Life History, Diet and Distribution of three Grenadier Species in South Africa

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Plagiarism Declaration

I know the meaning of plagiarism and declare that all of the work in the thesis, save for that which is properly acknowledged, is my own.

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19/07/2024

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Abstract

The Macrouridae are a diverse and varied family of deep-sea fishes which, barring a few commercially exploited species, have not received sufficient scientific attention. A lack of basic life history data in the species *Coelorinchus braueri*, *Coelorinchus simorhynchus*, and *Malacocephalus laevis* prevents assessments of their stocks and their vulnerability to bycatch mortality in the South African offshore trawl fishery. To remedy this, more than 500 specimens across the three species were collected over the course of a year from the South African west and south coasts, with sampling occurring every 1–3 months. These were measured and dissected to provide data on distribution, morphometrics, biometrics, growth, age structure, diet, reproduction, and parasites. A von Bertalanffy regression was fitted to *Coelorinchus braueri* growth data, and length-weight regressions were fitted for all three species. Stomach dissections were used to identify prey taxa and calculate their index of relative importance, reproductive seasonality was assessed, and the ovarian organisation of *Coelorinchus simorhynchus* and *Malacocephalus laevis* were described. Macroscopic and histological images of female and male gonads are presented here for the first time. These were used to measure sexual development phase and investigate reproductive seasonality. The life history data were interpreted in the context of the deep-sea habitat occupied by these species and the limitations inherent in studying trawl-captured deep-sea fishes and macrourids in general. Comparisons between information revealed here and previous studies on grenadiers were made where possible.

Morphometric estimations for total length (TL) from pre-anal fin length (PAFL) were determined to be as follows: TL = 2.22 * PAFL + 56.7 (*C. braueri*), TL = 2.84* PAFL + 66.0 (*C. simorhynchus*), and TL = 3.73 * PAFL + 136.0 (*M. laevis*). In all species females were larger than males. No clear patterns of PAFL or average mass with depth were found. Sex ratios did not consistently vary with depth, but were different on the west and south coasts. Gonado-somatic index (GSI) was typically less than 1% in males and between 2% and 8% in females. No evidence for strong reproductive seasonality was found.

C. braueri showed isometric growth (Mass = $8.36\text{x}10^{-5}$ * $\text{PAFL}^{2.97}$), and had a PAFL_{50} of 107 (females) and 89 mm (males). A von Bertalanffy regression for this species was estimated as $\text{PAFL}_t = 169.13*(1 – e^{-0.10*(t - (-1.73))})$, and the maximum observed age of 17 years was roughly in line with what is known from this genus. *C. braueri* preyed primarily on small crustaceans and teleost fish. The sex ratio in this species was biased towards females, with mean female GSI of 3.2%. The copepod *Sphyrion quadricornis* was found on this species, along with unidentified chondracanthid copepods in the gill chamber.

C. simorhynchus showed isometric growth (Mass = $1.12\text{x}10^{-4}$ * $\text{PAFL}^{3.08}$) and had a PAFL_{50} of 71 (females) and 32 mm (males). *C. simorhynchus* preyed primarily on a mix of crustaceans, ophiuroids and teleosts. The sex ratio in this species was biased towards females, with mean female GSI of 3.7%. The ovaries in this species were categorised as asynchronous. The copepod *Sphyrion quadricornis* was found on this species.

M. laevis showed hypoallometric growth (Mass = $2.09\text{x}10^{-3}$ * $\text{PAFL}^{2.59}$). *M. laevis* preyed primarily on teleosts and cephalopods, as well as some large prawns. The sex ratio in this species was roughly equal, with mean female GSI of 2.6%. The ovaries in this species were categorised as group synchronous. Unidentified chondracanthid copepod parasites were found in the gill chamber of this species.

External parasites were identified where possible. The parasite loads and their locations on the specimens were described. Both *Coelorinchus* species were found to be parasitised externally by copepod *Sphyrion quadricornis*, while *C. braueri* and *M. laevis* were beset by unknown chondracanthid gill copepods.

It is evident that much work remains to be done before these species, and other less well-researched macrourids may be incorporated into ecosystem and fisheries models or before their stocks and vulnerability may be assessed. Furthermore, it is clear that these species of grenadiers differ in many of their life history characteristics. Future models and fisheries policies must not treat grenadiers interchangeably, but rather consider them on a species-by-species basis where possible.

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1. Introduction

1.1 Characteristics and etymology

The grenadiers or rattails (Acanthopterygii: Macrouridae) are a diverse family of gadiform fishes found in deep waters throughout the world's oceans, and account for the majority of gadiform species (Cohen *et al*., 1990; Roa-Varón & Ortí, 2009). They are generally characterised by the following set of features: the body consists of a short anterior trunk and a very long tapered tail; pelvic fins are inserted below the pectorals thoracically; eyes are large; first dorsal fin is often very tall, and the second dorsal and anal extend to the posterior tip of the fish to give the appearance of a single continuous fin (Cohen *et al.,* 1990). The caudal fin is absent as there are no bones supporting it, except in the subfamily *Trachyrincinae* (Cohen *et al.,* 1990; Endo 2002). Fishes in the subfamily *Macrouroidinae* also differ from other macrourids in their general body shape, having greatly enlarged globose heads, small eyes, and lacking the free-standing dorsal fin (Endo 2002). Many macrourid species feature chin barbels and ventral subdermal light organs containing luminescent bacteria immediately anterior to the anus (Nelson, 1994). These barbels serve as mechanoreceptors and gustatory sense organs in some species, having high densities of taste buds and nerve endings, assisting in close-range foraging (Bailey *et al*., 2007). Insufficient research has been conducted on the function of light organs in macrourids, although it has been suggested that luminescence facilitates specific recognition (Marshall, 1965). Luminescence in other fishes is known to play a role in schooling behaviour, species-recognition for reproduction, prey attraction, and predator avoidance (Dunlap *et al*., 2007).

The large tail and anal fin give rise to the family name Macrouridae, from Greek *makros* (large) and *oura* (tail) (Romero, 2002). The colloquial name rattail or rat-tail is also likely derived from the thin, tapering tail and fin. While the term rattail is frequently used in South Africa, the globally more common name "grenadier" has a less certain etymology. Historically, *grenadiers* have been soldiers specialised in the use of thrown explosives (i.e. grenades). It is believed that the headwear of Napoleonic-era French grenadiers, being similar in shape to a Catholic mitre, somewhat resembles the snout from the grenadier as seen from below (Centre National de Ressources Textuelles et Lexicales, 2012), or possibly the tall first dorsal fin (STEM Newcastle, 2017), which could have given rise to this name. However, while plausible, these claims should be considered speculative until corroborated by a reliable source. The term is likely used for species targeted by fisheries for marketing reasons, due to potential consumer prejudice against eating fish containing the prefix "rat" in its name (Monterey Bay Aquarium Research Institute [MBARI], 2024). Unfortunately, the term “grenadier” is also occasionally used for non-macrourid fishes such as *Macrouronus capensis* in the family Macrouronidae, the so-called “Cape grenadier” (Cohen *et al*., 1990).

1.2 Taxonomy

1.2.1 Historical perspective

The clade Macrouridae was first erected in 1831 as *Macrourini*, a subfamily within the Gadidae, by French naturalist Charles Lucien Bonaparte, with only the sparse description of “*pinne ventrali quasi toraciche: squame ruvide e dure*” (near-thoracic ventral fins: rough and hard scales) separating them from other known Gadiformes (Bonaparte 1831, van der Laan *et al*., 2014). Scientific knowledge of grenadiers predates Bonaparte, however, as the first grenadier species described was *Coryphaenoides rupestris* Gunnerus 1975, the roundnose grenadier (World Register of Marine Species [WoRMS], 2023a).

The morphology-based cladistic analysis by Endo (2002) includes a more comprehensive account of the morphological and anatomical features of grenadiers that are used to place them within the Gadiformes and to resolve relationships within that family. Of note are the “presence of a transverse median process on pelvic girdle and the absence of a caudal fin”, which separate the macrourids and steindachnerids from all other Gadiformes, and the “presence of cartilaginous pb 1 and both interarcual elements and a reduced number of actinosts” in macrourids but not steindachnerids. Endo (2002) lists a variety of competing phylogenies for the Gadiformes which were proposed throughout the 20th century. Despite the prevalence of the Endo (2002) analysis in literature focused on gadiform fishes, later studies using genetic data or molecular data have challenged this interpretation (Roá-Varon & Ortí, 2009; Malmstrøm *et al.* (2016); Han *et al.* (2021)).

1.2.2 Diversity of known species

An exact figure for the number of described species is rarely given in published literature. Most authors describe the Macrouridae as comprising over 300 (e.g. Moranta *et al*., 2007; Acuña *et al*., 2008) or, in more recent works, over 400 species (e.g. Endo *et al*., 2010; Sobrino *et al*., 2012). The World Register of Marine Species lists 409 accepted species in 36 genera within the family Macrouridae (WoRMS, 2023b). However, the genus *Mesovagus* Nakayama and Endo, 2016 was created to replace the genus *Mesobius* Hubbs and Iwamoto, 1977, due to the latter name already being in use as a genus of centipede (Nakayama & Endo, 2016). WoRMS currently lists both genera as valid despite the fact that *Mesovagus antipodum* and *Mesovagus berryi* are the replacement names for *Mesobius antipodum* and *Mesobius berryi* respectively, and that neither of the latter two species are accepted. The unique accepted species of grenadiers therefore number 407, spread across 35 genera when *Mesobius* is discarded in favour of its replacement.

More than half of all described macrourids are currently placed in only three genera, those being *Coelorinchus*, *Coryphaenoides*, and *Nezumia* (*Table 1.2*). The notion of paraphyly of *Coelorinchus* was supported by genetic work (Roá-Varon & Ortí, 2009), suggesting that future revisions of this genus will perhaps see reassignment of some species to other or new genera. The period around the turn of the 20th century was the most productive era of macrourid taxonomy, as 15 genera were described between 1884 and 1925. By comparison, no new genera have been described since the 1980s.

*Table 1.2: Tally of described macrourid species by genus, along with the year the genus was erected, as per WoRMS. * Genus* Mesobius*, while still listed, should not be counted as it has effectively been renamed* Mesovagus*. **The total species count amounts to 407 when* Mesobius *is discounted, but 409 when included.*

Genus	Year	Number of species
Coryphaenoides	1765	66
Macrourus	1786	5
Coelorinchus	1809	119
Trachyrincus	1809	6
Lepidorynchus	1846	1
Malacocephalus	1862	7
Bathygadus	1878	14
Hymenocephalus	1884	28
Cetonurus	1887	2
Trachonurus	1887	6
Albatrossia	1898	1
Mataeocephalus	1898	6
Gadomus	1903	13
Nezumia	1904	53
Cynomacrurus	1909	1
Macrouroides	1912	1
Echinomacrurus	1916	2

*Table 1.2 (continued): Tally of described macrourid species by genus, along with the year the genus was erected, as per WoRMS. * Genus* Mesobius*, while still listed, should not be counted as it has effectively been renamed* Mesovagus*. **The total species count amounts to 407 when* Mesobius *is discounted, but 409 when included.*

Squalogadus	1916	1
Hymenogadus	1920	2
Lucigadus	1920	9
Ventrifossa	1920	24
Sphagemacrurus	1925	6
Odontomacrurus	1939	1
Pseudonezumia	1970	4
Spicomacrurus	1970	4
Kumba	1973	8
Paracetonurus	1973	1
Kuronezumia	1974	7
Mesobius	1977	2 (0)*
Haplomacrourus	1980	1
Idiolophorhyncus	1981	1
Asthenomacrurus	1982	2
Cetonurichthys	1982	1
Pseudocetonurus	1982	1
Macrosmia	1983	1
Mesovagus	2016	2*
Total:	407**	

The most recently described species currently accepted by WoRMS is *Coelorinchus ganymedes* Prokofiev 2021; however, three species have been described more recently and may soon become accepted. These are *Coelorinchus tricristiger* (Prokofiev & Iwamoto, 2022) and *Coelorinchus zinjianus* (Prokofiev & Iwamoto, 2023), both from the western Indian Ocean, as well as *Coelorinchus inventionis* (Prokofiev *et al.,* 2022) from the southeastern Atlantic Ocean.

1.2.3 State of macrourid phylogeny

The phylogenetic relationships within the Macrouridae have not been fully agreed upon, and it is likely that the taxonomy will undergo major revision in the near future. The families Macrouridae and

Steindachneridae constitute the suborder Macrouroidei within the Gadiformes, alongside the Steindachneriidae. Whereas Endo (2002) placed the Macruronidae within the suborder Gadoidei, Roá-Varon & Ortí (2009) include it as a third macrouroid family, based on genetic evidence. However, Malmstrøm *et al.* (2016) place it within the Macrourinae-Bathygadinae clade.

Many phylogenies (e.g. Endo 2002; Nelson 2006) split the family Macrouridae into the four constituent subfamilies Trachyrincinae, Macrouroidinae, Bathygadinae, and Macrourinae, with the last containing the majority of species. However, there is mounting evidence that the Macrouridae are not monophyletic. A 2009 genetic analysis (Roá-Varon & Ortí) showed only Macrourinae and Bathygadinae as well-supported within the Macrouridae, reassigning Trachyrincinae and Macrouroidinae to the Gadoidei as subfamilies within a monophyletic family-level clade, while also suggesting that Bathygadinae could be elevated to family level as Bathygadidae. These changes, if accepted, would remove nine species from the Macrouridae. Conversely, genetic work by Malmstrøm *et al.* (2016) and Han *et al.* (2021) casts doubt on the traditional split of the Gadiformes into its three suborders (Muraenolepidoidei, Macrouroidei, and Gadoidei), with the latter placing the Trachyrincinae as sister to the Muraenolepididae. It is evident that the family Macrouridae as accepted by WoRMS is likely not monophyletic, and that a number of the fish groups commonly called grenadiers are more closely related to other gadiform fish lineages. The name grenadier may arguably better be reserved for only those species within the Macrourinae, or the Macrourinae and Bathygadinae if that clade holds up to further scrutiny.

Roá-Varon & Ortí (2009) also found inconsistencies internal to subfamily Macrourinae, suggesting that the genus *Coelorinchus* is likely paraphyletic and should include at least some species from *Macrourus*. Both this phylogeny and work done by Wilson *et al.* (1991) suggest that *Albatrossia pectoralis* should be a species of *Coryphaenoides*, which would eliminate the monotypic genus *Albatrossia* entirely. These examples of the many proposed changes at all levels in the grenadier phylogeny show that, like many deep-sea fish groups, the clade has not received adequate taxonomic attention and is liable to change as further genetic studies are conducted.

1.3 Distribution

1.3.1 Depth ranges

The Macrouridae are one of the teleost families with the widest depth ranges. The deepest recorded species, *Coryphaenoides yaquinae*, is one of the few fish species known from the hadal zone at a depth of approximately 7000 m (Linley *et al.*, 2016). Conversely, Bigelow and Schroeder's 1953 *Fishes* *of the Gulf of Maine* relates an anecdote of a specimen of *Macrourus bairdii* (now *Nezumia bairdii*) trawled in only “9 fathoms” (16.2 m) of water off Massachusetts, although the species’ usual minimum depth is considered closer to 90 m (Cohen *et al*., 1990). Cohen *et al.* (1990) also list 100 m as the minimum depth for grenadiers in general. The claim of Marshall (1965) that “90 per cent or more” of then-known grenadier species occupy the bathyal zone on continental slopes, between roughly 200 and 2000m, is still widely quoted (Cohen *et al.* 1990; Moranta *et al.*, 2007; Sobrino *et al.* 2012). Evidence exists for ontogenetic shifts in depth range in some species, with larger fish generally being found at greater depths. This trend, known as the “bigger-deeper” phenomenon, has been observed in a variety of deep-sea fishes (Polloni *et al*., 1979), but is not universally shared among deep-sea fishes or even macrourids.

1.3.2 Pelagic habitats

Macrourids generally occupy benthic habitats, but a few have been captured in the pelagic zone. For example, Stein (1985) encountered *Coryphaenoides filifer* in abyssopelagic waters (2000–3000 m) and mentioned similar observations of *Coryphaenoides acrolepis*. Several species of grenadier are known to consume primarily pelagic prey based on stomach contents. While some of these may represent scavenging on sunken carcasses on the seabed, it is generally thought that at least some of these species hunt in the pelagic zones (Anderson, 2005; Drazen *et al.*, 2001). For example, *Mesovagus antipodum* is a specialised midwater predator at 800-1400 m, while *Coryphaenoides striaturus* is a generalist exploiting both the benthic and pelagic environments (Anderson, 2005).

1.3.3. Substrate and bathymetric features

Macrourids have been observed on a variety of substrates, including soft sediments, gravel, and exposed rock outcrops (Baker *et al*., 2012; Durán Muñoz *et al.*, 2012). In hurdle models, sediment heterogeneity was positively correlated with grenadier presence and abundance in some species, but negatively in others (Baker *et al*., 2012). The community composition of the coral fauna of the substrate also correlated with grenadier presence and abundance. Corals could directly benefit grenadiers by increasing prey abundance and reducing water current speeds (Baker *et al*., 2012).

There is evidence to suggest that the distribution and population structure of certain macrourids may be defined by bathymetric features such as seamounts and canyons. Some grenadiers appear to show fidelity to the specific seamounts they settle on as larvae. Régnier *et al.* (2017) examined genetic exchange between *Coryphaenoides rupestris* specimens sampled at depths of approximately

900–1050 m on adjacent seamounts, determining them to be discrete populations that do not intermix. White *et al*. (2010) also reported genetic differences between *C. rupestris* sampled from either side of the sub-polar front in the North Atlantic, which presents a barrier to larval dispersal. Furthermore, *C. rupestris* demonstrate a preference for areas of low current, and as such may aggregate in submarine canyons (Lorance *et al.*, 2008; Snelgrove & Haedrich, 1985). However, Baker *et al.* (2012) found variability in the presence and abundance of several grenadier species between different canyons in the same area, and therefore cautioned against generalising macrourids as preferring canyons. These studies show that, while it may not be possible to make generalisations about habitat preferences in at the family level, many species of grenadiers are strongly influenced by the structure of the seabed. Unlike for midwater gadoids, fisheries policies on macrourids will need to account for the structural effects of bottom trawling on macrourids beyond mere catches, while predictive models must evolve beyond mere location and depth-based ones to take into account the structure of the seabed and ecological composition of the benthos.

1.3.4 Geographic distribution and ranges

The distribution of macrourids is near-cosmopolitan, as representatives occur in every ocean from the Antarctic coast to Arctic latitudes. While no species have been found in the highest Arctic latitudes, with *Macrourus berglax* being one of the northernmost species at 82°N (Cohen *et al.*, 1990), it is possible that this simply reflects the difficulty of sampling fish below the Arctic sea ice rather than actual absence of grenadiers. The waters of the Indo-Pacific host the greatest known diversity of grenadiers (Nakayama & Endo, 2018), particularly the areas off Australia (Iwamoto & Graham, 2008), New Caledonia (Iwamoto & Merrett, 1997) and Taiwan (Iwamoto *et al.*, 2015). However, the high number of described species in the Indo-Pacific may be attributable partly to the high fishing effort in the region, as the western Pacific is one of the most heavily fished areas worldwide (Garcia & Newton, 1995).

The majority of *Coryphaenoides* species are known to be restricted to single ocean basins, but *C. armatus* and *C. rudis* occur in all basins and at a variety of latitudes (Gaither *et al.*, 2016). The same study showed that species at abyssal depths had broader depth and geographic distributions than shallow-living species. In general, *Coryphaenoides* grenadiers follow a unimodal diversity pattern with depth that peaks between 1000 and 1500 m (Gaither *et al.*, 2016). Such unimodal patterns have been observed in other groups of deep-sea animals, although the optimum depths vary considerably (Ramirez-Llodra *et al.*, 2010). For example, a review of pelagic teleost fishes in the Pacific considering

73 families showed that maximum diversity occurred in the 100 to 200 m depth range (Smith & Brown, 2002).

Whereas most macrourids are widely distributed, with several having extremely broad geographic ranges (e.g. *Cetonurus globiceps*, *Coryphaenoides armatus*, *Malacocephalus laevis*), a few have relatively narrow geographic ranges. For example, *Coelorinchus trunovi* is only known from waters off Mozambique and Kwa Zulu–Natal in northern South Africa, and *Nezumia brevibarbata* and *Nezumia umbracincta* are found only in South African waters, barring occasional catches in southern Namibia (Iwamoto & Anderson, 1994). Although grenadiers in general show wide-ranging geographic distributions and depth ranges, these are much narrower in some species, potentially indicating a mixture of generalist and specialist habitat adaptations in the family.

1.4 Grenadiers of South Africa

1.4.1 Species of the South African EEZ

Sources disagree on the precise number and identity of the species described in South Africa. Iwamoto and Anderson's 1994 *Review of the Grenadiers (Teleostei: Gadiformes) of Southern Africa, with descriptions of four new species* recorded 38 species in South African waters. FishBase lists 35 species in 14 genera that have been recorded off the coast of South Africa, all of which are considered native (Froese & Pauly, 2024). The Global Biodiversity Information Facility [GBIF] lists 48 species (GBIF, 2024).

The Iwamoto and Anderson (1994) review includes the three target species considered here, *Coelorinchus braueri*, *Coelorinchus simorhynchus*, and *Malacocephalus laevis*. Iwamoto and Anderson (1994) first recognised *C. simorhynchus* as a distinct species from *C. fasciatus*, which does not occur in South Africa. The three species were chosen based on their high rate of capture in the demersal hake trawl fishery (Cooper, personal communication 2022, February 07). What follows is a list of the species potentially found in South Africa (*Table 1.4*) and a discussion on the discrepancies in the species records.

Table 1.4: Comparison of records of macrourid species found in South African waters across three different sources. *C. fasciatus *now considered to be* C. simorhynchus. C. flabellispinis *now considered to be* C. trunovi.

Iwamoto & Anderson (1994)	FishBase	GBIF	Common name
Bathygadus cottoides	*Bathygadus cottoides*	*Bathygadus cottoides*	Codheaded rattail
Bathygadus favosus	*Bathygadus favosus*	*Bathygadus favosus*	-
-	*Bathygadus melanobranchus*	*Bathygadus melanobranchus*	Vaillant's grenadier
Cetonurus globiceps	*Cetonurus globiceps*	*Cetonurus globiceps*	Globehead grenadier
Coelorinchus acanthiger	*Coelorinchus acanthiger*	*Coelorinchus acanthiger*	Surgeon grenadier
Coelorinchus braueri	*Coelorinchus braueri*	*Coelorinchus braueri*	Shovelnose grenadier
Coelorinchus denticulatus	*Coelorinchus denticulatus*	*Coelorinchus denticulatus*	Filesnout grenadier
-	*Coelorinchus fasciatus**	*Coelorinchus fasciatus**	Banded whiptail
-	*Coelorinchus flabellispinis*	*Coelorinchus flabellispinis*	-
Coelorinchus kaiyomaru	*Coelorinchus kaiyomaru*	*Coelorinchus kaiyomaru*	Campbell whiptail
Coelorinchus karrerae	*Coelorinchus karrerae*	*Coelorinchus karrerae*	Karrer's whiptail
Coelorinchus matamua	*Coelorinchus matamua*	*Coelorinchus matamua*	Mahia whiptail
-	-	*Coelorinchus occa*	Swordsnout grenadier
-	-	*Coelorinchus parallelus*	Spiny grenadier
Coelorinchus simorhynchus	*Coelorinchus simorhynchus**	*Coelorinchus simorhynchus**	-
Coelorinchus trunovi	*Coelorinchus trunovi*	*Coelorinchus trunovi*	-
Coryphaenoides armatus	*Coryphaenoides armatus*	*Coryphaenoides armatus*	Abyssal grenadier
Coryphaenoides carapinus	*Coryphaenoides carapinus*	*Coryphaenoides carapinus*	Carapine grenadier
Coryphaenoides dossenus (as *Coryphaenoides* sp. A)	-	*Coryphaenoides dossenus*	Humpback whiptail
Coryphaenoides grahami	*Coryphaenoides grahami*	-	Graham's whiptail
-		*Coryphaenoides leptolepis*	Ghostly grenadier
Coryphaenoides mcmillani	*Coryphaenoides mcmillani*	*Coryphaenoides mcmillani*	McMillan's whiptail
Coryphaenoides striaturus	*Coryphaenoides striaturus*	*Coryphaenoides striaturus*	Striate whiptail
Coryphaenoides subserrulatus	*Coryphaenoides subserrulatus*	-	Longrayed whiptail
Gadomus capensis	*Gadomus capensis*	*Gadomus capensis*	-
Haplomacrourus nudirostris	*Haplomacrourus nudirostris*	*Haplomacrourus nudirostris*	Naked snout rattail
Hymenocephalus heterolepis	-	*Hymenocephalus heterolepis*	-
-	*Hymenocephalus italicus*	*Hymenocephalus italicus*	Glasshead grenadier
Kuronezumia bubonis	*Kuronezumia bubonis*	*Kuronezumia bubonis*	Bulbous rattail
Kuronezumia leonis	*Kuronezumia leonis*	*Kuronezumia leonis*	Snubnose whiptail
-	-	*Lucigadus nigromaculatus*	Blackspotted grenadier
Lucigadus ori	*Lucigadus ori*	*Lucigadus ori*	Bronze whiptail
Macrourus carinatus	*Macrourus carinatus*	*Macrourus carinatus*	Ridge scaled rattail
-	-	*Macrourus holotrachys*	Bigeye grenadier
Malacocephalus laevis	*Malacocephalus laevis*	*Malacocephalus laevis*	Softhead grenadier

*Table 1.4 (continued): Comparison of records of macrourid species found in South African waters across three different sources. **C. fasciatus *now considered to be* C. simorhynchus*.* C. flabellispinis *now considered to be* C. trunovi.

Mesovagus antipodum (as *Mesobius antipodum*)	*Mesovagus antipodum*	*Mesovagus antipodum* (as *Mesobius antipodum*)	Bathypelagic rattail
Nezumia brevibarbata	*Nezumia brevibarbata*	*Nezumia brevibarbata*	Shortbeard grenadier
Nezumia micronychodon	*Nezumia micronychodon*	*Nezumia micronychodon*	Smalltooth grenadier
-	-	*Nezumia milleri*	Miller's grenadier
-	-	*Nezumia polylepis*	-
Nezumia propinqua	*Nezumia propinqua*	*Nezumia propinqua*	Aloha grenadier
Nezumia spinosa	*Nezumia spinosa*	*Nezumia spinosa*	Sawspine whiptail
Nezumia umbracincta	*Nezumia umbracincta*	*Nezumia umbracincta*	-
Odontomacrurus murrayi	*Odontomacrurus murrayi*	*Odontomacrurus murrayi*	Roundhead grenadier
Sphagemacrurus richardi	*Sphagemacrurus richardi*	*Sphagemacrurus richardi*	Richard's whiptail
Trachonurus villosus	-	*Trachonurus villosus*	Furry whiptail
-	-	*Trachyrincus longirostris*	Slender unicorn rattail
-	*Ventrifossa divergens*	-	Plainfin grenadier
Ventrifossa mystax	*Ventrifossa mystax*	*Ventrifossa mystax*	-
Ventrifossa nasuta	*Ventrifossa nasuta*	*Ventrifossa nasuta*	Conesnout grenadier
-	-	*Ventrifossa petersonii*	Peterson's grenadier
Ventrifossa sp. indet.	-	-	-

Bathygadus melanobranchus is known from only one South African record on GBIF and is listed as a South African species on FishBase, but Iwamoto and Anderson (1994) noted that Southern African records of the species cannot be verified, and that the original material has been lost. Cohen *et al.* (1990) showed the distribution along the entire African west coast, but highlight the ease of confusion between this species and the sympatric *Bathygadus favosus*.

Coryphaenoides dossenus is well-documented in South African waters as *Coryphaenoides* sp. A (e.g. McMillan, 1999; Iwamoto & Anderson, 1994), although it is not listed as a South African species on FishBase.

It was recognised by Iwamoto and Anderson (1994) that specimens recorded as *Coelorinchus fasciatus* in South African waters are the morphologically similar *Coelorinchus simorhynchus*. FishBase and GBIF still list both species as occurring in South Africa despite *C. fasciatus* being restricted to South America, Australia and New Zealand (Iwamoto & Anderson, 1994).

Similarly, Iwamoto and Anderson (1994) assert that observations of *Coelorinchus flabellispinnis* on the South African east coast are misidentifications of *C. trunovi*. GBIF includes 21 observations in

South African waters, recorded between 1986 and 2010, while FishBase also lists this species as South African. The actual distribution of *C. flabellispinnis* appears to be limited to the northern Indian Ocean between the Arabian Sea and Bay of Bengal (Iwamoto and Anderson, 1994; Jawad and Al-Mamry, 2012).

Coryphaenoides grahami is placed in South Africa by Iwamoto and Anderson (1994) and is shown as widely distributed on both South African coasts as per FishBase, despite the absence of GBIF records.

Iwamoto and Anderson (1994) make no mention of *Coryphaenoides leptolepis* and the species is considered by FishBase to occur only in the northern hemisphere, in both the Atlantic and Pacific. GBIF has a single observation of the species from 1996 labelled as taken in South Africa, although the coordinates given point to a location southeast of Argentina the species. It seems likely that this species does not occur in South Africa and that the GBIF record is erroneous.

Although it is not mentioned by Iwamoto & Anderson (1994), there are 7 South African observations of *Coelorinchus occa* listed on GBIF, all from July 1988. However, the given coordinates point to a location off the coast of Angola. The Ocean Biodiversity Information System [OBIS] shows a number of records from both sides of the South Atlantic, but Cohen *et al.* (1990) caution that “identification of specimens taken off southern Africa must be confirmed”, as the species is generally considered to favour the Gulf of Mexico. Melo *et al.* (2010) record the species off Brazil only.

Coelorinchus parallelus is known from 72 records in South African waters (GBIF), however, the most recent of these are from 1925 (with later records off Namibia up to 1984) and Cohen *et al.* (1990) suggest these to be misidentifications of *Coelorinchus braueri* and/or *Coelorinchus acanthiger*. The actual distribution of *C. parallelus* is likely restricted to the western Pacific between Japan and the Philippines, potentially down to New Zealand (Cohen *et al.*, 1990). Iwamoto and Anderson make no mention of *C. parallelus*, but do list *C. pseudoparallelus* as a synonym of *C. acanthiger.*

Iwamoto and Anderson (1994) noted two specimens of *Coryphaenoides subserrulatus* taken on the Agulhas Bank. Cohen *et al.* (1990) also shows it as being distributed along the South African south coast, and it is considered a South African species by FishBase despite the lack of GBIF records.

Hymenocephalus heterolepis is described as being limited to the eastern Indian Ocean around Thailand on FishBase, while GBIF lists a single record from 2010 off the South African east coast. This species has been in a state of taxonomic uncertainty for some time, with some authors suggesting its synonymy with the Atlantic species *Hymenocephalus italicus* soon after it was described (Anderson, 1996), as these species differ only in the ratio of orbit diameter to head length and number of pyloric caeca. Iwamoto and Anderson (1994) confirm the presence of specimens of a species of

Hymenocephalus off the South African east coast that are "intermediate in their characters between *H. italicus* Giglioli, 1884 of the Atlantic and *H. heterolepis* of the Indian Ocean", and tentatively named the species as *H. heterolepis*. Anderson (1996) later synonymised *H. heterolepis* with *H. italicus*, giving the latter a wide distribution from the Atlantic to the east Indian. *H. heterolepis* is still accepted as a valid species on WoRMS.

Lucigadus nigromaculatus is listed in nine records from the east coast of South Africa between 1931-1932 on GBIF. Cohen *et al.* (1990) restrict the distribution to only Chile, Australia, and New Zealand (as its synonym *Ventrifossa nigromaculata*) but OBIS also lists records from the South Atlantic. Iwamoto and Anderson (1994) record only *Lucigadus ori* as a Southern African species, mentioning *L. nigromaculatus* as inhabiting the southwest Atlantic.

Macrourus holotrachys is listed by FishBase as occurring only off Patagonia and South Georgia, following Cohen *et al.* (1990), with the latter source suggesting that previous reports of the species elsewhere may likely be misidentifications of *M. carinatus*. GBIF lists four recent (2015) observations of *M. holotrachys* in South African waters northwest of the remote Prince Edward Islands. *M. carinatus* was shown to occur around the Prince Edwards islands by Cohen *et al.* (1990), although Iwamoto and Anderson (1994) list only *M. carinatus* as occurring in South African waters. This may simply be an omission on the part of the latter authors, as they do not mention the Prince Edward islands at any point in their review, suggesting that they focused only on the waters surrounding the South African mainland.

Nezumia milleri was initially only confirmed as occurring off Angola (Cohen *et al.*, 1990), but the range was later extended further south (Iwamoto and Anderson, 1994). It is recorded on the African west coast from Angola to southern Namibia as per FishBase, whereas GBIF lists a single observation just south of the border to South Africa. It is possible that *N. milleri* occasionally occurs in South African waters near the Namibian border.

Nezumia polylepis is restricted to the Indian Ocean north of Zanzibar by FishBase, while GBIF lists three observations in 1920, all west of Cape Point. There is no mention of *N. polylepis* by Iwamoto and Anderson (1994).

Iwamoto and Anderson (1994) tentatively list *Trachonurus villosus* as a species occurring in South African waters while cautioning that this may in fact be an undescribed species of *Trachonurus*. *T. villosus* is stated to have a "worldwide" distribution on FishBase, although it is not listed as one of the South African species. GBIF lists only four South African records, all off the south coast between 1976 and 1994. The genus *Trachonurus* has been undergoing revision for the past several decades.

Trachyrincus longirostris has been recorded 22 times on both South African coasts between 1923-1925 (GBIF), however it has not been recorded since and McMillan (1995) considers the species to be exclusive to New Zealand and the Australian south coast. Distribution maps by FishBase and OBIS also limit its distribution to these countries and do not consider it a South African species. Iwamoto and Anderson (1994) also list only *T. scabrus* as occurring in Southern African waters off Namibia.

Ventrifossa divergens has no South African records on GBIF but FishBase shows it as occurring on the South African east coast, mirroring their distribution in Cohen *et al.* (1990). Iwamoto and Anderson (1994) instead refer to this species as *Ventrifossa* sp. aff. *divergens* and re-describe it as *Ventrifossa mystax*, a species known to occur on both South African coasts.

There exist 10 documented observations of *Ventrifossa petersonii* in South Africa, all between 1920-1926. Cohen *et al.* (1990) considers the distribution to be limited to southeast Asia and the African east coast between Yemen and Kenya, but not further south. This matches the distributions given by FishBase and WoRMS. Iwamoto and Anderson (1994) do not mention *V. petersonii*, but discuss a record of an unknown individual of *Ventrifossa*, potentially from further north (*Ventrifossa* sp. *indet*.).

Iwamoto and Anderson (1994) also list a single individual in *Ventrifossa* taken off East London in 1901 which does not match any of the *Ventrifossa* known from the area, suggesting that the individual could be a rare vagrant from the northern Indian Ocean.

1.4.2 Distribution of trawl bycatch

The trawl fishery on the South African west and south coasts generates high amounts of macrourid bycatch every year. *Figure 1.4* maps the locations of trawls containing grenadiers reported by observers on hake-directed trawlers between November 2002 and January 2011 (South African Deep Sea Trawling Industry Association, 2024). Observers examined sub-samples of approximately 20% of the trawl haul by mass, either directly from the net or from ship decks during sorting. For discard species, a random sub-sample was kept for observers to examine prior to discarding. The sub-sampling observer procedure is described in detail by Attwood *et al*. (2011).

