbol '-' indicates a negative relationship.

Genus/species	N	W-L equation	r^2	S.E of b	95% C.I of b	Relationship
Epinephelus						
<i>E. fuscoguttatus</i>	271	$W = (1.36 \times 10^{-8})L^{3.048}$	0.979	0.036	(2.977 - 3.120)	Isometric
<i>E. polyphekadion</i>	242	$W = (9.399 \times 10^{-9})L^{3.093}$	0.955	0.049	(2.996 - 3.190)	Isometric
<i>E. ongus</i>	468	$W = (1.202 \times 10^{-8})L^{3.031}$	0.797	0.086	(2.861 - 3.201)	Isometric
<i>E. fasciatus</i>	576	$W = (4.551 \times 10^{-8})L^{2.790}$	0.797	0.080	(2.631 - 2.948)	Allometric -
<i>E. quoyanus</i>	129	$W = (5.371 \times 10^{-8})L^{2.767}$	0.944	0.077	(2.615 - 2.920)	Allometric -
<i>E. maculatus</i>	104	$W = (7.737 \times 10^{-9})L^{3.098}$	0.964	0.091	(2.918 - 3.278)	Isometric
<i>E. cyanopodus</i>	58	$W = (4.538 \times 10^{-9})L^{3.220}$	0.975	0.077	(3.067 - 3.373)	Allometric +
<i>E. spilotoceps</i>	37	$W = (2.681 \times 10^{-8})L^{2.901}$	0.887	0.175	(2.555 - 3.248)	Isometric
Anyperodon						
<i>A. leucogrammicus</i>	91	$W = (2.723 \times 10^{-9})L^{3.231}$	0.905	0.132	(2.969 - 3.493)	Isometric
Athaloperca						
<i>A. rogae</i>	41	$W = (9.871 \times 10^{-8})L^{2.726}$	0.966	0.113	(2.503 - 2.949)	Allometric -
Variola						
<i>V. louti</i>	156	$W = (1.213 \times 10^{-8})L^{3.050}$	0.965	0.056	(2.939 - 3.161)	Isometric
<i>V. albimarginata</i>	71	$W = (6.890 \times 10^{-9})L^{3.148}$	0.913	0.110	(2.929 - 3.366)	Isometric
Cephalopholis						
<i>C. argus</i>	341	$W = (8.123 \times 10^{-9})L^{3.127}$	0.938	0.051	(3.027 - 3.227)	Allometric +
<i>C. miniata</i>	35	$W = (6.558 \times 10^{-10})L^{3.540}$	0.963	0.134	(3.275 - 3.804)	Allometric +
<i>C. boenak</i>	36	$W = (1.669 \times 10^{-9})L^{3.413}$	0.870	0.214	(2.990 - 3.836)	Isometric
<i>C. microprion</i>	24	$W = (7.1412 \times 10^{-7})L^{2.255}$	0.842	0.226	(1.807 - 2.703)	Allometric -
<i>C. cyanostigma</i>	2596	$W = (4.106 \times 10^{-8})L^{2.808}$	0.683	0.039	(2.730 - 2.885)	Allometric -
<i>C. urodeta</i>	256	$W = (1.254 \times 10^{-8})L^{3.060}$	0.99	0.006	(3.048 - 3.071)	Isometric

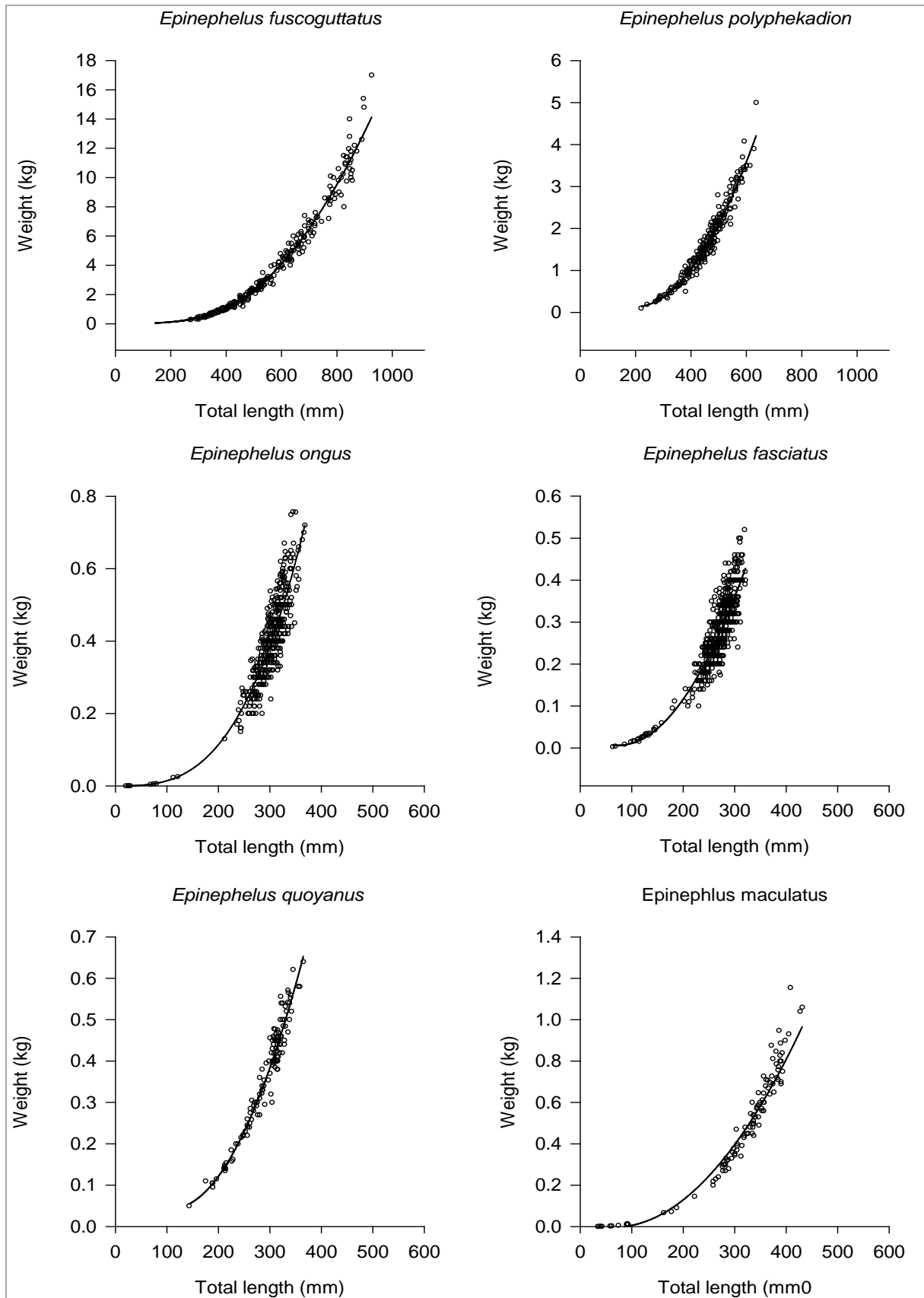


Figure 4 (continues to pages 20-21): Length data and fitted power curve for 18 species of Epinephelinae grouper sampled from the Great Barrier Reef. Sample sizes and length-weight estimates from fitted power curves are included in [Table 2](#).

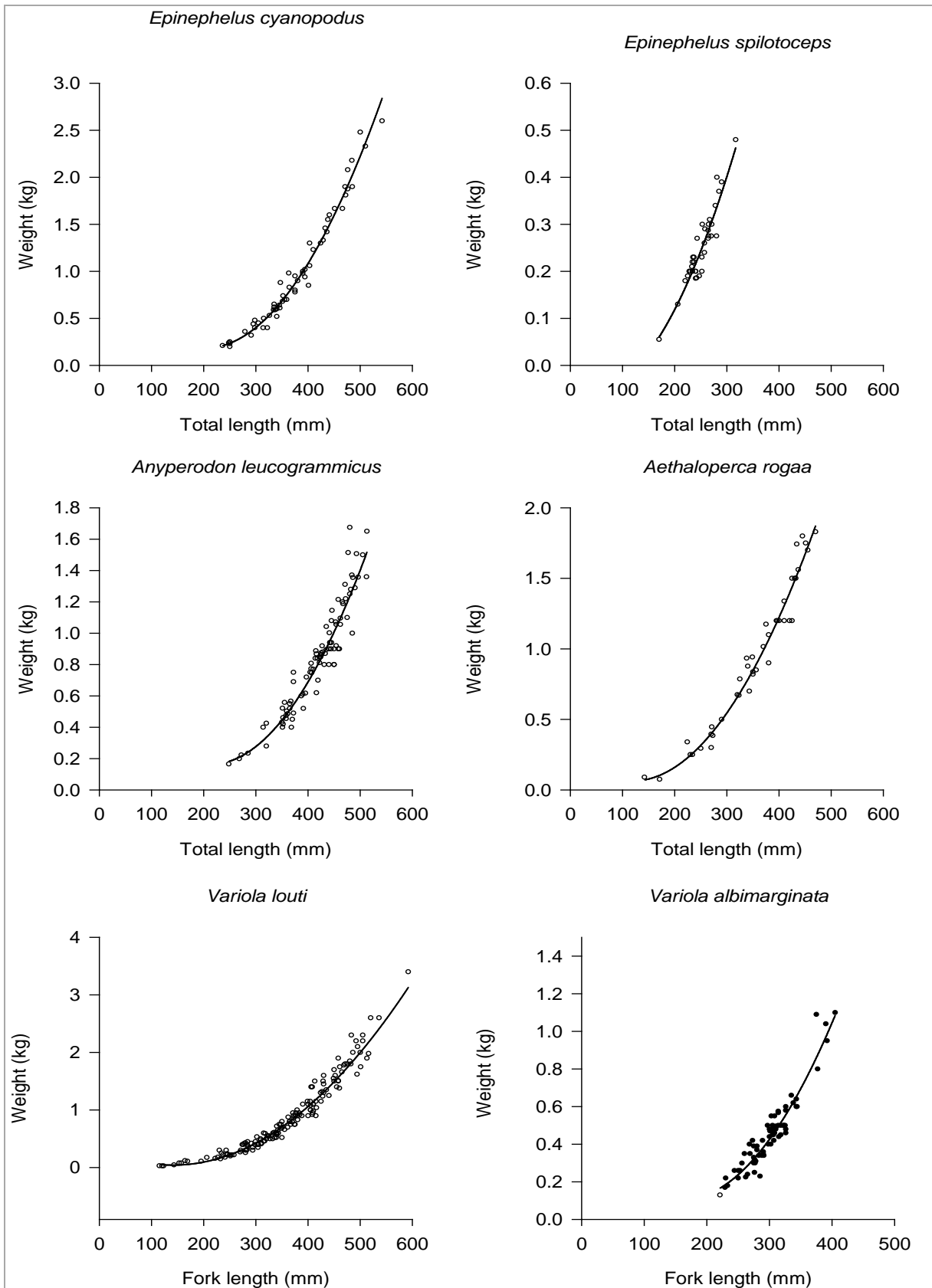


Figure 4 (continued).