The combined inshore and offshore trawl fishery operates from the Orange River estuary on the west coast to Gqeberha on the south coast at depths between 250 and 800 m on the west coast and between 80 and 400 m on the south coast (Department of Forestry, Fisheries and the Environment [DFFE], 2023). Grenadiers are not typically caught in the inshore trawl fishery, as *C. braueri*, *C. simorhynchus* and *M. laevis* all occur at minimum depths of more than 200 m. The discontinuity in the distributions at ca. 22° E reflects an absence of trawl effort (DFFE, 2023). It is likely that the actual distribution of these species completely follows the shelf edge.

Grenadiers were present in the trawl sample in 4726 out of 37289 trawls (12.7%) taken deeper than 200 m. Based on these data, *C. braueri* were present in 881 (2.4%) trawls, *C. simorhynchus* in 3553 (9.5%), *M. laevis* in 2509 (6.7%), and other macrourids in 238 (0.6%). Macrourids were present in 35 trawls out of 199 (17.6%) that were taken from waters shallower than 200 m. However, it is not possible to meaningfully compare the percentage of inshore fishery trawls (shallower than 200 m) containing macrourids with those of the offshore fishery due to differences in vessels and gear. Inshore fishery vessels are much smaller, resulting in a higher proportion of the haul in the observer sample, and use nets with smaller mesh sizes, potentially facilitating greater catches of smaller species such as *C. braueri*. These data cover only the west and south coast hake-directed trawl fishery. Grenadiers are also caught in other South African fisheries; for example, *M. laevis* is reported as a commonly discarded bycatch species in the prawn fishery on the east coast (Fennessy & Groeneveld, 1997).

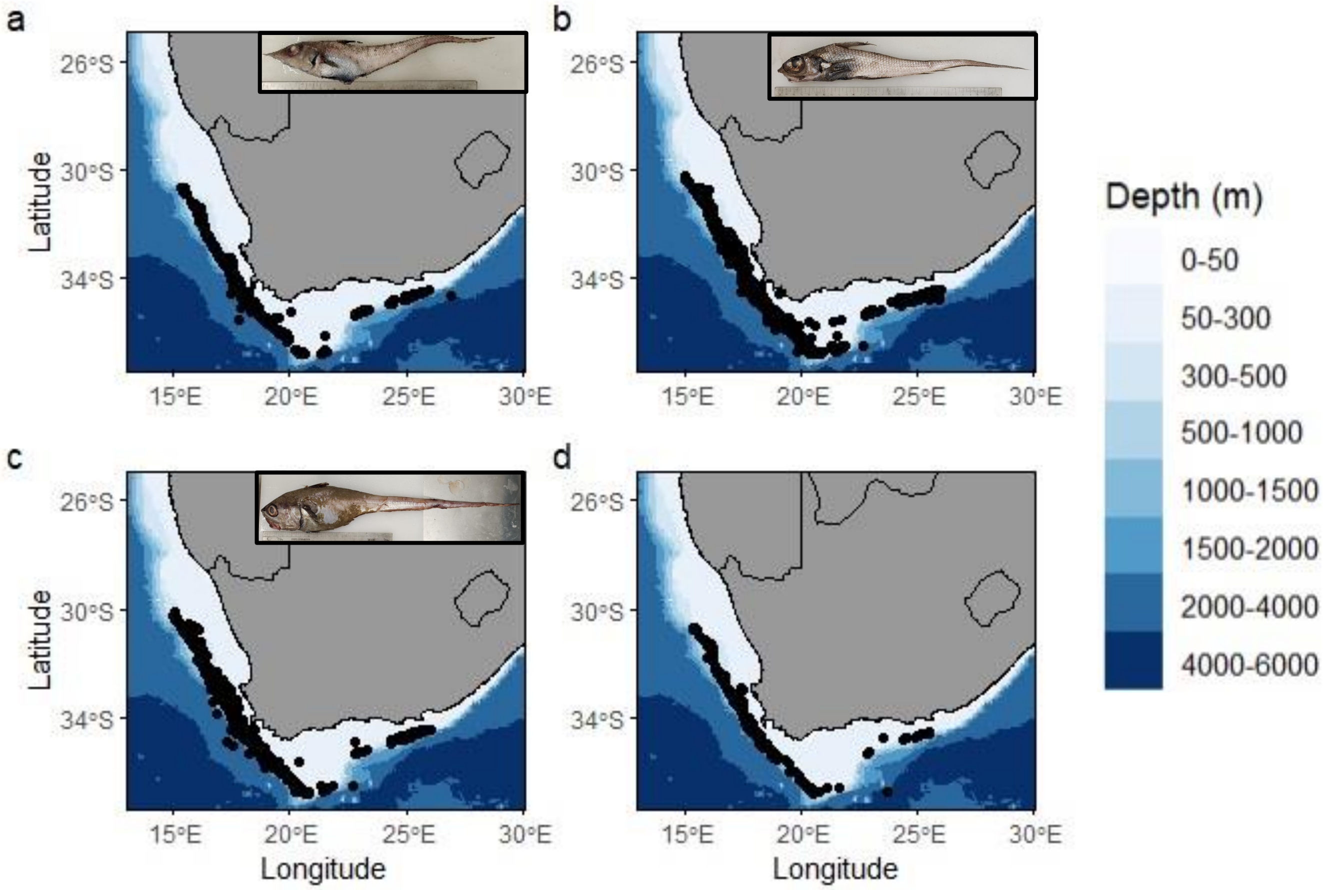

Figure 1.4: Bathymetric maps showing the locations of trawls containing (a) Coelorinchus braueri*, (b)* Coelorinchus simorhynchus*, (c)* Malacocephalus laevis*, (d) Non-specific Macrouridae ("rattails") based on an observer dataset of the offshore trawl fishery.*

1.5 Importance to Fisheries

1.5.1 Fisheries targeting macrourids

While grenadiers are widely distributed and often abundant at depth, their commercial utilisation remains limited (Matsui *et al.,* 1990). A 1990 FAO report on the family (Cohen *et al*., 1990) lists only *Coryphaenoides rupestris*, *Macrourus berglax*, *M. carinatus*, and *M. holotrachys* as targeted species, with a few others such as *C. acrolepis* and *Albatrossia pectoralis* landed occasionally in modest amounts. Since then, new fisheries have developed, with Tuponogov *et al.* (2008) denoting *C. acrolepis, C. cinereus* and *A. pectoralis* as commercially important; the latter having become a target species. *C. rupestris* in particular is considered one of the most commercially important fish within the Northeast Atlantic deepwater fishery (Lorance *et al.*, 2008).

There are few targeted fisheries for macrourids because they generally occur at depth and often relatively far from the coast, tend to be small, and are often regarded as having poor culinary quality (Lorance *et al.*, 2008; Matsui *et al.,* 1990). Their tapered body shape and long tail results in a considerably lower meat yield relative to length than in a fusiform fish of comparable length. Matsui *et al.* (1990) report a fillet to total mass ratio of only 25% for *C. acrolepis*, while even those species deemed most suitable for meat extraction, such as *C. cinereus*, only reach about 36% (Bykov *et al*., 2000). Their protein content is also typically below the mean for fish, averaging only about 15.2% for *C. acrolepis* (Matsui *et al.,* 1990) and 6.8% for *Albatrossia pectoralis* (Crapo *et al.*, 1999). Whereas some species are reported as having pleasant taste (e.g. *C. acrolepis, C. tokiensis, M. berglax*), others (e.g. *A. pectoralis*) are considered to be unpalatable (Matsui *et al.,* 1990), due to high moisture content caused by loose arrangement of muscle fibre bundles, as well as low protein content (Crapo *et al.*, 1999). Drazen (2007) showed the lipid content of muscles and livers in macrourids to relate to their mode of predation and mechanism for buoyancy control. Scavenging species, and those using their livers to remain buoyant in place of a gas bladder, had higher lipid contents and gelatinous muscle tissue. Most species of grenadiers are likely not suitable for human consumption, and may not hold much commercial value except for the generation of fishmeal.

1.5.2 Fisheries discards

As a result of their low perceived value, grenadier bycatch has historically been discarded - a practice which continues to this day in many fisheries. Some species, when taken as bycatch, are landed for the production of fishmeal and fertiliser (Matsui *et al*., 1990). Balsinger (2014) reported that within the Gulf of Alaska fishery in 2013, only 38 tonnes of caught grenadiers were taken to harbour, representing less than 0.5% of the total grenadier catch. Of these landings, 35 tonnes were used to produce fishmeal (Balsinger, 2014). In the case of more profitable species (e.g. *Coryphaenoides rupestris* in the north Atlantic), the entire catch may be landed, with unmarketable fish used for fishmeal production (Vinnichenko, 2019). The total value of grenadier discards of all species between 1950 and 2015, including those that were at some point commercially exploited, has been estimated at over 2.5 million tonnes (Victorero *et al.*, 2012).

Unfortunately, data on fisheries discards of macrourids have historically been insufficient, with catches often listed only as “grenadiers” or the equivalent local term. Trawl observer data from the South African west and south coast trawl fishery used to generate the distribution maps in section 1.4.2 split grenadier bycatch into only four groups: *Coelorinchus braueri*, *Coelorinchus simorhynchus*, *Malacocephalus laevis*, and a generic “Rattails” category for all other macrourid species. This practice has also occurred internationally – in the Northwest Pacific during the 1970s and 1980s, catches of grenadiers were identified only to species level for a handful of commercially exploited species such as *C. rupestris,* and assigned to the group “grenadiers *nei*” (*not elsewhere included*) for all other species. Macrourid discards in this region were not reported at all prior to 1977 (Victorero *et al.*, 2012). Many Macrouridae have large gas bladders used to control their buoyancy, which expand due to the rapid pressure decrease when they are caught and damage other internal organs. As a result of this intense barotrauma experienced by fish caught in deepwater fisheries, macrourid discards can generally be assumed to suffer total mortality (Lorance *et al.*, 2008).

1.5.3 Sustainability of macrourid fisheries

Grenadier fisheries are likely to be unsustainable unless conducted cautiously, as exemplified by the Northwest Atlantic fishery between 1975 and 1995. Large numbers of *Coryphaenoides rupestris* (peaking at 80000 t annually) were taken as bycatch while targeting halibut, which is highly likely to have been one of the factors leading to the collapse of that stock (Devine & Haedrich, 2008). Today, *C. rupestris* is red-listed as critically endangered (International Union for Conservation of Nature [IUCN], 2012), with ICES reporting a total catch of only 1378 t in the Northeast Atlantic in 2019 (International Council for Exploration of the Sea [ICES], 2023). Devine and Haedrich (2008) described a comparable decrease in abundance of *Macrourus berglax* in the same fishery over that time period, but found this to be correlated more strongly with changes in the environment than measures of exploitation. This species was less abundant, with catches never exceeding 9000 tonnes annually (Devine & Haedrich, 2008). It is currently listed as least concern in Europe (IUCN, 2014).

Analysis of life history characteristics of six grenadier species that are frequently taken as bycatch in the North Atlantic, North Pacific and Southern Ocean indicated their potential vulnerability to fishing pressure (Devine *et al.*, 2012). Four of the species examined had ages at 50% maturity exceeding 10 years, with both *Coryphaenoides acrolepis* and *Albatrossia pectoralis* taking 20 years or more to mature. Only the popeye grenadier *Coryphaenoides cinereus* was found to reach maturity at the relatively low age of between three to six years. Fecundity estimates were low, ranging from a minimum estimate of 2500 eggs annually for *C. rupestris* to 231000 for *A. pectoralis*, with four species estimated to produce less than 100 000 eggs per year. It was also noted that these fecundities may be overestimating the realised output of eggs due to possible biennial spawning in certain species. As a result of their long lives, slow growth, low fecundity, and high trophic level, these species could be very vulnerable to fishing pressure. While the results of the productivity-susceptibility analysis carried out by Devine *et al.* (2012) did not reveal any of the six macrourids as particularly vulnerable under current conditions, the development of new targeted fisheries could increase their susceptibility. Based on current knowledge of grenadier life histories, it is likely that many species could suffer stock collapse if targeted or caught as bycatch under strong fishing pressure.

1.5.4 The future of grenadier fisheries

Tuponogov *et al*. (2008) considered grenadiers to hold promise as yet-underexploited fisheries resources, with their market value potentially set to increase as more uses – such as canned roe, liver, or surimi paste – are developed. This sentiment was shared by Devine *et al.* (2012) who noted that the global development of deep-sea fisheries could see an increase in targeted exploitation of grenadier stocks. However, the conservative life histories shared by many macrourids suggest that the case of the North Atlantic “boom and bust” *C. rupestris* fishery could repeat itself for other macrourids, even those which are only taken as bycatch.

1.6 Ecology of grenadiers

1.6.1. Diet and feeding strategy

The tendency of macrourids to occupy relatively deep habitats has hindered the study of their ecology, but it is generally assumed due to their large size and abundance that they are important meso- or apex predators in deep-sea food webs (Drazen *et al.*, 2001; 2008). The trophic levels of the six grenadiers whose life histories were examined by Devine *et al.* (2012) ranged from 3.54 in

Coryphaenoides rupestris to 4.48 in *Macrourus berglax*. However, little useful data are available to quantify the effect which grenadiers have in mediating deep-sea prey populations, and their feeding rates are poorly understood (Drazen *et al.*, 2001).

Most grenadiers are thought to be generalised feeders and have a diverse range of diets and foraging methods, including benthic epifauna, infauna, pelagic nekton and scavenged carcasses (Drazen *et al.*, 2001; Laptikhovsky, 2005). However, some grenadiers may also have relatively narrow diets; for example, the high incidence of infaunal prey in stomachs of macrourids with long rostra such as *Trachyrinchus trachyrinchus* suggests these specialise in infauna (Macpherson, 1979). It has been suggested that, at least within the Mediterranean, grenadier species occupying depths of between 200 and 800 m were specialists, whereas those occurring below 1000 m tended to be generalists (Carrassón & Matallanas, 2002), following the general hypothesis that species occupying the food-scarce deep sea have broader dietary niches to take advantage of the food that is present.

An analysis of several South African macrourids found the majority of species to be micro- and mesocarnivores targeting benthic epi- and infauna, while opportunistically taking midwater prey (Anderson, 2005). One species, *Mesovagus antipodum*, was found to be a specialised midwater mesopredator, and several more employed a mixture of both foraging strategies. Diets of individual species were broad, with more than 35 species identified in stomachs of *Coelorinchus simorhynchus* and more than 25 in *C. braueri* despite the difficulties of analysing stomach contents of deep-sea fish. Similarly, a diet study of *Macrourus holotrachys* and *M. carinatus* in the Southwest Atlantic (Laptikhovsky, 2005) identified 30 and 49 prey species respectively among only about 150 individual food items. More specialised macrourid predators do exist, however. *Mesovagus antipodum* stomachs were found to contain only penaeid and carid prawns, cephalopods, and teleosts (Anderson, 2005), with no more than ten prey species identified. These species were all bentho- and mesopelagic, with no benthic epi- or infauna found, although the total number of stomachs examined was low.

Several studies have examined the importance of carrion in the diet of macrourids. Stein (1985) analysed pelagic prey in *Coryphaenoides armatus* stomachs, and found beaks from cephalopods which would have been too large for the macrourids to consume alive. This suggests carrion-feeding on animals that have sunk to the benthos, rather than pelagic predation by *C. armatus.* Baited camera observations on a continental slope in the North Atlantic (Mahaut *et al.*, 1990) have shown macrourids to be the first group of fishes to arrive at a large carcass; although they were not observed feeding and were eventually displaced by the arrival of sharks. A later baited camera study in the North Pacific captured four macrourid species feeding on carrion, all with short arrival times

(Yeh & Drazen, 2011). Drazen *et al.* (2008), through examination of stomach contents and stable isotope analysis, found carrion to be an important dietary component in North Pacific abyssal *Coryphaenoides armatus* (though not in the smaller *C. yaquinae*) larger than 20 cm, comprising nearly 70% of the diet by mass, and 33% of the index of relative importance (%IRI). Similar trends were observed in an earlier study of *C. acrolepis* (Drazen *et al.*, 2001). Smaller specimens of both species did not exploit carrion to nearly the same extent, likely due to an inability to consume large quantities of flesh (Drazen *et al.*, 2001; 2008). While macrourids appear to have a keen sense of chemoreception, allowing them to quickly locate sunken carrion, their ability to exploit these food sources is likely affected by both size and depth, with larger specimens in deeper waters being more likely to feed on carrion (Yeh & Drazen, 2011). It is evident that macrourids as a family show considerable variation in trophic level, dietary niche breadth, and foraging methods.

1.6.2 Variability in diet

The types of prey taken by macrourids, and by extension their foraging methods, have been shown to differ between juveniles and adults in several species (Mauchline & Gordon, 1984; Drazen *et al.*, 2001; 2008; Anderson, 2005). Whereas juveniles of *C. simorhynchus* may feed exclusively on benthic fauna, adults consume most prey taken by juveniles in addition to larger benthic epifauna as well as cephalopods and teleosts from the water column. A similar trend of increasing dietary diversity with size was shown for *C. braueri*, while *C. striaturus* showed not only an expansion of prey categories with age, but a significant turnover as penaeid prawns, teleosts, and cephalopods replaced gammarids, tanaids and euphausiids as the most important prey categories in adults (Anderson, 2005). This trend of ontogenetic changes in diet could be explained both by an increased ability to take larger prey as the fish grows and a shift towards occupying greater depths observer in larger specimens of some macrourid species (Stein & Pearcy, 1982; Devine & Haedrich, 2008).

Additionally, there was significant variation in the prey species listed in Anderson (2005) and comparable diet studies focusing on the same species in different geographic areas. Not only did the prey species composition change by location, but entire higher order taxa varied in their dominance as prey items – Anderson (2005) found mysids, ophiuroids, and anomurans only in small quantities in *Coelorinchus simorhynchus* stomachs, whereas these were all identified as important prey taxa for the species in an earlier study (Meyer & Smale, 1991). Changes in diet across different locations were also observed for *Coryphaenoides mediterraneus* and *C. guentheri* in the Atlantic and Mediterranean (Carrassón & Matallanas, 2002). This dietary plasticity within species supports the idea of macrourids as generalist feeders, which can adjust their diet based on availability of prey organisms within their habitat. Some macrourid diets vary seasonally as grenadiers may adjust their feeding strategy based on temporal fluctuations in the abundance of certain prey species (Carrassón & Matallanas, 2002; Mauchline & Gordon, 1984; Laptikhovsky, 2005).

1.6.3 Niche segregation

In light of their generalised diets, it is thought that depth, and to a lesser extent prey size, plays an important role in niche segregation among co-occurring species of grenadiers (Laptikhovsky, 2005), with specimens of some species changing their depth distribution as they age and grow (Carrassón & Matallanas, 2002; Lin *et al.*, 2012, Massuti *et al.*, 1995). This "bigger-deeper" trend observed, for example, in Mediterranean species *Coelorinchus coelorinchus*, *Hymenocephalus italicus*, *Nezumia aequalis*, *Trachyrinchus trachyrinchus* and *Trachyrinchus scabrus* (Fernandez-Arcaya *et al.* 2012; Massuti *et al.*, 1995), or *Coryphaenoides rupetris* off Newfoundland (Snelgrove & Haedrich, 1985), is not universally supported, with various studies failing to find evidence for such a trend (Lee *et al*., 2008; Snelgrove & Haedrich, 1985; Stein & Pearcy, 1982). Additionally, the dietary plasticity of macrourids allows the less competitive species to adjust their diet in cases of interspecific food competition (Lee *et al*., 2008). A study of stomach contents of *Macrourus carinatus* and *Macrourus holotrachys* showed the two species to be segregated by depth, albeit with some overlap, and to occupy different feeding niches even when comparing similarly sized specimens within the same depth range. *M. carinatus* demonstrated an ontogenetic niche shift, with larger specimens taking additional prey (fish and cephalopods) not captured by smaller conspecifics, despite the large dietary niche overlap (Laptikhovsky, 2005). Environmental factors such as temperature and dissolved oxygen have also been shown to be important in determining niche in certain species, potentially even more so than diet or size (Cruz-Acevedo & Aguirre-Villaseñor, 2020).

1.6.4 The role of macrourids as prey species

Although a number of studies have analysed the diet of various macrourid species, almost no data exists on the role of grenadiers as prey. Orlov *et al.* (2012) reported significant complete or partial losses of *Albatrossia pectoralis* caught in traps in an experimental Bering Sea fishery due to scavenging by amphipods. Although the usage of traps creates an artificial situation, this shows that scavengers will consume macrourid carcasses if the opportunity arises. It seems likely, given their relatively high trophic level (Chuchukalo & Napazakov, 2012; Devine *et al.*, 2012) and widespread presence in deep-sea ecosystems, that some macrourids are an important food source for scavengers, thereby playing a role in deep-sea ecological energy transfer (Pearcy and Ambler, 1974). They are also taken by predatory fish, including other macrourids. Stevens (2012) reported *Bathygadus cottoides* and *Trachyrinchus longirostris* as prey species of *Coryphaenoides mcmillani* and *C. murrayi* respectively, although comprising less than 2% of the %IRI in either case. Similarly, Anderson (2005) found "Unidentified Macrouridae" in stomachs of *C. striaturus*, comprising less than 4% of the %IRI. This may constitute a regional difference in diet, as Stevens (2012) found no macrourids in their *C. striaturus*.

Macrourids in South Africa, including *C. braueri*, *C. simorhynchus,* and *M. laevis* have been found in the diet of hakes *Merluccius capensis* and *M. paradoxus* (Punt and Leslie, 1995; Roel and Macpherson, 1988), in which they occurred in similar numbers to myctophids in larger hake, but were sparse or absent in the diet of small hake. Punt *et al*. (1992) shared this finding, and explicitly name *C. simorhynchus* (recorded as *C. fasciatus*) from the diets of both hake species in South African waters. Three species are also reported (Macpherson, 1983) from South African kingklip (*Genypterus capensis*), namely *C. simorhynchus* (as *C. fasciatus*), *Trachyrhinchus trachyrhinchus*, and *Nezumia aequalis*, although only in larger specimens and never exceeding 4% of the diet by mass. Beukes (2020), on the other hand, found *C. braueri* and *C. simorhynchus* to be important prey of kingklip, and *M. laevis* to be important prey of the commercially fished monkfish *Lophius vomerinus*.

1.6.5 Larval development and reproductive characteristics

The early life stages of macrourids are not well-studied as they are rarely encountered and difficult to identify, although the planktonic eggs and larvae of several species have been described (e.g. Fukui *et al.*, 2008; 2010). Larvae generally resemble adults with the exception of stalked, discoid pectoral fins (Endo *et al.*, 2010). According to a hypothesis proposed by Marshall (1965), grenadiers spawn benthically, and their buoyant eggs rise into the epi- or mesopelagic zones close to the thermocline, where the warmer sunlit waters are relatively abundant in plankton (Lin *et al.*, 2012).

This interpretation was challenged due to the apparent scarcity of pelagic macrourid larvae despite the abundance of macrourids, and the subsequent discovery that the eggs of most species of macrourids, especially those with deeper adult distributions, had raised "ornamentation" on the egg envelope. This feature has been hypothesised to inhibit movement through the water column to keep larvae at depth (Merrett 1978; Merrett & Barnes, 1996). However, the life cycle originally proposed by Marshall (1965) has since found support in a number of planktonic surveys which have found grenadier larvae and eggs in the pelagic environment. A mesopelagic *Coryphaenoides* *pectoralis* larva was described by Endo *et al.* (2010) from the North Pacific off Japan, and pelagic eggs and larvae of *Coelorinchus kishinouyei* from the same area (Fukui *et al*., 2010) all showed the hexagonal ornamentation of the chorion typical of grenadiers.

Larvae are hypothesised to develop into juveniles either during or immediately after their descent to the bottom, which may be followed by a further downward migration of the juveniles in some species. Isotopic analyses of $\delta^{18}O$ values in otoliths have suggested that in some — but not all — macrourid species, larvae settle at shallower depths than those occupied by adults (Gerringer *et al*., 2018). The length of the pelagic larval stage may be linked to the extent of ontogenetic migration, with deeper-dwelling adults having a longer larval development and higher larval metabolic rate compared to their adult stage, shown by a study based on ^{18}O stable isotope content in otoliths (Lin *et al.*, 2012).

The reproductive characteristics of different species of grenadiers appears to differ greatly, making generalisations difficult. The spawning season of *Trachyrinchus scabrus* in the Mediterranean begins in autumn and lasts into winter (Fernandez-Arcaya *et al.*, 2012), whereas that of *Macrourus berglax* can last from winter to spring (Geistdoerfer, 1979) or spring to summer (Savvatimsky, 1984), depending on their spawning location in the North Atlantic. Spawning season can also be far more protracted, as in *Coryphaenoides rupestris*, which begins spawning as early as July (Kelly *et al.*, 1996), and lasts until winter. Spawning can last throughout the year as in Mediterranean *Nezumia aequalis*, albeit usually with a peak during a certain season. The timing of this peak may vary by location within a species; Mediterranean *N. aequalis* reach peak reproductive output in winter, whereas those of the Northeast Atlantic do so in spring and summer (Fernandez-Arcaya *et al.*, 2013). Although unconfirmed, there is evidence to support the idea that some species, including *Coryphaenoides acrolepis*, may have two spawning periods within a year (Drazen, 2002; Stein & Pearcy, 1982). Similarly, while most species are iteroparous, Drazen (2002) suggests that *Coryphaenoides filifer* may be semelparous based on its relatively high reproductive investment.

Ovarian organisation can be synchronous (e.g. *Trachyrinchus scabrus* as per Fernandez-Arcaya *et al.*, 2012), group-synchronous (e.g. *Macrourus berglax* as per Murua *et al*., 2000) or asynchronous (e.g. *Hymenocephalus italicus* as per D'onghia *et al.*, 1999). Merrett (1987) posited that, at least in the Northwest Atlantic, ovarian developmental organisation is strongly correlated with latitude and therefore seasonality of the environment. The oligotrophic and less variable systems at lower latitudes were thought to benefit asynchronous continuous development, whereas eutrophic seasonal environments of higher latitudes are inhabited by macrourids with distinct spawning seasons. However, even between two species inhabiting similar depth ranges within the

Mediterranean, *T. scabrus* and *Nezumia aequalis*, ovarian organisation varies. The former is a synchronous batch spawner while the latter is asynchronous (Fernandez-Arcaya *et al.*, 2012; 2013).

Sex ratios in macrourids tend to vary with size within a species, with females comprising a greater proportion of the largest size classes (Massutí *et al.*, 1995). There is also evidence that some species show depth-based segregation by sex even among similarly sized specimens of the same species (e.g. *Albatrossia pectoralis* as per Datsky, 2017), which naturally affects the sex ratio of fishes caught in that depth range. Many species show a roughly 1:1 overall ratio (Fernandez-Arcaya *et al.*, 2012; 2013), although in some species females dominate (Fernandez-Arcaya *et al.*, 2013; Stein & Pearcy, 1982).

Fecundity varies greatly between species. Stein and Pearcy (1982) report an average fecundity of 2.5 million eggs for *Coryphaenoides armatus* but only 26 000 and 70 000 for congeners *C. acrolepis* and *C. filifer*. Most species exhibit fecundity ranges in the 10 000 to 100 000 spread, for example *C. rupestris* (11 000 - 55 000 per Kelly *et al.*, 1996), *M. berglax* (14 000 – 79 000 per Murua *et al*., 2000), or *M. whitsoni* (7 000 – 76 000 per Prut'ko, 2012). Fecundity is generally believed to scale with fish size (Fernandez-Arcaya *et al.*, 2013; Murua *et al*., 2000; Stein & Pearcy, 1982), although this relationship is often weak due to high variability in fecundity (Alekseyev *et al.*, 1992; Kelly *et al.*, 1996). While such a relationship has sometimes failed to be detected (Fernandez-Arcaya *et al.*, 2012), it has been suggested that variation in environmental factors such as food supply, or the inclusion of partially spent batch-spawners in fecundity analysis may be responsible. As with distribution, depth range, and diet, the reproductive characteristics of macrourids are variable between and even within species.

1.6.6. Parasites of Macrouridae

Studies of deep-sea parasitism remain challenging due to the difficulty of sampling, particularly without dislodging ectoparasites from their hosts (Quattrini & Demopoulos, 2016). Consequently, the parasite communities of only a fraction of described deepwater fish have been investigated (Klimpel *et al.*, 2006).

Host specificity can be high for some taxa and regions (e.g. monogeneans and digeneans in New York Bight (Campell, 1990)), but is generally considered to be low compared to shallower-living parasites. This is likely due to the difficulty of encountering hosts, which occur in lesser density with increasing depth (Boxshall, 1998). Endoparasitic helminths, especially nematodes, are the most abundant parasites in deepwater fishes (Campbell, 1990) In deep-sea fishes, metazoan parasites are more common in species that migrate vertically than in those that remain permanently near the bottom, due in part to the spread of parasitic larvae from their mid-water prey species (Campbell, 1990). However, parasitic copepods are more common among demersal and shallow-water species that mesopelagic ones (Boxshall, 1998).

Although sources conflict on the prevalence of parasites in the deep sea, it is thought that many macrourid species host a high diversity of parasites, with more than 30 species reported from some (Chai, 2022; Ñacari & Oliva, 2016). Parasitological studies play an important role in delineating phylogenies (Chai, 2022) and improving the understanding of deep-sea ecosystems, as parasite communities are influenced by host ecology and evolutionary history (Ñacari & Oliva, 2016). Diet, depth, bathymetric environmental features such as canyons, and host density influence parasite load and infection frequency in macrourids (Campbell, 1990; Quattrini & Demopoulos, 2016).

1.7 Extent of literature on the Macrouridae in South Africa

Despite the lack of scientific focus on macrourids, a number of authors have written on South African and southern African species. The seminal paper on this topic is Iwamoto & Anderson's (1994) monograph on Southern African grenadier species, giving descriptions, distributions, and keys to the species in the region. Meyer and Smale (1991) included two grenadiers in a diet analysis of demersal predatory fish on the south and west coasts. Anderson (2005) also described the diet and feeding strategies of ten South African species of grenadiers, as well as providing some anatomical descriptions and measurements for *Hymenocephalus italicus* in Anderson (1996). Macrouridae also appear incidentally in other studies, including as part of fish community studies (Roel, 1987; Fennessy, 2016), as hosts of the parasitic copepods such as *Sphyrion spp.* (Dippenaar & Sebone; 2022; 2023), and in a number of diet studies of other fish (e.g. Macpherson, 1983).

1.8 Extent of literature on *C. braueri*, *C. simorhynchus*, and *M. laevis*

Macpherson (1985) investigated daily food intake and feeding periodicity in Namibian *C. simorhynchus* (as *C. fasciatus*). Sobrino *et al.* (2012) showed bathymetric and geographic distribution patterns for the three species, among others, on the African Atlantic coast. Lombarte & Morales-Nin (1995) described the ultrastructure of the sagittal otoliths of five Namibian species of *Coelorinchus*, including *C. simorhynchus* (as *C. fasciatus*) and *C. braueri*. More considerable research has been carried out on *Malacocephalus laevis* due to its global distribution and its value in producing fish meal and fish oil (Cohen *et al.*, 1990). This includes the weight-length relationship (Borges *et al.*, 2003; Torres *et al.*, 2012) and further diet studies (Mauchline and Gordon, 1984).

1.9 Aims and limitations of the present study

The aim of this work is to provide basic data on the distribution and life history of three understudied species of macrourids which have either never been investigated, or only investigated outside of South African waters. This includes distributions, morphometric data, length-weight regressions, maximum ages and von Bertalanffy regressions, diet, reproductive strategy and seasonality, and parasites. Aspects of their biology which have been studied before, such as diet, were compared to earlier findings to assess any across different regions, and to strengthen the assessments. The three different species were compared to test the validity of the perception that grenadiers may be treated collectively in ecosystem models and fisheries assessments.

The macrourids examined here were all captured by hake-directed demersal trawlers. Due to the realities of obtaining small, non-target specimens from heavily loaded nets (with bag sizes frequently exceeding five t), many of the fish examined were in poor condition. It was not possible to obtain samples of equal sizes for all three species, nor were they sampled with equal frequency at all depths on both coasts, or even across their entire depth distribution. As a result, the findings reported here should be interpreted in the context of the limitations of the study. The variability of life history characteristics in these species is likely to be greater than what was observed in the limited number of samples here. Observed life history characteristics can be assumed to apply to fish within the size, geographic and depth ranges sampled, but cannot be extrapolated outside of those ranges reliably.

2. Methods

2.1 Sampling

Grenadier samples were collected by fisheries observers of CapMarine (SA) stationed on trawl vessels which operate on the South African west coast shelf and on the Agulhas Bank off the south coast. Observers were asked to collect samples of *Coelorinchus braueri*, *Coelorinchus simorhynchus*, *Lucigadus ori*, and *Malacocephalus laevis*. These were identified prior to sampling as the most common grenadier species in the bycatch of the hake fishery (Cooper, personal communication 2022, February 07).

Sampling took place between March 2022 and May 2023, in latitudes between 30° 39.5' S and 36° 18.84' S, and longitudes between 15° 30.5' E and 25° 34.15' E, at depths of 244-622 m. During this time, 64 *C. braueri*, 318 *C. simorhynchus*, and 134 *M. laevis* were collected. After six months of sampling, it was decided to forego collecting *Lucigadus ori*, as only two specimens had been collected until then. The date, vessel name, trawl number, trawl depth, and start and end positions of the trawl were recorded where possible (some samples lacked the appropriate labels). *Figure 2.1.2* shows the location of all samples for which position data are available. Grenadiers were identified by observers using photographs of the target species, and species were confirmed in the laboratory using keys and descriptions in Iwamoto and Anderson (1994). Observer identification was very accurate, with all fish collected belonging to one of the four targeted species with the exception of a single notacanthid specimen (which may have simply been a mix-up during sample storage).

Figure 2.1.1: Typical specimens of (a) Coelorinchus braueri*, (b)* Coelorinchus simorhynchus*, and (c)* Malacocephalus laevis.

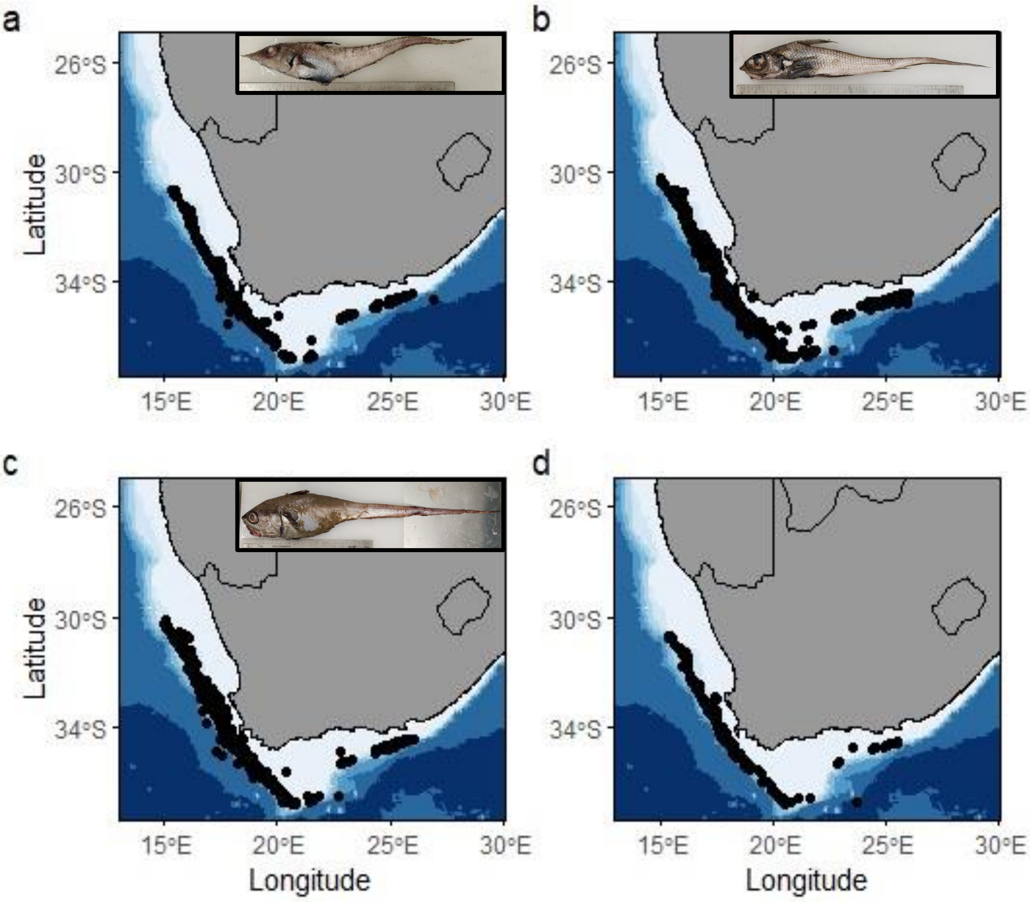

Figure 2.1.2: Bathymetric maps showing the locations of trawl samples containing (a) Coelorinchus braueri*, (b)* Coelorinchus simorhynchus*, (c)* Malacocephalus laevis and *(d) all three species combined.*

2.2 Measurements and dissections

The head length (HL), pre-anal fin length (PAFL) and total length (TL) were measured. These measurements are common among grenadier studies (e.g. Iwamoto & Anderson, 1994) and are used as per Iwamoto and Sazonov (1988), where they are defined as follows: HL – length from tip of snout to upper posterior angle of opercle; PAFL – length from tip of snout to origin of anal fin; TL – length from tip of snout to the most posterior point. Measurements of TL often did not represent the true total length of the fish, as the tails of grenadiers were frequently partially missing. While some tails may have lost *in situ*, it was assumed that most sustained this damage during capture, freezing, or storage, as this occurs commonly in macrourids (Middleton & Musick, 1986). In cases where parts of the tail were missing, this was recorded. Additionally, the relatively fragile facial bones that gave rise to the name *Coelorinchus* (Greek, "hollow snout") resulted in a few specimens having broken or missing snouts. This was most common in the long-snouted *C. braueri*. If the snout was merely broken, it was straightened into position prior to measurement of the lengths, but when it was completely absent, this was recorded, and these lengths were excluded from the analysis. Each fish was photographed prior to dissection. A selection of photographs of the three species may be found at https://drive.google.com/drive/folders/1MXS5BeuAKWBk_eLiV9QELmahsTuMAnVc?usp=sharing.

The two *Coelorinchus* species are easily differentiated from *M. laevis* by the presence of a pointed snout and hard ridges covered in coarse scales leading from the snout tip over the eyes to the angle of the opercle. The species *C. braueri* is distinguished from *C. simorhynchus* by its snout length, which constitutes 40 to 50% of the HL in *C. braueri* (23 to 29% in *C. simorhynchus*), and is greater than the orbit diameter in *C. braueri* but considerably less than the orbit diameter in *C. simorhynchus* (Iwamoto & Anderson, 1994). Generally, the species are simple to differentiate in the laboratory. The smallest species is *C. braueri* (*Figure 2.1.1a*) — although the largest specimens can overlap with small *C. simorhynchus* and *M. laevis* — and has a distinctive thin, shovel-shaped snout. Their eyes are smaller in proportion to their head compared to *C. simorhynchus*, and tend be angled slightly upwards. In comparison, the eyes of *C. simorhynchus* (*Figure 2.1.1b*) are oriented completely laterally. The jaw is visible from a lateral perspective even when the mouth is closed, unlike in *C. braueri*. This species also tends to be slightly darker and have a less well-developed anal fin than *C. braueri*. By far the largest of the three species is *M. laevis*. These fish are characterised by their minute scales, blunt snout, large jaw, and greater proportion of body mass in the trunk and head compared to the *Coelorinchus* species (*Figure 2.1.1c*). Their skin is toned uniformly grey, as opposed to the white and blue scales of *Coelorinchus*, and frequently covered in a dark green or grey algal growths.

Fish were drained of residual water from the thawing process, photographed, weighed to the nearest 0.1 g, and inspected for external parasites. For this inspection, the fish were briefly examined from all angles; followed by a thorough check under the pelvic and pectoral fins, along the bases of the dorsal and anal fins, inside the buccal cavity, between the gills, and in the skin folds around the jaw. Wounds or marks that were likely to be the result of previous parasite attachment were also noted. Parasites were counted and representatives of each species were preserved in a 99% ethanol solution.

Fish were dissected via ventral incision. The liver was removed and, when possible, weighed to the nearest 0.1 g for the calculation of hepatosomatic index (HSI), a measure of stored energy potentially linked to reproductive effort. In a number of specimens, the liver had partially or entirely liquefied. It is not known whether this was due to the barotrauma experienced during capture, pressure exerted on them within the net, overheating during sampling or storage, or as a consequence of freezing and thawing. In the case of fish with damaged livers, liver mass was not recorded, and as much of the liver as possible was removed by dabbing away liquefied tissue using paper towels.

The stomach was removed via incisions at the posterior end of the oesophagus and the pylorus, weighed, and preserved in a 99% ethanol solution for dissection. In a large number of fish of all three species, stomachs were everted due to the expansion of the gas bladders during capture. While in some specimens this presented as a fully everted stomach inside the buccal cavity (*Figure 2.2c*), partial eversion where the stomach remained in the abdominal cavity but was folded in on itself also occurred. In the case of either full or partial eversion, the stomachs were removed but not weighed or preserved. Any prey items or other objects in the buccal cavity or oesophagus were removed but not preserved, as these could represent net-feeding during capture. Gutted mass was calculated by subtracting stomach mass from total mass.

Figure 2.2: Grenadiers showing symptoms of catch damage and barotrauma, including (a) the loss of part of the tail, (b) the loss of the snout (compare with Fig. 2.1.1(b), and (c) stomach eversion.

Where possible, gonads were removed and weighed for the determination of gonadosomatic index (GSI). Fish were sexed based on the presence of ovaries or testes. Fish in which gonads were absent or too damaged to be accurately sexed were labelled as sexually indeterminate. In both sexes, some specimens had only one gonad (usually larger than each individual gonad in specimens with a regular gonad pair); this was recorded but such fish were not excluded from the analysis unless there was strong suspicion that the gonad had been lost due to damage. The phase of reproductive development was estimated based on the macroscopic appearance of the gonads, using the phases outlined in Brown-Peterson *et al.* (2011). The term *reproductive phase* is used here to refer exclusively to the macroscopic assessment of the developmental state of the gonad, while *reproductive stage* instead refers to the developmental state of gametes, as per Brown-Peterson et al. (2011).

Gonads were preserved in a 10% formalin solution. Not all fish had macroscopically identifiable gonads. In some specimens, particularly in small males, the gonads were too damaged to accurately determine their mass. In others, gonads were entirely absent or possibly completely destroyed prior to dissection, as was the case with the livers in some fish.

Fish were inspected for internal parasites in the abdominal cavity or on the exterior surfaces of the organs; when found, this was noted, and parasite specimens were preserved in 99% ethanol solution. However, due to the high numbers of very small parasites in some fish, no effort was made to quantify parasite load. Also, with the exception of the stomach, no organs were dissected specifically to find parasites, although incidental discoveries, such as parasites spilling out from the anterior end of the intestine after removal of the stomach, were noted.

Following the removal and measurement of the liver, stomach, and gonads, an incision was made into the dorsal surface of the buccal cavity to remove both sagittal otoliths, which were cleaned, dried, and stored in envelopes.

2.3 Aging

One otolith was selected randomly from each pair, except in cases in which one otolith was damaged or lost, in which case the undamaged otolith was selected. The position of the *sulcus acusticus* near the centre of the otolith was marked at the widest point on the otolith with a pencil. The otolith width (dorsoventral dimension), was measured to the nearest 0.01 mm using callipers. Otoliths were encased in Kristal 30 clear epoxy resin and set to cure for 48 hours. From each resin-encased otolith, a 2 mm thick transverse slice was cut using a dual-bladed saw, centred on the pencil marking. The resin slice thickness was set at 2 mm as attempts to use thinner slices resulted in shattered otoliths that were difficult to age, while thicker slices did not transmit sufficient light for counting bands.

Resin slices were mounted to a microscope slide using DPX mounting fluid, with an additional drop of DPX placed on top of the resin slice centred on the otolith to improve visibility. The addition of cover slips was initially attempted but later avoided when it was found to increase the likelihood of the otolith slice cracking.

Linear regressions of otolith width by PAFL were generated for each species to estimate nucleus width. The y-intercepts of these regressions were taken as estimates of otolith width at a PAFL of 8 mm. This value of 8 mm PAFL was used as an estimate of PAFL at the time of larval metamorphosis, based on measurements of the largest pelagic larval stage of Japanese *Coelorinchus kishinouyei*, one of the few macrourids for which larval length data have been published (Fukui *et al*., 2010). The estimates of nucleus width were used to help identify the extent of the nucleus within otoliths of each species. These estimates facilitated counting otolith annuli, as they provided an approximate guide to where the first annual bands began in otoliths (the first band was often difficult to discern from the dark nuclear core).

A subset of 25 otolith slices of each species was initially examined to count annuli by an observer with knowledge of both the PAFL of the fish and the otolith width. Only rings whose diameter exceeded the estimated nucleus width, and never intersected the nucleus at any point, were considered to be yearly annuli. After a period of at least 48 hours, the same otoliths were re-examined by the same observer in a random order without knowledge of PAFL or otolith width to ensure that consistent readings were possible. For *C. simorhynchus* and *M. laevis*, < 50% of readings coincided, and it was deemed that these species could not be consistently aged using otolith annuli according to this methodology.

In *C.baueri*, for which consistent aging was possible, all otoliths were examined by two observers independently and without knowledge of length or otolith width. If counts agreed exactly, the reading was recorded as the age of the fish. If readings disagreed, both observers re-examined the otolith and discussed until a consensus was reached, at which point it was recorded as the age. In cases in which no consensus was able to be reached, a third observer was called on to resolve this disagreement. If no consensus was able to be reached between any two of the three observers, or if one observer felt strongly that the otolith was not accurately readable, it was excluded from the analysis.

The annulus count was incremented by one for every opaque band, starting with the first opaque band beyond, but not touching, the nucleus of the otolith. In all three species, the problem of grouping bands arose, as there often appeared to be several thinner opaque and translucent bands within a broad opaque band. After examining a substantial number of otoliths, and with consideration of the initial readings with knowledge of length and otolith width, both observers agreed that generally the first two to three opaque bands were very broad (and should be read as single bands even when there appeared to be thin opaque sub-bands within them), followed by a sharp decrease in the thickness and contrast of opaque bands. The third band situated dorsally of the *sulcus acusticus* in *Figure 2.3b* is an example of sub-bands that were grouped due to clear confluence farther along the dorso-ventral axis.

The clearest area in which to read bands depended on the otolith. It was seen as preferable to count bands on either the dorsal or ventral side of the medial surface immediately adjacent to the *sulcus acusticus*, which follows Morales-Nin and Panfili (2005) who suggested that otolith growth in deep-sea fish occurs primarily along this surface. When these areas were obscured, it was sometimes possible to count bands directly on the sulcus acusticus, or along the medio-lateral axis, although this latter method proved to be very subjective as it always required some grouping of sub-bands. Counting rings on the lateral side of the nucleus was possible in a few cases, but was found to be unreliable, often failing to detect fainter outer rings beyond the fifth or sixth opaque band. Annulus counts were based on opaque bands — in cases where the outermost band was translucent, the estimated age was rounded down. Without prior knowledge of a define spawning season, it was decided not to use half-year estimates, given that there was no guarantee of all specimens hatching in the same season. Ideally, each observer counted rings in multiple areas and reached consensus between readings. If this was not possible due to differing band counts, the area with the clearest bands, or in the case of two equally clear areas, the lower count, was chosen. *Figure 2.3* shows micrographs of transverse sections through otoliths of all three species.

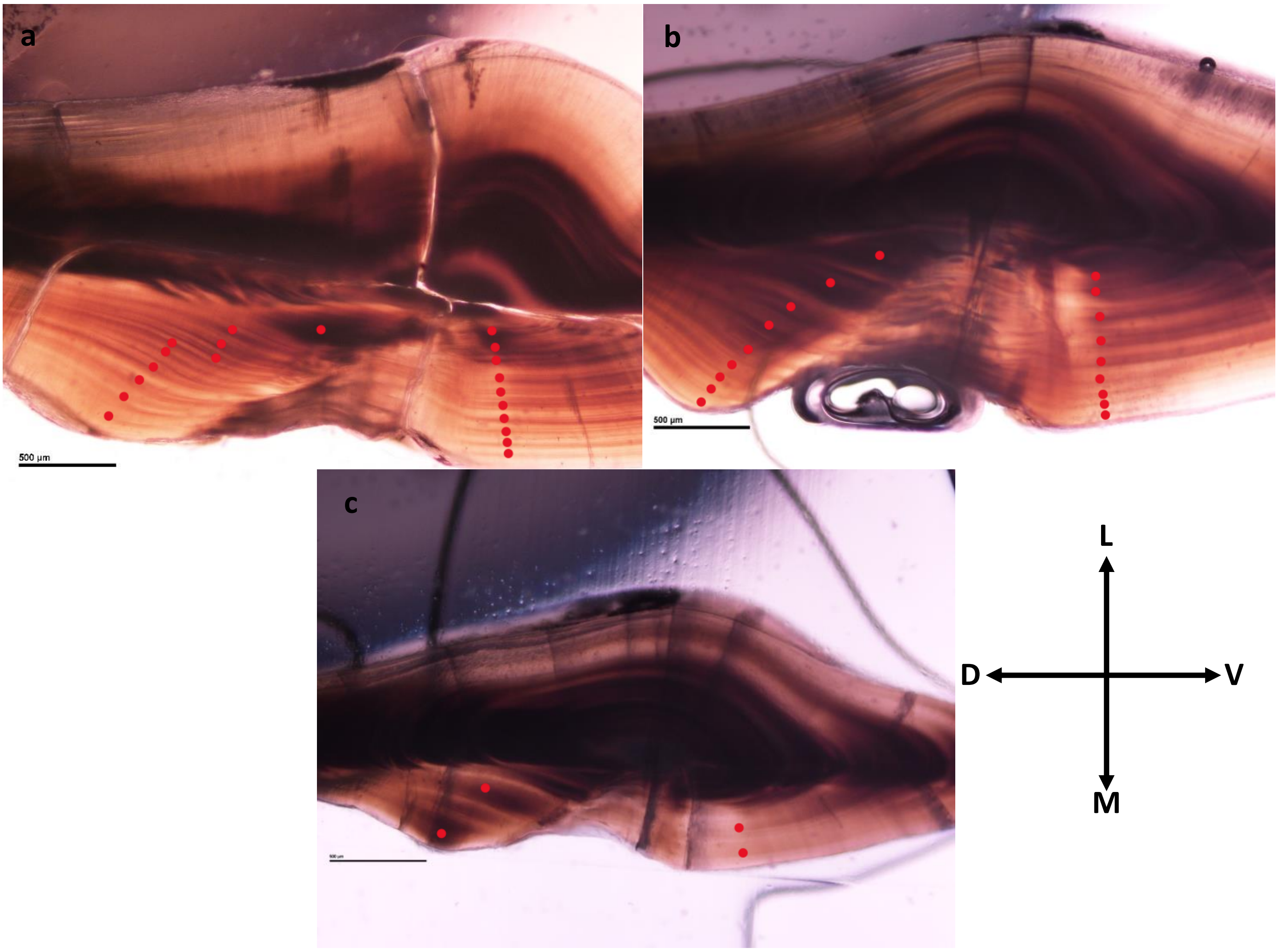

Figure 2.3: Otolith sections of (a) 10-year-old Coelorinchus braueri*, (b) 9-year-old* Coelorinchus simorhynchus*, (c) A 2-year-old* Malacocephalus laevis*. All scale bars = 500 µm. Arrows indicate alignment of section dimensions on otolith. D: Dorsal side, V: Ventral side, L: Lateral side, M: Medial side*

2.4 Stomach dissections

Stomachs were dabbed clean of ethanol and cut open between the oesophageal and pyloric openings, and any prey items were removed. For stomachs taken from *M. laevis*, this involved scraping the internal folds of the stomach, which were frequently filled with a thin lining of partially digested prey. The stomach interiors of both *Coelorinchus* species, by comparison, were smooth and had no such lining.

Empty stomachs were weighed to determine the total mass of stomach contents by subtracting the empty stomach mass from the mass of the full stomach. Prey items were categorised, identified to the lowest taxonomic level reliably possible, and each group of prey items was counted and weighed. Identification of prey items was aided by the following works: *Field Guide to the Offshore Marine Invertebrates of South Africa* (Atkinson & Sink; 2018), *Two Oceans: A guide to the marine life of southern Africa (Fourth Edition)* (Branch *et al.*, 2016), *Shrimps and Prawns of Southern Africa* (Kensley, 1972), *Guide to the Marine Isopods of Southern Africa* (Kensley, 1978). In the case of teleost fish remains with intact heads, sagittal otoliths were extracted where possible and identified using the *Otolith Atlas of Southern African Marine Fishes* (Smale *et al.*, 1995) in conjunction with *Smith's Sea Fishes* (Smith & Heemstra, 1986). Cephalopod beaks were identified, where possible, using a combination of *A Handbook for the Identification of Cephalopod Beaks* (Clarke, 1986) and *Cephalopod beak guide for the Southern Ocean* (Xavier & Cherel, 2009).

In rare cases (accounting for <1% of all stomachs) in which stomach contents were comprised of more than ca. 100 individual prey items of the same type (e.g. amphipods), counts were estimated from subsamples as per Gelwick and McIntyre (2017). To achieve this, the prey items were evenly distributed in a petri dish, and specimens in a quarter subsection of the dish were counted, from which the total number was then estimated. In the case of identifications based only on small parts (vertebrae, eyeballs, otoliths, claws, *etc*.) counts were made as conservatively as possible by grouping prey fragments which could conceivably have originated from the same specimens as per Pinkas *et al.* (1970). For example, if a stomach contained 31 crustacean eyeballs, it was assumed that 16 crustaceans were ingested. In cases in which multiple structures of the same prey type were present, it was assumed that they originated from the same individual (e.g. teleost vertebrae and two otoliths found in the same stomach were assumed to originate from the same fish) unless it was obvious that multiple specimens must have been present (e.g. ophiuroid remains with multiple disks).

Stomachs which were empty or in which contents consisted entirely of a digested slurry were considered non-informative and excluded from diet analysis. Each prey item type in a stomach was graded on a scale of digestion level ranging from 1 to 3. This scale, in which 1 represents prey items that were barely digested and 3 represents prey that was extremely digested, is largely subjective and intended only to give an overview of the average condition of prey, rather than a testable metric. Generally, prey items scored a 1 if they were largely intact, with no limbs or other major structures missing, 2 if they were damaged but still easily identifiable to order or family level, and 3 they were extremely damaged (e.g. crustaceans missing heads or shell plates) or if only a minor part of the entire organism was present (e.g. teleost eyeballs, crustacean antenna segments, or polychaete chaetae).

2.5 Preparation of gonads

Where possible, from the preserved gonads of *C. simorhynchus* and *M. laevis* three samples of each phase of reproductive development per sex were used to prepare tissue sections for histological staging and observation. No phase 5 testes were identified in *C. simorhynchus*, and there were only two phase 1 testes in *M. laevis*, resulting in a total of 57 tissue sections. No sections were prepared for *C. braueri* due to the high number of indeterminate specimens and low overall sample size.

To this end, a transverse section approximately 3-4 mm in width was taken from the centre of each gonad and dehydrated, then embedded in paraffin wax. A dehydration protocol developed specifically for fish tissues (Yalsui *et al*., 2021) was used with a Leica TP 1020 Processor. To start, samples were heated in 70% ethanol for one hour, followed by two cycles in 96% ethanol for one hour each. This was followed by four more hour-long cycles in 100% ethanol, then two one-hour cycles in xylol. Finally, wax was applied, and any remaining moisture was removed by heating for two cycles of two hours each at 55-60°C. The wax-encased gonads were then sectioned on a microtome to a width of 5 µm and placed on a specimen slide.

Tissue samples were rehydrated and stained with Mayer's Haemalum solution, a haematoxylin/eosin-based stain, then mounted to the slide with Entellan mounting medium. The staining procedure was as follows, as per Culling (1974):

To start, the slide was immersed three times consecutively for one minute each in xylol. This was followed by three one-minute immersions in 100% ethanol, then two one-minute immersions in 96% ethanol, and one minute in 70% ethanol. Next, a one-minute water bath at room temperature; then nine minutes in haematoxylin followed by a rinse under running water. This was followed by three minutes each in Scott's water, water, and 1% eosin solution. Finally, the slide was rinsed in alcohol and glycol.

2.6 Analyses

Statistical tests were carried out in R, using functions from the car (Fox & Weisberg, 2019), tidyverse (Wickham *et al*., 2019), and dunn.test (Dinno, 2017) packages, in addition to those present in Core R (R Core Team, 2023). Data visualisation was primarily done using ggplot2 (Wickham, 2016), but also required functions from PieGlyph (Wishvakarma *et al*., 2023). The package ggOceanMaps (Vihtakari, 2023) was used to create all bathymetric maps in this study. Several variables were found to not follow a normal distribution during analysis. In cases in which non-parametric tests were used, medians are reported in place of means.

2.6.1 Distribution

A large dataset of trawl observations from the South African trawl fishery on the west and south coasts between July 2002 and July 2011 was provided by CapMarine (SA), a Cape Town-based company specialising in marine and fisheries observing (CapMarine, 2023). This dataset contained location and depth data for trawls, along with trawl species compositions and records of abundances and biomass of different species in a sample of the trawl (typically 3-10% of the total haul) counted and measured by a trawl observer. The data were used to illustrate the relative distribution of the three species of grenadiers, as well as compare their abundance and biomass between coasts and depth intervals.

The following adjustments to the dataset were made: Average depth was calculated as the mean of the starting and ending trawl depths (in cases in which these were not equal, they typically differed by only a few metres) and assigned to a 100 m depth interval. Each trawl was assigned a single coordinate position calculated as the midpoint of its start and end positions, which in turn was used to assign a trawl to either the west or south coast, depending on whether the midpoint lay west or east of the 20th meridian respectively. The 20th meridian was used as it is the longitude of Cape Agulhas, a landmass traditionally taken as the division between the Atlantic and Indian Oceans (“Agulhas, Cape”, 2024). Whereas the continental shelf on the west coast is relatively narrow, on the south coast it extends considerably southwards to form the Agulhas Bank. The Agulhas Bank is considered part of the south coast for the purpose of analyses.

The total mass of all species in each trawl sample was summed to derive the mass of the sample, and this was divided by the total trawl haul mass to obtain the sample fraction. The inverse of this fraction was then used to estimate an estimate of trawl abundance and trawl biomass by multiplying it by the recorded abundance and biomass of the different grenadier species in the trawl sample, respectively.

The trawl distances were calculated based on the trawl start and end coordinates using the Haversine formula for great circle distance (Yunardi *et al.*, 2024) and an assumed radius of the Earth of 6371 km. Together with an estimated horizontal net opening of 60 m, this allowed for calculation of swept area (trawl distance * horizontal net opening), which was used to normalise the estimated abundances and biomasses to a swept area of 1000 m^2.

Potentially inaccurate data were filtered from the dataset, including trawls from depths of less than 50 m, trawls in which the average fish mass was less than the lowest measured mass of that species in this study, trawls in which the sample fraction was less than 1% or greater than 100%, and those in which the trawl distance was less than 1 km or exceeded 60 km. As these observations stem from the open trawl fishery, it is possible that some fish may have been captured in shallower waters than the intended trawl depth when the net was pulled up. However, these are not likely to represent a considerable fraction of total samples, and their influence on the analyses should be rendered negligible by the large sample size.

The relative normalised abundance of each grenadier as a fraction of all three species was calculated and used to produce a distribution map, where each grid square of one degree latitude by one degree longitude holds a pie chart of the relative abundance by species. The same was done for relative normalised biomass. Due to the strong deviation from the normal distribution, comparisons by depth interval of normalised abundance and biomass were carried out using non-parametric Kruskal-Wallis tests, with Dunn's test used for the post-hoc comparisons. For comparisons by coast, the similarly non-parametric Wilcoxon Rank-sum test was used.

The normalised abundance and biomass are estimates based on a fisheries observer dataset and therefore reflect to a large extent the spatial bias of the fishery. Therefore, these data represent the abundance and biomass of grenadiers caught by trawl fishery vessels, without accounting for factors such as a differential ability of grenadier species to escape the net due to differing swimming speeds, reaction time, response to threats, *etc*. The estimates in normalised abundance and biomass are used here only for comparisons between species, depth intervals, and coastlines.

2.6.2 Morphometrics

For each species, linear models of TL against PAFL and TL against HL were generated. These models were based on only those specimens which did not exhibit broken tails, as this would decrease measured TL below the true total length, nor snouts, as this would decrease PAFL, HL, and TL. TL was then estimated in specimens with broken tails based on the model parameters. Specimens with broken snouts were excluded entirely from the morphometric analyses, while in specimens with unbroken tails and snouts, the measured TL was used. The TL estimations for each species were compared via two-sided paired Wilcoxon signed-rank tests. The Wilcoxon test was used in lieu of a paired t-test due to strong deviations from normality in the difference of the estimated TL using both methods.

For all statistical analyses relating to length, PAFL was used, as this did not require estimation and was found to correlate better with TL. Kruskal-Wallis tests were used to detect significant differences in PAFL between the different sex categories (female, male, indeterminate). These tests were utilised in preference to two-sided ANOVAs due to significant deviations from normality in the PAFL lengths of *C. simorhynchus* and *M. laevis*, and non-homogeneity of variance in all three species. Post-hoc tests to identify which sex categories differed significantly in their median PAFL were administered via pairwise two-sided Wilcoxon signed-rank tests with Holm's method of p-adjustment.

For the purpose of checking for differences in body length with depth, the trawl depths were split into 50m depth intervals, beginning at 200 to 250m and ending at 600 to 650m. As with the distribution data, non-parametric Kruskal-Wallis and Dunn's post-hoc tests were employed due to deviations from the normal distribution and non-homoscedasticity of the data. Linear models of PAFL by depth were also employed to check for the presence of "bigger-deeper" (or conversely, "smaller-deeper") trends common to some species of grenadiers.

2.6.3 Biometrics and growth

The length-weight relationship was assumed to follow the curve $W = aL^b$, where W is the total mass, L is a measure of length, and a and b are constants. To analyse the length-weight relationship, linear regressions of the natural logarithm of the total mass were plotted against the natural logarithm of the PAFL, and the significance of the relationship and its parameters was assessed. The slope coefficient of this relationship was taken as an estimate of b, while the intercept was back-transformed ($a = e^{\log(\text{intercept})}$) to derive an estimate of a.

Furthermore, the growth type was assessed based on the estimate of b. For $b \approx 3$ (specifically, if the estimate of b lay within ±1.96 SE of 3), growth was considered isometric. When the estimate deviated from a value of 3, growth was considered allometric (i.e. $b < 3$ represents hypoallometric and $b > 3$ represents hyperallometric growth).

While the large dataset used in the analysis of distribution did not contain direct information on fish lengths nor masses, it did feature the number of fish in the sample and their total mass, which was used to generate an estimate of average mass of fish in that sample. This average mass was used to check for linear trends with depth, as well as for 100 m interval comparisons using Kruskall-Wallis and Dunn's post hoc tests.

Maturity ogives were calculated using the gonad_mature() function of the R package sizeMat (Torrejon-Magallanes, 2020), based on PAFL and the macroscopic maturity assessments. Fish in reproductive phase 1 were considered immature as per Brown-Peterson *et al*. (2011). Separate curves were produced for females and males.

2.6.4 Von Bertalanffy growth models

Following the determination of age estimates of the fish based on otolith annuli, von Bertalanffy regressions were fitted to the plots of age by PAFL for *C. braueri*. No consistent method of counting otolith annuli was developed for *C. simorhynchus* and *M. laevis*, precluding the fitting of von Bertalanffy regressions. Based on the results of Kruskal-Wallis tests and subsequent Wilcoxon tests for differences in PAFL among females and males, it was deemed appropriate to produce separate regressions for each sex. However, given the low number of *C. braueri* in this study (n = 64), of which nearly a third were sexually indeterminate, a combined regression for females, males, and sexually indeterminate fish was fitted for *C. braueri*.

The von Bertalanffy equation in the form $L(t) = L_{inf} * (1 – e^{-k(t-t_0)})$ was fitted to the data, where L(t) is the PAFL at age t, L_{inf} is the asymptotic maximum PAFL, k is the growth coefficient, and t_0 is the theoretical intercept (i.e. the age at which PAFL would equal zero). This equation was used to produce a set of predicted PAFL based on the estimated age of the fish in Microsoft Excel. The difference between predicted and observed PAFL for each individual was used to derive residuals for each fish, the sum of which was stored. The Excel add-in SOLVER was used to heuristically minimise this sum of squared residuals by systematically altering the von Bertalanffy parameters. The parameters were initialised as follows: L_{inf} was set to the value of the largest observed PAFL, k was set to 0.2, and t_0 was set to zero. The standard SOLVER Large-Scale Generalised Reduced Gradient (LSGRG) non-linear model was applied with the constraints that neither L_{inf} nor k could be ≤ 0. The LSGRG model was chosen over the Simplex or Evolutionary models, as the former is appropriate only for modelling linear relationships (the von Bertalanffy relationship is non-linear), while the latter is designed for complex, discontinuous relationships, rendering it less efficient and accurate for continuous modelling. The LSGRG model was run several times while iterating the initial parameters within reasonable values, to ensure a consistent model answer. The Evolutionary model was also applied with the same parameters to ensure it produced the same result. The parameter values adjusted by the model were then produced, along with curves of estimated age based on otolith readings against observed PAFL.

An estimated age-length key for *C. braueri* was produced using the lencat() function in the FSA package (Ogle *et al*., 2023).

2.6.5 Diet

For each species, the percentage index of relative importance (IRI) was calculated based on stomachs which contained identifiable prey. Percentage IRI was calculated as %IRI = %F * (%N + %W), where %F is the percentage frequency of occurrence of a prey group, %N is the number of prey items in that group as a percentage of total prey items, and %W is the total mass of that prey group as a percentage of total prey mass across all groups. A mass-based approach was taken (using %W) rather than the volume-based approach (which replaces %W with %V) of Anderson (2005), as measuring volume accurately would have been substantially more difficult than measuring mass.

Identified prey were assigned to groups at the family level or higher. These prey groups were mostly taken from Anderson (2005), although a few that did not appear in that study were added. The following prey groups as per Anderson were recorded: Amphipoda (unidentified), Anomura, Brachyura, Caridea, Euphausiacea, Gammaridea, Gastropoda, Hyperiidea, Isopoda, Mysida, Ophiuroidea, Ostracoda, Penaeidea, Polychaeta, Stomatopoda, Tanaidacea, Teleostei, Cephalopoda. The following groups that were not present in Anderson (2005) were also recorded, although most of these constituted extremely minor elements of the diet: Anthozoa, Aristeidae, Caprellidae, Chondrichthyes, Flabellifera, Nematoda, and Porifera. Additionally, the Sergestidae were treated as a unique prey group rather than as penaeid prawns in Anderson (2005).

Anderson (2005) divided prey into major and minor groups, but no explanation of what constitutes either was offered (although it seems likely to be based on IRI). For this study, major prey groups are defined as those groups, in descending order of IRI, which collectively comprise ≥ 90% of the IRI. A number of prey groups were represented rarely and in extremely small amounts while also contributing little to mass, and may in some cases have been ingested incidentally while targeting other prey (e.g. fragments of sponges or corals). As a result, prey groups with an IRI less than 10 were listed but not considered in detail. In all three species of grenadiers, these negligible groups comprised less than 1% of the total IRI when summed. As a result, minor prey groups are defined as those which are not major (i.e. have IRI smaller than any of those which sum to 90% of the total IRI across all prey groups) but have an IRI exceeding 10.

2.6.6 Reproduction

Gonad tissue sections of *C. simorhynchus* and *M. laevis* were examined under a compound microscope and staged histologically according to the criteria of Brown-Peterson *et al.* (2011). The histological stages were compared to the macroscopic reproductive stages assigned during dissections. Due to poor agreement between macro- and microscopic assessments, all gonads were re-staged after histological examination. Initial staging of macroscopic reproductive phases had been carried out during dissection without any comparative material, whereas the macroscopic re-staging at this point was carried out with more experience of the study species and with the benefit of a range of gonad phases. Photomicrographs of each reproductive stage present in the tissue sections for both sexes in *C. simorhynchus* and *M. laevis* were taken at 100x and 400x magnification. The diameters of several cells of each stage of oocyte development were measured using an eyepiece graticule to give an approximate indication of their size ranges.

Fisher's exact tests were used to test for relationships between sex and depth; as none were found, no post-hoc tests were conducted. Sex ratios were calculated as the percentage of females relative to females and males combined, with sexually indeterminate fish excluded from the sex ratio calculation. Plots of sex ratio by depth interval and coast were generated, as well as by PAFL, split into intervals of 10 mm.

The gonado-somatic index (GSI) was determined as follows: GSI = $\frac{Gonad\ mass}{Total\ mass} * 100$. GSI was calculated using total mass rather than gutted mass as the former is more common in the literature (D'onghia, 1999; Prut'ko, 2012). Sex ratios were calculated as the percentage of female fish relative to all sexually determinate fish for each species. The hepato-somatic index (HSI) was also determined: HSI = $\frac{Liver\ mass}{Total\ mass} * 100$. This was used as an index of condition of the fish. Log-log models of gonad mass by total mass were created. Plots of GSI and HSI by season and species were generated, and differences in GSI by species and season were examined using Kruskal-Wallis and Dunn's post hoc tests. Seasons were defined as follows: Summer: Dec-Feb, Autumn (Fall): Mar-May, Winter: Jun-Aug, Spring: Sep-Nov.

2.6.7 Parasites

Some external parasites were identified after consideration of Dippenaar and Sebone (2022), Ho (1994), and Leigh-Sharpe (1930). Mean and ranges of parasite loads were calculated for exoparasites, and the frequencies of occurrence were recorded for both external and gill parasites as well as those inhabiting the abdominal cavity and stomach, although no attempt was made to identify the latter.

3. Results

3.1 Distribution

The most common grenadier on both the west coast and the south coast was *C. simorhynchus*. *C. simorhynchus* was present in every degree square and made up the majority of the total abundance of grenadiers in all but two grid squares (*Figure 3.1.1a*). The exceptions are grid squares bounded by 35-36°S and 23-24°E, in which *C. braueri* comprised about two thirds of the abundance of the three grenadier species, and 20-31°S and 15-16°E, in which *M. laevis* comprised ca. 60% of the total abundance. In all other grid squares, *C. simorhynchus* comprises more than 50% of the abundance in trawl catches, including two on the south coast where it makes up nearly 100% of the grenadier observer samples. When summing the normalised abundance of the three species across all grid squares on the west coast (defined here as all grid squares west of the 20th meridian), *C. braueri* constituted 8.5% of the normalised abundance, while *C. simorhynchus* and *M. laevis* made up 72.3% and 19.2% respectively. On the south coast, *C. braueri* made up 9.3% of normalised abundance, whereas *C. simorhynchus* and *M. laevis* constituted 78.5% and 12.2% respectively.

C. braueri was missing from five of the 22 grid squares that were sampled, two of which are in the far north on the west coast, with the remaining three on the south coast. Considering the grid-squares where it was present, *C. braueri* was relatively more abundant on parts of the south coast east of the 22nd meridian, where it comprised more than 10% of the abundance of the three grenadiers in three squares, including the square where it comprised the majority. *M. laevis* was found in all but one grid square (25-36°S by 21-22°E) and its greatest relative abundance occurred on the west coast north of the 34th parallel, where it comprised up to roughly 60% of trawl abundance. Samples from several grid squares included *M. laevis* in excess of 25% of the abundance of the three species.