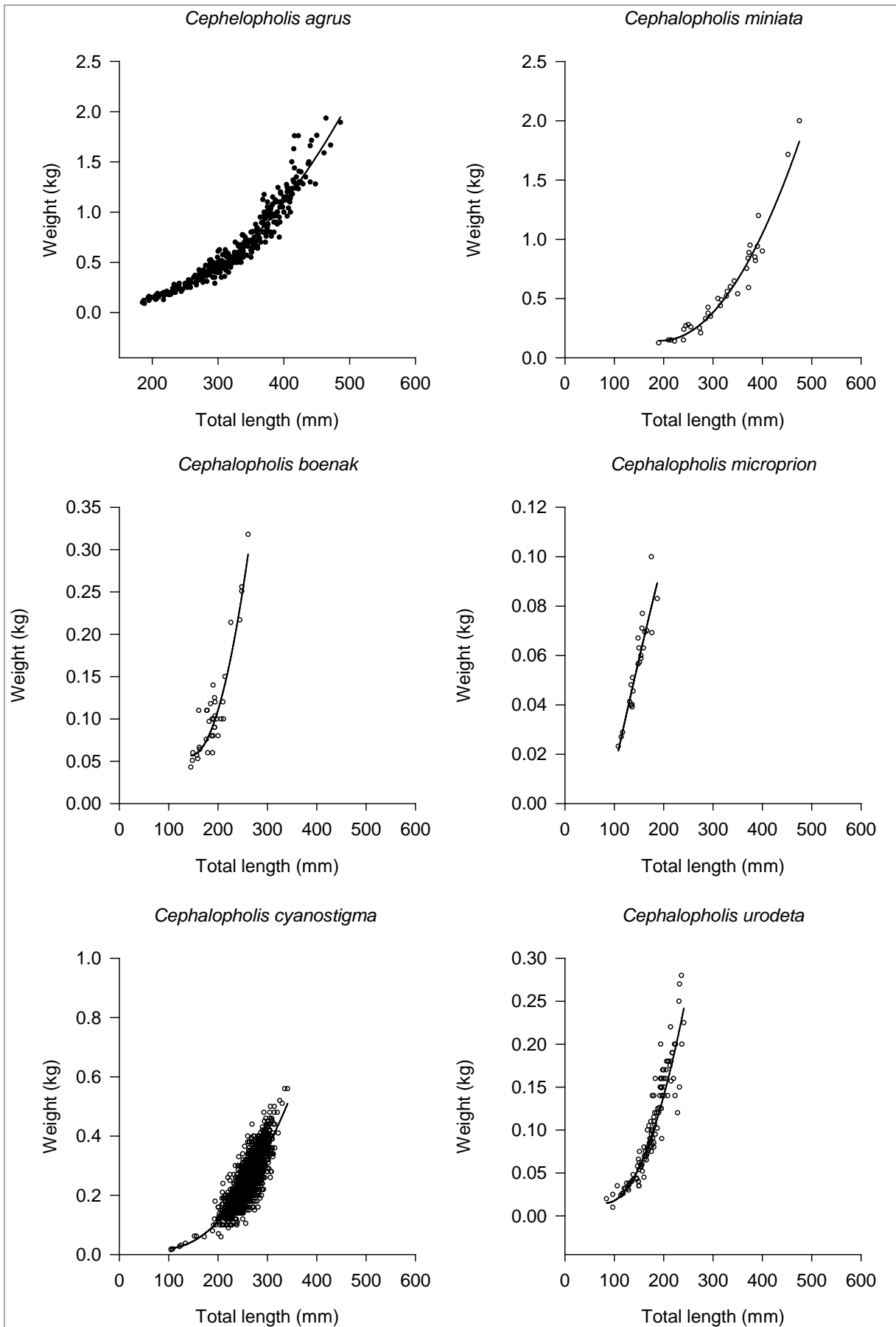


Figure 4 (continued).

Growth

Growth curves were fitted to length-at-age data for 16 species, with growth parameters varying between species (Figure 5, Table 4). Growth for a number of species was asymptotic, in these cases there was generally both young and old individuals included in the sample. A number of the growth curves were relatively flat due to the limited number of smaller individuals. There are other instances where larger older individuals have not been sampled, and in these instances the growth curve has not yet reached an asymptote. The fitted growth curves and VBGF parameter estimates for some of the larger and more commonly sampled species appear to be more meaningful. Most *Cephalopholis* species had a consistently low K and high negative t_0 values which suggests that growth curves were not providing reliable growth estimates for species within this genus. The fitted growth curves varied between species within the same genus (Figure 6).

Table 4: Sample sizes and parameter estimates for the VBGF. L_∞ is the mean asymptotic fork length, K is the von Bertalanffy growth coefficient, and t_0 is the theoretical age at length of zero.

Genus/species	N	L_∞	K	t_0
Epinephelus				
<i>E. fuscoguttatus</i>	401	846.936	0.093	-3.741
<i>E. polyphkadion</i>	330	562.345	0.194	-0.081
<i>E. ongus</i>	843	326.284	0.175	-3.906
<i>E. fasciatus</i>	1047	281.814	0.405	-0.685
<i>E. quoyanus</i>	214	326.595	0.523	-0.740
<i>E. maculatus</i>	58	638.683	0.093	-5.538
<i>E. cyanopodus</i>	45	787.186	0.113	-3.629
Anyperodon				
<i>A. leucogrammicus</i>	127	518.483	0.132	-4.949
Athaloperca				
<i>A. rogaea</i>	10	441.948	0.212	-0.225
Variola				
<i>V. louti</i>	58	1558.917	0.038	-3.978
<i>V. albimarginata</i>	55	316.252	0.479	-0.155
Cephalopholis				
<i>C. argus</i>	232	485.499	0.049	-14.145
<i>C. miniata</i>	33	420.033	0.101	-2.041
<i>C. boenak</i>	16	262.216	0.059	-11.113
<i>C. microprion</i>	20	189.655	0.062	-13.196
<i>C. cyanostigma</i>	2607	311.294	0.040	-27.006

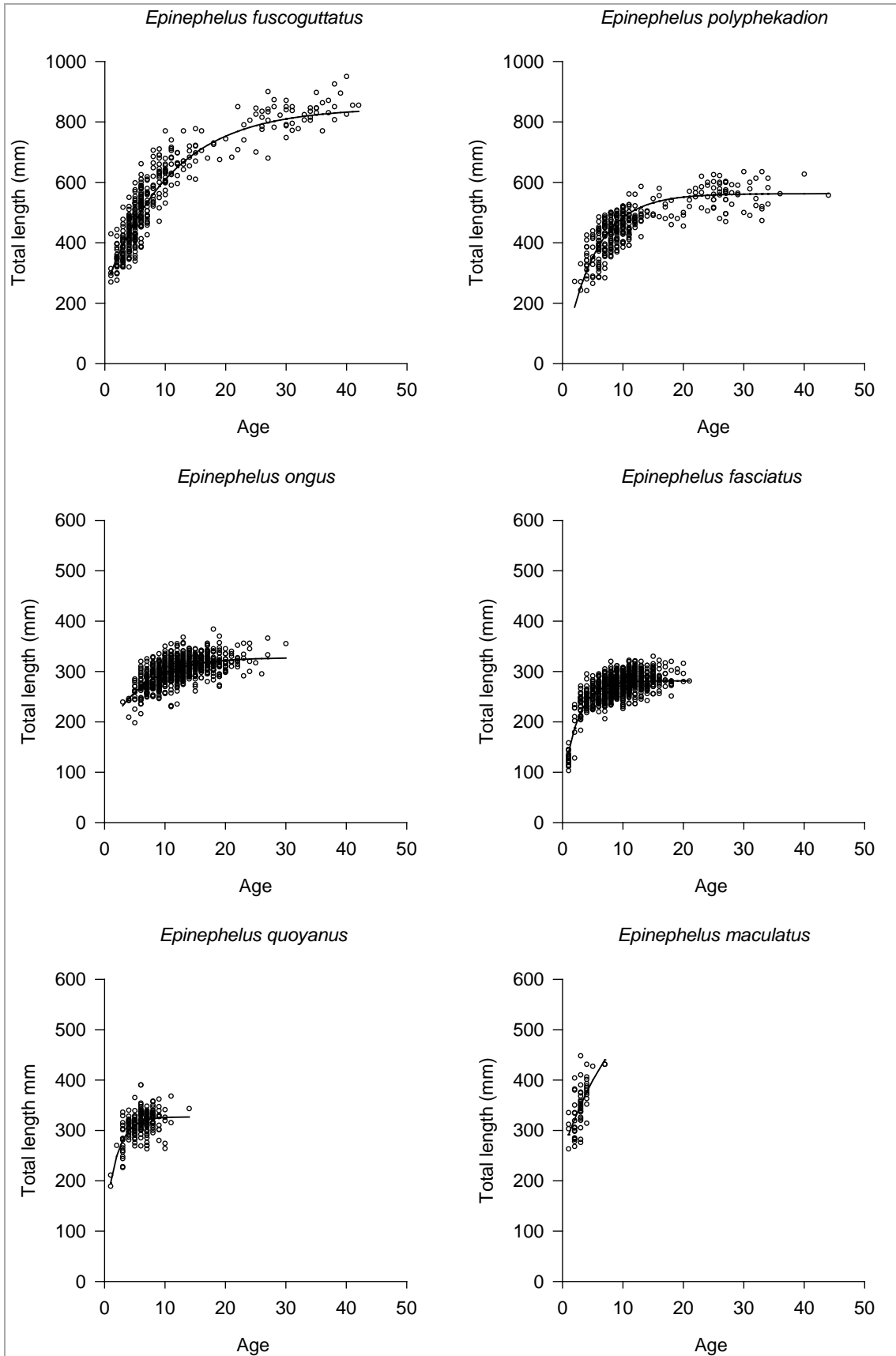


Figure 5 (continued to pages 24-25): Length-at-age data and fitted VBGF curves for 16 species of Epinephelinea grouper. Parameter estimates from the fitted curves and sample numbers are included in [Table 4](#).

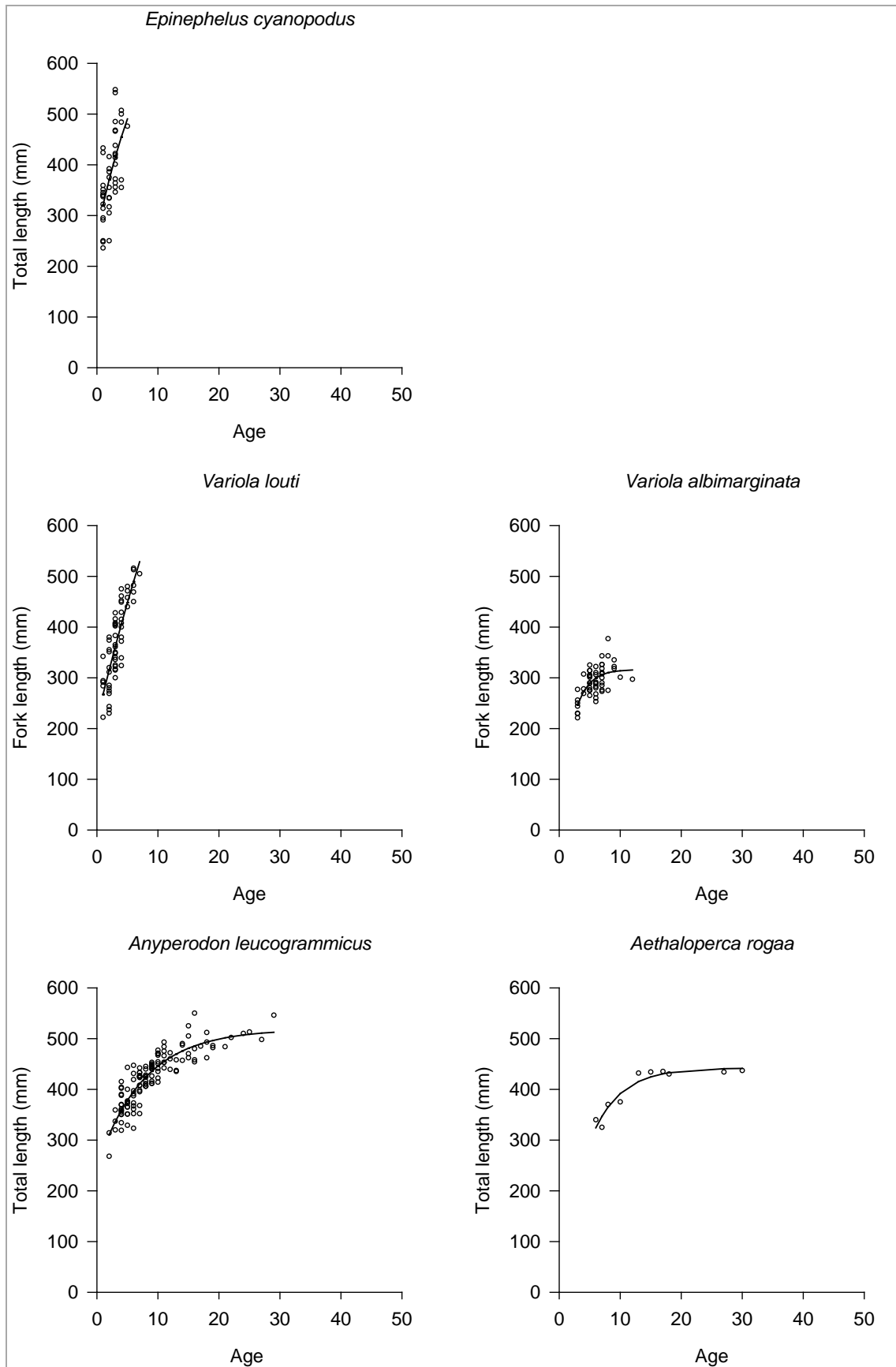


Figure 5 (continued).