A similar map of normalised biomass in trawl catches (*Figure 3.1.1b*) largely showed the same trends. *C. simorhynchus* was found in every square, *C. braueri* was more proportionally abundant on the south coast but and absent or very rare in several squares, and *M. laevis* was most proportionally abundant on the west coast. However, there are some notable differences. *M. laevis* occupied a greater relative proportion of the biomass in all squares where it was present when compared to the map of abundance, while *C. braueri* showed the opposite trend, reflecting the greater average mass of *M. laevis* and smaller average mass of *C. braueri* relative to each other and *C. simorhynchus.* This was especially noticeable on the west coast, where *M. laevis* dominated the biomass in five of the six grid squares west of the 17th meridian. When summing the normalised biomass of the three species across all grid squares on the west coast, *C. braueri* constituted 5.2% of the normalised biomass, while *C. simorhynchus* and *M. laevis* made up 49.3% and 45.5% respectively. On the south coast, *C. braueri* made up 6.6% of normalised biomass, whereas *C. simorhynchus* and *M. laevis* constituted 71.7% and 21.7% respectively.

Plots of normalised abundance by coast revealed a higher mean normalised abundance on the south coast compared to the west coast in all three species (*Figure 3.1.2a, c, e*). The overall highest mean abundance was found in *C. simorhynchus*, followed by *C. braueri* and *M. laevis*.

The plots of normalised biomass (*Figure 3.1.2b, d, f*), on the other hand, suggested a slightly different pattern. Differences in biomass by coast were less pronounced than those in abundance, with the south coast being slightly higher in mean biomasses for both *Coelorinchus* species but slightly lower in mean biomass of *M. laevis*. *M. laevis* had the highest biomass on the west coast, followed by *C. simorhynchus* and *C. braueri*. On the south coast, *C. simorhynchus* biomass was followed by that of *M. laevis* and then *C. braueri*.

Normalised abundance and biomass respectively differed significantly by coast in *C. braueri* ($W = 185457$, $p < 0.0001$; $W = 191241$, $p < 0.0001$), in *C. simorhynchus* ($W = 5022066$, $p < 0.0001$; $W = 5282025$, $p < 0.0001$), and in *M. laevis* ($W = 1290587$, $p < 0.0001$; $W = 1044186$, $p < 0.01$). These comparisons revealed that both normalised abundance and biomass differed significantly ($p < 0.01$ for *M. laevis* biomass, $p < 0.001$ for all other comparisons) by coast for all three species (*Table 3.1.1*).

C. braueri occurred only rarely at depths shallower than 200 m. Since only depth intervals containing ten or more trawls were used for statistical comparison, the 100 to 200 m interval for *C. braueri* and the 700 to 800 m intervals for all three species were excluded (*Table 3.1.2*).

Kruskal-Wallis tests by depth interval retuned significant differences in *C. braueri* normalised abundance ($X^2 = 72.157$, $p < 0.0001$) and biomass ($X^2 = 58.134$, $p < 0.0001$). The distributions in abundance and biomass for *C. braueri* were bimodal*,* peaking between 700 and 800 m but with a lesser peak at 300 to 400 m, and there was an overall trend of increasing abundance and biomass with depth (*Figure 3.1.3*). Kruskal-Wallis tests also retuned significant differences in *C. simorhynchus* normalised abundance ($X^2 = 311.92$, $p < 0.0001$) and biomass ($X^2 = 175.86$, $p < 0.0001$). In *C. simorhynchus*, the trend with depth was opposite to that of *C. braueri*, with peaks at 100 to 200 m and 300 to 400 m. The *C. simorhynchus* patterns differ slightly between abundance and biomass; for example, the biomass reaches its maximum in the 300 to 400 m interval, whereas abundance is maximised at 100 to 200 m. *M. laevis* also showed significant differences in normalised abundance ($X^2 = 130.09$, $p < 0.0001$) and normalised biomass ($X^2 = 166.9$, $p < 0.0001$) by depth interval. The incongruity between abundance and biomass is even more pronounced in *M. laevis*, the largest of the three species. *M. laevis* biomass also peaks at 300 to 400 m, but the highest abundance is found in the 700 to 800 m interval.

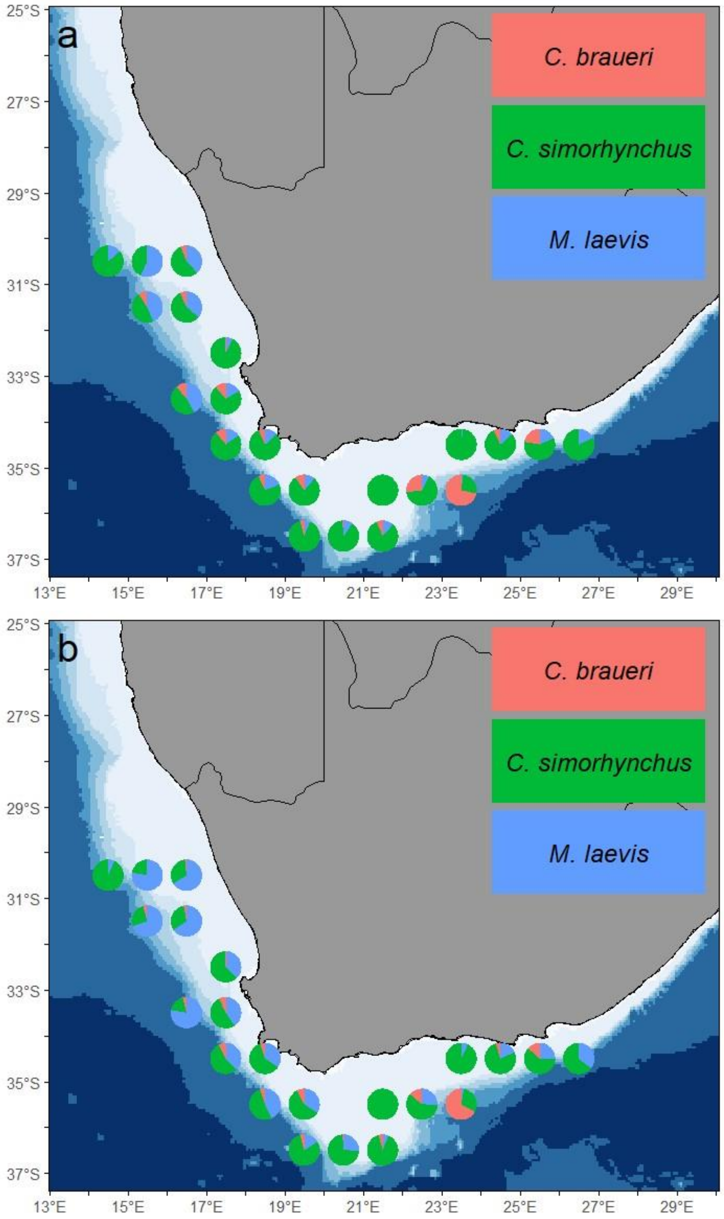

Figure 3.1.1: Relative distribution of (a) normalised abundance and (b) normalised biomass of C. braueri*,* C. simorhynchus*, and* M. laevis *within trawls on the South African west and south coasts.*

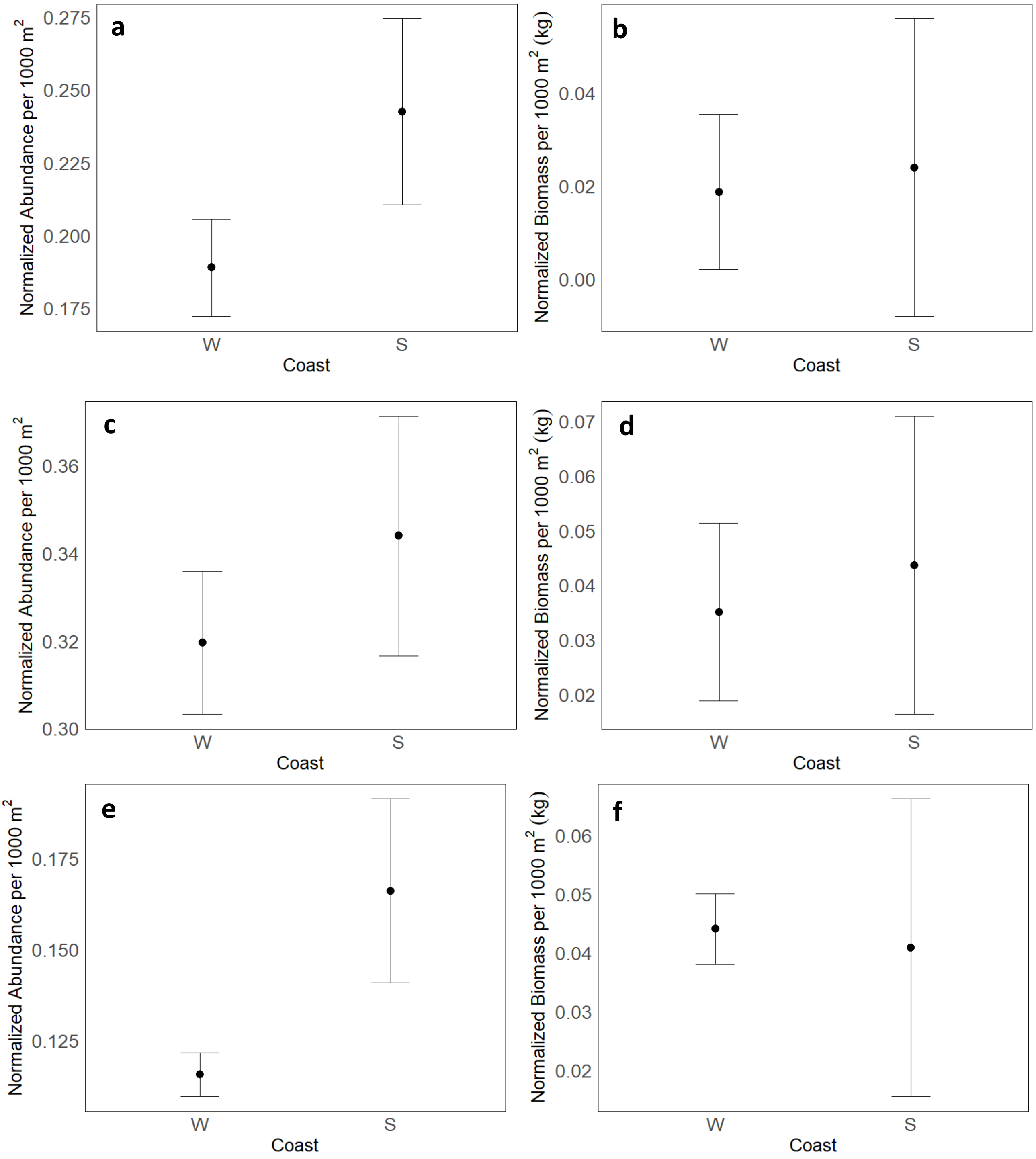

Figure 3.1.2: Means and 95% confidence intervals of normalised abundance per area and normalised biomass (kg/1000 m^2) in trawls from the west and south coasts for (a, b) C. braueri*, (c, d)* C. simorhynchus*, and (e, f)* M. laevis.

Table 3.1.1: Results of Wilcoxon Rank-sum comparisons of normalised abundance (/1000m^2) and normalised biomass (kg/1000 m^2) by coast.

	Median		W (test statistic)	p-value
	West	**South**		
C. braueri				
Abundance	0.0943	0.1405	185509	< 0.0001
Biomass	0.0098	0.015	191241	< 0.0001
C. simorhynchus				
Abundance	0.1484	0.1694	5045162	< 0.0001
Biomass	0.0172	0.0228	5298024	< 0.0001
M. laevis				
Abundance	0.0617	0.0786	1353726	< 0.0001
Biomass	0.0226	0.0205	1092380	< 0.01

These comparisons show that the *C. braueri* biomass and abundance in the 600 to 700 and 700 to 800 m intervals were higher than in all shallower intervals (*Table 3.1.2*). In *C. simorhynchus*, the 300 to 400 m interval differed from both intervals on either side, confirming the peak seen in both abundance and biomass at that interval in *Figure 3.1.2*. The lesser peak at 700 to 800 m was not significant compared to the intervals between 500 to 600 and 600 to 700 m. The depth distribution of *M . laevis* resembled that of *C. simorhynchus*, with a significant peak at 300 to 400 m, although the abundance at 700 to 800 m did differ significantly from 500 to 700 m in this species.

Across all three species, normalised abundance differed in a greater number of depth interval comparisons than normalised biomass (seven compared to six in *C. braueri*, ten compared to fourteen in *C. simorhynchus*, and ten compared to nine in *M. laevis*), although there were also two comparisons in which the difference in biomass was significant while that in abundance was not. Insofar as the depth preferences of the three species can be ranked, for the 100 to 800 m depth range, *C. braueri* favours the greatest depths while *C. simorhynchus* favours the shallowest waters, although this range does not cover the deepest layers in which these three species may be found.

While all models returned significant to highly significant p-value outputs for the slope coefficient estimates, model fits were extremely poor with all $R^2 < 0.03$ (*Table 3.1.3*). Relationships between abundance or biomass and depth cannot be approximated with a linear trend. Attempts at log-transforming either the dependent variable or depth, or both, did not improve the R^2 to more than 0.05 in any of the models.

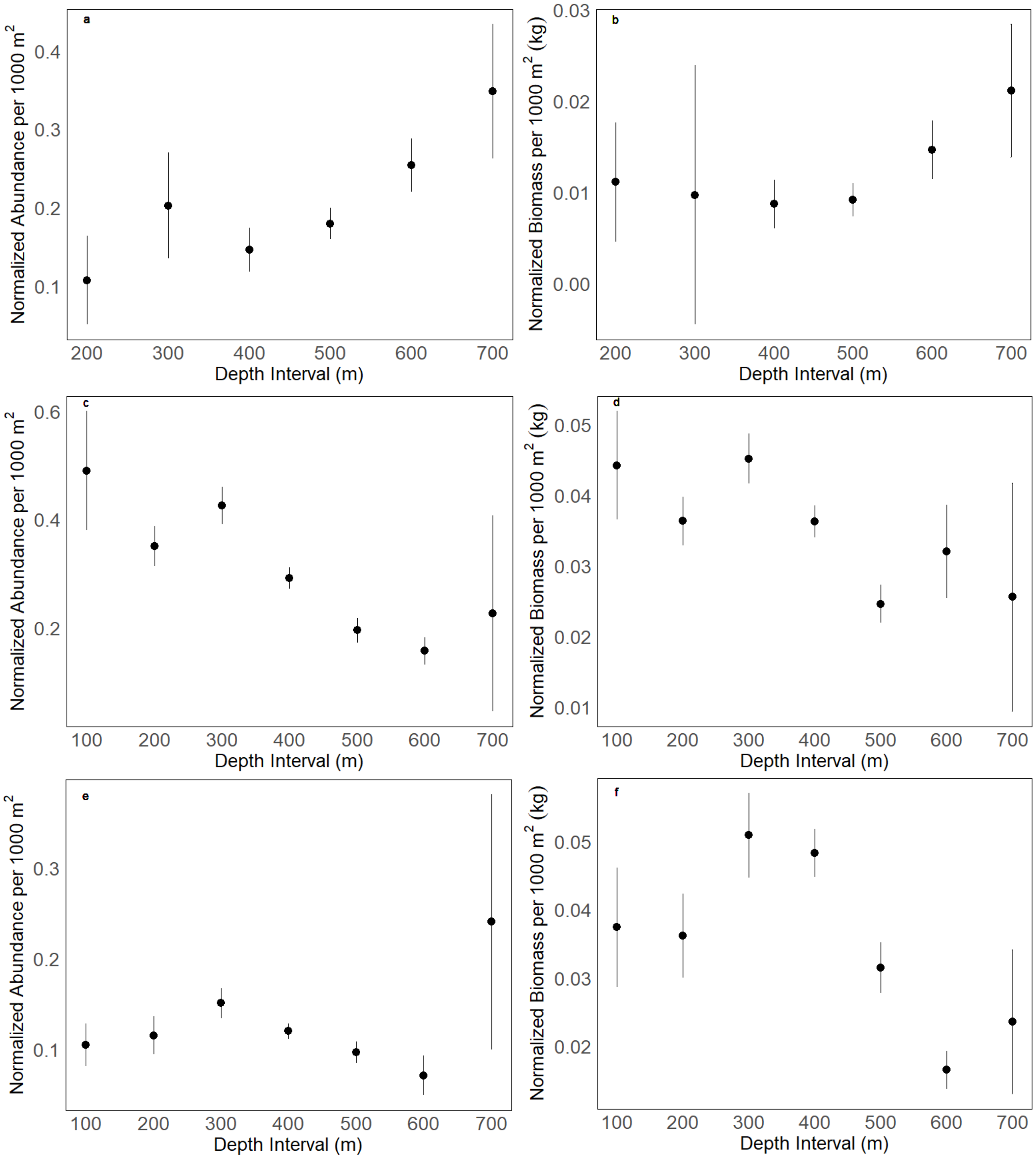

Figure 3.1.3: Means and 95% confidence intervals of normalised abundance per area and normalised biomass (kg/1000 m^2)in trawls at various 100 m depth intervals for (a, b) C. braueri, *(c, d)* C. simorhynchus, *and (e, f)* M. laevis. *Only depth intervals with n > 10 samples are shown. Depth ranges are grouped to their lower bounds.*

Table 3.1.2: Dunn's post-hoc comparisons of normalised abundance and normalised biomass by depth interval. Only comparisons significant at p < 0.05 are shown. Rows are greyed-out where there is an absence or low numbers of trawls (n < 10).

Intervals (m)	**p-value**					
	C. braueri		*C. simorhynchus*		*M. laevis*	
	Abundance	**Biomass**	**Abundance**	**Biomass**	**Abundance**	**Biomass**
100 vs 200	▨	▨	< 0.01	< 0.01		
100 vs 300	▨	▨				
100 vs 400	▨	▨	< 0.001	< 0.05		
100 vs 500	▨	▨	< 0.0001	< 0.0001		
100 vs 600	▨	▨	< 0.0001	< 0.0001	< 0.0001	< 0.0001
100 vs 700	▨	▨	< 0.01			
200 vs 300			< 0.0001	< 0.0001	< 0.0001	< 0.0001
200 vs 400						< 0.0001
200 vs 500			< 0.0001	< 0.0001		
200 vs 600	< 0.01		< 0.0001		< 0.0001	< 0.0001
200 vs 700	< 0.001					
300 vs 400			< 0.0001	< 0.0001	< 0.001	
300 vs 500			< 0.0001	< 0.0001	< 0.0001	< 0.0001
300 vs 600		< 0.05	< 0.0001		< 0.0001	< 0.0001
300 vs 700	< 0.01	< 0.001	< 0.05 *			
400 vs 500			< 0.0001	< 0.0001	< 0.0001	< 0.0001
400 vs 600	< 0.0001	< 0.0001	< 0.0001	< 0.0001	< 0.0001	< 0.0001
400 vs 700	< 0.0001	< 0.0001				
500 vs 600	< 0.0001	< 0.0001			< 0.001	< 0.001
500 vs 700	< 0.0001	< 0.0001				
600 vs 700					< 0.01	

Table 3.1.3: Results of linear models of normalised abundance (/1000 m^2) and normalised biomass (kg/1000 m^2) against depth.

	Estimate	**Std. Error**	**p-value**	**R^2**
C. braueri				
Intercept (Abundance)	$-6.12x10^{-2}$	$4.44x10^{-2}$	> 0.05	0.026
Slope (Abundance)	$4.86x10^{-4}$	$8.00x10^{-5}$	< 0.0001	
Intercept (Biomass)	$9.44x10^{-3}$	$5.58x10^{-3}$	> 0.05	0.003
Slope (Biomass)	$2.05x10^{-5}$	$1.01x10^{-5}$	< 0.05	
C. simorhynchus				
Intercept (Abundance	$5.79x10^{-1}$	$2.88x10^{-2}$	< 0.0001	0.011
Slope (Abundance)	$-6.26x10^{-4}$	$6.94x10^{-5}$	< 0.0001	
Intercept (Biomass)	$5.24x10^{-2}$	$4.25x10^{-3}$	< 0.0001	0.002
Slope (Biomass)	$-3.43x10^{-5}$	$1.02x10^{-5}$	< 0.001	
M. laevis				
Intercept (Abundance	$1.72x10^{-1}$	$1.49x10^{-2}$	< 0.0001	0.003
Slope (Abundance)	$-1.17x10^{-4}$	$3.41x10^{-5}$	< 0.001	
Intercept (Biomass)	$6.30x10^{-2}$	$5.38x10^{-3}$	< 0.0001	0.002
Slope (Biomass)	$-4.14x10^{-5}$	$1.23x10^{-5}$	< 0.001	

3.2 Morphometrics

Comparing the total lengths as estimated from pre-anal fin lengths, *C. braueri* was the shortest of the three species, with a mean estimated TL of 283 mm, and a maximum TL of 416.6 mm (*Table 3.2.1*). *C. simorhynchus* had mean and maximum estimated TL of 316.9 mm and 498.0 mm respectively. *M. laevis* was the largest species, with mean and maximum TL of 500.3 mm and 781.7 mm, respectively. In all cases, mean TL as estimated from head length was slightly shorter than the estimation from PAFL, differing by 1.1% in *C. braueri* and *M. laevis* and 0.2% in *C. simorhynchus.* Of these differences, only that in *C. braueri* was significant (V = 275, p = < 0.01, *Table 3.2.2*).

The relationships between TL and PAFL were modelled using linear regressions. Comparing these regressions revealed differences between the three species. While *C. braueri* TL was smaller compared to *C. simorhynchus*, their mean PAFL is greater (compare mean PAFL of 92.69 mm in *C. braueri* to only 86.79 mm in *C. simorhynchus*). This difference is more extreme in a comparison of HL, where the mean HL of 51.2 mm in *C. simorhynchus* was 12.6% shorter than the 58.59 mm mean HL of *C. braueri*.

A difference was also apparent in the number of specimens with damaged snouts, of which *C. braueri* accounted for the majority (four), while only a single *C. simorhynchus* and no *M. laevis* showed snouts that were too damaged to accurately measure length. A total of 198 fish across the three species lacked the posterior portion of their tails, accounting for 39%, 25%, and 69% in *C. braueri*, *C. simorhynchus*, and *M. laevis* respectively.

Regressions of PAFL and HL against total measured lengths in specimens with unbroken tails and snouts yielded highly significant linear relationships with good fit (all $R^2 > 0.8$) in all three species, allowing for the estimation of TL based on either metric in those specimens with broken tails (*Table 3.2.3*, *Figure 3.2.1*).

Table 3.2.1: Means and (ranges) of pre-anal fin length (PAFL), head length (HL), and total length (TL). Total lengths are given as recorded from specimens with unbroken tails, and as estimations from pre-anal fin length and head length. All lengths given in mm.

Species	**PAFL**	**HL**	**TL from unbroken**	**TL from PAFL**	**TL from HL**	**Broken snout (%)**	**Broken tail (%)**
C. braueri	93 (56-149)	59 (37-94)	263 (181-395)	283 (181-417)	280 (181-395)	6	39
C. simorhynchus	87 (42-130)	51 (28-76)	313 (181-446)	317 (181-498)	316 (181-505)	0	25
M. laevis	95 (63-149)	67 (50-100)	490 (372-695)	500 (304-782)	495 (312-708)	-	69

Table 3.2.2: Comparison between estimated total lengths (TL) based on pre-anal fin length (PAFL) and head length (HL). Results given as the median of the difference between both estimations (TL from PAFL - TL from HL) *and a two-sided paired Wilcoxon signed-rank test between estimated TL for each individual.*

Species	**Median difference (mm)**	**V statistic**	**p-value**
C. braueri	11.97	275	< 0.01
C. simorhynchus	2.09	1990	> 0.05
M. laevis	-0.46	2448	> 0.05

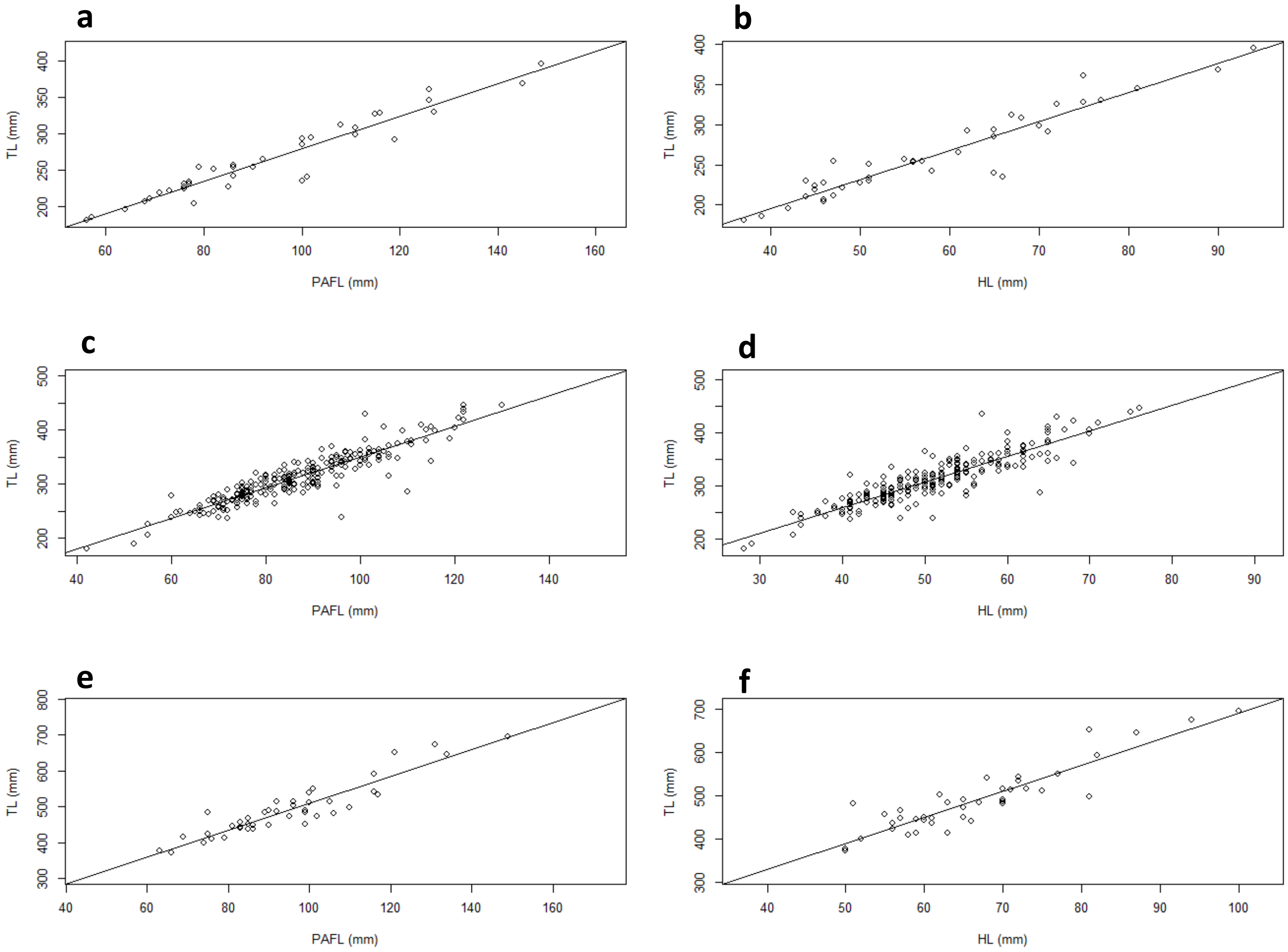

Figure 3.2.1: Regression plots of measured total length (TL) against pre-anal fin length (PAFL) and head length (HL) for (a, b) C. braueri *(c, d)* C. simorhynchus, *(e, f)* M. laevis.

Table 3.2.3: Results of linear models of total length (TL) of specimens with unbroken tails against pre-anal fin length (PAFL) and head length (HL), used to estimate total length in specimens with broken tails. All lengths given in mm.

	Estimate	**Std. Error**	**p-value**	**R^2**
C. braueri				
Intercept (PAFL)	56.70	10.08	< 0.0001	0.923
Slope (PAFL)	2.22	0.11	< 0.0001	
Intercept (HL)	50.85	12.07	< 0.001	0.895
Slope (HL)	3.61	0.20	< 0.0001	
C. simorhynchus				
Intercept (PAFL)	65.97	7.21	< 0.0001	0.837
Slope (PAFL)	2.84	0.08	< 0.0001	
Intercept (HL)	65.64	8.11	< 0.0001	0.802
Slope (HL)	4.83	0.16	< 0.0001	
M. laevis				
Intercept (PAFL)	135.96	23.23	< 0.0001	0.857
Slope (PAFL)	3.73	0.24	< 0.0001	
Intercept (HL)	90.77	29.47	< 0.01	0.825
Slope (HL)	5.99	0.44	< 0.0001	

In both *Coelorinchus* species, female median PAFL exceeded that of males (*Figure 3.2.2a, b*). Median female PAFL was 26 mm greater than that of males in *C. braueri* and 7 mm greater in *C. simorhynchus.* Male *C. braueri* were longer than indeterminate fish (21 mm), whereas in male *C. simorhynchus* and *M. laevis*, indeterminate median PAFL was not significantly greater than that of males (*Figure 3.2.2c*). Female *M. laevis* also had greater median PAFL than males (by 16 mm) or indeterminate fish (16 mm). Size differences by sex were most pronounced in *C. braueri*, while in the other two species medians of all categories were more similar.

Significant differences in PAFL by 50 m depth interval were detected in *C. braueri* ($X^2 = 21.533$, $p < 0.0001$) and *C. simorhynchus* ($X^2 = 28.849$, $p < 0.0001$). While the Kruskal-Wallis test of PAFL by depth interval in *M. laevis* returned a significant difference ($X^2 = 8.5325$, $p < 0.05$), none of the post-hoc comparisons were significant at $p < 0.05$. In order to avoid Simpson's paradox, comparisons were re-assessed using 100 m depth intervals instead, resulting in no significant differences of PAFL by depth interval ($X^2 = 5.2639$, $p > 0.05$).

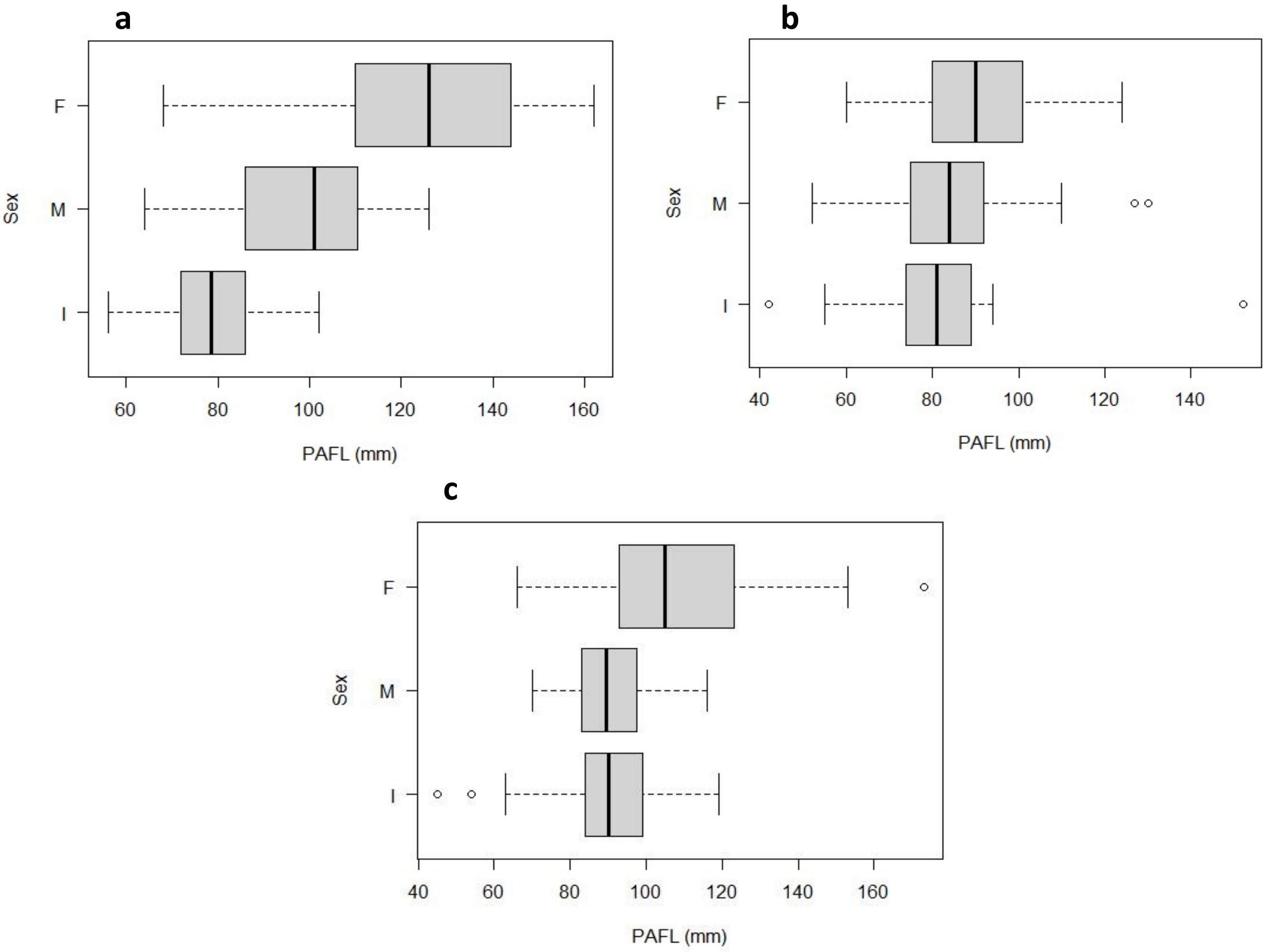

Figure 3.2.2: Boxplots of pre-anal fin length by sex for C. braueri *(a),* C. simorhynchus *(b)* M. laevis *(c). F – female, M – male, I – indeterminate.*

In *C. braueri*, specimens caught between 250 and 300 m showed higher median PAFL than those caught at greater depths (*Figure 3.2.3; Table 3.2.4*). The maximum PAFL was also recorded from this depth category. The lowest PAFL and lowest median PAFL were recorded between 500 and 550 m. Only one further depth category, 600 to 650 m, yielded *C. braueri* samples, and in such low numbers (n = 3) as to preclude comparisons. While the difference between the 250 to 300 m and 500 to 550 m intervals was significant ($p < 0.0001$), all fish in the 250 to 300 m interval came from the same trawl sample, potentially conflating location-based differences in PAFL with depth-based differences. For this reason, no comparisons involving *C. braueri* are presented here.

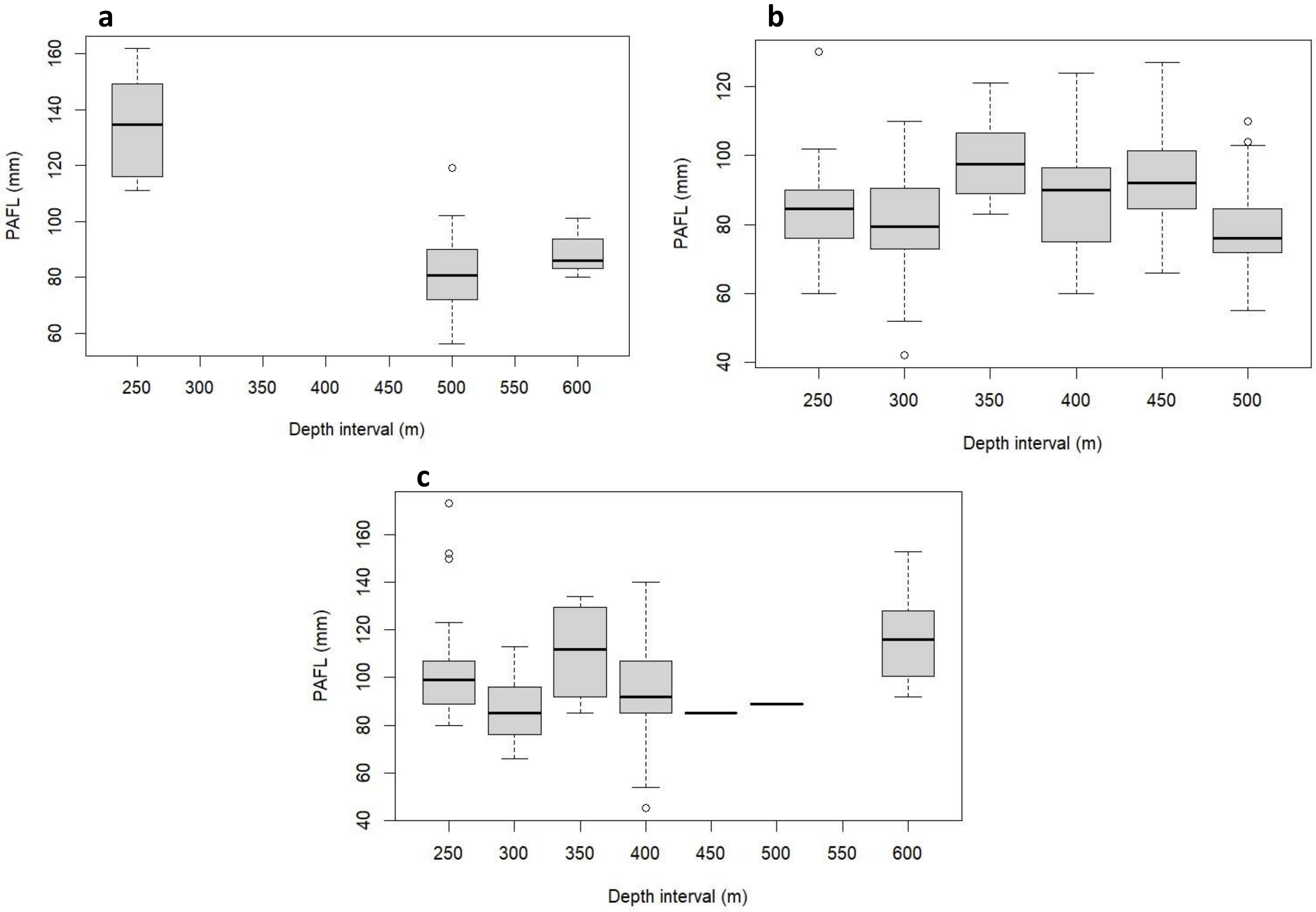

Figure 3.2.3: Boxplots of pre-anal fin length by depth interval for C. braueri *(a),* C. simorhynchus *(b)* M. laevis *(c). F – female, M – male, I – indeterminate. Depth intervals are 50 m in width and grouped by their lower bounds.*

C. simorhynchus showed a smaller depth range compared to the other species (250 to 550 m), although, unlike its congener, every depth interval in this range yielded multiple fish. The greatest median PAFL occurred between 350 and 400 m, with the shallowest depth interval having the third-lowest median PAFL. The minimum PAFL and lowest median PAFL in this species were found in the 300 to 350 m interval, albeit closely followed by 450 to 500 m. The peak in PAFL in the 350 to 400 m depth stratum differed significantly from the shallowest (250 to 300 m) and deepest (500 to 550 m) intervals ($p < 0.01$ and $p < 0.0001$, respectively), as well as the 300 to 350 m interval ($p < 0.01$).

Specimens of *M. laevis* showed the same overall depth range as *C. braueri*, from 250 to 650 m. Samples containing this species were obtained from seven depth intervals, although two of these were represented by only one individual each, with the majority if fish caught between depths of 250 to 450 m and 600 to 650 m. This last interval contained the greatest median PAFL, although as in the other species, the greatest overall PAFL was found in the shallowest interval of 250-300 m. This value represents one of several positive outliers within that depth interval. The lowest median PAFL value lies in the 300 to 350 m interval, while the overall lowest PAFL is one of two negative outliers between 400 to 450 m.

Table 3.2.4: Dunn's post-hoc comparisons of pre-anal fin length by depth interval for C. simorhynchus*. Only comparisons significant at $p < 0.05$ are shown.*

Interval (m)	Median PAFL (mm)	Comparisons	p-value
250	84.5	250 vs 300	
		250 vs 350	< 0.01
		250 vs 400	
		250 vs 450	< 0.001
		250 vs 500	
300	79.5	300 vs 350	< 0.01
		300 vs 400	
		300 vs 450	< 0.01
		300 vs 500	
350	97.5	350 vs 400	
		350 vs 450	
		350 vs 500	< 0.001
400	90.0	400 vs 450	
		400 vs 500	< 0.01
450	92.0	450 vs 500	< 0.0001
500	76.0	-	-

The only grenadier species that exhibited a trend in PAFL with depth was *C. braueri* (*Figure 3.2.2 d-f, Table 3.2.5*). A linear regression of PAFL by depth showed a significant ($p < 0.0001$) decrease in PAFL with increasing depth of 0.18 mm/m, with adequate goodness of fit (multiple $R^2 = 0.61$). No interaction terms of sex and depth were considered given that no significant relationship between sex and depth interval was discovered (*Table 3.6.1*). No linear trends of PAFL with depth were detected in *C. simorhynchus* or in *M. laevis* (both $R^2 < 0.1$). No linear trends were detected in the models of average mass with depth in any species (*Table 3.2.6*).

Table 3.2.5: Results of linear regressions of pre-anal fin lengths (mm) against depth (m)

	Estimate	**Std. error**	**p-value**	**R^2**
C. braueri				
Intercept (mm)	177.98	10.59	< 0.0001	0.609
Slope	-0.18	0.022	< 0.0001	
C. simorhynchus				
Intercept (mm)	80.16	3.96	< 0.0001	0.013
Slope	0.018	0.01	> 0.05	
M. laevis				
Intercept (mm)	90.31	8.13	< 0.0001	0.009
Slope	0.02	0.02	> 0.05	

Table 3.2.6: Results of linear models of average mass (g) by depth (m)

	Estimate	**Std. Error**	**p-value**	**R^2**
C. braueri				
Intercept (g)	2.436×10^{-1}	1.829×10^{-2}	< 0.0001	0.030
Slope	-2.147×10^{-4}	3.295×10^{-5}	< 0.0001	
C. simorhynchus				
Intercept (g)	3.784×10^{-1}	1.760×10^{-2}	< 0.0001	5.05×10^{-3}
Slope	6.071×10^{-5}	4.016×10^{-5}	> 0.05	
M. laevis				
Intercept (g)	7.932×10^{-2}	5.995×10^{-3}	< 0.0001	0.012
Slope	1.736×10^{-4}	1.443×10^{-5}	< 0.0001	

Significant differences in average total mass by depth interval were found in *C. braueri* (X^2 = 19.537, $p < 0.05$), *C. simorhynchus* (X^2 = 104.44, $p < 0.0001$), and *M. laevis* (X^2 = 115.73, $p < 0.0001$). The only depth interval in which mass differed in *C. braueri* was the 200 to 300 m category, in which fish were consistently heavier than in other depth intervals (*Figure 3.2.4; Table 3.2.7*).

The mass of *C. simorhynchus* in the 700 to 800 m interval was lower than in all intervals shallower than 600-700 m. In *M. laevis*, it was the 600 to 700 m interval in which the highest average mass occurred, differing from all intervals other than 700 to 800 m. The mass of *M. laevis* in the 500 to 600 m interval was also consistently higher than in the intervals ranging between 100 to 400 m, while mass in the 400 to 500 m interval differed from both the 200 to 300 and 300 to 400 m intervals.

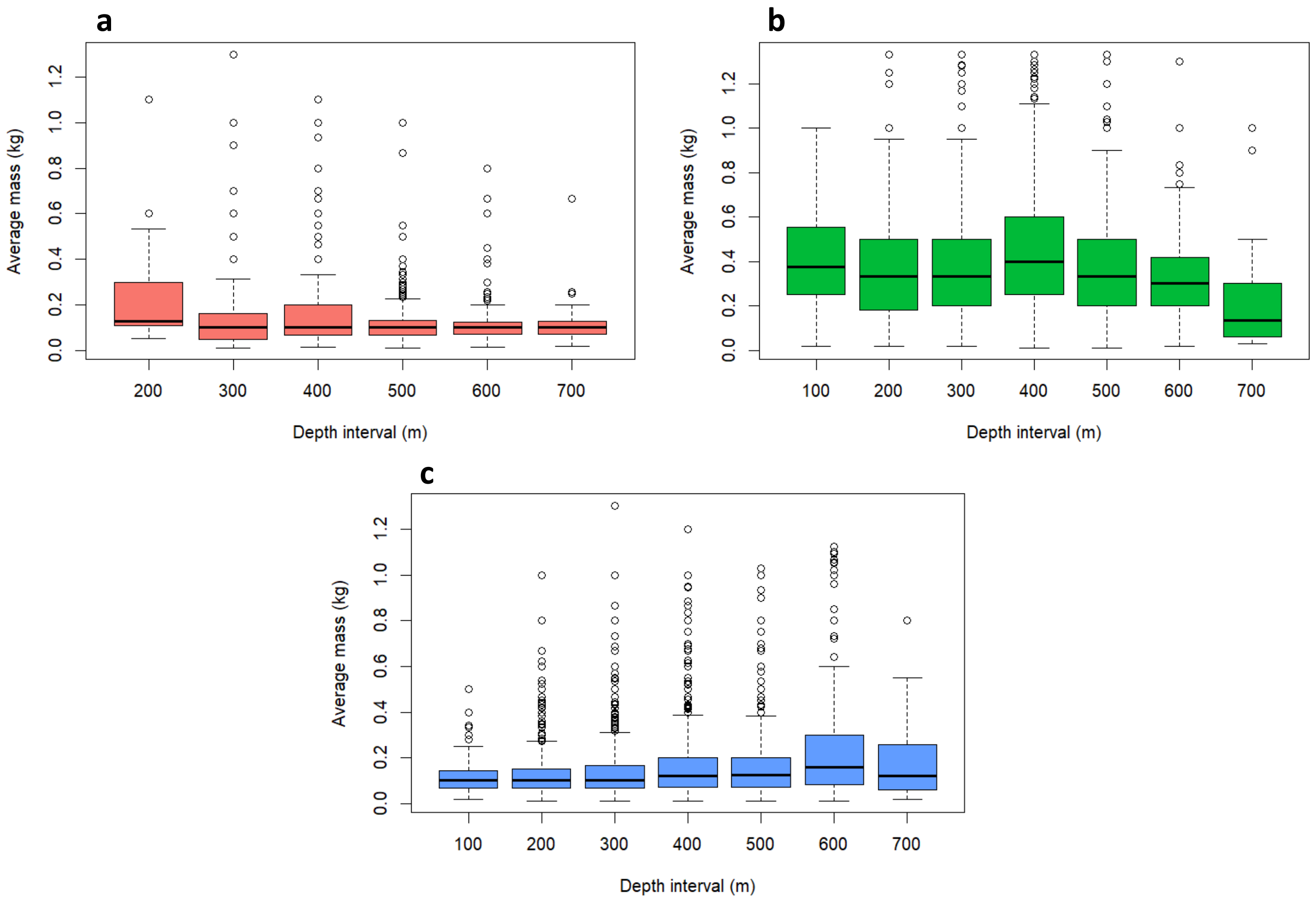

Figure 3.2.4: Boxplots of average mass by depth interval for (a) C. braueri, *(b)* C. simorhynchus, *(c)* M. laevis. *Only intervals with n ≥ 10 are shown. Depth intervals are 50 m in width and grouped by their lower bounds.*

Table 3.2.7: Dunn's post-hoc comparisons of average mass by depth interval. Only comparisons significant at $p < 0.05$ are shown. Rows are greyed-out where there is an absence or low numbers of specimens ($n < 10$).

Intervals (m)	**p-value**		
	C. braueri	*C. simorhynchus*	*M. laevis*
100 vs 200	▨		
100 vs 300	▨		
100 vs 400	▨		
100 vs 500	▨		< 0.05
100 vs 600	▨		< 0.0001
100 vs 700	▨	< 0.01	
200 vs 300	< 0.01		
200 vs 400	< 0.05	< 0.0001	< 0.0001
200 vs 500	< 0.001		< 0.0001
200 vs 600	< 0.01		< 0.0001
200 vs 700	< 0.01	< 0.05	
300 vs 400		< 0.0001	< 0.0001
300 vs 500			< 0.0001
300 vs 600			< 0.0001
300 vs 700		< 0.01	
400 vs 500		< 0.0001	
400 vs 600		< 0.0001	< 0.0001
400 vs 700		< 0.0001	
500 vs 600			< 0.001
500 vs 700		< 0.05	
600 vs 700			

3.3 Biometrics and growth

The trend in masses followed that in TL, with *C. braueri* being the lightest with a mean of 92.1g and range of 12.9 to 294.6 g , followed by *C. simorhynchus* at 122.3 g and 14.6 to 743.5 g, and *M. laevis* the heaviest at 339.3 g mean mass and ranging between 30.8 to 1346.6 g. All three species followed significant power relationships of mass against PAFL (*Figure 3.3.1*).

The power relationship models were based on sample sizes of 44, 300, and 120 for *C. braueri*, *C. simorhynchus*, and *M. laevis* respectively, and covered similar PAFL ranges in all three species. Minimum PAFL lay between 52-66 mm, and maximum between 130-173 mm, with *C. simorhynchus* having the lowest minimum and maximum values and *M. laevis* the highest.

The growth type was isometric (b–1.96*SE < 3 < b+1.96*SE) in *C. braueri* and *C. simorhynchus*, with b = 2.97 (SE 0.11) and b = 3.08 (SE 0.05) respectively (*Table 3.3.1*). *M. laevis* was hypoallometric with b = 2.59 (SE 0.09). Despite having the lowest exponent b, *M. laevis* showed the steepest growth curve due to its comparatively high value of the a-term, followed by *C. simorhynchus* and *C. braueri*.

Table 3.3.1: Results of linear log-log models of total mass (g) against pre-anal fin length (mm).

	Estimate	**Std. Error**	**p-value**	**R^2**	**Growth type**
C. braueri					
Intercept	-9.39	0.38	< 0.0001	0.955	Isometric
Coefficient	2.97	0.08	< 0.0001		
C. simorhynchus					
Intercept	-9.10	0.24	< 0.0001	0.914	Isometric
Coefficient	3.08	0.05	< 0.0001		
M. laevis					
Intercept	-6.17	0.43	< 0.0001	0.851	Hypoallometric
Coefficient	2.59	0.09	< 0.0001		

Females of *C. braueri* reached maturity at a $PAFL_{50}$ that was 18 mm greater than that of males (107 mm and 89 mm respectively; *Figure 3.3.2*). Females of *C. simorhynchus* reached maturity at a $PAFL_{50}$ of only 71 mm, but the $PAFL_{50}$ of *C. simorhynchus* males could not be accurately estimated despite the substantial number of immature males (12 out of 37 immature *C. simorhynchus*), possibly due to failure to capture fish in the smallest length intervals. Nonetheless, the data suggested that males of *C. simorhynchus* mature at lower PAFL than females. No immature females and only two immature male *M. laevis* were captured.

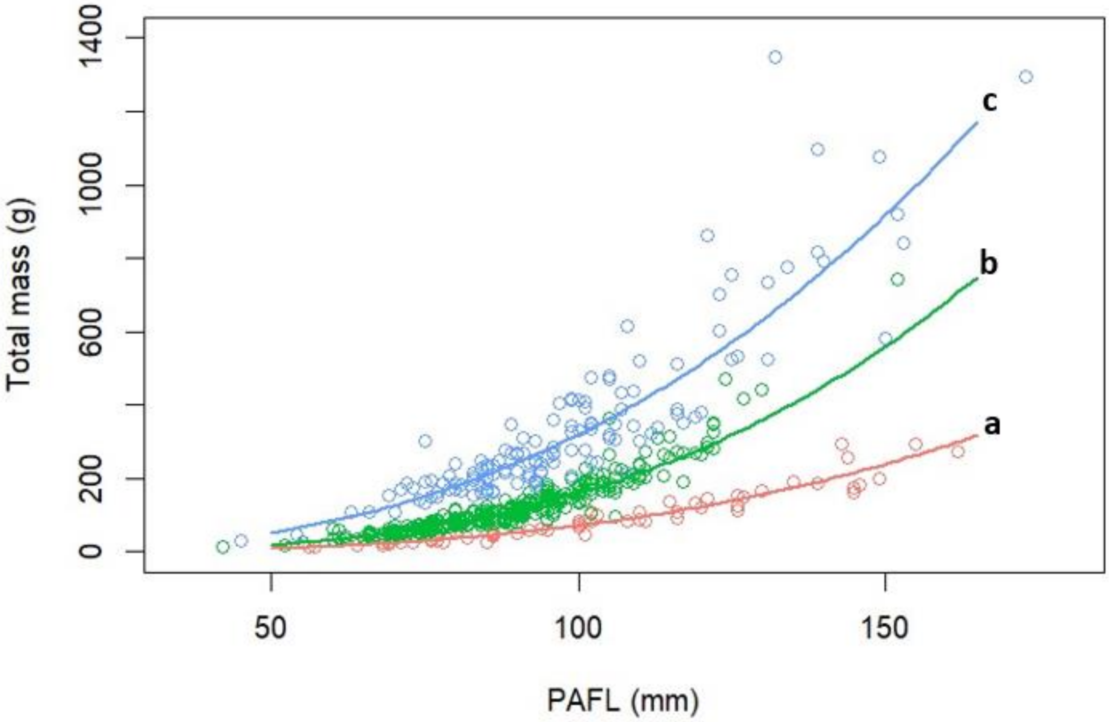

Figure 3.3.1: Power regressions of the type $W = a*PAFL^b$ *of total mass (W) against pre-anal fin length (PAFL) for (a)* C. braueri*, (b)* C. simorhynchus*, and (c)* M. laevis.

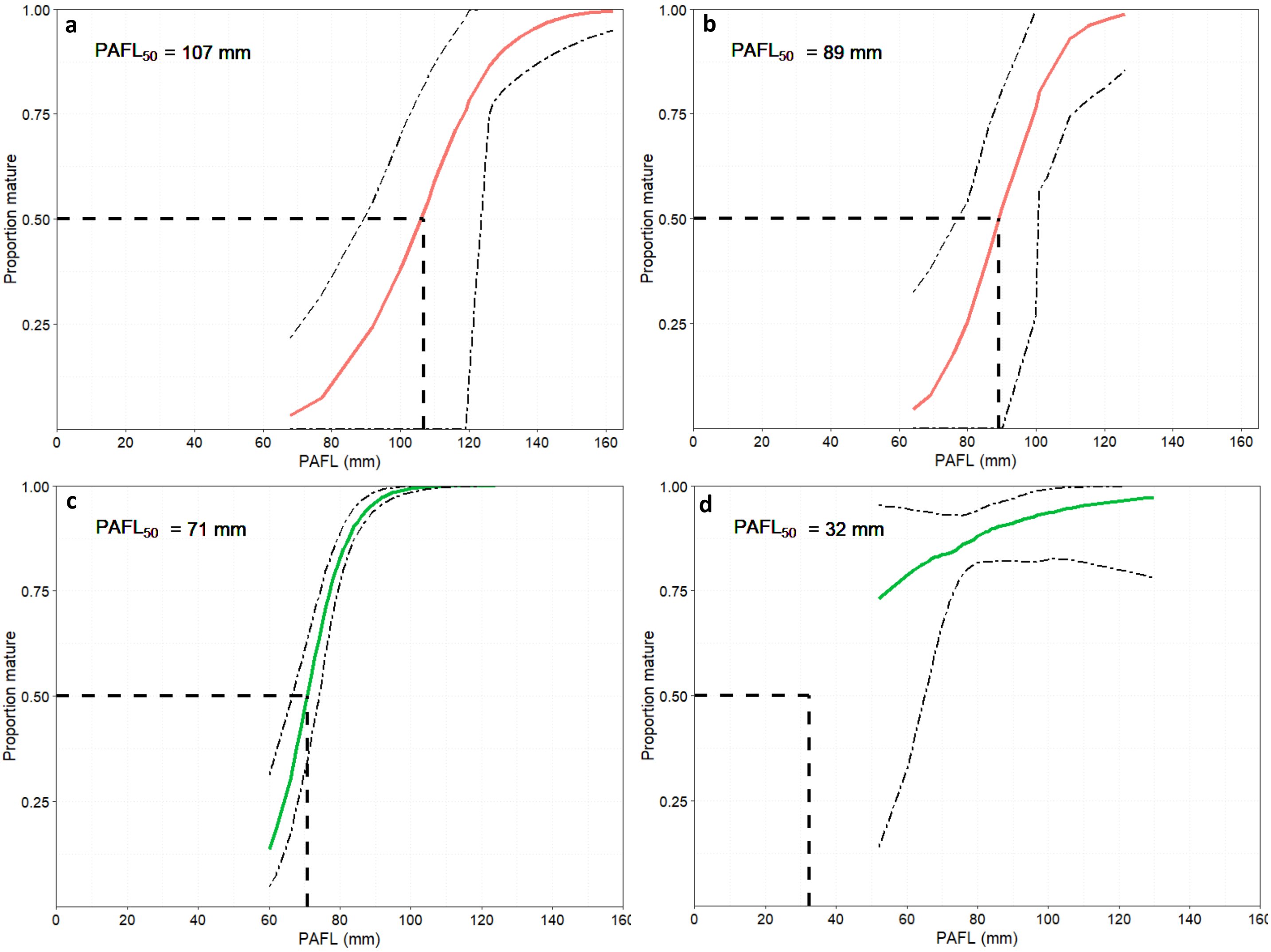

Figure 3.3.2: Maturity ogives with 95% confidence intervals of pre-anal fin length at 50% maturity for C. braueri *females (a) and males (b), and* C. simorhynchus *females (c) and males (d)*

3.4 Von Bertalanffy Growth Models

C. braueri had the smallest estimated otolith nucleus width at 2.76 mm, as well as the largest range of probable nucleus widths, ranging between 2.18 and 3.35 mm (*Table 3.4.1*). In all three species, linear models of otolith width against PAFL were highly significant (*Figure 3.4.1; Table 3.4.2*). Model fits in *C. braueri* and *M. laevis* were reasonable and producing R^2-values of 0.75 and 0.72 respectively, but were relatively poor in *C. simorhynchus* (R^2 = 0.54).

Table 3.4.1: Means and ranges of otolith widths, as well as results of linear regressions of otolith widths (OW) against pre-anal fin lengths, including the estimated nucleus width (NW) and its 95% confidence interval (CI). All measurements given in mm.

	Range OW	**Mean**	**NW**	**95% CI**
C. braueri	3.78-9.02	6.30	2.76	2.18-3.35
C. simorhynchus	4.24-7.56	5.91	3.63	3.37-3.90
M. laevis	4.54-8.53	6.25	3.88	3.59-4.17

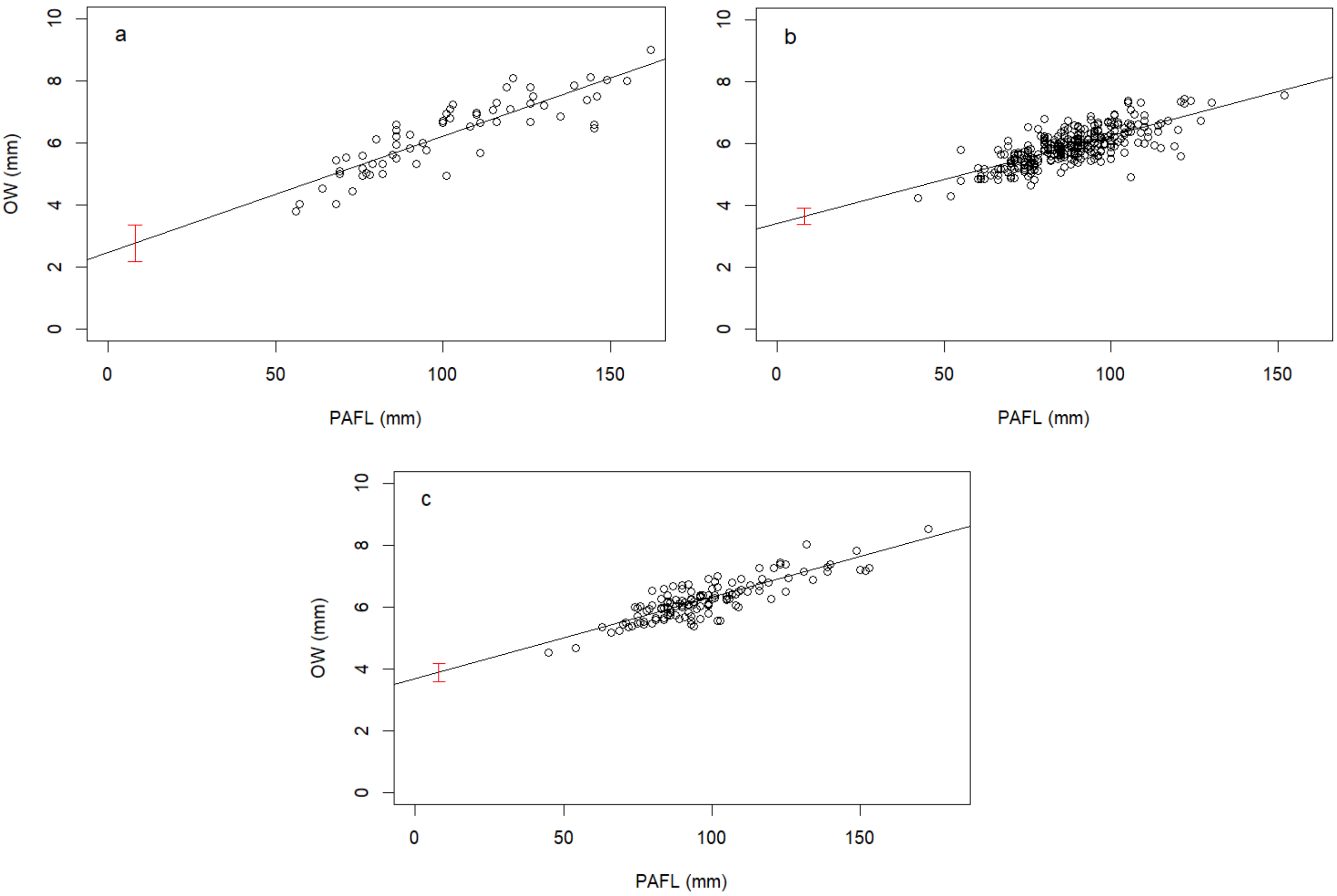

Figure 3.4.1: Plots of linear regressions of otolith width against pre-anal fin length for (a) C. braueri, *(b)* C. simorhynchus*, and (c)* M. laevis*. 95% confidence interval of the estimated nucleus width at a PAFL of 8 mm shown as (I)*

Table 3.4.2: Results of linear models of otolith widths against pre-anal fin lengths

	Estimate	Std. Error	p-value	R^2
C. braueri				
Intercept (mm)	2.46	0.29	< 0.0001	0.752
Slope	0.04	2.75×10^{-3}	< 0.0001	
C. simorhynchus				
Intercept (mm)	3.40	0.135234	< 0.0001	0.544
Slope	0.03	1.52×10^{-3}	< 0.0001	
M. laevis				
Intercept (mm)	3.67	0.146111	< 0.0001	0.717
Slope	0.03	1.47×10^{-3}	< 0.0001	

A von Bertalanffy regression was estimated for *C. braueri*, with females, males, and sexually indeterminate specimens combined (*Figure 3.4.2*), and an age-length key was generated for this species (*Table 3.4.3*). The model had good fit ($R^2 = 0.80$). The von Bertalanffy model equation for *C. braueri*, where t is the age in years, is given by:

$$PAFL_t = 169.13 * \left(1 - e^{-0.10*(t - (-1.73))} \right)$$

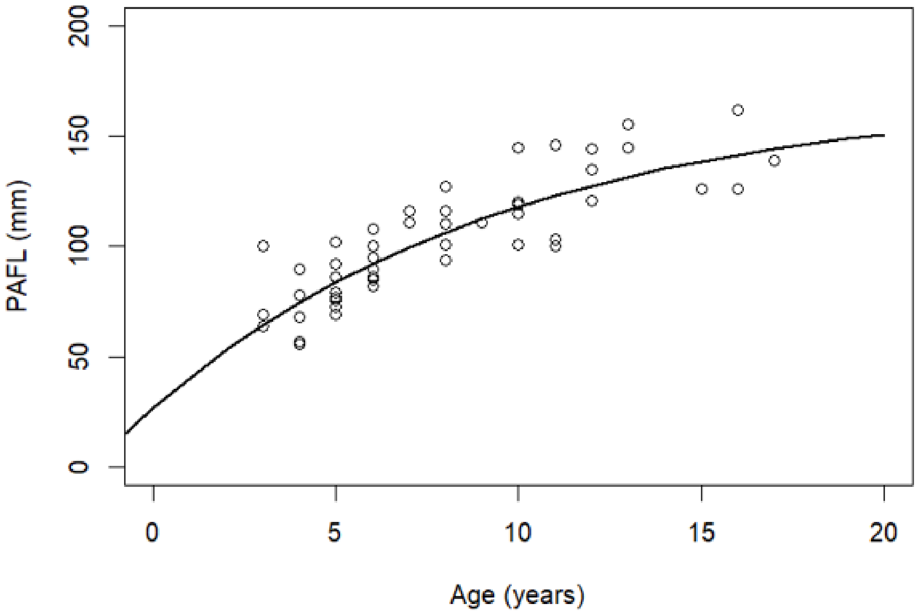

Figure 3.4.2: Curve of the von Bertalanffy regression of C. braueri*, using pre-anal fin length and estimated age from otolith annuli.*

Table 3.4.3: Age-length key for C. braueri. *Length categories given as the lower bounds of 10 mm intervals.*

Pre-anal fin length (mm)	Age (years)														
	3	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**	**14**	**15**	**16**	**17**
50		1.00													
60	0.40	0.40	0.20												
70		0.12	0.75	0.12											
80			0.22	0.67	0.11										
90		0.20	0.20	0.40		0.20									
100	0.11		0.11	0.22		0.11		0.11	0.33						
110					0.25	0.38	0.12	0.25							
120						0.17		0.17		0.17			0.17	0.33	
130										0.50					0.50
140								0.20	0.20	0.20	0.20			0.20	
150											1.00				
160														1.00	

3.5 Diet

The high incidence of stomach eversion, stomachs which contained no food, and stomachs which contained food remains but without identifiable items limited the number of stomachs which yielded useful dietary information. The proportion of everted stomachs was greatest in *C. braueri* at 69%, followed by *M. laevis* (24%) and *C. simorhynchus* (19%). This left a total of 13, 188, and 66 stomachs containing one or more identifiable prey items for analysis in *C. braueri*, *C. simorhynchus*, and *M. laevis* respectively.

Generally, prey digestion was very advanced, making order- or family-level identification difficult and usually prohibiting identification to the level of genus or species (*Table 3.5.1*). On average, the best-preserved prey was found in stomachs of *M. laevis*, with about 10% of prey items being ranked at digestion level 1. Conversely, in *C. simorhynchus* less than 4% of prey items were ranked at digestion level 1, while 63% were at digestion level 3.

Table 3.5.1: Summary of stomach dissections, including the eversion status, state of stomach contents or lack thereof, and frequency of digestion levels among prey.

	Everted	**Non-everted**	**Stomach contents**			**Level of digestion**		
			Empty	**Fully digested**	**Identifiable prey**	**1**	**2**	**3**
C. braueri	44	20	1	6	13	2	5	17
C. simorhynchus	62	256	4	64	188	11	114	213
M. laevis	32	102	0	36	66	12	49	50

Two major prey groups were found in the stomachs of *C. braueri*, the larger of these being unidentified crustaceans at an IRI value of about 8674, and the smaller being teleost fish at about 2235. Complete teleosts found in this species did not exceed 8 cm in length. Unidentified crustacea dominated both in frequency of occurrence (69%) and number (83%) while teleosts had the greatest percentage mass (56%). The only teleost whose condition permitted identification to lower taxonomic rank was an unidentified myctophid. Squids were among the three minor prey groups with a relatively high frequency of occurrence (31%). Despite being the third-highest group by IRI, the IRI of squids was only about 91 due to their low numbers and masses (both < 3%). The other minor prey groups were euphausiids (IRI of 82) and ostracods (IRI of 26). Among these, the only metric exceeding 10% was the frequency of occurrence of ostracods (15%).

Table 3.5.2: List of prey taxa of C. braueri

Crustacea
Unidentified crustaceans
Amphipoda
Unidentified gammarideans
Euphausiacea
Unidentified euphausiids
Ostracoda
Unidentified ostracods

Mollusca
Cephalopoda
Unidentified cephalopods
Teleostei
Unidentified teleosts
Unidentified myctophids

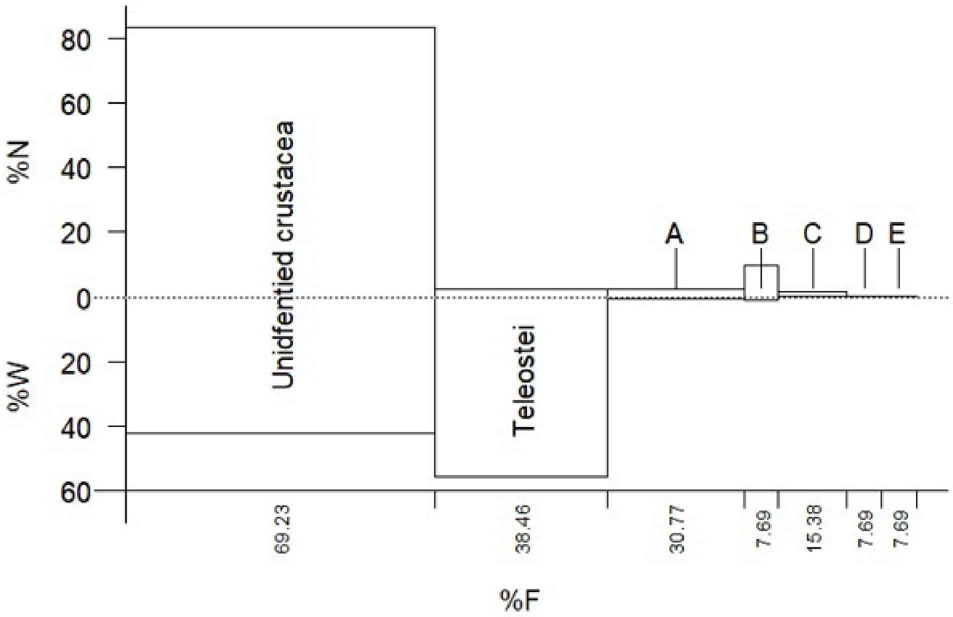

Figure 3.5.1: Prey IRI components of C. braueri (n = 13)*. IRI values for major prey groups are as follows: Unidentified* crustacea *(8674.3),* Teleostei *(2235.4). IRI values for minor groups:* Cephalopoda *(A, 90.6),* Euphausiacea *(B, 82.3),* Ostracoda *(C, 26.2). The remaining prey groups, in descending order of IRI, are as follows:* Gammaridea *(D), Unidentified* amphipoda *(E), all with IRI < 10.*

Unidentified crustaceans also constituted by far the largest prey category by IRI in the stomachs of *C. simorhynchus*, at 2620, while also being the greatest individually by number (34%), mass (26%), and frequency of occurrence (43%). The composition of identifiable crustacean prey groups suggested that gammarid and hyperiid amphipods, hermit crabs, penaeid and carid shrimps, and isopods likely comprised the bulk of this group. There were five major prey categories, the other four being of comparable importance to each other: gammarid amphipods (436), polychaetes (300), ophiuroids (246) and teleost fish (206). Among these four, the most frequently occurring was the ophiuroids (27%), the most numerous were the gammarid amphipods (27%) and the largest percentage mass was represented by the polychaete worms (16%), followed closely by teleosts (12%). Among the six minor prey groups, the anomurans and ostracods were notable for their frequency of occurrence (17% and 10% respectively), the penaeid prawns for their numbers (13%), and the hyperiid amphipods for their contribution to mass (14%).