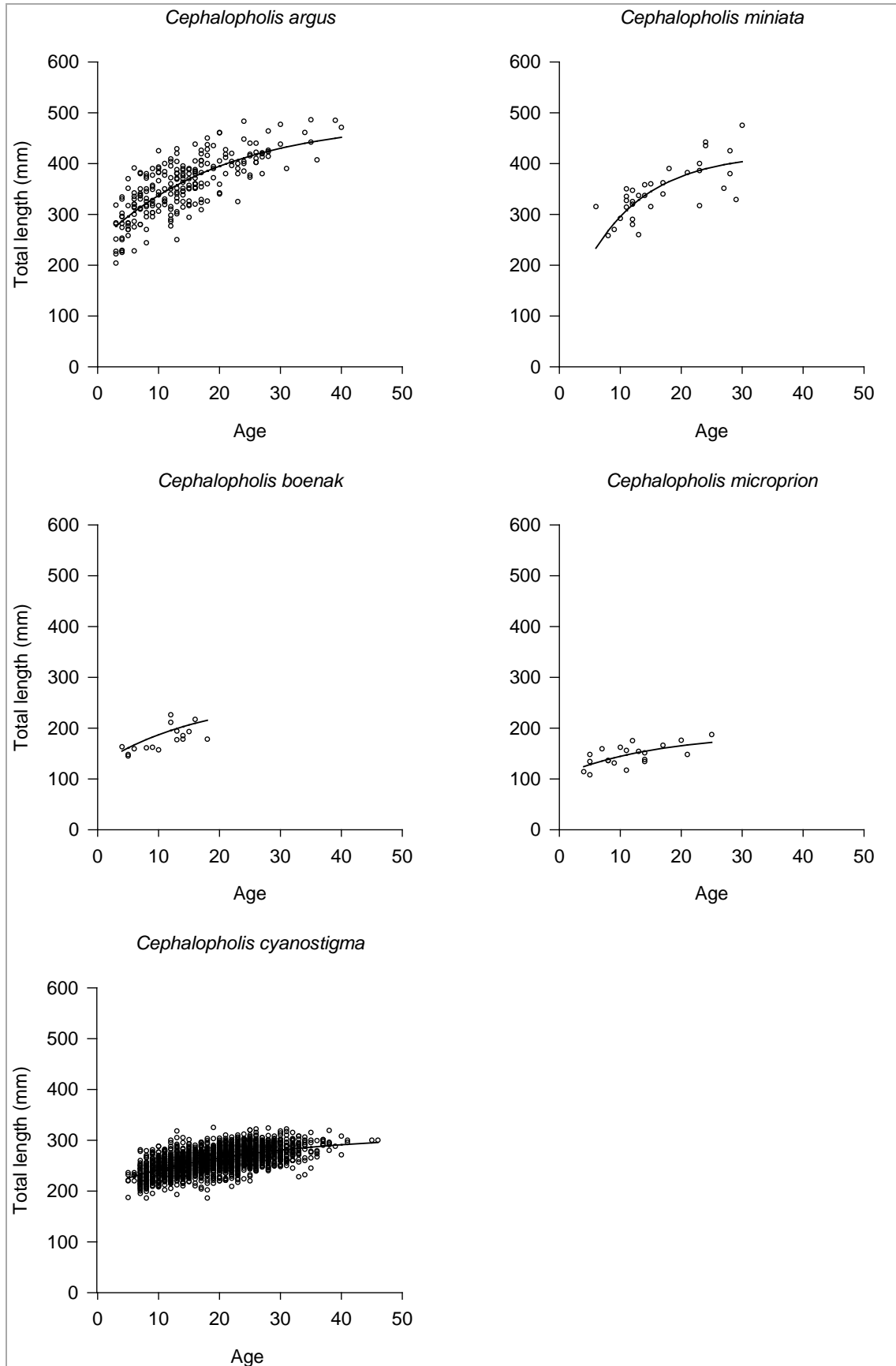


Figure 5 (continued).

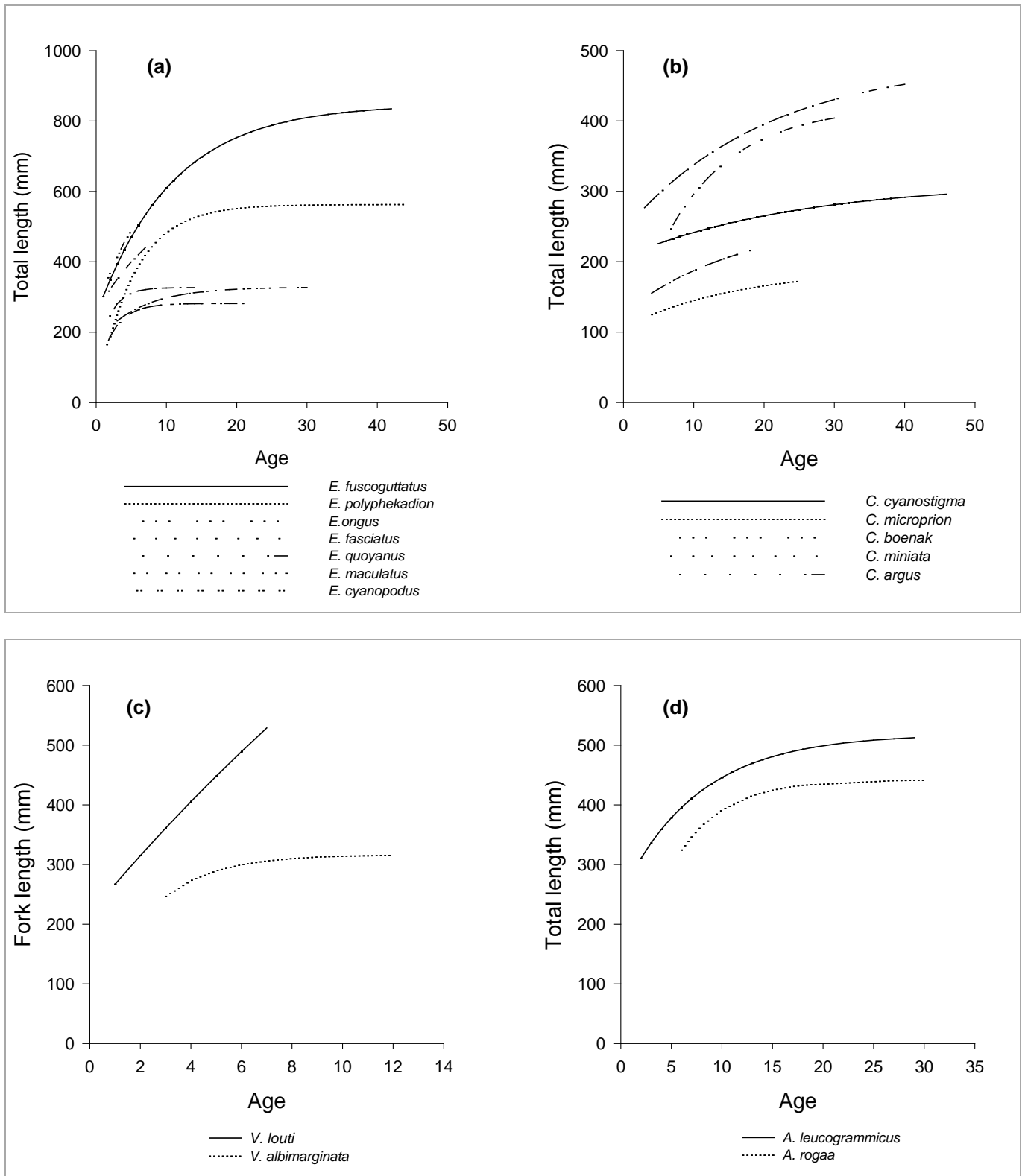


Figure 6: Fitted VBGF curves for 16 species of Epinephelinae grouper. Species have been grouped by genus for (a) *Epinephelus*, (b) *Cephalopholis* and (c) *Variola*. The last two species, *Athaloperca rogae* and *Anyperodon leucogrammicus* have been plotted together (d).

Mortality

Estimates of total mortality (Z), derived from catch curves varied between species and within each genus (Figure 7, Table 5). The lowest estimates of Z were calculated for the two largest species *E. fuscoguttatus* and *E. polyphkadion*. Alternate mortality estimates were calculated for *E. fuscoguttatus*, *E. polyphkadion* and *C. cyanostigma* following natural breaks in the catch curves. Using a reduced age range which did not include the less numerous older age classes for *E. fuscoguttatus* and *E. polyphkadion* provided higher estimates of mortality (b), for both of these species. Different age ranges were used to estimate Z for the longest lived species, *C. cyanostigma*. The lowest estimate was for the youngest age range where fish had fully recruited to the gear and the highest was when the older age classes were included.

Table 5: The instantaneous rate of natural mortality Z and associated r^2 values. For three species, additional estimates were given using different age ranges (b) and (c).

Genus/species	Z (yr ⁻¹)	r ²
Epinephelus		
<i>E. fuscoguttatus</i>	(a) -0.07	0.47
	(b) -0.20	0.74
<i>E. polyphkadion</i>	(a) -0.07	0.36
	(b) -0.23	0.80
<i>E. ongus</i>	-0.82	0.90
<i>E. fasciatus</i>	-0.38	0.92
<i>E. quoyanus</i>	-0.68	0.94
<i>E. maculatus</i>	-0.82	0.90
<i>E. cyanopodus</i>	-0.39	0.81
Anyperodon		
<i>A. leucogrammicus</i>	-0.14	0.53
Variola		
<i>V. louti</i>	-0.67	0.88
<i>V. albimarginata</i>	-0.44	0.88
Cephalopholis		
<i>C. argus</i>	-0.13	0.75
<i>C. miniata</i>	-0.18	0.65
<i>C. cyanostigma</i>	(a) -0.16	0.80
	(b) -0.02	0.26
	(c) -0.29	0.94