Some prey items, particularly teleosts, were sufficiently intact to enable more specific identification. Two of the ophiuroids in two stomachs resembled *Ophiura trimeni*, although the majority of ophiuroid prey appeared to be a different species, which it was not possible to determine. Among the polychaetes, one common species was large, thick but short, and had relatively fine chaetae, matching the description of *Chloeia inermis*. A total of 17 specimens of this polychaete were found in 12 stomachs of *C. simorhynchus*. This figure likely accounts for most of the *C. inermis* present in this species, as they were not easily confused with the other much thinner, longer polychaetes. Among the crustaceans, one amphipod individual was placed in genus *Leucothoe*, while a very common anomuran was identified as *Parapagurus pilosimanus*, a hermit crab utilising colonial cnidarians instead of gastropod shells as their retreat. *P. pilosimanus* was present in 22 stomachs and accounted for by 61 specimens, and it seems plausible that most of the unidentified anomurans (those heavily digested or know only from fragments) were also this species.

Among the teleosts, the most commonly identified species was the ladder dragonet *Paracallionymus costatus* (family Callionymidae), with three specimens in two stomachs. Two myctophids (lanternfishes) were found in different stomachs, one of which was identified as *Symbolophorus sp.* One macrourid was found in each of two stomachs, apparently juvenile *C. simorhynchus*, while a different stomach contained the head of a hake (*Merluccius capensis* or *M. paradoxus*). The dragonets and myctophids measured 6–9 cm, while the hake head was estimated to have belonged to a ca. 15 cm specimen. Only one cephalopod beak was able to be identified from *C. simorhynchus* stomachs, belonging to the oegopsid squid *Lycoteuthis lorigera.*

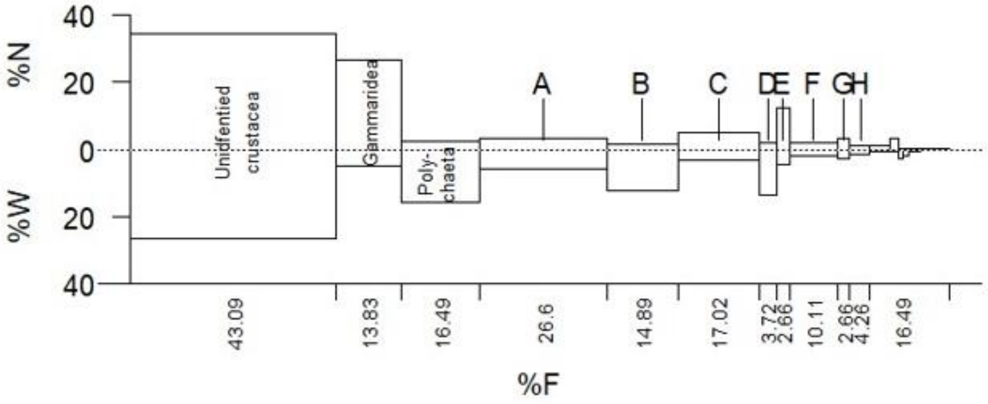

Figure 3.5.2: Prey IRI components of C. simorhynchus (n = 188). *IRI values for major prey groups are as follows: Unidentified* crustacea *(2621.1),* Gammaridea *(435.5),* Polychaeta *(300.3),* Ophiuroidea *(A, 246.3),* Teleostei *(B, 205.9). IRI values for minor groups:* Anomura *(C, 139.8),* Hyperiidea *(D, 59.3),* Penaeidae *(E, 45.8),* Ostracoda*, (F, 39.2),* Caridae *(G, 16.4),* Isopoda *(H, 10.6). The remaining prey groups, in descending order of IRI, are as follows: Unidentified* amhipoda*,* Euphausiaceae*,* Brachyura*,* Stomatopoda*,* Cephalopoda*,* Tanaidae*,* Anthozoa*,* Caprellidea*,* Flabellifera*,* Sergestidae*,* Mysida*, all with IRI <10.*

In *M. laevis* stomachs, two major and five minor prey groups were found. Of the two major groups, teleosts were the larger, with an IRI of 6852; and were also by far the most important by mass (72%). Teleosts also had the highest frequency of occurrence (83%) but were not particularly numerous, comprising less than 11% of all prey items. A number of these teleosts were identifiable to lower taxonomic ranks. The most important prey fish seemed to be other macrourids, identified by seven specimens in four stomachs. Six of these appeared to be *C. simorhynchus* while the seventh was too heavily digested to draw conclusions beyond family level, but was of similar size and shape as the others and is likely of the same species. These were the largest teleosts in *M. laevis* stomachs, and measured 12–18 cm. Two unidentified myctophids and two hake were also found, with each represented in two stomachs. Furthermore, one *Paracallionymus costatus* dragonet was found. One barracudina (family Paralepididae) was also tentatively identified, although its level of digestion prohibited further identification.

Table 3.5.3: List of prey taxa of C. simorhynchus

Cnidaria
  Unidentified anthozoans
Crustacea
  Unidentified crustaceans
  Anomura
  Unidentified anomurans
  Parapagurus pilosimanus
  Amphipoda
  Unidentified hyperiids
  Unidentified gammarideans
  Unidentified caprellids
  Leucothoe sp.
  Caridea
  Unidentified carids
  Decapoda
  Unidentified dromiids
  Euphausiacea
  Unidentified euphausiids
  Isopoda
  Unidentified isopods
  Unidentified flabelliferids
  Unidentified sphaeromatids
  Mysida
  Unidentified mysids
  Ostracoda
  Unidentified ostracods
  Penaeidae
  Unidentified penaeids
  Sergestidae
  Unidentified sergestids
  Stomatopoda
  Unidentified stomatopods
  Tanaidaecea
  Unidentified tanaids
Echinodermata
  Ophiuroidae
  Unidentified ophiuroids
  Ophiura trimeni
Mollusca
  Cephalopoda
  Unidentified cephalopods
  Lycoteuthis lorigera
Polychaeta
  Unidentified polychaetes
  Chloeia inermis
Teleostei
  Unidentified teleosts
  Unidentified myctophids
  Coelorinchus simorhynchus
  Merluccius sp.
  Paracallionymus costatus
  Symbolophorus sp.

The other major group, penaeid prawns (IRI 494), was present in far higher numbers (with 59% making it the most numerous category), but had frequencies and percentage masses of less than 8%. Unlike in the *Coelorinchus* species, unidentified crustaceans made up only the fifth-most important prey group, with an IRI of 94, due to the higher frequency of prey items at low levels of digestion. Among the minor prey groups, relatively abundant categories were squids (39%), ostracods (15%), and unidentified crustaceans (11%), while aristeid prawns contributed a relatively large mass (11%). The four Aristeidae were found in the same stomach and appeared to be the deepwater prawn *Aristeiopsis edwardsiana*.

Of the cephalopod beaks identified from *M. laevis* stomachs, the majority belong to *Lycoteuthis lorigera*, with this species being identified from at least ten beaks. Another common beak (encountered six times) was that of an unknown species in the subfamily Todarodinae, belonging to either *Todaropsis emblanae* or *Todarodes sp*. A squid beak belonging to *Cranchia scabra* was also recovered, along with a beak of the kind possessed by Sepiida. The only polychaete found resembled the ones suggested to be *Chloeia inermis* in *C. simorhynchus* stomachs.

Table 3.5.4: List of prey taxa of M. laevis

Chondrichthyes
- Batoidea
- Unidentified batoid

Crustacea
- Amphipoda
- Unidentified amphipods
- Unidentified hyperiids
- Unidentified gammarideans
- Aristeidae
- *Aristeiopsis edwardsiana*
- Decapoda
- Unidentified decapods
- Ostracoda
- Unidentified ostracods
- Penaeidae
- Unidentified penaeids

Mollusca
- Gastropoda
- Unidentified gastropods
- Unidentified gastropod
- Cephalopda
- Unidentified cephalopods
  - Unidentified cranchiid
  - *Cranchia scabra*
  - Unidentified *Todarodinae*
  - Unidentified *Sepiida*
  - *Lycoteuthis lorigera*

Nematoda
- Unidentified nematodes

Polychaeta
- Unidentified polychaetes
- *Chloeia inermis*

Porifera
- Unidentified sponge

Teleostei
- Unidentified teleosts
- Unidentified paralepididid
- Unidentified macrourid
- Unidentified myctophids
- *Coelorinchus simorhynchus*
- *Merluccius sp.*
- *Paracallionymus costatus*

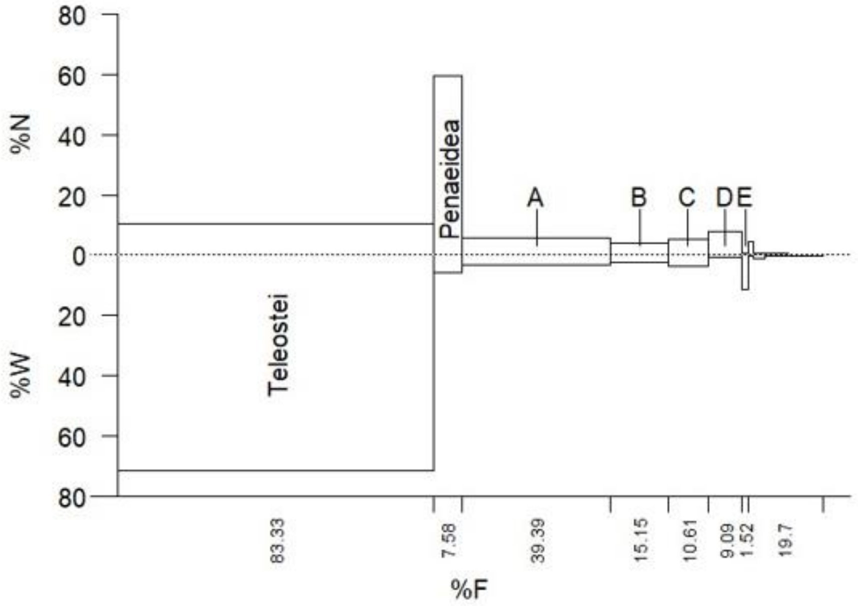

Figure 3.5.3: Prey IRI components of M. laevis (n = 66)*. IRI values for major prey groups are as follows:* Teleostei *(6851.5),* Penaeidea *(493.5). IRI values for minor groups:* Cephalopoda *(A, 340.1),* Ostracoda *(B, 95.9), Unidentified* crustacea *(C, 93.8),* Hyperiidea *(D, 78.5),* Aristeidae *(E, 18.1). The remaining prey groups, in descending order of IRI, are as follows:* Nematoda*,* Polychaeta*,* Porifera*,* Gammaridea*, Unidentified* amphipoda*,* Chondrichthyes*,* Gastropoda*, all with IRI < 10.*

3.6 Reproduction

No relationships between sex as a categorical variable and depth interval were detected in any of the three grenadier species (*Table 3.6.1*). In *C. simorhynchus*, females were considerably more abundant than males. Females comprised about 68% of fish once sexually indeterminate specimens are excluded. *C. braueri* samples also consisted of slightly more females than males, as about 57% were female. Only in *M. laevis* was the sex ratio roughly equal, with 51% females.

Figure 3.6.1 shows plots of sex ratio by depth interval and PAFL interval respectively. Intervals with less than ten specimens, or ones in which all specimens came from the same trawl, were excluded. The only species in which there appeared to be a clear trend with depth is *C. braueri*, in which the sex ratio dropped by over 25% between 250 to 300 m and 500 to 500 m, suggesting females may have been more common in shallower depths. All three species, conversely, showed a clear trend of increasing sex ratio (proportion females) with increasing PAFL.

Table 3.6.1: Results of Fisher's exact tests of sex and depth interval, frequencies of sexes, and sex ratios (% females).

	p-value	**Female**	**Male**	**Indeterminate**	**Sex ratio (%)**
C. braueri	> 0.05	25	19	20	56.8
C. simorhynchus	> 0.05	204	97	17	67.8
M. laevis	> 0.05	61	59	14	50.8

Plots of sex ratio by coast also show marked differences: the sex ratio of *C. braueri* on the south coast was more than twice that of the west coast, while the pattern was essentially reversed in *C. simorhynchus*, with females being twice as common on the west coast. No comparison of this type was possible for *M. laevis*, as none were captured on the south coast.

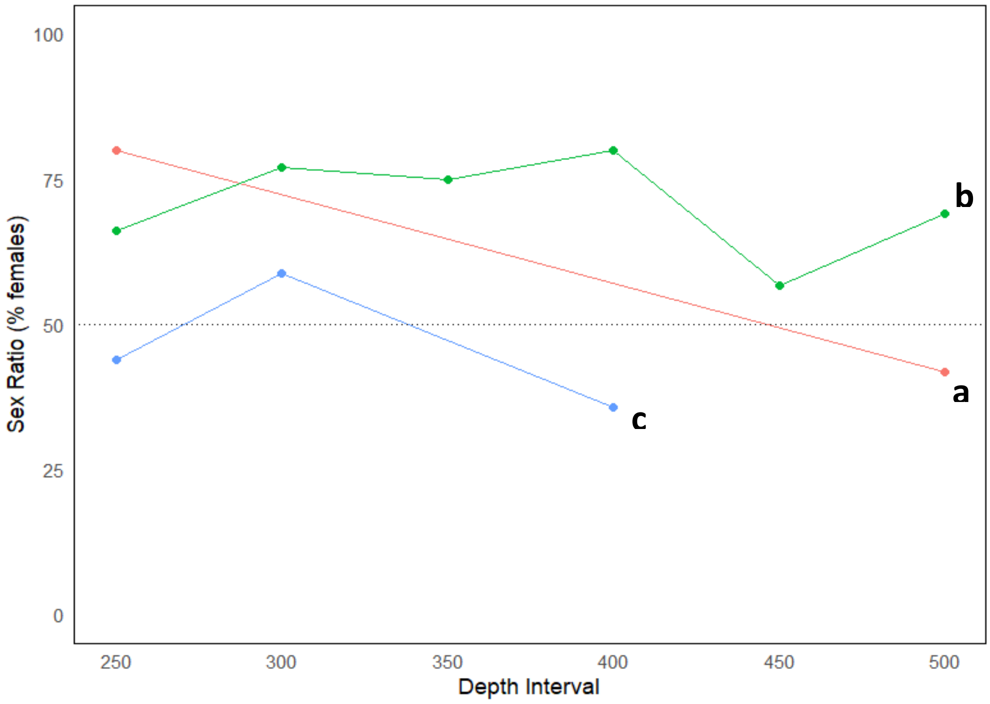

Figure 3.6.1: Sex ratios (females as a percentage of sexually determinate fish) by 50 m depth intervals for (a) C. braueri, *(b)* C. simorhynchus, *(c)* M. laevis. *Only intervals with n ≥ 10 are shown.*

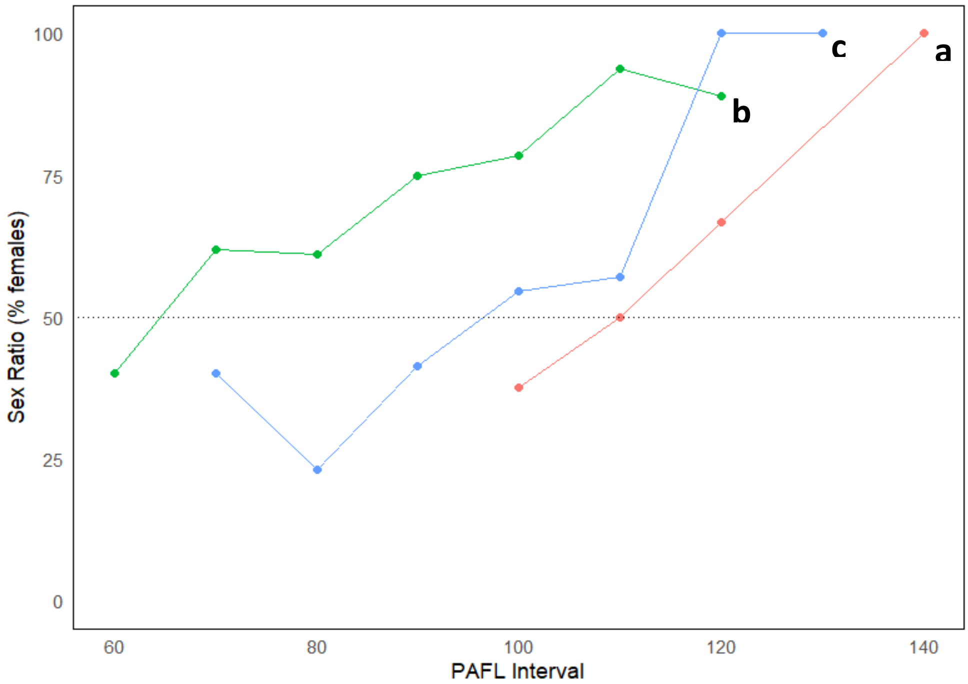

Figure 3.6.2: Sex ratios (females as a percentage of sexually determinate fish) by 10 mm intervals of pre-anal fin length for (a) C. braueri, *(b)* C. simorhynchus, *(c)* M. laevis. *Only intervals with n > 5 are shown.*

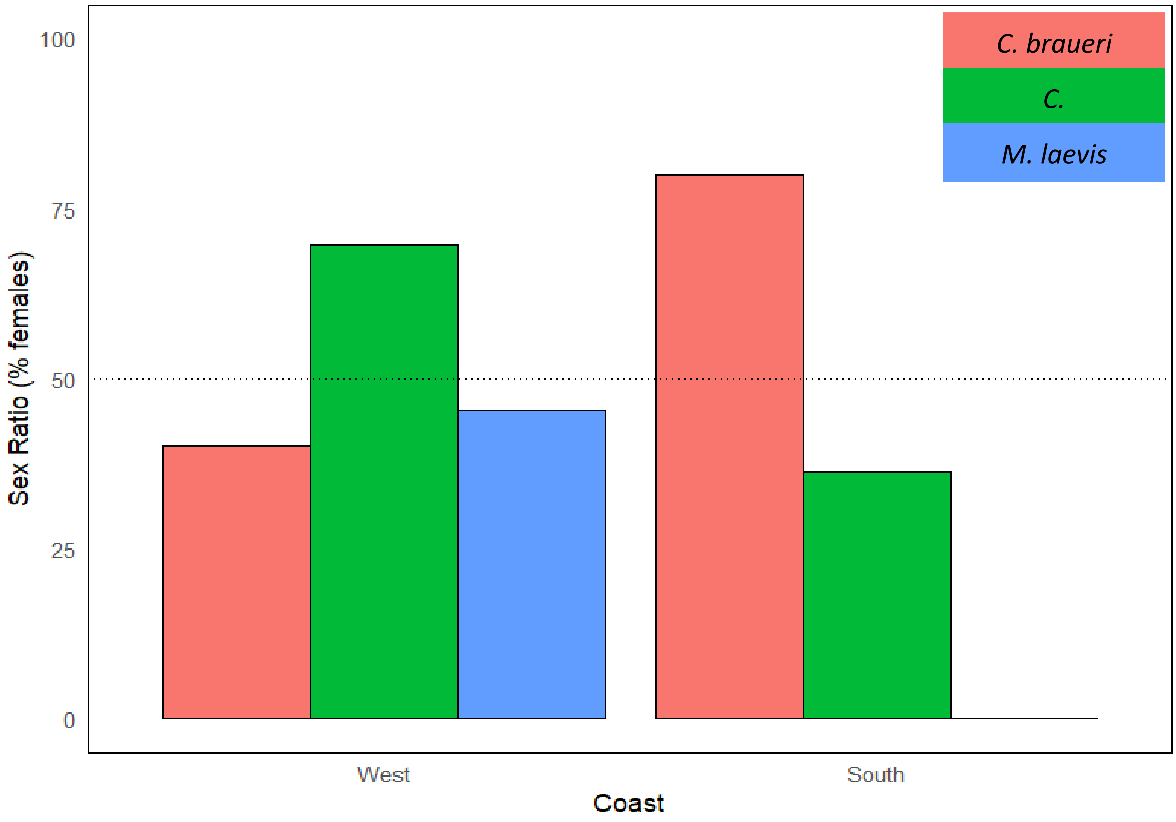

Figure 3.6.3: Sex ratios (females as a percentage of sexually determinate fish) by coast.

Representative examples of all phases found are given in *Figure 3.6.4*, although it is worth noting that these gonads had previously been preserved in formalin for over a year in some cases, and may not match fresh gonads in colour, particularly those of *M. laevis*.

Coelorinchus ovaries were generally beige to orange-yellow, with phase 1 and phase 2 ovaries often covered by a dark lattice of connective tissue. Vascularisation in these species was usually poorly developed, often visible only in phase 4. In some cases, phase 1 and phase 5 gonads appeared very similar; the length of the fish was taken into account when assigning these reproductive phases. Naturally, ovary size was an important determinant in assigning reproductive phase, with phases 3 and 4 being the largest, followed by phase 2 and phases 1 and 5. However, ovary size must be considered relative to the size of the fish it originated from — a phase 2 ovary from a very large fish could be larger than a phase 3 ovary from a fish in its first reproductive season, for example. This could be seen in *Figure 3.6.8c*, in which the phase 4 ovary came from a much larger individual than the phase 3 ovary, and is therefore more than twice its size. In Ovaries of phases 3 and 4 from comparably sized specimens were similar in size, but phase 4 ovaries often appeared smaller due to their flaccid nature. This also applied to *M. laevis* ovaries.

The following characteristics were used to assign macroscopic phases in females, and are applicable to both *C. braueri* and *C. simorhynchus.* Phase 1: Ovaries were round but not turgid, off-white in colour and usually covered by a grey or brown covering of connective tissue. Phase 2: Ovaries were turgid but with no oocytes visible from an external perspective, darker in base colour and often with darker connective tissue covering it. Phase 3: Ovaries were completely turgid, evidently brown to yellow in colour, with no connective tissue or only small remnants thereof; vascularisation could be present but usually weak; oocytes were clearly visible from the outside of the ovary. Phase 4: Ovaries were flaccid or partially flaccid. Vascularisation could be visible fairly clearly in this phase. Some oocytes could be visible externally, but not as densely as in phase 3. Connective tissue could sometimes be seen, but not very dense if it was present. Phase 5: Ovaries were flaccid, similar in colour and appearance to phase 1.

Coelorinchus males were more difficult to stage macroscopically than females. Testes did not undergo noticeable changes in colour or presence of connective tissue between phases. Instead, testes are generally off-white and relatively free of connective tissue or vascularisation in all phases, with only their turgidity and shape changing from phase to phase. Phase 1: Testes were elongated, straight, flaccid, and stringlike. Phase 2: Testes were rounded and curled inward, but still flaccid. Phase 3: Testes were turgid and strongly curled, somewhat resembling a pair of wings in shape; only in this phase did they approach the triangular cross-section that often describes fish testes. Phase 4: Testes were similar in shape to those in phase 3, but completely flaccid. Testes in this phase were typically only 1–2 mm thick. Phase 5: Testes resembled those in phase 1, but generally larger and even more elongated. Generally, the size of the testes was far less dependent on the length of the individual than that of ovaries in the same species, so that the size of the testes was also a reasonably good indicator of reproductive phase. While the testes were longest in phase 5, the overall largest and heaviest testes were found in phases 3 and 4. No milt release was observed on applying pressure to the testes in any of the specimens, although this may be a consequence of barotrauma or the freezing process; its presence would have been taken as indicative of phase 3.

Differences in ovarian reproductive phases in *M. laevis* were less apparent than in females of the *Coelorinchus* species, with colour changes in the ovaries being far more subtle. In general, ovaries of this species are off-white with occasional pink areas, with no connective tissue covering them in any phase. There is a slight darkening in phase 3 (and to a lesser extent phase 4) due to the orange oocytes being visible externally. These differences are most apparent during dissection, as colour becomes more uniformly off-white in formalin. Vascularisation was more obvious in this species than in *Coelorinchus*, but only during dissection. *Malacocephalus* blood vessels faded to a far greater extent than those of *Coelorinchus* when preserved in formalin, although the shape of the larger blood vessels could sometimes still be noticeable even when the colour had faded from red to white. Phase 1: No ovaries of this phase were found, as all ovaries were either too turgid (and hence staged as phase 2) or came from large specimens (and were assigned to phase 5), but were speculated to be essentially identical to phase 5. Phase 2: Ovaries were turgid and round, without visible oocytes. Phase 3: Ovaries were turgid, with externally visible orange oocytes giving a darker appearance, vascularisation occasionally present. Phase 4: Ovaries were flaccid or partially so, with occasional oocytes still visible. Vascularisation was not always present, but could be extremely clear in larger ovaries during this phase. Phase 5: Ovaries were rounded and completely flaccid, with no oocytes or vascularisation.

Testes of *M. laevis*, were staged similarly to those of *Coelorinchus* males, although their overall shape was often harder to discern due to testes being discontinuous with constrictions between sections, which were often coiled at angles to each other, possibly due to damage during capture or the freezing process.

Figure 3.6.4: Examples of formalin-preserved ovaries (left) and testes (right) of C. braueri *(a, b),* C. simorhynchus *(c, d), and* M. laevis *(e, f) at each reproductive phase (1-5 from left to right). No phase 1 female* M. laevis *were found. All scale bars 20 mm.*

Gonad mass increased non-linearly with total mass. Slopes of log-log regression models of gonad mass by total mass were all significant at $p < 0.0001$ and significantly higher than one (i.e. all slopes ≥ 1 + 1.96*SE). Only females were considered, as males had very small gonad masses relative to total mass, which were not nearly as variable between gonad development phases compared to females. Model fit was good in *C. braueri* and *M. laevis*, but poor in *C. simorhynchus* (*Table 3.6.2*). HSI did not have a linear relationship with body mass (all $R^2 < 0.15$).

Table 3.6.2: Linear regressions of the log of female gonad mass by the log of total mass.

	Estimate	**SE**	**p-value**	**R^2**
C. braueri				
Intercept	-12.40	1.02	< 0.0001	0.88
Slope	2.69	0.21	< 0.0001	
C. simorhynchus				
Intercept	-7.34	0.49	< 0.0001	0.60
Slope	1.78	0.10	< 0.0001	
M. laevis				
Intercept	-11.44	0.67	< 0.0001	0.87
Slope	2.23	0.11	< 0.0001	

Based on the macroscopic identifications of reproductive phases, both sexes across the three species showed a distinct GSI peak in phase 3, with this pattern being more pronounced in the females (*Figure 3.6.5*). Phases 1 and 5 typically had the lowest GSI values. GSI in females typically varied between 1 to 10%, but reached as high as 15% in *M. laevis*. Male GSI values were lower, barely reaching 1% in phase 3 *C. simorhynchus* and *M. laevis*, and never exceeding 0.3% in *C. braueri*. No female phase 1 *M. laevis* were captured.

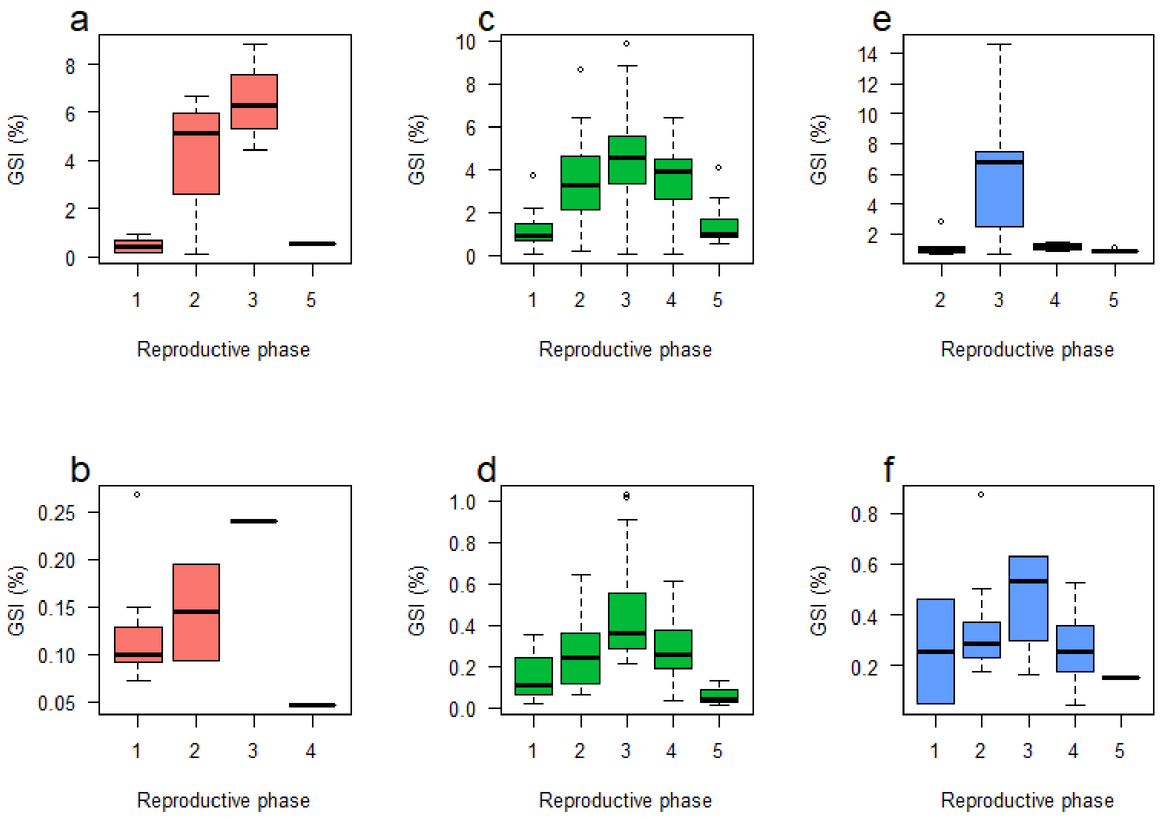

Figure 3.6.5: Plots of gonadosomatic index (GSI) across the five reproductive phases for C. braueri females (a) and males (b), C. simorhynchus females (c) and males (d), and M. laevis females (e) and males (f).

About 25% of *C. braueri* were in phase 3 during both autumn and winter (*Figure 3.6.6a*). Female GSI in this species also peaked in winter (*Figure 3.6.7a*). Phase 3 *C. simorhynchus* were captured throughout the year (*Figure 3.6.6b*), but most commonly in spring, although the GSI of females of this species reached its highest value in winter (*Figure 3.6.7a*). *M. laevis* similarly occurred in phase 3 in all seasons, with this phase comprising about 50% of all fish in all seasons except winter (*Figure 3.6.6c*). The female GSI reached its highest values in summer in females of this species (*Figure 3.6.7a*). In males of all three species, average GSI values did not vary much throughout the year (*Figure 3.6.7b*).

Generally, differences in GSI by season were not significant; the only differences were found among females of *C. braueri* and *C. simorhynchus*. In *C. simorhynchus*, GSI was significantly higher in winter than in autumn ($p < 0.001$). Winter GSI was also higher than in autumn in *C. braueri* ($p < 0.05$), although this comparison was also the only possible one that can be made, given that *C. braueri* was only captured in autumn and winter.

In females, mean GSI was highest in *C. simorhynchus* (3.7%), followed by *C. braueri* (3.2%) and *M. laevis* (2.6%), with all differences being significant ($p < 0.001$). In males, *C. simorhynchus* and *M. laevis* had similar mean GSI (both 0.3%) while the mean GSI of *C. braueri* was significantly lower at 0.2% ($p < 0.001$). When comparing gonadosomatic indices across all seasons and reproductive phases, in females only one set of comparisons was significant ($p < 0.001$), namely *C. simorhynchus* having a greater GSI than *M. laevis* (*Table 3.6.3)*. In males, the GSI of *C. braueri* was significantly lower than that of *C. simorhynchus* and *M. laevis* (both $p < 0.001$).

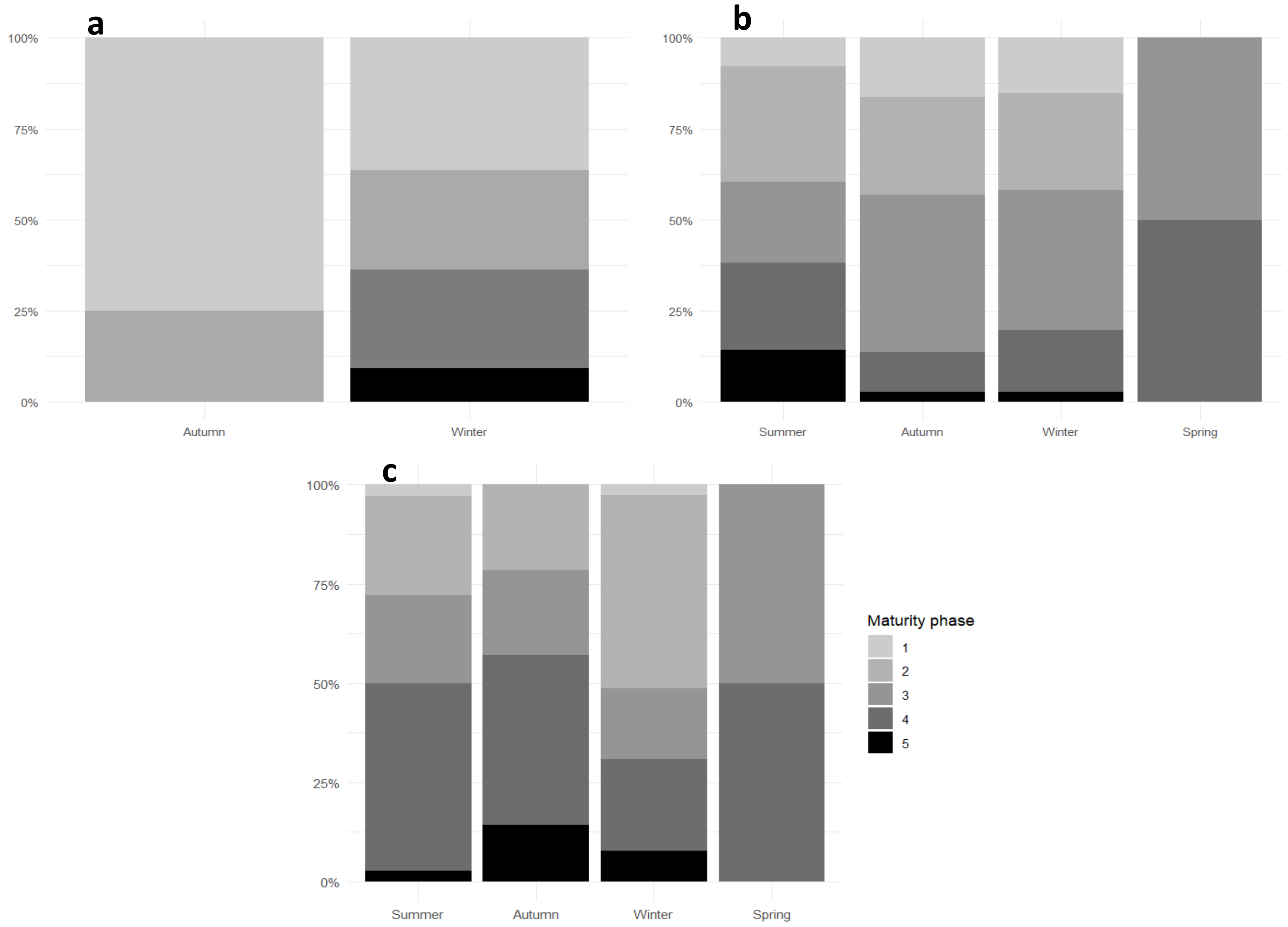

Figure 3.6.6: Frequency of gonad maturity phases by season for (a) C. braueri*, (b)* C. simorhynchus*, (c)* M. laevis*.*

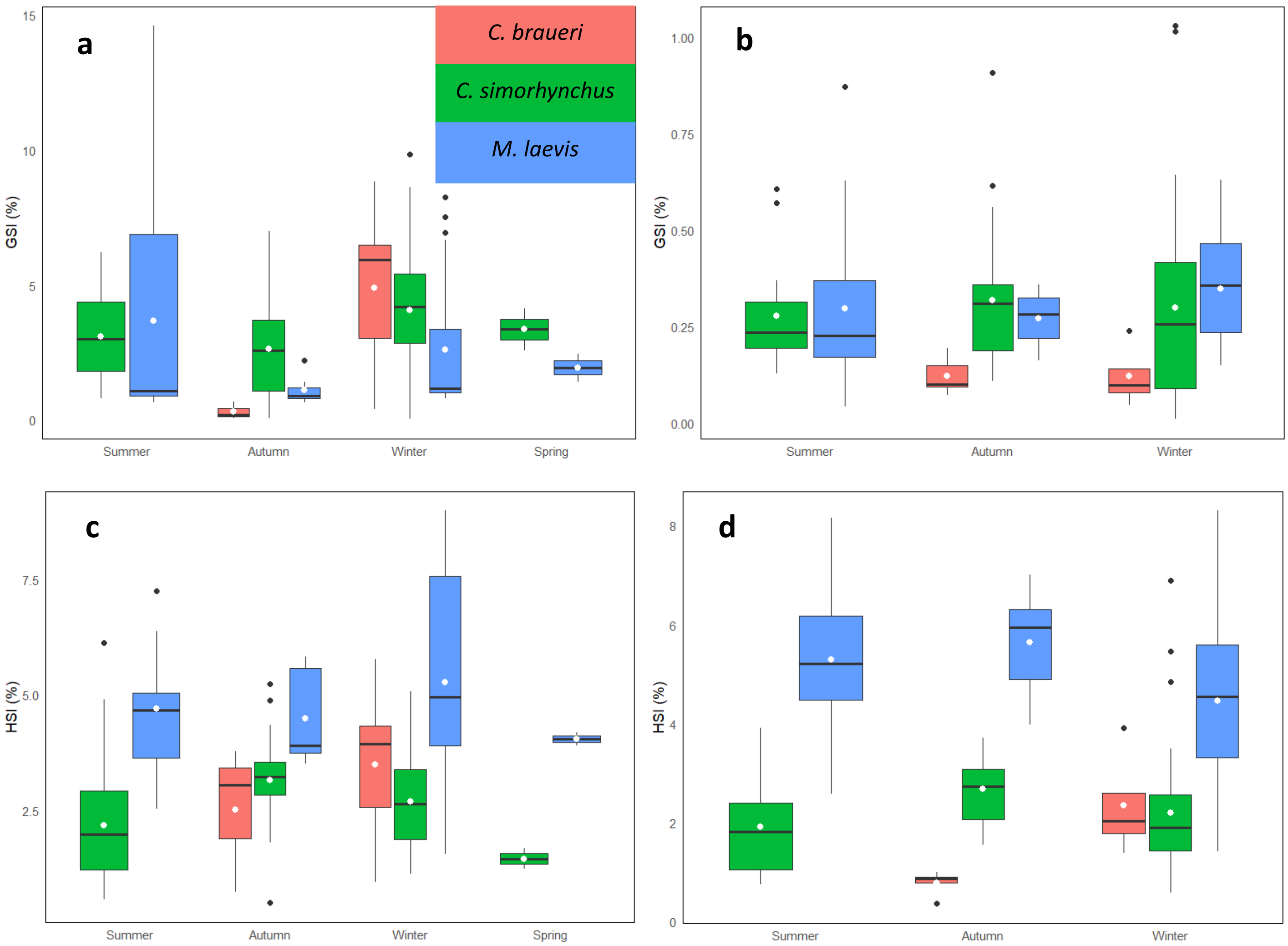

Figure 3.6.7: Boxplots of gonadosomatic (GSI) and hepatosomatic (HSI) indices for females (a, c) and males (b, d) across different seasons for C. braueri, C. simorhynchus, and M. laevis. Black bars give medians, white dots represent means.

Table 3.6.3: Results of Dunn's post hoc comparison p-values of gonadosomatic index (GSI) by species.

	C. braueri	***C. simorhynchus***
Females		
C. simorhynchus	> 0.05	-
M. laevis	> 0.05	< 0.001
Males		
C. simorhynchus	< 0.001	-
M. laevis	< 0.001	> 0.05

In both females and males, median HIS values did not differ significantly among gonad phases for any of the three species (all $p > 0.05$). No significant linear relationships between GSI and HSI were detected in any species in females or males (all $R^2 < 0.15$), including in models in which only phase 3 (ripe) gonads were considered.

Diameter ranges of oocyte stages in *C. simorhynchus* and *M. laevis* are given in *Table 3.6.4*. These were not exhaustive, being based on a handful of measurements from gonad tissue sections examined histologically, and should be taken only as rough guidelines when examining ovaries in these species. As a result, these ranges were likely conservative, with the true upper and lower bounds being higher and lower, respectively, for each stage, to the point where diameter ranges of consecutive stages would overlap (e.g. as can be seen in primary growth oocytes and cortical alveoli oocytes of *M. laevis*). Oocyte diameters at each stage of cell development were roughly similar in *C. simorhynchus* and *M. laevis*.

Ovaries of *C. simorhynchus* contained oocytes in various stages of development (e.g. *Figure 3.6.8b, c*), with no clear patterns of adjacent oocytes forming distinct clutches. Ovarian development was therefore asynchronous.

Table 3.6.4: Oocyte size ranges at various stages of cell development in C. simorhynchus *and* M. laevis

	Oocyte diameter (µm)	
	C. simorhynchus	*M. laevis*
Primary growth	30-108	29-88
Cortical alveoli	125-196	78-118
Early vitellogenic	166-343	118-157
Advanced vitellogenic	303-490	147-539
Germinal vesicle migration	490-784	392-882
Hydrated		805-931

In *M. laevis*, oocyte development is more uniform, with ovaries containing a noticeable clutch of similarly developed oocytes as well as less developed oocytes in the primary growth or cortical alveoli stages (e.g. *Figure 3.6.9b*). In addition, hydrated oocytes co-occurred with advanced vitellogenic and germinal vesicle migration oocytes in this species, suggesting that not all yolked oocytes are hydrated and released simultaneously. *M. laevis* was therefore described as a likely group-synchronous batch spawner. Atresia was common in all ovaries which contained post-ovulatory follicles.

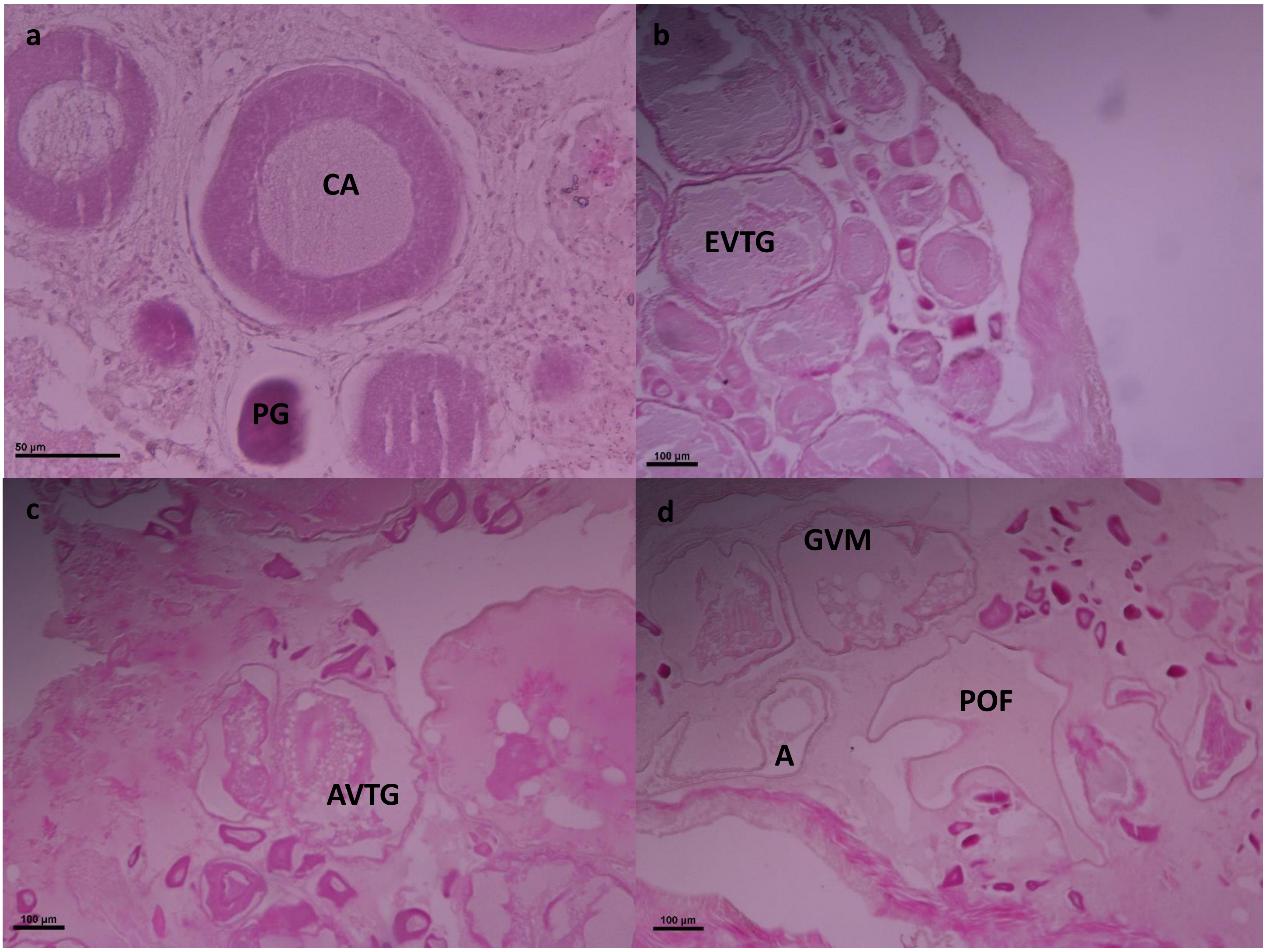

Figure 3.6.8: Ovarian tissue of C. simorhynchus in different reproductive phases*. (a) Phase 2, (b) Phase 3, (c) Phase 3 (advanced), (d) Phase 4. PG – Primary growth, CA – Cortical alveoli, EVTG – Early vitellogenic, AVTG – Advanced vitellogenic, GVM – Germinal vesicle migration, POF – Post-ovulatory follicle, A – Atretic oocyte*

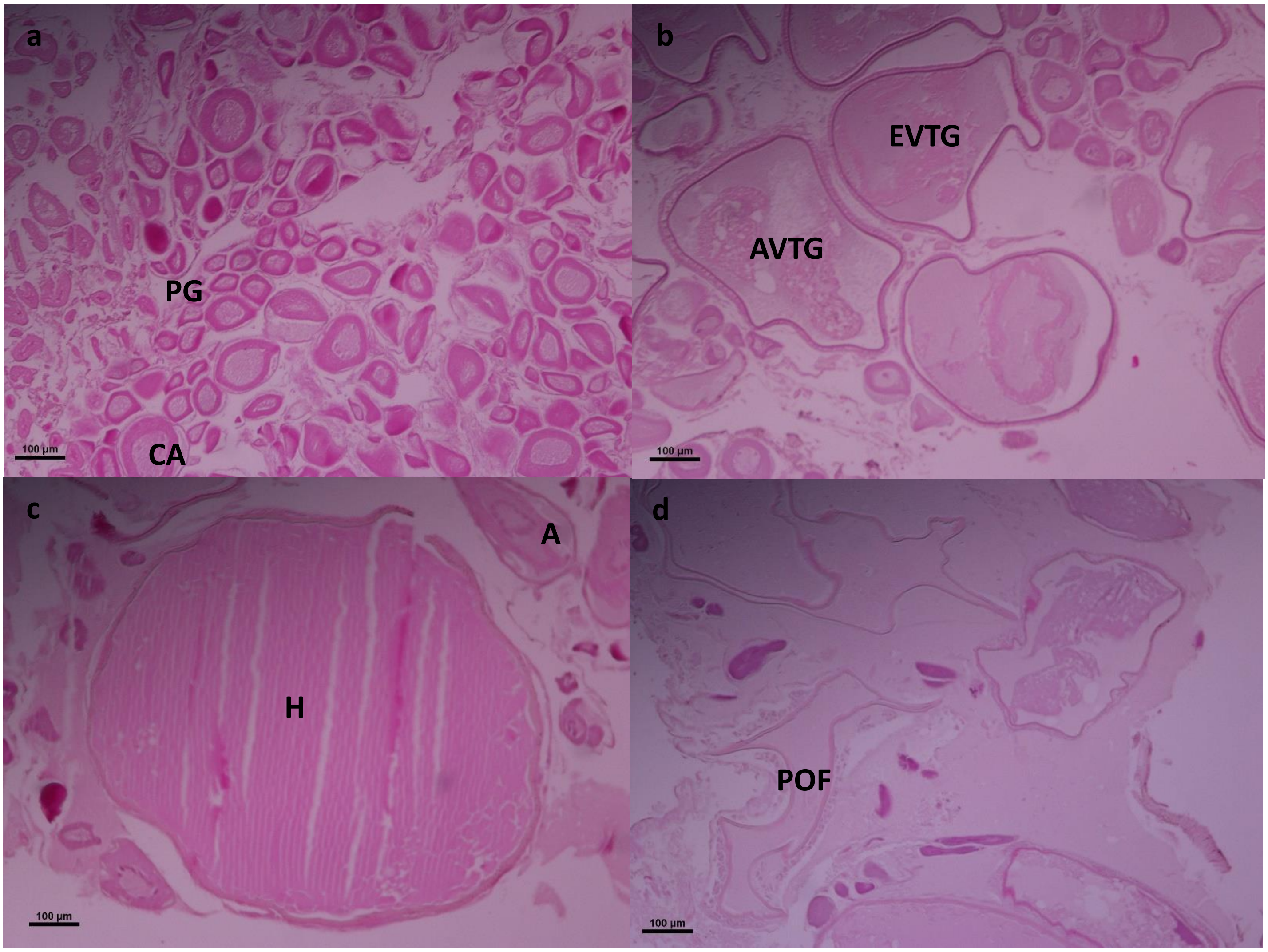

Figure 3.6.9: Ovarian tissue of M. laevis in different reproductive phases. *(a) Phase 2, (b) Phase 3, (c) Phase 3 (advanced), (d) Phase 4. PG – Primary growth, CA – Cortical alveoli, EVTG – Early vitellogenic, AVTG – Advanced vitellogenic, H – Hydrated, POF – Post-ovulatory follicle*

3.7 Parasites

Eight *C. simorhynchus* and one *C. braueri* were found to be parasitised externally by sphyriid copepods. These were identified in all cases as *Sphyrion quadricornis.* One further *C. simorhynchus* had two lesions consistent with those suffered during *Sphyrion* attachment, and was assumed to have been parasitised as well. The majority of parasitised fish were beset by one or two copepods, although one individual numbered seven and another three. Attachment occurred dorsally and laterally on the trunk of the fish, posterior to the paired fins (*Figure 3.7*).

A total of 40 specimens were parasitised by chondracanthid copepods. The hosts were primarily *M. laevis*, although three *C. braueri* were also affected. Those in *M. laevis* specimens were a good match for *Chondracanthus neali,* a known parasite of *M. laevis*. Those in *C. braueri* were in poor condition but closely resembled *C. neali*. Of the three parasitised *C. braueri*, one specimen was also observed to host *S. quadricornis*, being the only fish on which both copepods were found. These copepods were found exclusively in the gill cavities, usually parasitising both gills of an individual although 13 specimens were found to contain only a single parasite. Mean parasite load among affected fish was 2.7, with one *M. laevis* specimen containing as many as 20 parasites.

Figure 3.7: Two S. quadricornis *copepods attached laterally, posterior to the base of the pectoral fin of a* C. simorhynchus individual.

Concerning endoparasites, a total of 31 fish across all three species contained nematodes either loosely in the abdominal cavity or embedded in or on the organs. These nematodes did not appear distinct in the different macrourids, and were not identified, although they visually resembled *Anisakis spp.* common to many fish species. A further 23 specimens across all three species contained what appeared to be white cestodes; these occurred singly or in pairs towards the posterior of the abdominal cavity, in all cases unattached. In 45 fish, primarily *C. simorhynchus* but also in two *C. braueri* and two *M. laevis*, the abdominal cavity and organs were covered in what appeared to be pinhead-sized cysts; these were particularly common among the liver, stomach, and pyloric caeca. These cysts rarely co-occurred with nematodes or cestodes, but were most often found among otherwise unparasitized fish.

Parasite load was not quantified for internal parasites due to the ease with which they may be missed when embedded in soft organs (e.g. gonads, liver) and the difficulty distinguishing between intestinal parasites and those of the abdominal cavity when the gut is ruptured, as was the case in many fish. Gut parasites were occasionally noticed within the intestine, but not recorded.

The same nematodes found in the abdominal cavity were also found to be present during stomach dissections. A total of five *C. braueri*, 39 *C. simorhynchus*, and 13 *M. laevis* contained nematodes cf. *Anisakis*, while two *C. simorhynchus* contained a different, longer species of nematode. One *M. laevis* stomach contained 30 perfectly straight nematodes of a third species; however, due to their number and lack of attachment to the interior of the stomach, they were assumed to have been free-living and interpreted as part of the *M. laevis* diet (*Figure 3.5.3*).

4. Discussion

4.1 Distribution

The maps of the distribution of macrourid abundance and biomass show that grenadiers, particularly *C. simorhynchus* and *M. laevis*, are caught in all areas exploited by the South African offshore trawl fishery. These two species are known to comprise an important fraction of trawl discards in the west coast trawl fishery. *C. simorhynchus* constitutes between 12.7% and 26.1% of discards by number, depending on the depth interval considered. *M. laevis* is less abundant in discards, constituting between 0.9% and 3.5% (Walmsley *et al*., 2007).

Proportional normalised abundance and biomass of *M. laevis*, relative to the other two species in trawl samples, are generally higher in grid squares on the west coast than on the south coast. However, the absolute normalised abundance of *M. laevis* is higher on the south coast than on the west coast, and *M. laevis* has the lowest absolute abundance on the west coast among the three species. The greater proportion of *M. laevis* relative to the *Coelorinchus* species on the South African west coast contrasts against distribution data from the Atlantic coast off Namibia (Sobrino *et al*., 2012), where *M. laevis* yields from Namibia are considerably lower than those of *C. braueri* and *C.*

simorhynchus. In Namibia, the proportions are more extreme, with *M. laevis* yields being less than 1% of the combined yields of *C. braueri* and *C. simorhynchus*. The South African distribution data differs from that of Namibia in that *C. braueri* is not more common than *C. simorhynchus* on the South African west coast, whereas in Namibia *C. braueri* is over six times as common in trawl catches than *C. simorhynchus*. These comparisons show that the grenadier community composition varies strongly between the South African west and south coasts, as well as between the South African west coast and the Namibian coast.

The Namibian study by Sobrino *et al*. (2012) sampled down to 2000 m, far deeper than the South African surveys. As *C. braueri* is abundant between 800 and 1000 m, its abundance is inflated when considering the full depth range on the Namibian coast. However, even considering only depths shallower than 800 m, *C. braueri* is still more than four times as common as *C. simorhynchus* in Namibia. Unfortunately, no distribution data exist for the South African west or south coast for the sake of comparison. Differences between the South African and Namibian west coasts may potentially be attributed to the fact that they belong to the Southern and Northern Benguela systems respectively, whose upwelling cycles respond differently to climate events such as the El Niño Southern Oscillation (Rouault & Tomety, 2022). Further research is needed to determine the distribution and habitat preferences of these common grenadier species in Southern Africa.

The higher abundance and biomass of both *Coelorinchus* species on the south coast compared to the west coast could potentially be attributed to the higher oxygen content at depth on the Agulhas Bank (Hutchings, 1994) allowing for higher metabolic rates. Dissolved oxygen (DO) concentrations below 50 m on the Agulhas Bank average 4–5 ml/l (Chapman & Shannon, 1987), whereas off St Helena Bay on the west coast, they are reported as 1–2 ml/l at depths of 50–100 m (Pitcher & Probyn, 2017). Higher metabolic rates benefit predatory fishes that lead an active lifestyle. Grenadiers are not ambush predators (Priede *et al*., 1990), and likely cover large distances in search of prey aided by their well-developed chemoreceptive abilities (Yeh & Drazen, 2011). Due to this active hunting strategy, coupled with the inefficient sinusoidal movement inherent to their body shape, it can be assumed that their metabolic requirements are higher than other deep-sea demersal predatory fish such as *Helicolenus dactylopterus* or *Lophius vomerinus*. The importance of dissolved oxygen content is known to limit the distribution of some grenadiers, such as *Coelorinchus scaphopsis* in the Gulf of California (Cruz-Acevedo & Aguirre-Villaseñor, 2020). Other factors, such as temperature, body mass, and hunting method, are known to play a role in determining metabolism in deep-sea fishes, suggesting that the drivers of metabolism of South African grenadiers are likely more complex (Drazen & Seibel, 2007).

However, oxygen concentration would not explain the higher biomass of *M. laevis* on the west coast, where it is 8% greater than on the south coast. As the largest of the three species, and based on the high IRI of mobile prey such as fish and squid in its diet, *M. laevis* would likely benefit most from increased oxygen availability. It is possible that *M. laevis* may be adapted to lower oxygen environments to a greater extent than the two *Coelorinchus* species, allowing it to thrive on the west coast. Low-oxygen adaptations have been observed in grenadier species such as *Coryphaenoides anguliceps* and *C. capito* in the Pacific (Cruz-Acevedo & Aguirre-Villaseñor, 2020).

The west coast is characterised by higher biological productivity (Hutchings, 1994) than the south coast due to upwelling generated by prevailing easterly offshore winds. Additionally, the influx of fish larvae carried to the west coast by the Agulhas current (Largier *et al*., 1992), supports a high forage-fish biomass, which sustains pelagic, and ultimately benthic production.

Fishing pressure has historically been higher on the west coast due to topographic difficulties in trawling large areas of the shelf on the Agulhas Bank (Hutchings, 1994). Higher fishing pressure on the west coast could explain the lower abundances of all three species in this area, as well as the lower biomass of the *Coelorinchus* species. It seems unlikely that the higher biomass of *M. laevis* on the west coast could be explained plausibly in terms of a greater capability in avoiding fishing mortality, given that its peak biomass occurs in a heavily trawled depth interval and its tissue is very watery and soft, suggesting that it is likely a slow-swimming species.

Perhaps, due to a lower average trophic level in the *Coelorinchus* species, these species prefer the south coast in spite of its lower level of productivity. Analysis of the relative magnitude of the effects of fishing effort and primary productivity on hake in the Southern Benguela (west coast) system has shown that demersal fish stocks are controlled through a combination of top-down and bottom-up processes, although fishing seems to be the more dominant driver (Mackinson *et al*., 2009). Cape hake *Merluccius capensis* have a higher trophic level on the south coast due to a higher dietary importance of fish than on the west coast (Pillar & Wilkinson, 1995). However, in some demersal predatory fish west coast populations exhibit greater sizes and growth rates than on the south coast, such as the white stumpnose (Attwood *et al*., 2010). Thus, species-specific responses to primary productivity differences between the west and south coast could explain why *M. laevis* biomass is higher on the west coast whereas that of the *Coelorinchus* species is higher on the south coast.

Predation may also play a role in explaining the greater biomass of *M. laevis* on the west coast, in spite of the lower abundance. Large demersal predators such as chondrichthyans are known to be more abundant, diverse, and influential in structuring the community on the Agulhas Bank compared to the west coast (Smale, 1992). A number of South African cartilaginous fish species consume macrourids, including species of Rajidae (Ebert *et al*., 1991), Squalidae (Ebert *et al*., 1992), and the sixgill shark *Hexanchus griseus* (Ebert, 1994). Another potentially important predator is *Lophius vomerinus*. Walmsley *et al*. (2005) calculated an IRI of *C. simorhynchus* in adults of this monkfish species as ten times greater on the west coast than the south coast. *C. braueri* and *M. laevis* were found only in west coast *L. vomerinus* stomachs (Walmsley *et al*., 2005; Beukes, 2020). Skates and *L. vomerinus* are important demersal predators of fish along both coasts (Smale, 1992).

While *L. vomerinus* presents an example of elevated predation on the west coast, rather than the south coast, it does demonstrate how predator-prey interactions may differ between areas in which the same species are present. It is therefore not implausible that predators, particularly sharks and skates, target adult *M. laevis* on the south coast more frequently than on the west coast, restricting the abundance of large adults. Furthermore, *M. laevis* itself may be partially responsible for the lower abundance and biomass of the *Coelorinchus* on the west coast. Smale (1992) identifies it as an influential deep demersal fish predator in their assessment of west coast trophic relations, but do not mention it for the south coast. *M. laevis* were found to prey on *C. simorhynchus* in this study.

The higher *M. laevis* biomass and greater average size on the west coast could theoretically be a result of ontogenetic westward migration of recruits from the south coast. This seems unlikely, however, given that the documented fish migrations in South African waters typically involve egg or larval dispersal from the Agulhas Bank to nurseries on the productive Atlantic coast, followed by older fish returning south and east to spawn. The majority of fish migration studies in South African waters have focused either on this westward movement of pelagic fish eggs from spawning grounds on the Agulhas Bank by jet currents (e.g. Hutchings *et al*., 2002; Roel *et al*., 1994), seasonal inshore-offshore migrations in commercially important species (Japp *et al*., 1994) or vertical migrations (e.g. Pillar & Barange, 1995).

A range of possible factors have been considered here in attempting to explain the high biomass of *M. laevis* on the west coast in spite of its low abundance, including oxygen concentrations, productivity, predation, and ontogenetic migration. In the absence of concrete data on environmental preferences and tolerances, as well as detailed analysis of the ecology of *M. laevis*, none of these speculative explanations can be confirmed. It is also possible that variation in biomass of *M. laevis* between the west coast and south coast may be attributed to a more complex combination of abiotic and biotic factors. This was the conclusion drawn by Stefanescu *et al*. (1992) to explain differences in size of grenadiers *Coryphaenoides guentheri* and *Chalinura mediterranea* between the Atlantic and Mediterranean sea, which were attributed to a complicated "combination of factors of disparate origin".

The peak in abundance of *C. braueri* at between 700 and 800 m also matches the results from the Namibian coast, where this species achieves greatest abundance between 600 and 800 m, although no Namibian *C. braueri* were found at depths shallower than 400 m (unlike in South Africa). Namibian *C. simorhynchus* were only found between 400 and 600 m, whereas in South Africa they peaked in abundance between 100 and 300 m. *M. laevis* along the African Atlantic coast were also most abundant at 400 and 600 m according to Sobrino *et al*. (2012), a depth range that represents some of the lowest abundances in South Africa. It is clear that depth preferences in these macrourids are not consistent between South Africa and Namibia. Therefore, data on abundance and biomass, as well as any potential size-depth patterns, should not be generalised across their entire geographic range.

Iwamoto and Anderson (1994) report a minimum depth of 455 m for *C. braueri,* and Cohen *et al*. (1990) similarly place the minimum depth at 457 m, whereas here it is recorded in the much shallower 200 to 300 m interval. Similarly, both Iwamoto and Anderson (1994) and Cohen *et al*. (1990) record *M. laevis* between 200 and 1000 m, while here it was also present in the 100 to 200 m interval. *C. simorhynchus*, here reported from 100 to 800 m, matches well with Iwamoto and Anderson's 139 to 986 m, while Cohen et al. (1990) report *C. fasciatus* as shallow as 73 m, although it is unclear whether this refers specifically to misidentified South African *C. simorhynchus* or actual *C. fasciatus* from elsewhere. Depth ranges estimated from South African trawl data place extend the bathymetric ranges of *C. braueri* and *M. laevis* to shallower depths than previously reported, while the depth range of *C. simorhynchus* was found to agree with the published data.

4.2 Morphometrics

Broken snouts occurred only in *C. braueri* (while *C. simorhynchus* snouts were occasionally damaged, their much shorter snouts made differences in length negligible). Accounting for snout breakage is important when taking length measurements in this species, particularly partial measurements such as pre-anal fin length or head length, as the snout can make up 30-40% of the HL. Broken tails occurred most frequently in *M. laevis*, potentially due to their softer, unscaled flesh and their longer and thinner tails compared to the *Coelorinchus* species. PAFL accounts for only 19% of total length in *M. laevis*, but 27-32% in the two *Coelorinchus* species.

Estimations of the TL of grenadiers are based on either the PAFL or HL (e.g. Atkinson 1991, Swan & Gordon, 2001), although the former is more common. Both metrics are linearly related to TL in grenadiers, as well as to each other (Massutí *et al*., 1995). A third metric, pre-anal length, is used occasionally (e.g. Moranta *et al*., 2007), but this is inadvisable as barotrauma can expand or distort the anus considerably (Atkinson, 1991). In many specimens in this study, particularly *in M. laevis* and small specimens of all species, the thin abdominal wall on the ventral side of the fish would be torn from the anus anteriorly, thereby rendering accurate measurement of pre-anal length impossible.

The use of both methods of estimation is largely validated here, as both gave significant estimates of the model coefficients and had good fit, and the estimates of TL were negligibly different in *C. simorhynchus* and *M. laevis*. In *C. braueri*, the PAFL-derived estimate was significantly larger than that based on HL, likely due to the disproportionately large snout that is present even in small specimens. As PAFL-based estimation yielded a slightly better fit, this method of calculating TL seems superior in this species and others with similar snouts. All three species are long-tailed when comparing their PAFL/TL ratio to that of *Macrourus berglax* (38%) reported in Atkinson (1991).

In all three species, females were significantly larger than males. This corresponds to similar patterns of larger females observer in a number of other grenadier species, including *Trachyrinchus trachyrinchus*, *Nezumia aequalis*, *Hymenocephalus italicus*, *Coelorinchus caelorinchus* (Massutí *et al*., 1995), *Macrourus carinatus* (Lee *et al*., 2019), and *Coryphaenoides rupestris* (Lorance *et al*., 2003). Females attaining larger sizes than males is common in fish, as female fecundity often scales with body mass, and therefore length. Higher fecundity confers fitness benefits in species which do not practise parental care. Exceptions occur mostly in cases in which there is strong male-male competition for mates beyond sperm competition, or when males exhibit a significantly higher growth or lower mortality rate (Parker, 1992). Considering the strong disparity in GSI of females and males observed here, the larger size of females is most likely driven by a benefit in maximising fecundity, and there is little to no direct physical competition among males.

Males were not significantly larger than sexually indeterminate specimens except in *C. braueri*, in which sexually indeterminates accounted for nearly a third of all fish sampled. This high proportion of sexually indeterminate fish may be due to sampling mostly from the upper two thirds of their distribution, as they can be found down to depths of 1200 m (Iwamoto & Anderson, 1994), and may prefer depths of over 1000 m in some regions (Sobrino *et al*., 2012). It is therefore possible that sampling the entire age-range in *C. braueri* necessitates trawling at depths greater than 800 m. However, the trend of size with depth in this species appears to be negative (i.e. “smaller-deeper”). Assuming this pattern holds through the entire depth range, it would suggest that sexually indeterminate *C. braueri* should be more abundant at greater depths, and therefore should have been sampled less frequently in this study than sexually determinate fish.

A number of fish examined here were damaged through extreme barotrauma (and possibly also as a result of handling and freezing/thawing prior to dissection), with organs sometimes hanging out of the anus and partially lost, torn, or liquefied. It is therefore assumed that some of the fish identified as sexually indeterminate were males, most likely in reproductive phases during which the testes were strongly reduced or immature, and would have been sexed as male if not for their condition. A more likely explanation for the high proportion of sexually indeterminate *C. braueri* may simply be that they were, by and large, affected the most by these damages due to their small size and fragility.

A tendency of small males being misclassed as indeterminate likely also applies in the other two species, and could account for the slightly higher median PAFL of indeterminate *M. laevis* compared to their males. The overall high PAFLs of sexually indeterminate fish lend credence to this idea, as their median PAFLs in all species exceed 80 mm. In comparison, in four of the five species analysed in Massutí *et al*. (1995) the maximum PAFL of sexually indeterminate fish lies between 40 and 60 mm, including two *Coelorinchus* species. Only in *Trachyrinchus scabrus* are there larger indeterminates, rarely reaching up to 130 mm. Potential misclassification of the smallest males of *C. simorhynchus* and *M. laevis* as sexually indeterminate is likely to have raised the maximum size of indeterminate fish in this species to the point where it overlaps with the smallest correctly identified males, explaining the lack of significant size difference between males and indeterminates in these species.

The concept of a general relationship of increasing size and mass with depth in marine fishes, known as Heincke's Law, has been discussed and debated frequently over the past 30 years (e.g. supported by Macpherson & Duarte 1991, questioned by Stefanescu *et al*., 1992, and invoked by Fernandez-Arcaya *et al*., 2012 and Santos *et al*., 2019). Macpherson and Duarte (1991) found significant linear relationships between depth and fish TL among a variety of demersal fish species, among them *Coelorinchus fasciatus* (i.e. *C. simorhynchus*) and *Malacocephalus laevis*. They identified bigger-deeper trends in *C. fasciatus* (b = 0.40 mm TL per m depth) and five other macrourid species, all from datasets with an excess of 400 specimens per species. Only *M. laevis* did not follow this pattern, showing a smaller-deeper relationship instead. These trends contrast with the morphometric data presented here, in which there were no linear relationships between abundance and depth in either *C. simorhynchus* or *M. laevis*. Macpherson and Duarte (1991) sampled off Namibia, suggesting that, as is the case with depth ranges, size-depth trends in macrourids may vary geographically within the same species.

Iwamoto and Anderson (1994) suggest caution when interpreting references to *C. fasciatus* in works published prior to their review of the southern African species (e.g. Macpherson & Duarte, 1991), as *C. fasciatus* may have been confused with *Coelorinchus matamua*, *Macrourus carinatus*, or both. It is therefore possible that data reporting on characteristics of southern African *C. fasciatus* may have been based on any of these three species (although *M. carinatus* is not known to occur in Namibia). Nevertheless, it seems unlikely that *M. laevis* could be confused with another common species of grenadier.

The lack of size-depth trends in *C. simorhynchus* and *M. laevis* cannot be attributed to incomplete sampling across the depth range, given that most of their depth range was sampled. Conversely, *C. braueri* was sampled from only the upper two thirds of its depth range, yet this species does show a negative linear trend of size with depth (i.e. "smaller-deeper"). Unfortunately, no published size-depth data exist for *C. braueri* against which this could be compared.

Below 1000 m, some demersal teleosts show a smaller-deeper trend due to decreasing resource availability limiting maximum size (Stefanescu *et al*., 1992). This may apply to certain grenadiers as well, considering *Trachyrinchus scabrus* shows a bigger-deeper trend above 1100 m, but the reverse below that depth (Fernandez-Arcaya *et al*., 2012). *C. braueri* is the smallest of the three species and occurs at the greatest maximum depth out of the three species considered here, although sampling was largely limited to the upper two thirds of its depth range. Therefore, it cannot be confirmed that the smaller-deeper trend observed in *C. braueri* may not hold true for depths greater than 800 m.