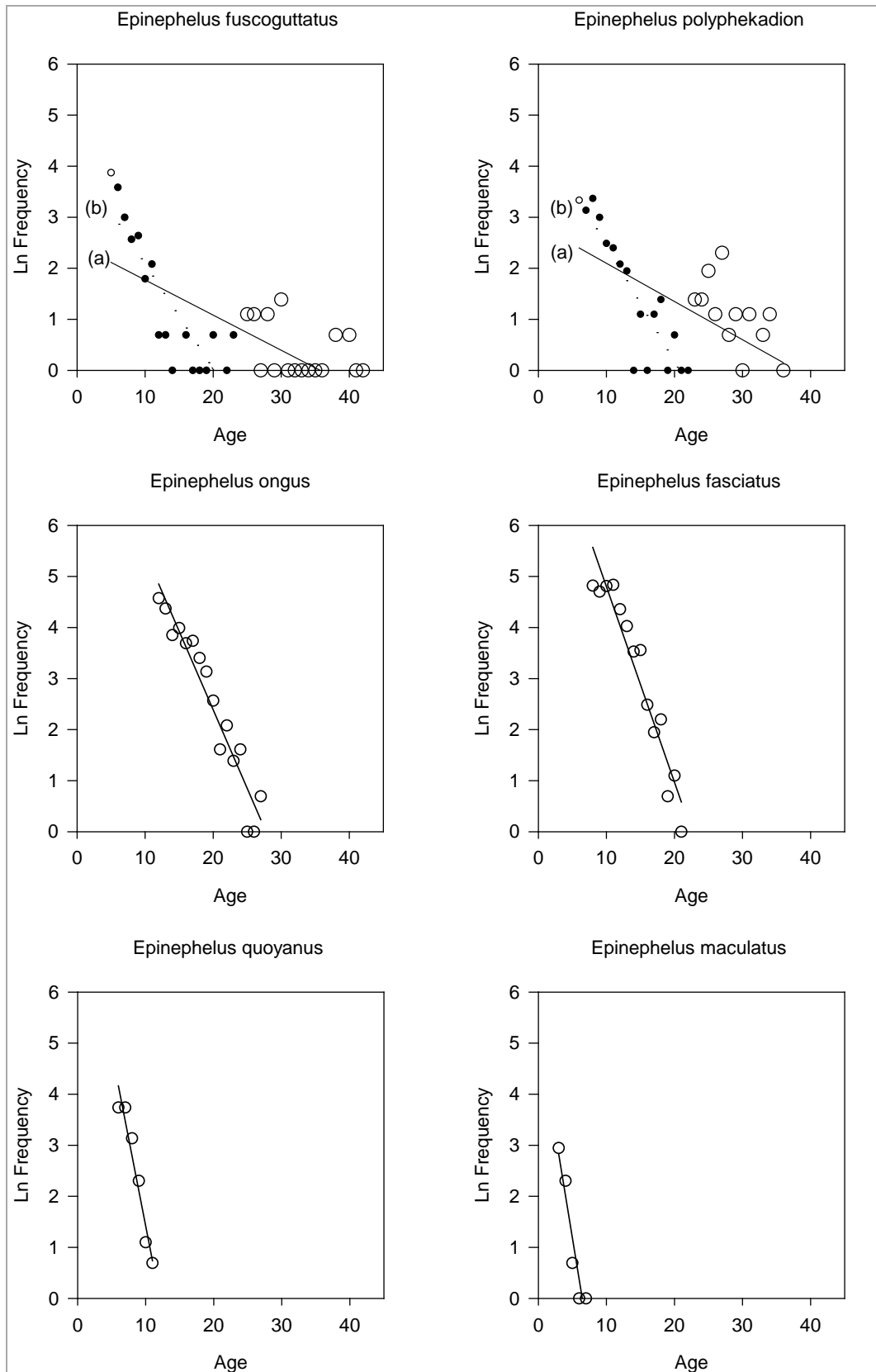


Figure 7 (continued to pages 29-30): Catch curves for seven species of grouper. The slopes of the regressions are an estimate of the total mortality (Z) for each species. The first estimate (a) uses all of the data. Alternate estimates of mortality are provided for three species using natural breaks in the data (b and c).

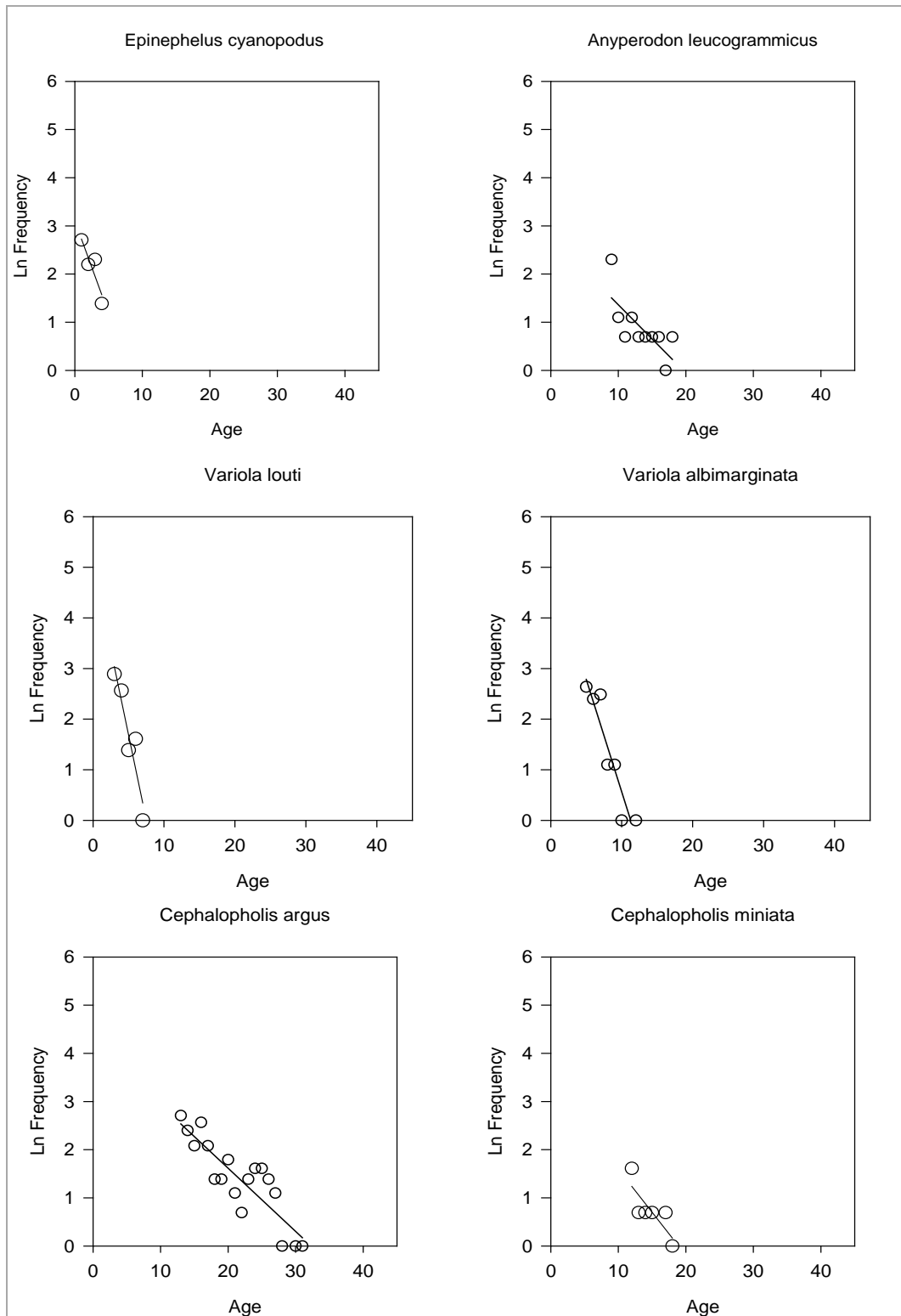


Figure 7 (continued).

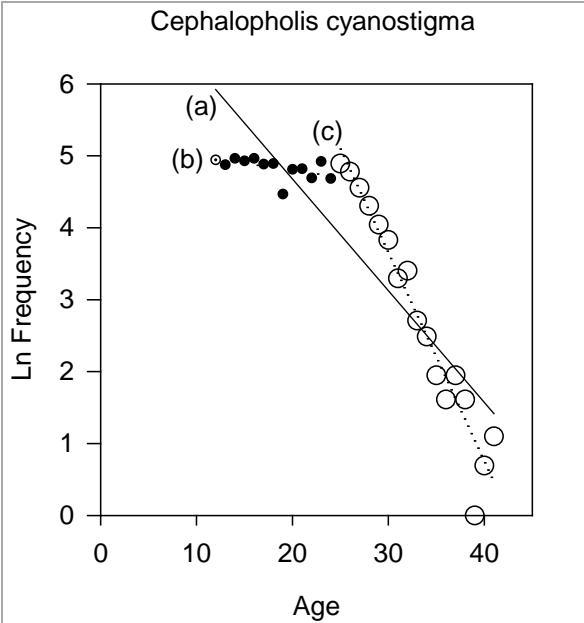


Figure 7 (continued).

Spawning seasonality and sex change

There was not a very even temporal spread in the collection of reproductive data for any species, which made it difficult to accurately determine seasonal reproductive cycles. However, generalisations about the likely peak spawning times can be made for many species. Running ripe females (fish with hydrated ovaries) were observed in each month from October until January ([Figure 8](#)). Spent female fish were also observed in October and November for *E. fuscoguttatus*, and October, November January and May for *C. cyanostigma*. Spent male fish were collected in seven of the months from January through to December. Monthly GSI for mature female grouper were usually highest between October and December, matching closely to the months when running ripe fish were collected ([Figure 8](#)). Similarly, male monthly GSI was consistently higher in December. This suggests that spawning for some species such as *E. fuscoguttatus*, *E. polyphkadion*, *E. ongus*, *E. fasciatus* and *V. albimarginata* occurred during the Austral spring and summer. There is however a lack of data for June and July for both male and female fish of most species. This reduced the certainty with which we can positively identify the spawning season.

There was a large overlap in the length range of females and males for many species, though the trend in most species was for females to dominate the smaller length classes and males to dominate the larger length classes ([Figure 9](#)). Very few male *E. cyanopodus* and *E. maculatus* appear in the sample. The length distributions of both these species were dominated by undetermined inactive females, immature females and mature females. Transitional individuals were identified in the samples of five species: *E. polyphkadion*, *E. ongus*, *E. fasciatus*, *C. argus* and *C. cyanostigma*. Transitional fish accounted for less than five percent of the catch for each of these species. There were also a small number of bisexual individuals identified in the catch of *E. fasciatus* (1.14 %). The length at 50% sex change varied between species ([Table 6](#)). The maximum value was for the largest species and the minimum value was for one of the smallest.

There were some younger male fish in the age distributions ([Figure 10](#)). There was still a similar pattern as in the length distribution, with younger females and older males. There were very different estimates of the age at 50% sex change. The estimates for the two largest species were in excess of twenty years. Other estimates were less than ten years with the estimate for *C. cyanostigma* between these two groups.

Table 6: Sample numbers and the length and age at sex change (mature female to mature male) for 50% (L_{50} , A_{50}) of fish and 95% (L_{95} , A_{95}) the fish.

Genus/species	Length			Age		
	N	L_{50}	L_{95}	N	A_{50}	A_{95}
Epinephelus						
<i>E. fuscoguttatus</i>	327	846	1085	310	29	50
<i>E. polyphemadion</i>	242	550	634	215	24	52
<i>E. ongus</i>	651	272	330	562	7	14
<i>E. fasciatus</i>	438	262	300	351	9	31
<i>E. quoyanus</i>	170			103		
<i>E. maculatus</i>	97			49		
<i>E. cyanopodus</i>	65			33		
Anyperodon						
<i>A. leucogrammicus</i>	98	430	573	85		
Variola						
<i>V. louti</i>	82	476	525	31		
<i>V. albimarginata</i>	58	286	320	43	5	9
Cephalopholis						
<i>C. argus</i>	91	365	449	48	24	53
<i>C. miniata</i>	34			13		
<i>C. boenak</i>	22			14		
<i>C. microprion</i>	16			14		
<i>C. cyanostigma</i>	722	251	328	608	14	28

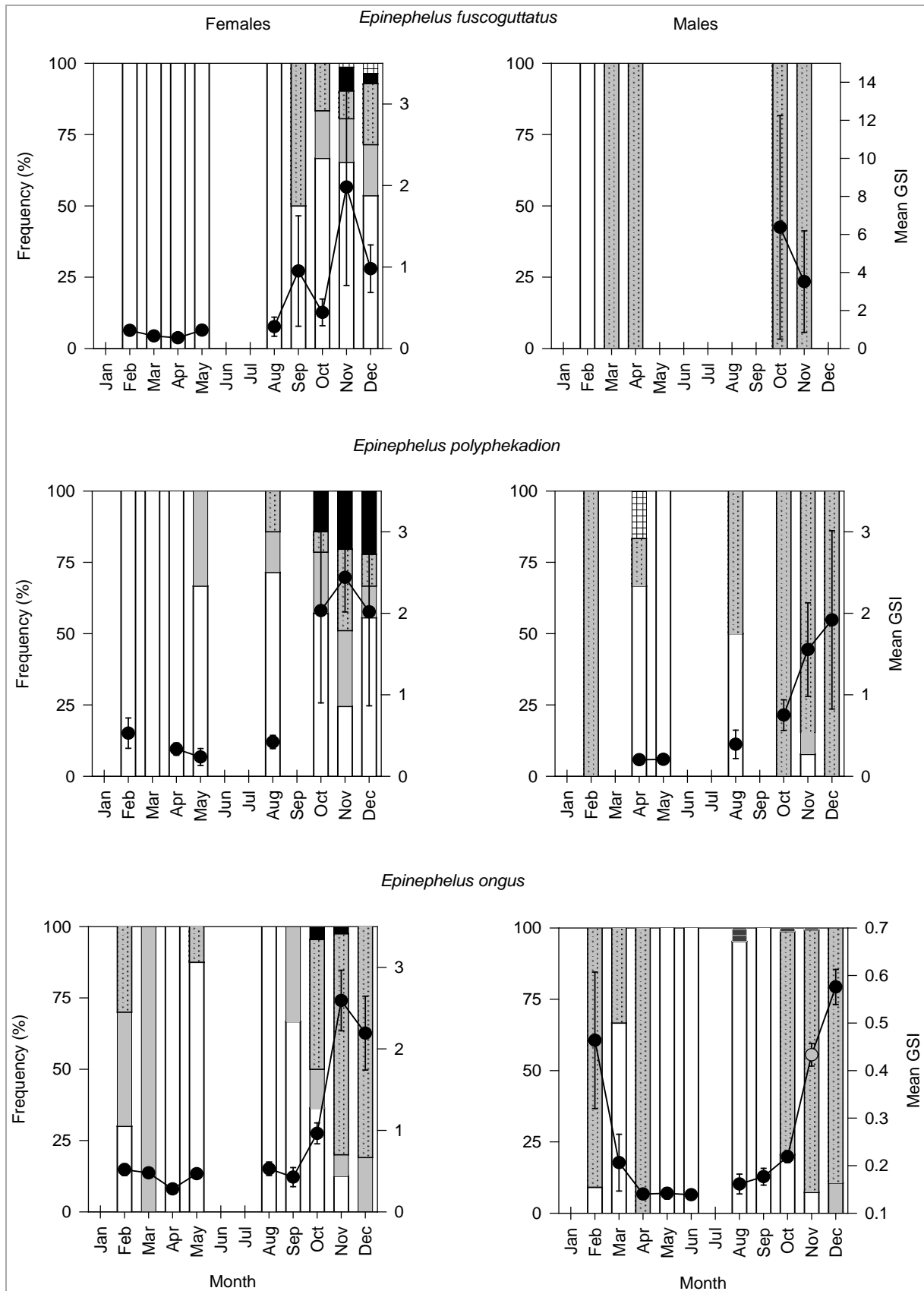
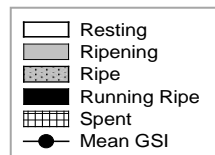


Figure 8 (continues to pages 34-36): Monthly frequencies of mature ovarian stages (bars) for female and male Epinephelinae grouper and mean monthly gonadosomatic index (GSI) values (lines).



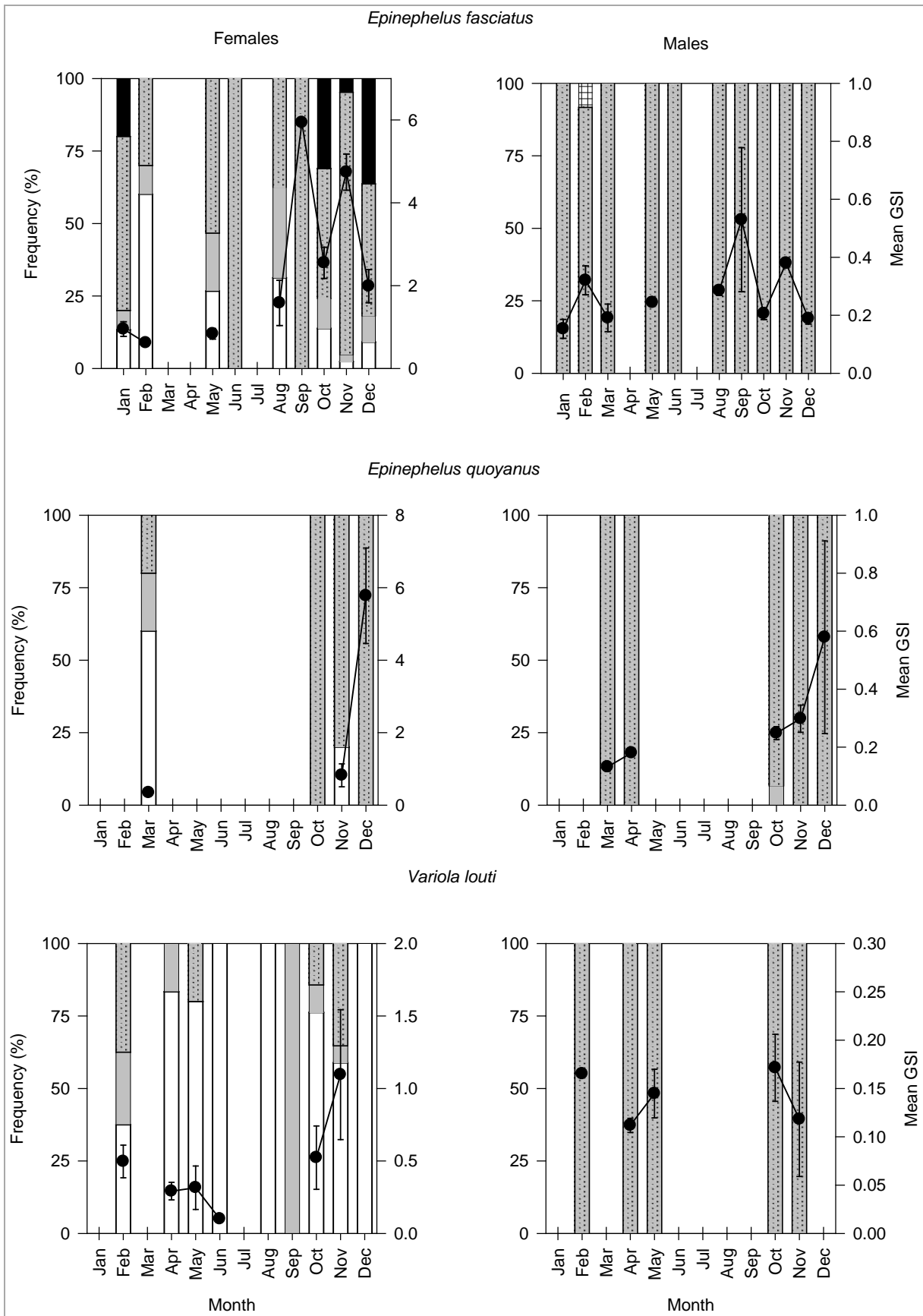


Figure 8 (continued).

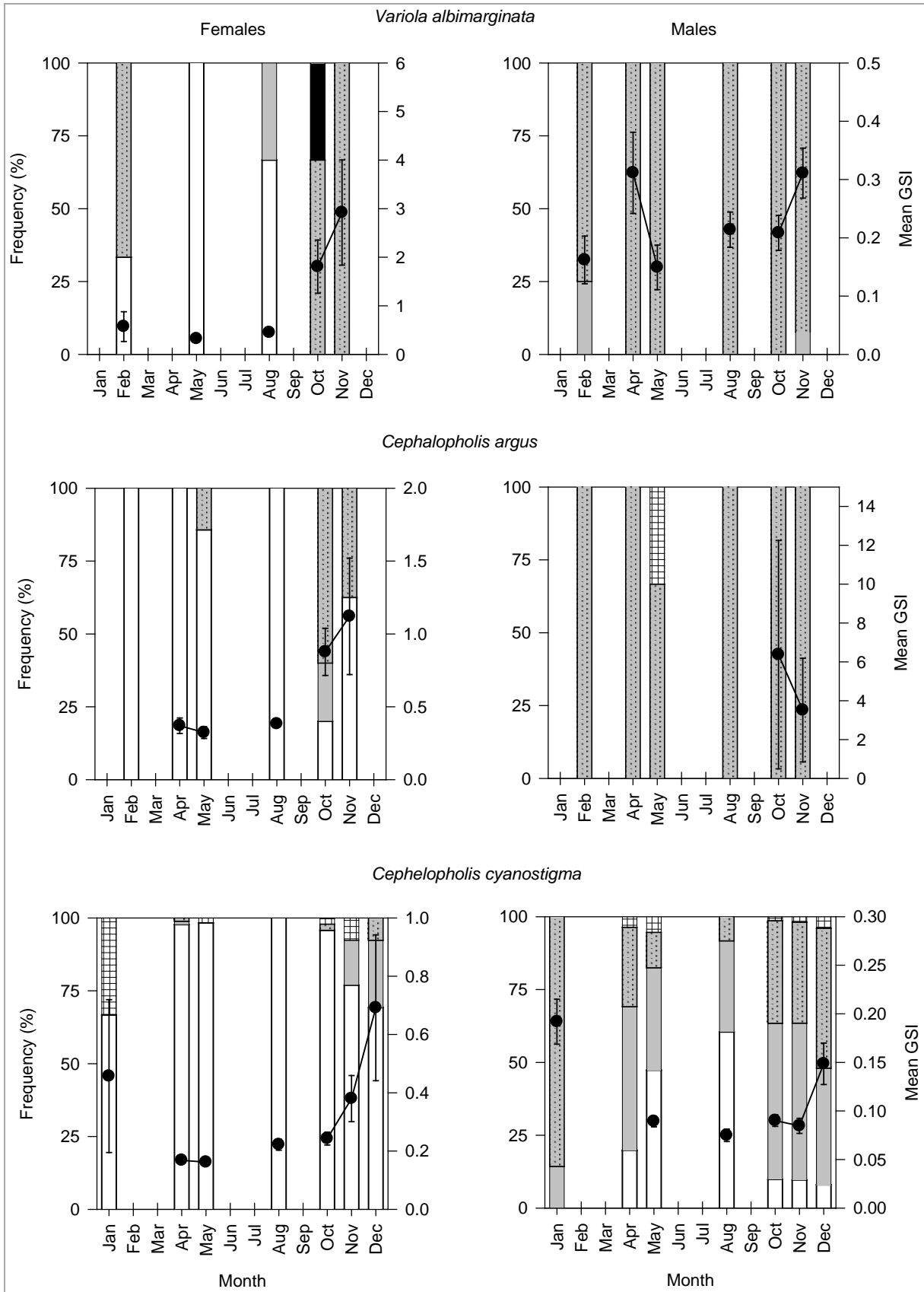


Figure 8 (continued).

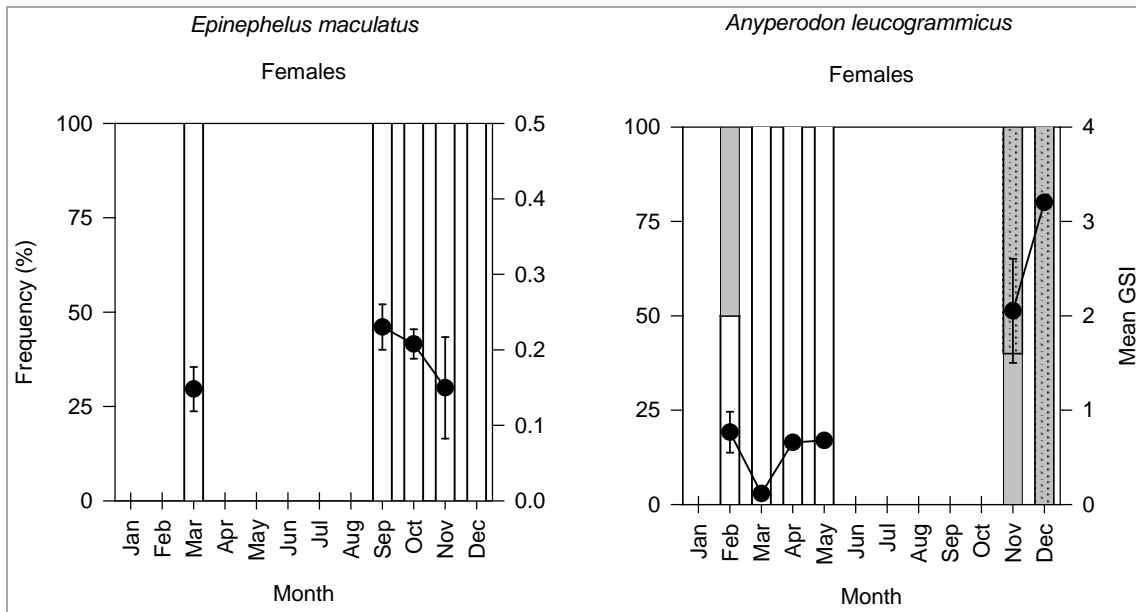


Figure 8 (continued).

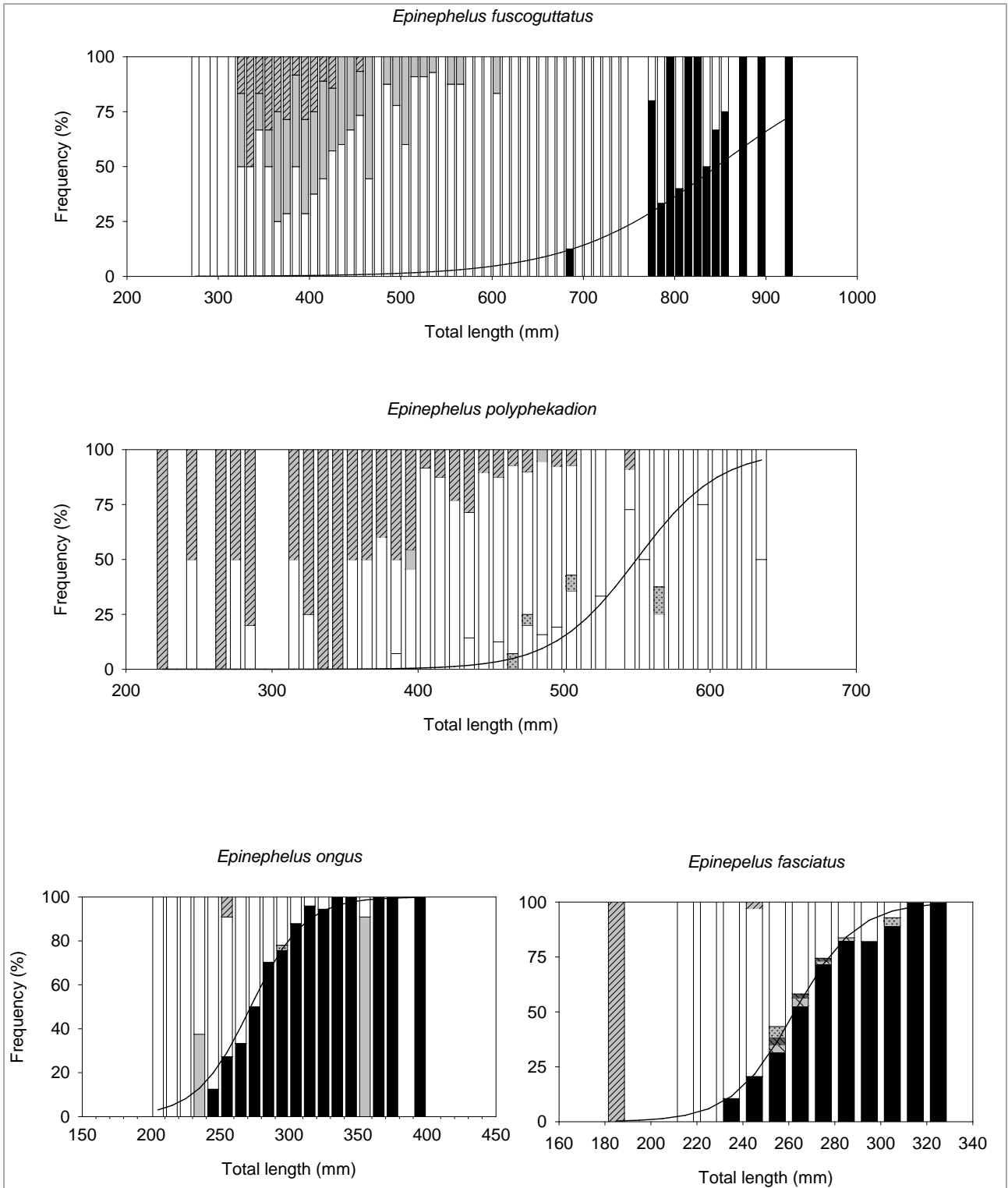


Figure 9 (continues to pages 38-39): Proportion of males and females in each length class. Logistic curves are plotted for some species to determine the length at sex change.

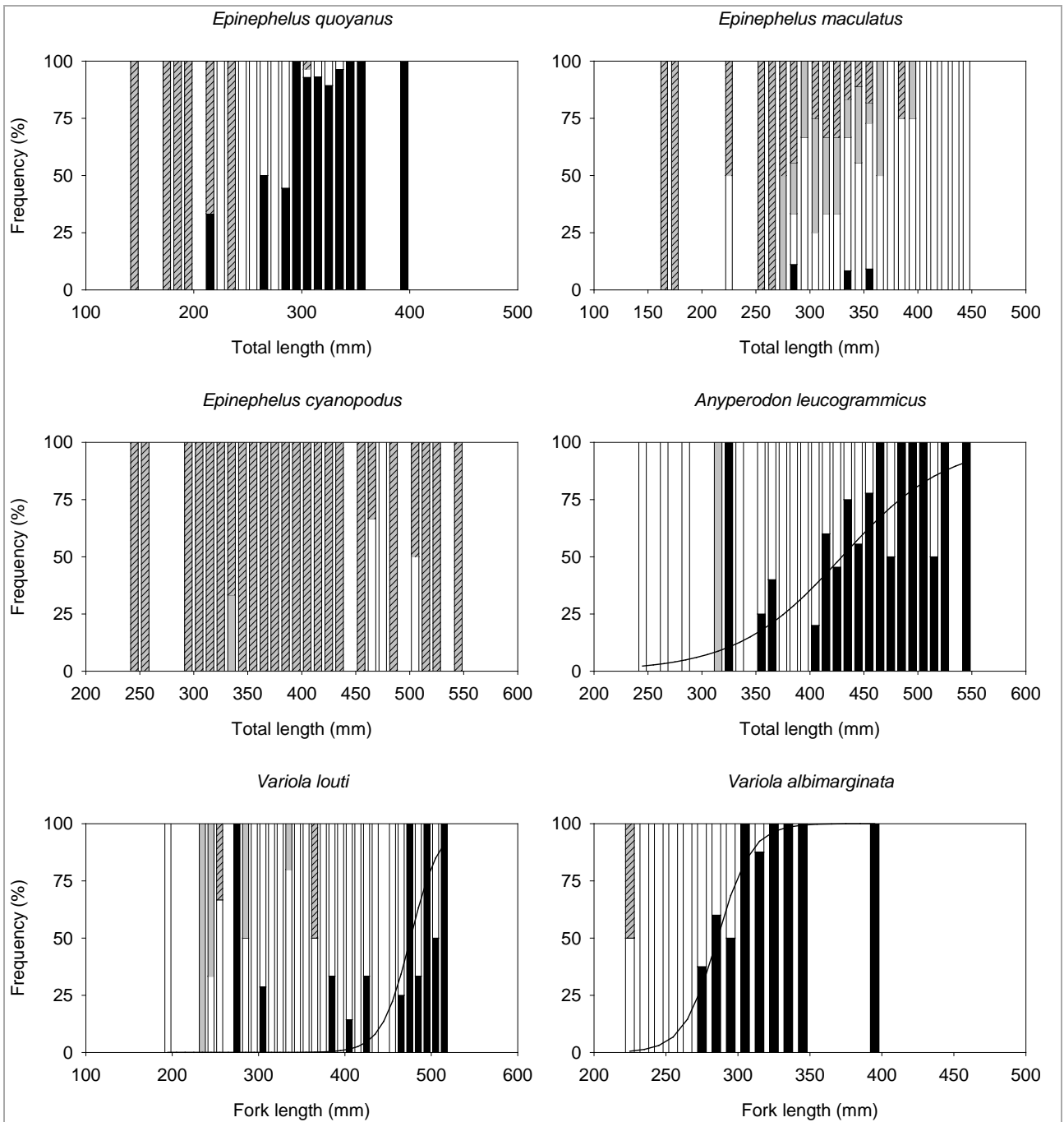


Figure 9 (continued).

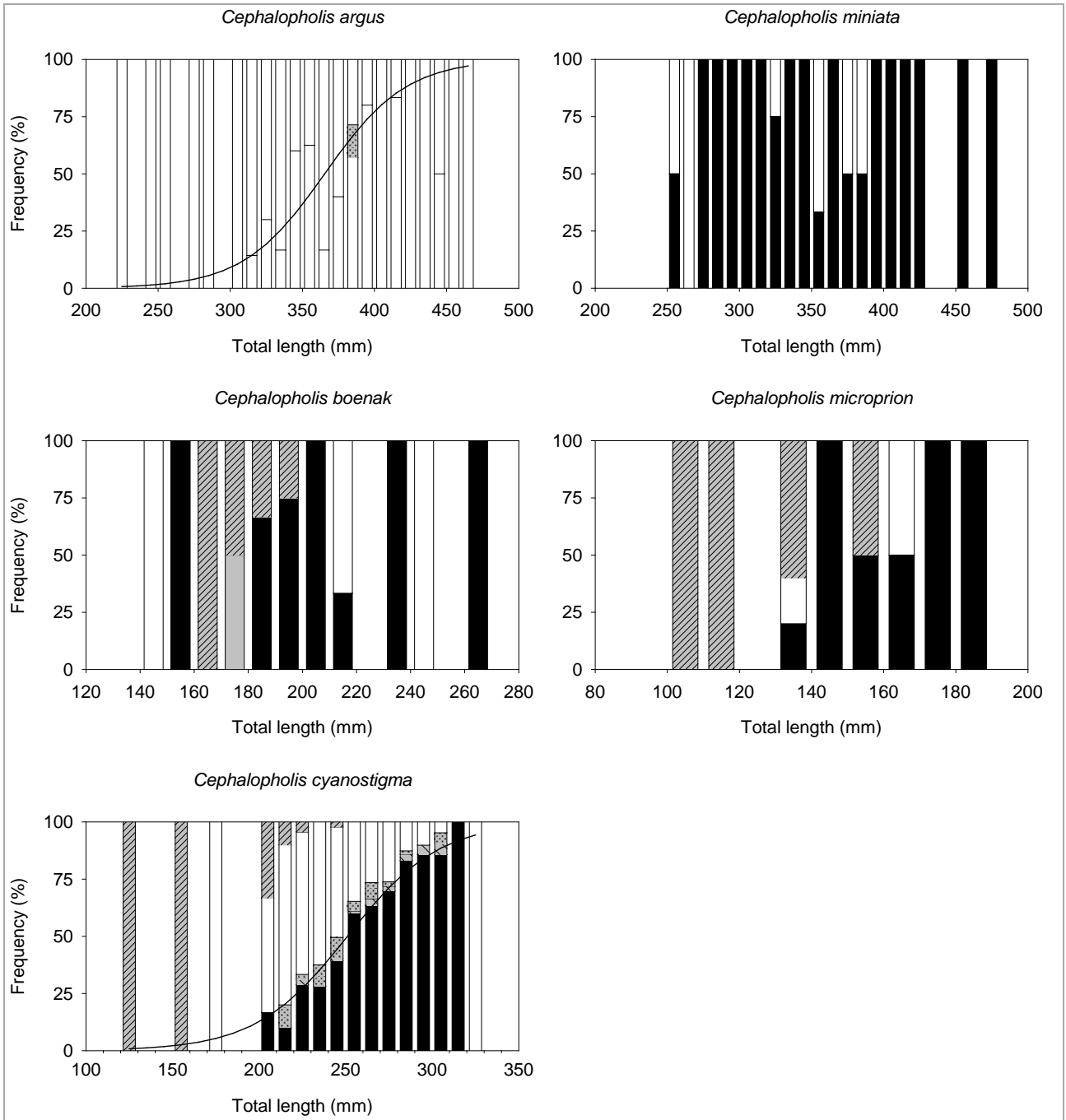


Figure 9 (continued).

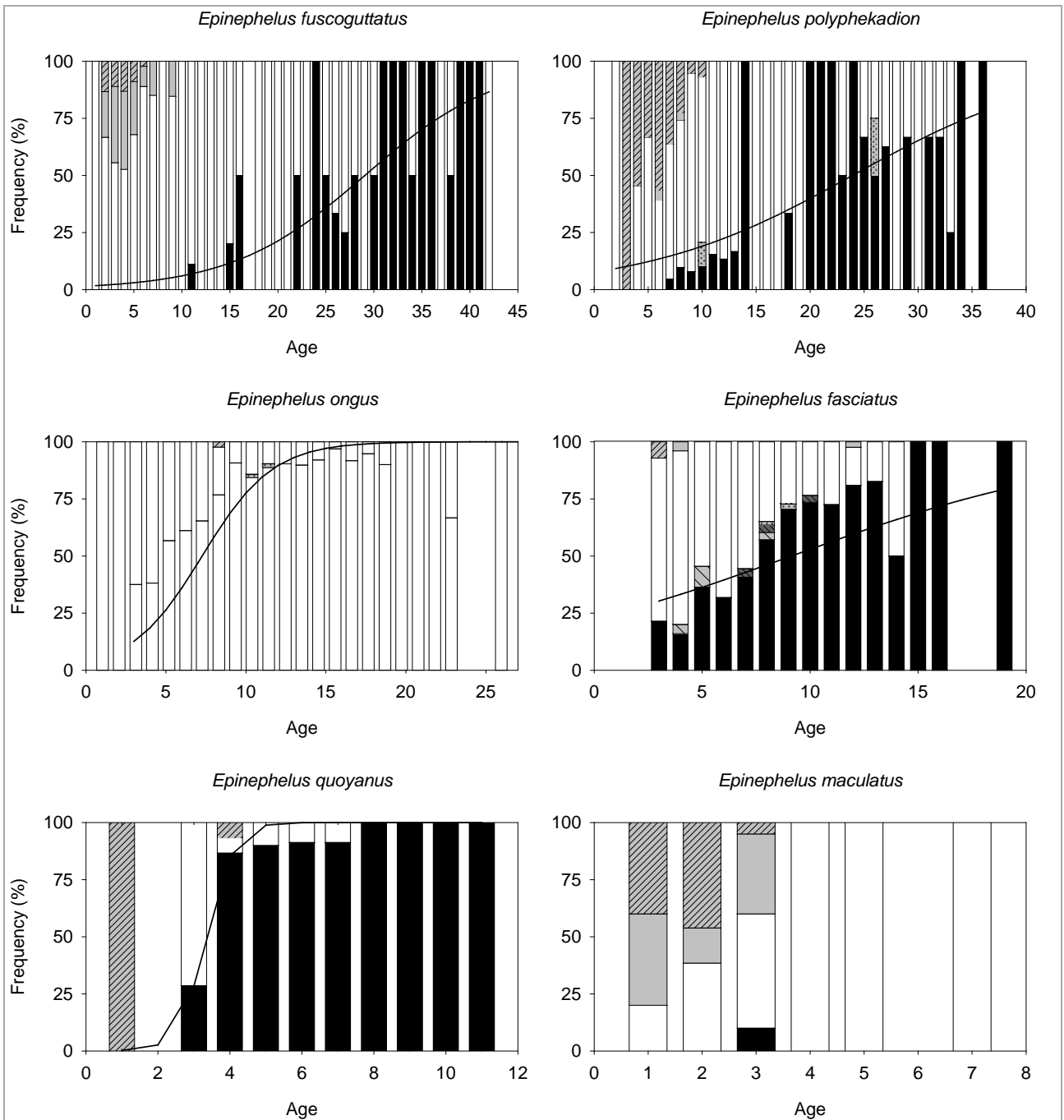
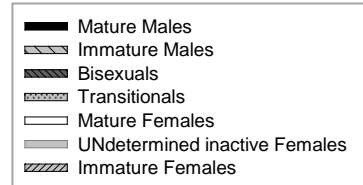


Figure 10 (continues to pages 41-42): Proportion of males and females in age class. Logistic curves are plotted for some species to determine the age at sex change.



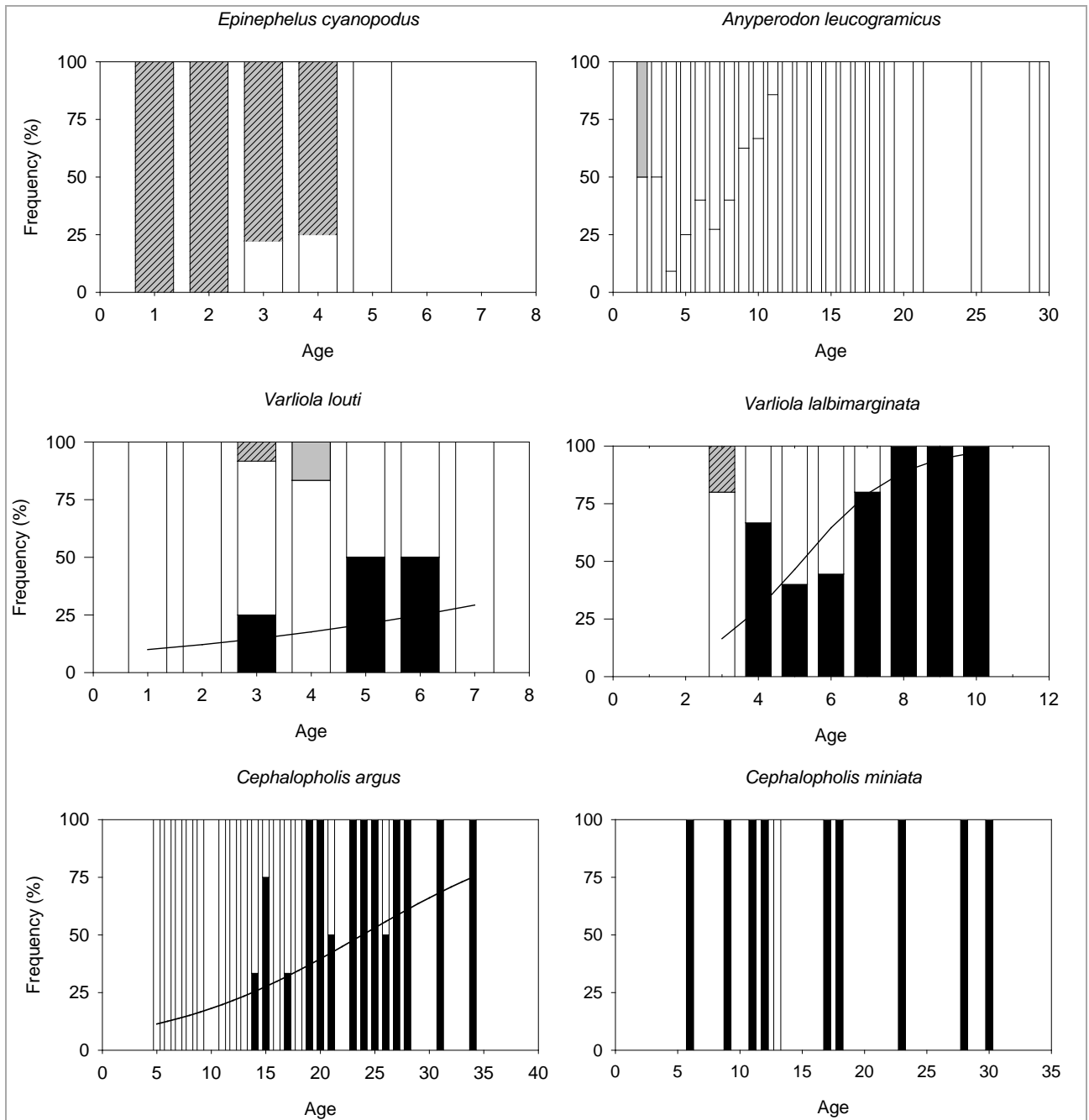


Figure 10 (continued).

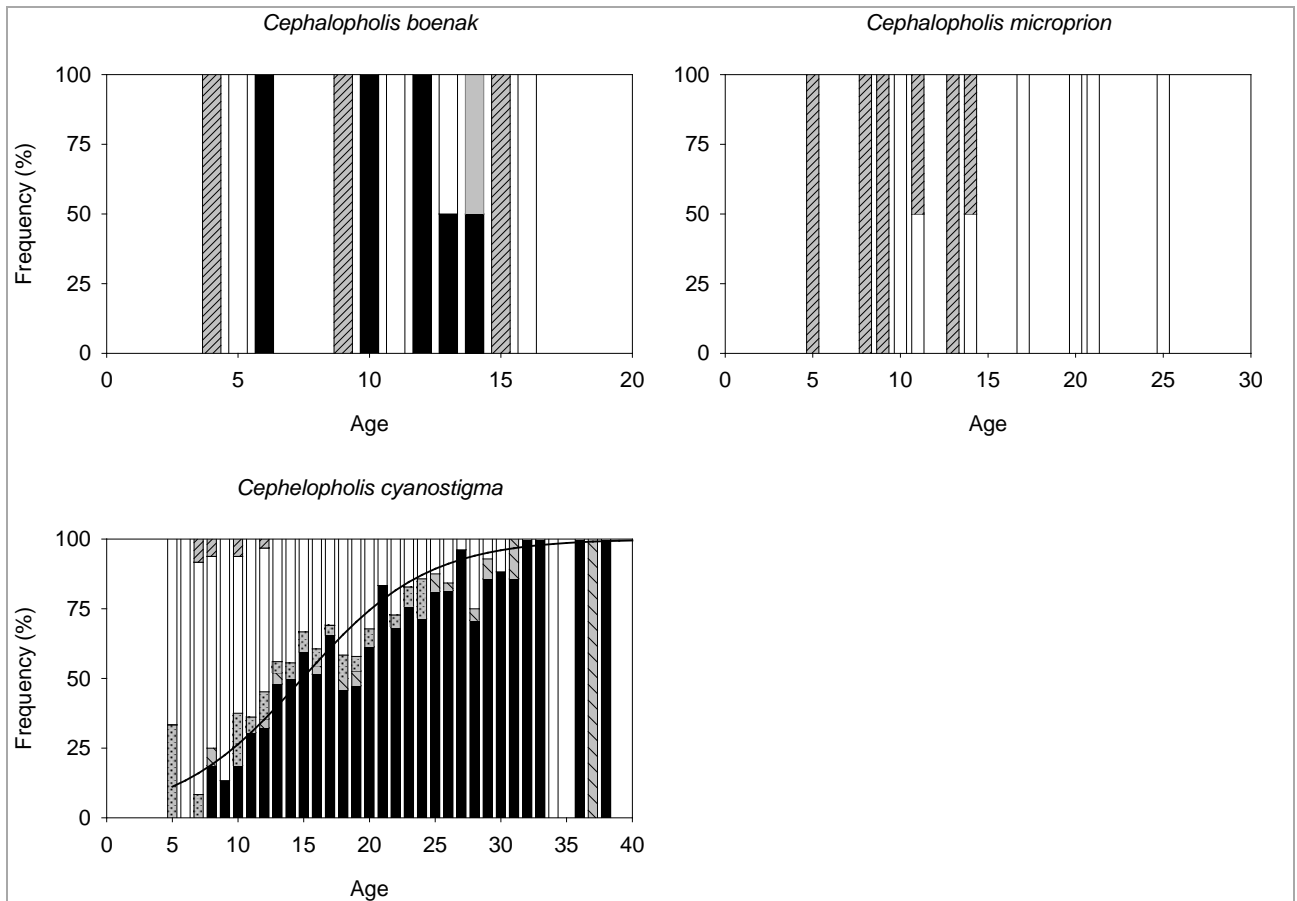


Figure 10 (continued).

Discussion

The data presented in this report is evidence that epinepheline serranids captured as part of the Great Barrier Reef line fishery include species with a range of life histories that would preclude these species from being managed effectively as a single group. Life history parameters such as growth, length and age at sex change and longevity were not consistent for all species or even species within the same genus. The outcome from increasing levels of harvest for individual species would therefore be very different, and if harvest were quite high could potentially result in over-exploitation of some species. Management strategies which focus on these more vulnerable species may be one option. Alternatively it may be important to provide species-specific management options. Either option requires more research focused on providing accurate biological parameters for individual species. This highlights the difficulty in managing multi-species coral reef fisheries.

Using data collected from the ELF experiment surveys, length and age distributions varied between species. Both young and old species as well as small and larger species were represented in the sample. Because these samples were collected using standardised hook and line gear, the length and age distribution of each species has been affected by gear selectivity. For each species, smaller younger individuals would be less vulnerable to the gear than larger older individuals. Alternatively, smaller younger individuals may not have been present in the habitats that were sampled. The largest species sampled, *E. fuscoguttatus* and *E. polyphkadion* were two of the oldest species, but not as old as *C. cyanostigma* (46 years), one of the smallest species sampled. Each of these species had maximum ages greater than forty years, which make these some of the oldest epinepheline serranids aged to date. Age ranges varied between species within those genera with more than one species. The genus *Cephalopholis* tended to have a greater number of longer lived species. Previous studies of *Cephalopholis* species have provided maximum age estimates ranging from 11-26 years (Chan and Sadovy, 2002; de Araujo and Martins, 2006). These species had been collected from areas where they are an important target species within the fishery. This is not the case with *Cephalopholis* species on the Great Barrier Reef where they are either a byproduct or bycatch species. Variation in the maximum can result from variation in regional demographic patterns, differences in exploitation levels, as higher levels of catch are more likely to deplete the oldest age classes, differences in the otolith reading method (whole or sectioned) or environmental conditions.

Though some species were long lived and slow growing it is not clear that this is the case for all grouper species. A number of the species included in this study had maximum ages which were more moderate when compared to the longest lived species. More moderate age ranges are also common for other epinepheline serranids within the genus *Plectropomus* (Ferreira and Russ, 1994; Russ *et al.* 1998; Williams *et al.* 2008). However for some species it was clear that larger older fish were missing from the sample. There were very few male fish collected in the samples of *E. cyanopodus* and *E. maculatus*. Epinepheline serranids are generally considered to be protogynous so it would have been expected that larger older individuals would be predominantly male. The absence of males in the sample suggests larger individuals may be associated with habitats which were not sampled. Only emergent reefs were fished during the ELF experiment surveys, no samples were collected from depths greater than ~20 m. Ontogenetic shifts associated with growth may have resulted in larger older individuals moving to deeper water. Other reef species in the family Lutjanidae have been found to undertake movements associated with growth and maturation (Russell and McDougall, 2005; Nakamura *et al.* 2008). In the case of protogynous species, evidence of movements associated with sex change has not been recorded.

The parameter estimates from the VBGF and length-weight estimates provided further evidence of the variability between species. The growth types identified in the length-weight

relationships highlighted the morphometric differences between species. In the case of the VBGF parameters, at times the smaller younger individuals were missing from the sample and for other species larger older individuals were absent from the catch. The absence of smaller individuals can result in biased estimates for the VBGF with higher estimates of L_{∞} and t_0 and an underestimate of K (Ferreira and Russ, 1994; Williams *et al.* 2008). The growth estimates in this case still provide an indication of the variation in growth between species. Generally where both younger and older fish were collected growth models were asymptotic, with most of the growth occurring while fish were younger. This highlights the importance of collecting both length and age data when estimating life history parameters for grouper species. For the long lived species size may not be a very good predictor of age and the VBGF may not be as accurate when predicting size-at-age.

The effect of gear selectivity on species with a variety of age ranges and length ranges resulted in varying estimates of mortality because of the different catch curves. Two of the largest species, *E. fuscoguttatus* and *E. polyphkadion* had the lowest estimates of mortality (0.07 yr^{-1}). Of the other species, the *Cephalopholis* species had lower estimates of mortality compared with estimates for *Epinephelus* and *Variola* species. There was no clear separation of mortality based on the size of species (Beverton and Holt, 1957). The older age estimates for *Cephalopholis* species contributed to the generally lower mortality rates for these species. The alternative mortality rates derived for *E. fuscoguttatus* (0.2 yr^{-1}), *E. polyphkadion* (0.23 yr^{-1}) and *C. cyanostigma* (0.02 yr^{-1} and 0.29 yr^{-1}) revealed that for some species mortality rate was not consistent across ages. For *C. cyanostigma* mortality was negligible over a wide age range, after which mortality increases at a certain age, perhaps due to senescence. The cryptic nature of some smaller serranids such as *C. cyanostigma* may result in these fish being able to avoid predation thus resulting in lower rates of mortality.

Reproductive data was collected for a number of species indicating the peak spawning period to be in the Austral spring and summer from October until January. Females with hydrated ovaries and increases in mean GSI were observed during this time. This indicates that for a number of species spawning occurs over the same period. A large number of epinepheline serranid species are known to aggregate during spawning (Shapiro, 1987; Sadovy, 1996). At these times species become vulnerable to fishing if aggregations can be reliably targeted. Within the Great Barrier Reef, Coral trout (*P. leopardus*) are known to form spawning aggregations during the new moons from August until December (Samoilys, 1997). Within the Great Barrier Reef there is currently no information about the spawning behaviour for any of the species included in this study. These species are not primary target species within the fishery so it is unlikely that much effort has gone into identifying and targeting spawning aggregations if they exist. Because the majority of data was collected via the ELF experiment there was not a very even temporal spread in data collection. Further sampling for some species throughout the period from March until August would complement the data which has already been collected.

The observed distribution of sexes by length and age strongly indicate that the sexual development of a number of species follows the pattern of a monandric protogynous hermaphrodite, with individuals first functioning as females, and later some mature females changing sex to function as males. The age and length at 50% sex change was variable across species. For a number of species there was often a large overlap in the size and age range of males and females. The large overlap in length and age ranges of male and female individuals is similar to other epinepheline serranids (Sadovy and Shapiro, 1987; Williams *et al.* 2008). This suggests that the cue for sex change for these species is not based solely on an endogenous developmental schedule, with individuals reaching a specific length or age and all becoming male. Exogenous mechanisms such as the maintenance of a threshold sex ratio within the population could influence the timing of sex change, or a combination of both exogenous and endogenous mechanisms. For three of the species, *E. fuscoguttatus*,

E. polyphkadion and *C. argus*, sex change occurred very late in life with the age at 50% sex change greater than the 90th percentile in age. Both *E. fuscoguttatus* and *E. polyphkadion* were also very large at the point of 50% sex change, measuring 846 mm and 550 mm respectively. In the case of both species there were a number of older larger females sampled. These larger older female fish may play an important role in the population. For both of these species there may have been a close relationship between length and the timing of sex change as there was only a narrower overlap in the length distribution of female and male *E. fuscoguttatus*. The life history characteristics, longevity, late sex change, and large size identified for both *E. fuscoguttatus* and *E. polyphkadion* indicate a potential for susceptibility to overharvest.

A number of species had female biased sex ratios while other species had male biased sex ratios and some sex ratios were not significantly different from 1:1. This variability is likely due to the effect of gear selectivity, the differences in the length of the species, and also the inconsistency in the length at sex change. Furthermore, for both *E. cyanopodus* and *E. maculatus* it appears that males were absent from the areas which were sampled. This would account for the high female bias in the catch of *E. maculatus*. Female bias sex ratios were more common for larger species and male biased sex ratios were more common for smaller species. The outcome of increasing harvest on the reproductive capacity of species will be different depending on the bias of the sex ratio. The removal of greater numbers of females could result in a compensatory response such as a smaller length at maturity, as larger more fecund females are removed (Olsen *et al.* 2005). The removal of male fish could result in a shortage of sperm to fertilise eggs, and depending on the behaviour of spawning fish it could disrupt social cues for mating (Huntsman and Schaaf, 1994; Coleman *et al.* 1996). Either situation results in a disruption of the natural sex ratio and a reduction in the reproductive output of species. Other concerns over size selective fishing relate to the removal of larger individuals from the population. For a number of species a greater proportion of the sample included larger older individuals. The removal of these individuals from a population can reduce fecundity and change food webs as larger predators are removed and reduce the genetic heterogeneity of a population (Birkeland and Dayton, 2005). All of these outcomes reduce the resilience of species to fishing or changes in the environment.

Management Implications

It is difficult to make broad generalisations about this species group using the information which was collected. Some species are long lived and slow growing however others had a more moderate age range and growth rate. The reproductive development of each species when related to age and length, and accounting for the influence of gear selectivity, was similarly highly variable. Management options for individual species such as minimum or maximum size limits become extremely complex, considering the number of species and differences between individual species. The introduction of size limits for individual species is further confused by the difficulty in distinguishing between species and the need to account for cryptic mortality associated with post release survival if large numbers of fish are likely to be discarded.

The current management arrangements for these species within the Great Barrier Reef include minimum (500 mm) and maximum size limits (700 mm) for *E. fuscoguttatus* and *E. polyphkadion*, which have been grouped as they are similar looking species, and a 380 mm minimum size limit for all other species. Both *E. fuscoguttatus* and *E. polyphkadion* were identified as being particularly susceptible to fishing, being long lived and changing sex when older and larger. Pears *et al.* (2006) outlined the implications of excessively large maximum size limits on *E. fuscoguttatus*, explaining the importance of protecting the larger older male and female individuals. Subsequent to the publishing of this paper the maximum size limit for these species was reduced from 1,000 mm to the current size. While the current

arrangements are successful in protecting larger male *E. fuscoguttatus* there is no protection for large male *E. polyphkadion*. However in the case of *E. polyphkadion*, the 500 mm minimum size limit offers some protection for smaller male fish. This shows the compromise involved in setting size limits for species groups rather than individual species. The current minimum size limit of 380 mm applies to species with a wide range of different biological parameters and in some instances it may be well matched to the biology (eg. *A. leucogrammicus* and *V. lout*), considering species length and age ranges and the presence of mature females and size at sex change. There are many instances where the current 380 mm minimum size limit leads to the exclusive harvest of males and large mature females. This may not be a desirable management outcome and consideration should be given to reviewing the size limit for these species. Currently none of these species are important target species within the fishery and this is likely due to either the small size of the species or their low abundance in the catch. If targeting behaviour were to change or if there was a market demand for smaller groupers it would be difficult to effectively manage these species using conventional fisheries measures such as size limits alone.

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