The goodness of fit of the linear relationships of mass with depth are worse than those for length in all three species, with *C. braueri* having the best among them. Given that length in this species is largely determined by the long tail and snout, and that feeding and reproductive success are likely affected more by the mass of the fish than the length of its tail, it is possible that while the observed negative linear size-depth trend is statistically significant, it is not particularly impactful in *C. braueri*.

Future studies of grenadier ecology may provide reasons for the trend in size with depth in *C. braueri*, and lack thereof in *C. simorhynchus* and *M. laevis*. Additionally, *C. braueri* must be sampled across its entire depth range to see if the trend remains consistent. All three species should be sampled across their entire geographic distribution in southern Africa (and elsewhere in the case of *M. laevis*) to determine if growth and size trends are uniform. Specimens sexed immediately post-capture could potentially facilitate determining differences in size by sex due to reduced damage to gonads.

4.3 Biometrics and growth

The difference in masses among the three species is more extreme than the difference in PAFL, not only due to mass scaling with the cube of length, but also because the majority of the mass of macrourids is concentrated in the head and body anterior to the anal fin. *C. braueri*, the shortest species, is 43% shorter (in terms of TL as estimated from PAFL) than the largest, *M. laevis*, but is has 73% less mass on average. Similar ratios may be obtained comparing *C. simorhynchus* to *M. laevis* and, to a lesser extent, *C. braueri* and *C. simorhynchus*.

Both PAFL (Murua, 2003; O'Hea *et al*., 2013) and TL (Borges *et al*., 2003; Filiz & Taskavak, 2008) have previously been used in length-weight assessments of macrourids. Regressions of the log of mass against the log of length were generated based on both PAFL and total recorded length. In theory, one would expect total recorded length to correlate better with total recorded mass, since the partial loss of a tail would impact both. However, as the tails of macrourids are so thin, they contain only a small fraction of the mass of a fish. Therefore, the mass of a macrourid tends to be less variable than its length. Consequently, the regressions based on PAFL fit better than those based on TL in all species, hence PAFL was used in this study.

This distinction of PAFL- or TL-based interpretations of the length-weight relationship should be accounted for when comparing growth types. For example, Borges *et al*. (2003) claim a b-coefficient of 3.28 for *M. laevis* in the North Atlantic based on TL, whereas Torres *et al*. (2012) cite a value of 2.66 based on PAFL. The latter is in line with the 2.59 calculated here. On the other hand, reported length-weight relationships in grenadiers seem to be variable within a species even when using a consistent model. For example, a comparison of such regressions for *Coelorinchus caelorhincus* in Filiz and Taskavak (2008) shows b-coefficients based on TL to vary between 2.13 and 3.14, despite all comparisons using TL (O'Hea *et al*. (2013) cite b as lows as 1.35 in this species, although their estimate is based on PAFL and has a very low R^2 value of 0.64). Similarly, O'Hea *et al*. (2013) cite two different estimates of b (3.25 and 1.79) in *Coryphaenoides guentheri*, both from the North Atlantic. Considering these strong differences in allometry, it is likely unwise to generalise the relationships for a species across its entire distribution.

No length-weight regressions have previously been carried out on *C. braueri* or *C. simorhynchus*, although FishBase gives estimates calculated via Bayesian estimation (Froese *et al*., 2014) based on their size and body shape. Notably, the FishBase estimate for *C. simorhynchus*, b = 3.08, corresponds exactly to that calculated here, although that of *C. braueri* is slightly higher than the b = 2.97 in this study. For South African macrourids, the use of Fulton's condition factor K (where $K = M/L^3$) is appropriate for *C. braueri* and *C. simorhynchus*, but not *M. laevis* (although it may be appropriate for *M. laevis* in other regions or if using TL), provided that the regression is based on PAFL (Ricker, 1975).

The curves of PAFL at 50% maturity for *C. braueri* and *C. simorhynchus* were produced using the reproductive phases assigned based on macroscopic assessment of the gonads. Although macroscopic staging was easier in the *Coelorinchus* species than in *M. laevis*, histological sections of *C. simorhynchus* gonads revealed some mismatch, particularly in the phase one and phase five gonads. In particular, ovaries which were deemed immature (phase one) based on visual assessments often contained some oocytes in more advanced stages. Nevertheless, the macroscopic staging data were used in this study to calculate length at maturity as well as assessing reproductive seasonality, as plots of gonadosomatic index by reproductive phase in all species and sexes generally show the expected pattern of highest GSI at phase three and lowest at phases one and five, with phases two and four at intermediate values. Therefore, the estimates of length at maturity are assumed to be representative of the actual length at maturity values within the population. Any deviations from those estimates would be more likely to be overestimates than underestimates (based on the assumption that some fish identified as immature may have been classed mature if assessed histologically). The accuracy of macroscopic staging in *C. braueri* was not able to be assessed, as no histology was carried out for this species due to low sample size.

No data on length at maturity has been published for any of the three species. Length at maturity between macrourid species can be fairly variable, as seen in three Ionian Sea macrourids (D'onghia *et al*., 1999). They report *Coelorinchus caelorinchus*, *Nezumia sclerorhynchus*, and *Hymenocephalus italicus* to have PAL_{50} of 61 mm, 37 mm, and 27 mm respectively. *Nezumia aqualis* was found to measure 45 mm at PAL_{50} (Masuttí *et al*., 1994). While comparisons between different length metrics such as PAFL, PAL, or TL should be interpreted with caution, and one would expect PAFL-based estimates to exceed ones based on PAL, the findings in this study estimate greater lengths at 50% maturity for *C. braueri* and *C. simorhynchus* than in most other macrourids studied previously. These estimates are exceeded by *Albatrossia pectoralis*, one of the largest grenadiers, which matures at between 650 to 1000 mm TL in the Bering Sea (Tupogonov *et al*., 2008), from which one can infer its $PAFL_{50}$ to be well over 100 mm. The lengths at maturity obtained in this study for the two *Coelorinchus* species are therefore larger than expected, but not implausible.

Length at maturity estimates are frequently reported only for females (e.g. Masuttí *et al*., 1994; Tupogonov *et al*., 2008), since females are the dominant driver of a population's reproductive output. While D'onghia *et al*. (1999) show very similar minimum PALs for all three of their species across both sexes, the example of *C. braueri* in this study highlights the importance of running separate ogives on males and females, as the estimated lengths at maturity are liable to differ considerably. Using a combined length of maturity for both sexes in a species should therefore be avoided. Future studies of *M. laevis* should aim to capture immature specimens of both sexes in order to generate a maturity ogive for this species.

4.4 Von Bertalanffy growth models

It is important to note that the otolith readings for the three species of macrourids presented here have not been validated. Otolith validation is necessary to demonstrate that annuli do in fact represent one-year increments, as is commonly assumed in fish life history studies. This was not attempted during this study due to the effort and difficulty involved; consequently all age estimates presented here are to be interpreted with caution, even those for *C. braueri* where a von Bertalanffy regression was generated. As the most reliable methods of age validation in shallow-water fishes such as chemical marking, laboratory rearing, and mark-release-recapture are not feasible in deep-sea fishes, validation of the otolith readings would require either analysis of growth-zone characteristics or radiometric dating (Cailliet *et al*., 2001). As the former is difficult for species living in deep waters, especially ones with broad depth ranges throughout their lives, radiometric dating using ^{210}Pb and ^{226}Ra disequilibria is likely the most promising method (Cailliet *et al*., 2001).

The longevity of macrourid species is highly variable even among congeners, ranging from five years in *Coryhaenoides guentheri* (Morales-Nin, 1990) to 73 in *Coryphaenoides acrolepis* (Andrews *et al*. 1999). However these are among the most extreme estimates, with the majority of species estimated to reach a maximum age of between 11 and 20 years (e.g. *Coelorinchus caelorinchus* and *Trachyrinchus scabrus* per Massutí *et al*., 1995), while it is less common for long-lived species to reach ages of over 50 years (e.g. *Coryphaenoides rupestris* per Andrews (1997)). Deep-sea fishes generally show higher ages at maturity and slower growth rates than shallower-living species, even when phylogenetic differences between deep- and shallow-water species are accounted for. For example, Drazen and Haedrich (2012) report highly significant positive correlations of age at 50% maturity (A_{50}) and highly significant negative correlations of the log of the von Bertalanffy growth coefficient, ln(k), with increasing depth. However, depth is not the sole driver of growth in the deep sea; as depth explains only 42% of variation in A_{50} and 40% of variation in k in Gadiformes at depths up to 700 m (Drazen & Haedrich, 2012).

Age estimates are also highly variable within species. The 73-year estimate of Andrews *et al*. (1999) for *C. acrolepis* contrasts with the 10 to 11 years reported for the same species in Brothers *et al*.

(1975). In both papers, the age estimates were obtained by counting annuli. While it is not unreasonable to assume that maximum age can differ in different populations of the same species, these differences are large enough to suspect under- or overcounting in at least one of the papers. Andrews *et al*. (1999) supplemented their counts with radiometric dating, the latter reaching estimates of 56 years plus an error of ±10 years, which supports their larger estimate for maximum age and led them to disregard very large counts in some fish, reaching beyond 90 years of age. These cases show the difficulty of aging macrourids based on otolith annuli alone. Further examples of age estimate variability based on grenadier otoliths and scales can be found in Swan and Gordon (2001).

It was possible to generate von Bertalanffy parameters for *C. braueri* by combining the regressions for both sexes. In macrourids, von Bertalanffy functions are typically fitted separately for males and females based only on sexually determinate fish due to the different growth patterns (e.g. Massutí *et al*., 1995; Lee et al., 2019), although a combined-sex model is sometimes given in addition or when sample sizes are low. Females typically attain larger asymptotic lengths, as was the case in the three species examined here. Due to the low sample size (n = 64) of *C. braueri*, of which almost one third could not be assigned to a sex, it was decided to create a combined-sex model. The parameters of this regression are likely to be intermediate to those that would have been obtained for females and males separately if given a larger sample size. However, the von Bertalanffy regression fits well (R^2 = 0.80), and the maximum age of 17 years is not unreasonable given the findings of Lombarte and Morales-Nin (1989), who recorded a maximum age of 14 years in *C. simorhynchus*.

Unfortunately, even with estimates of expected nucleus width, it was not possible to achieve a consistent method of aging in either *C. simorhynchus* or *M. laevis*. While rings were generally easily visible, they were often extremely diffuse and did not form predictable patterns of thickness, nor did readings on different parts of the same otolith consistently agree. In many cases, rings on the lateral side of the nucleus were very clear, but numbered only one or two, while on the medial side there could easily be two or three times as many. Nor did counts on the dorsal and ventral sides of the sulcus (which was considered the most consistent place to count) line up – what appeared to clearly be a single annulus on the dorsal side could be split into 2-3 bands on the ventral side, or vice versa. Annuli also did not always follow the expected pattern of decreasing width with increasing distance from the centre, with the first or second rings sometimes being thinner than the third and fourth ones. The difficulty lay not in being able to see rings, but rather defining what counted as an annulus. As a result, counts of annuli differed not only between different observers, but between counts by the same observer on different days.

Aging by counting otolith annuli was successful for *C. fasciatus* (i.e. *C. simorhynchus*) off Namibia by Lombarte and Morales-Nin (1989). They attained an asymptotic PAFL of 119 mm, a growth coefficient of 0.15, and a t_0 of -0.22, with the maximum recorded age being 14 years. Aging has not previously been attempted in *M. laevis*. Specimens of both species were fairly young, with most specimens having between 1-4 annuli, and the highest counts reaching 6-7. The authors did not elaborate on their counting protocol or provide micrographs, but reported good agreement between observers, and presumably did not struggle with aging the otoliths. Assuming that the data of Lombarte and Morales-Nin (1989) relate to *C. simorhynchus*, the data suggest that annuli in this species were strongly undercounted here, by as much as a factor of two. Given the absence of published aging data for *M. laevis*, it is difficult to assess the counting protocol.

Difficulties in aging deep-sea fish may be attributed to a number of factors. Historically, the idea of decoupling between primary production which occurs at the surface, and is strongly seasonal, and the arrival of food at depth, has been used to characterise the deep sea as less strongly seasonal. The downwards flux of energy was thought to occur slowly, via sinking of organic matter or vertical migration in prey species, thereby damping the seasonal impulse. However, this idea has gradually fallen out of favour following the discovery of surprisingly strong seasonal trends in deep-sea species and ecosystems (Hudson *et al*., 2003; Morales-Nin and Panfili, 2005; Corliss *et al*., 2009). Seasonality in the deep sea can be driven by variation in primary productivity at the surface or seasonal processes inherent to a species, such as a well-defined spawning season. Abiotic factors, such as changes in temperature due to seasonal upwelling or variability in ocean currents can also affect the growth of fishes (Glover *et al*., 2010). Only light availability is guaranteed unaffected by seasonality at the aphotic depths below 200 m. Studies on North Pacific grenadiers in particular have shown some *Coryphaenoides* species to be tied more closely than might be expected to the dynamics of the epipelagic zone due to their propensity for scavenging on sunken carrion (Drazen *et al*., 2008; 2009).

While it is plausible that there is some damping of the seasonal impulse, other factors are likely to play a role in the diffuse nature of the otolith annuli found in many macrourids (Swan & Gordon, 2001). For one, the larvae of grenadiers are pelagic and live much shallower than juveniles and adults; it is therefore to be expected that growth before juvenile settlement at depth occurs much faster than afterwards (Morales-Nin & Panfili, 2005). Variability in the length of this pelagic phase could explain the difficulties in defining the extent of the nucleus and position of the first ring.

Future efforts aimed at aging these species should focus on generating sex-disaggregated von Bertalanffy curves of all three species but especially *M. laevis*, as no such curve has been generated for this species before. Additionally, otolith readings should be validated for all three species, and alternative methods of age estimation such as radiometric ones should be considered to avoid the problems of inconsistent aging using annuli altogether.

4.5 Diet

The diet analysis was hindered by a large proportion of everted stomachs, as in other studies of macrourids (e.g. Laptikhovsky, 2005; Stevens *et al*., 2020). Stomach eversion was highest in *C. braueri*, with less than a third of specimens containing non-everted stomachs. While *C. braueri* was generally found deeper than the other two species, with a mean depth exceeding 400 metres, its high rate of stomach eversion cannot be simply attributed to the greater barotrauma accompanying these greater pressure changes, as all but one individual from a 265 m sample also had everted stomachs. The observed differences in species-specific rates of stomach eversion may be attributable to physiological attributes such as the size and position of the gas bladder, or behavioural ones such as a stress response during capture.

Five empty stomachs were found in the *Coelorinchus* species, suggesting they either underwent a long period without successfully feeding, or regurgitated the stomach contents during capture without everting their stomach. No empty stomachs were found among the specimens of *M. laevis*, perhaps because this species had an intricately folded interior stomach wall which typically contained a lining of strongly digested food, as opposed to the smooth interiors of the *Coelorinchus* species. This feature could suggest that *M. laevis* is less likely to fully regurgitate all stomach contents on capture, potentially explaining why none had completely empty stomachs.

Potential prey items were commonly found in the buccal cavity or oesophagus. Treatment of organic matter outside of the stomach in diet analyses varies; some authors choose to include it in IRI calculations (e.g. Anderson, 2005), while others discard stomachs from such fish entirely (Stevens *et al*., 2020). In this study, stomachs from these fish were not discarded – while this potentially introduces an element of bias due to smaller prey items being regurgitated more easily, sample sizes of non-everted stomachs were not high enough to comfortably discard a majority of them. However, it was not appropriate to include these items in the diet analysis, as it was not possible to definitively know whether they represented regurgitation or net feeding. The high frequency of grenadier scales in the buccal cavity shows that at least some items were consumed while in the net, as these were too large to have come from prey consumed while alive and must have been ingested while in the net.

The level of digestion of stomach contents in all three species was generally high. Most prey items were strongly fragmented. While *C. simorhynchus* had the highest proportion of stomachs with "identifiable prey items", confident identification to species level was the exception. Heavily digested prey were typically assigned to higher taxonomic levels. In practice, many *Coelorinchus* stomachs contained small fragments of shell plates, eyes, or red-tinted flesh, which could be identified comfortably as Crustacea, but no further. Taxonomic resolution was higher in *M. laevis* due to the high proportion of cephalopods and teleost fish found in the diet of this species, which contained hard beaks, statoliths, and otoliths that were resistant to digestion.

Crustacea which could not be identified to the level or order or lower composed a notably large proportion of the percentage frequency of occurrence (%F), and of the percentage number of prey items (%N), due to large numbers of crustacean eyes. As a result, unidentified crustacea emerged as the most important prey category in *C. braueri* and *C. simorhynchus*. One of the two previous diet studies in the region by Meyer and Smale (1991) similarly reported a high importance of this category. On the other hand, Anderson (2005) had no such category for any of the species considered. It is not known whether this is due to a higher success rate in identifying prey items (due to lower levels of digestion or better prey identification skills), disregarding of crustacean prey that could not be identified to at least class level, or a proportional allocation of the unidentified crustacean metrics to identified crustacean groups. Unidentifiable crustacean prey were not discarded in this study, as it would severely misrepresent the relative importance of crustacean vs non-crustacean prey groups. Proportional assignment was considered, but not carried out so as not to exacerbate existing biases in the data due to likely differences in the digestion/regurgitation rates of different crustacean taxa (e.g. anomurans were generally in much better condition than prawns or amphipods), and differences in the ability to identify highly digested taxa (e.g. the unique shape of ostracods generally allowed them to be identified even when digested).

Comparisons with other grenadier diet studies were made more difficult by several factors. *C. braueri* was not one of the species covered in Meyer and Smale's (1991) diet study of demersal teleosts. *C. fasciatus* was investigated and is treated as synonymous with *C. simorhynchus* here, although that comes with the aforementioned caveat of possible misidentifications of other macrourids. Meyer and Smale (1991) is directly mentioned in Iwamoto and Anderson (1994) following their cautionary note on this taxonomic uncertainty. Meyer and Smale (1991) also did not calculate the index of relative importance, but instead displayed individual IRI components only, and split off important species into separate "principal prey" groups from their families. Their study was also based on macrourid samples from the west coast only. As sample sizes in this study were far lower than in either of the previous studies, (especially for *C. braueri*), diet for juveniles and adults was not analysed separately. In general, diet composition resembled that of adult macrourids reported in Anderson (2005) and Meyer and Smale (1991) more so than that of juveniles. In *C. simorhynchus* and *M. laevis* especially, the large IRI of teleosts, ophiuroids and cephalopods reported here were found to characterise adult diets by these studies. In part, this is doubtlessly influenced by the greater ease with which these prey taxa may be identified even when partially digested compared to smaller, more fragile prey such as the mysids, euphausiids, and hyperiids that characterise juvenile prey.

Coelorinchus braueri

Both in this study and in the diet analysis of Anderson (2005), crustaceans were found to compose the majority of stomach contents. The diet of *C. braueri* analysed in Anderson (2005) was dominated by gammarid amphipods in juveniles with an IRI of over 6700, a very high value compared to other macrourid prey groups — in most species examined by Anderson (2005), the highest prey IRI values were less than 2000. Gammarids were followed in importance by tanaids and euphausiids, and by hyperiids, euphausiids, tanaids, and gammarids in adults, whereas in this study, very few crustacean remains could be attributed to a lower taxon. The Amphipoda, Tanaidacea and Euphausiacea of Anderson (2005) contribute over 99% of the total IRI in juveniles and 96% in adults and are the only major prey groups. Conversely, the various crustacean groups contribute about 80% of total IRI in this study, with the remaining 20% mainly accounted for by teleost fish including myctophids. While Anderson (2005) did find myctophid teleosts in *C. braueri*, they were an extremely minor prey group in that study, and counterintuitively only occurred in juveniles.

Several prey groups identified by Anderson (2005) were not found here, such as carid prawns, polychaetes, and stomatopods, although it is likely that carids composed part of the unidentified crustaceans here, and the sample size of *C. braueri* stomachs in this study was only one tenth that of Anderson (2005). More interesting is the lower frequency of occurrence of cephalopod remains in Anderson (2005), which were recovered from 30% of stomachs here. Cephalopods composed the largest of the minor prey groups here, but were absent from juveniles and found in less than 10% of adults of the Anderson (2005) study.

Of the *C. braueri* stomachs analysed in this study, only one contained gammarid remains. It is possible that the importance of gammarids is underestimated here due to some being lumped into the unidentifiable crustacean category, however it is worth noting that stalked eyes were far more common in stomachs from all three species than unstalked eyes. Based off this and circumstantial observations about the size and shape of crustacean remains, it seems more likely that a majority of the unidentified crustacean group was composed of euphausiids or small prawns (which possess stalked eyes), rather than amphipods (with unstalked eyes) or tanaids (most of which are eyeless). The Euphausiacea were identified by Anderson (2005) as the prey group with the third highest IRI in juveniles and second highest in adults, supporting their proposed importance within the unidentified crustaceans.

Coelorinchus simorhynchus

The Gammaridae are the most important prey group in this grenadier. After unidentified Crustacea, Gammaridae make up the identifiable prey taxon with the highest IRI in both juveniles and adults in Anderson (2005) and juveniles in Meyer and Smale (1991), although exceeded by ophiuroids, anomurans and euphausiids in Meyer and Smale's (1991) adults. Among these gammarids, both Anderson (2005) and Meyer and Smale (1991) were able to identify species of *Ampelisca*, *Gammaropsis*, *Heterophoxus, Hippomedon,* and *Leucothoe.* The only gammarid identified to genus level in this study was a species of *Leucothoe*.

Polychaetes composed the prey taxon with the third highest IRI after unidentified crustaceans and gammarid amphipods but was only a minor prey group in juveniles and adults of Anderson (2005) and Meyer and Smale (1991). Ophiuroids were important in all three studies, composing the fourth-largest prey group here, the second largest among adults in Anderson (2005), and the largest among adults in Meyer and Smale (1991). In particular, the species *Ophiura trimeni* was found in all studies.

The fifth largest and last major prey group, the teleosts, was important only in adult *C. simorhynchus* according to Anderson (2005), after the Gammaridae, Ophiuroidea, and Caridae. Meyer and Smale (1991) only list a species of lanternfish, *Lampanyctodes hectoris*, among the principal prey groups in adults. *Lampanyctodes hectoris* was not listed here, although it could easily fall within the group of unidentified myctophids. A dragonet, *Paracallionymus costatus*, was found in this study as well as those of Anderson (2005) and Meyer and Smale (1991). The latter two studies also identified a species of *Maurolicus* which were not found here, and Meyer and Smale (1991) noted predation on other macrourids but did not identify these as *C. simorhynchus.* Meyer and Smale's (1991) discovery of a head of anchovy *Engraulis capensis* strongly suggested scavenging behaviour in *C. simorhynchus*, as the inferred length of the anchovy was 50% greater than the grenadier that had eaten it.

The most important of the minor prey groups, the Anomura, seemed to be composed mostly of a single species, although some anomurans could not be identified and may represent closely related species. *Parapagurus pilosimanus*, a hermit crab which finds refuge under colonial anthozoans rather than mollusc shells, was identified in this study and by Anderson (2005) as prey of *C. simorhynchus*. Meyer and Smale found a congener, *P. dimorphus*, as well as unidentified *Parapagurus*. In that study, anomurans (particularly the Paguridae) constituted the second most important prey taxon in adults after ophiuroids.

Cephalopoda were an extremely minor prey group in this study, with an IRI of less than ten, which matches the findings of Anderson (2005) and Meyer and Smale (1991). Cephalopods were identified from their beaks, meaning the percentage mass is not representative of the true contribution to the diet, as they make up only a small fraction of the mass of a cephalopod. Conversely, the ability of beaks to remain undigested within the stomach until regurgitated likely resulted in an overestimation of the percentage occurrence and percentage numbers. The only cephalopod identified here was *Lycoteuthis lorigera*, which was also found by Meyer and Smale (1991), who listed it under the synonym *L. diadema*. Anderson (2005) listed *Rossia enigmata* as the only cephalopod identified at species or genus level.

Malacocephalus laevis

The diet of *M. laevis* was dominated by teleost fishes, which constituted over 85% of total IRI. This matches the findings of Anderson (2005), who found that Teleostei made up ca. 86% of the total IRI in adults. In juveniles of that study, teleosts were second in importance to hyperiid amphipods, with gammarids constituting the third main prey group. Hyperiidae were also recovered as a main prey group in Anderson's (2005) adults. In this study, hyperiids were the fourth most important among the minor prey groups and even the summed IRI of all unidentified crustaceans and hyperiids would make up less than 3% of total IRI, while gammarids were of extremely minor importance with an IRI of less than 10. Instead, the other major prey taxon was the penaeid prawns, which accounted for 6% of total IRI. Meyer and Smale (1991) also identified hyperiids as a principal prey taxon in juveniles, particularly the species *Themisto gaudichaudi*, although it was exceeded in importance by teleosts. In adults, they found the diet to be dominated by cuttlefish and squid, followed by teleosts, with no hyperiids or other crustaceans among the principal prey. Penaeid prawns were of minor importance in juveniles and adults per Anderson (2005), making up less than 1% of IRI, but the prawn *Funchalia woodwardi* was one of the less important principal prey groups of Meyer and Smale's (1991) adults. *F. woodwardi* was also found by Anderson (2005), and is one of the most abundant prawns in South African waters.

Among the teleosts identified here, macrourids and merluccids were the largest and most common prey of *M. laevis*. Meyer and Smale (1991) did not discover any macrourids in stomachs, whereas several *C. simorhynchus* were found in this study and that of Anderson (2005). Both Anderson (2005) and Meyer and Smale (1991) noted *Merluccius* hakes to be important prey of adult *M. laevis*. The merluccids recovered here were likely all *Merluccius paradoxus*, the deep-water hake, as the shallow-water congener *M. capensis* mainly occurs at depths shallower than 200 m. However, while all hakes found were small enough to feasibly have been predated by *M. laevis*, it cannot be ruled out that some were *M. capensis* carrion that had sunk to the bottom. The presence of batoid cartilage found within a stomach strongly suggests that this species acts as a scavenger, as the skate it had originated from must have been many times larger than the grenadier. The dragonet *Paracallionymus costatus* was found in all three studies, but was only considered important as teleost prey in juveniles by Meyer and Smale (1991). These authors additionally identified *Symbolophorus barnardi*, *Lampanyctodes hectoris*, and myctophid and ophichthid fishes, while Anderson found *Helicolenus dactyolpterus*, *Maurolicus walvisensis*, *L. hectoris*, and other myctophids. The only new teleost group identified here was a single individual in the barracudina family Paralepididae. Mauchline and Gordon (1984), in their investigation of foraging strategies of demersal fish in the North Atlantic, were unable to characterise those of several grenadiers including *M. laevis* due to the advanced state of digestion of prey, but did note that upwards of 60% of prey contents in this species were fish.

The importance of cephalopods varies greatly across the three studies. Anderson (2005) found them to be of minor importance among both juveniles and adults, with less than 1% of total IRI contribution. On the other hand, Meyer and Smale (1991) found them to constitute the majority of the IRI in adults, but did not list them among the principal prey of juveniles. The findings in this study show their importance as intermediate to the two previous studies (potentially a weakness of not analysing juveniles and adults separately), as they made up the most important among the minor prey taxa at about 4% of the total IRI. The cephalopods found include *Lycoteuthis lorigera*, as well as cranchiid and todarodine squid and sepiid cuttlefish. *Lycoteuthis* and cuttlefish beaks were the most abundant. Anderson (2005) found *L. lorigera* and the sepiids *Austrorossia enigmatica* (as *Rossia enigmatica*) and *Sepia australis*. The latter species was also found by Meyer and Smale (1991), as well as *L. lorigera* (as *L. diadema*) and the todarine squid *Todaropsis eblanae*, and loliginid and enoploteuthid squids.

More data in needed to determine the effects of depth, fish size, and geographic location on the dietary niche, as well as their interactions. It seems likely given the discrepancies between this study and past diet studies that these species have great dietary variability, and likely undergo ontogenetic shifts in diet, as well as potential seasonal or geographic shifts.

4.6 Reproduction

In both *Coelorinchus* species, the overall proportion of females was higher than that of males, while the sex ratio in *M. laevis* was close to 1:1. These ratios are similar to those in other macrourids. Stein and Pearcy (1982) found 64% females in *Coryphaenoides armatus* and *C. leptolepis*, but roughly equal sex ratios in *C. filifer* and *C. acrolepis*. Fernandez-Arcaya *et al*. (2013) found 55% females in *Nezumia aequalis* and 65% in *Coelorinchus mediterraneus*. *Trachyrinchus scabrus* was found to have an overall ratio of 54% females (Fernandez-Arcaya *et al*., 2012). Sex ratios in macrourids tend to be even or moderately in favour of females. Triay-Portella *et al*. (2023) observed an exception in *Bathygadus favosus*, in which females made up more than 80% of the specimens observed, while *B. melanobranchus* was more in line with other species at 69% females. Although Morley *et al*. (2004) observed a sex ratio as high as 97% in *Macrourus holotrachys*, this was attributed to sex-selection by the fishing gear, as the extreme ratio only appeared in longline samples. It has been suggested previously, in light of low capture rates of immature females and discrepancies between trawl and submersible-based sampling, that male grenadiers are more likely to be caught in trawls than females, such that catch rates do not accurately reflect the actual sex ratio in the population, at least in the smaller size classes (Merrett & Haedrich, 1997; D'Onghia *et al*., 2000).

Fish sex ratios that are biased towards females generally indicate high male reproductive success and low levels of inter- and intrasexual competition in males, as males will encounter more spawning-capable females (Forsgren *et al*., 2004). This is supported by the small testes and low male GSI found in this study, which imply that male grenadiers do not need to invest heavily into sperm production.

In a study of sex ratios of various mesopelagic fishes, Clarke (1983) proposed two explanations for the greater proportion of mature females observed in several species. Firstly, in cases in which the proportion of females increases with increasing size, this may be attributed to higher growth rates or larger maximum sizes among female mature fish compared to males. A higher female growth rate compared to that of males may be selected for in fishes as it influences the size of eggs, number of batches, and larval survivability. This is likely the case in the grenadiers examined, given that in all species, the proportion of females increases with PAFL.

The idea that these characteristics scale with the mass of the mature female spawning them has been explored in a number of species including South African deepwater hake *Merluccius paradoxus* (Field *et al*., 2008). Female gonad mass increased non-linearly with body size in all three species, and GSI has been shown to increase with total mass in other grenadiers, including *Coelorinchus caelorinchus* (D'onghia *et al*., 1999). Clarke (1983) further suggests that males may also be smaller and less abundant than females in food-poor environments to reduce interspecific food competition.

Secondly, a disproportionate female abundance could also be maintained in a population through higher male mortality rates among mature fish, either through differences in their ecology or as part of sexual selection. Clarke (1983) highlights the potential importance of light organs in fishes in this regard, suggesting that sexual dimorphism in the structure of a light organ could indicate that only one sex (i.e. males) utilises this during mate attraction, thereby drawing the attention of predators. This explanation is largely speculative, given that the function of the light organ in macrourids is poorly understood and may not relate to reproduction at all. Ecological differences, such as ontogenetic vertical migration, could also explain differential mortality rates. The proportion of females of *C. braueri* was shown here to decrease with depth, perhaps affording females of this species a slightly different habitat and associated prey and predators than their male conspecifics.

In all three species, the proportion of females increased from ca. 40% to over 80% with increasing PAFL. This is in line with the overall greater length of females compared to males observed in *C. braueri*, and suggests that despite the failure to detect significant differences in PAFL by sex in *C. simorhynchus* and *M. laevis* (which may be attributed to the large number of sexually indeterminate specimens), females are generally larger than males in these species as well. A trend of increasing sex ratio with size has been observed in a variety of macrourids, including *Bathygadus favosus* and *Bathygadus melanobranchus* (Triay-Portella *et al*., 2023), *Coryphaenoides rupestris* (Bergstad, 1990), *Hymenocephalus italicus*, *Nezumia sclerorhynchus*, and *Coelorinchus caelorinchus* (D'Onghia *et al*., 2000). While sex roles and reproductive investment in macrourids has not been studied in detail, the findings of this study broadly agree with previous studies in that females are larger and equally or more abundant than male conspecifics.

Depth was not a good predictor of sex in any of the species, and no clear trends in sex ratio with depth were observed, with the possible exception of *C. braueri*. Sex ratio in this species decreased from 80% at 250 m to less than 45% at 500 m. However, whether this decrease represents a consistent trend of decreasing sex ratio with depth could not be assessed, as only two depth intervals had sufficient fish to calculate meaningful sex ratios. Furthermore, *C. braueri* was not sampled through its entire depth range to begin with, as the distribution of this species extends to 1200 m.

Previous studies have identified trends in sex ratio with depth, such as an increase in the proportion of males of *Coelorinchus aconcagua*, *C. chilensis*, and *Nezumia pulchella* in deeper waters (Acuña *et al*., 2008), or the opposite in *Coelorinchus coelorinchus* (D'Onghia *et al*., 2000). A lack of a trend in sex ratio across depth strata would, however, not be too unusual, as D'Onghia *et al*. (2000) found no trend in sex ratio between 250 and 750 m in *Hymenocephalus italicus* and *Nezumia sclerorhynchus*.

Stein and Pearcy (1982) also failed to find a trend in sex ratio with depth in *Coryphaenoides filifer* and *C. armatus*, but did note that the proportion of males increased from 45% to more than 90% with increasing distance offshore.

Given the well-supported trend of an increasing female proportion with size in macrourids, and in the absence of definitive evidence of same-sex aggregation at specific depths (Stein & Pearcy, 1982), it seems plausible that any trends in sex ratio with depth in grenadiers could be explained by changes in depth preference as specimens age, likely due to the ontogenetic shifts in diet observed in a number of macrourids (e.g. Meyer & Smale, 1991; Anderson, 2005).

The comparison of sex ratio between coasts shows strong but inconsistent variation in the proportion of females in the *Coelorinchus* species. *C. braueri* is female-dominated on the south coast, but male-dominated on the west coast. The opposite trend was found in *C. simorhynchus*. Some of the south coast samples were taken extremely far offshore, at the southern extent of the Agulhas Bank. It is possible that the variation by coast is caused by same-sex offshore aggregations similar to what may have been observed in male *Coryphaenoides spp.* by Stein and Pearcy (1982). However, this is highly speculative and would only apply to *C. braueri*, while the opposite trend, a same-sex aggregation of females offshore (or males inshore) would be needed to explain the difference in coastal preference by sex in *C. simorhynchus*.

GSI values in macrourids varies between species. Female *Hymenocephalus italicus*, *Nezumia sclerorhynchus*, and *Coelorinchus caelorinchus* had minimum GSI values of zero and maximum values of 10%, 8%, and 4% respectively, with the majority lying in the 2-5% range (D’onghia et al., 1999). Conversely, mature females of *Macrourus berglax* and *Macrourus whitsoni* had average GSI of over 14% and 9% respectively at a certain time of the year (Eliassen & Falk-Petersen, 1985; Prut’ko, 2012). Only three of the six comparisons of GSI by species and sex were significant, owing to the high degree of GSI variation even within a reproductive phase (e.g. female phase 3 *C. simorhynchus* vary between close to zero and ten percent).

The GSI lies primarily between 2 and 8% and 2 and 6% respectively for mature females of *C. braueri* and *C. simorhynchus*, not too dissimilar from that reported in *C. coelorinchus* (D’onghia *et al*., 1999). While female *M. laevis* had the largest maximum GSI at 15%, its mean GSI was lower than that of *C. simorhynchus*.

GSI values in males were low, with the highest value occurring in a phase 3 *C. simorhynchus* at just over 1%. These values were usually less than one tenth of the corresponding female GSI in the same species and reproductive phase. Published information on male GSI is rare, but Eliassen and Falk-

Petersen (1985) report mean male GSIs of at most 2% in *Macrourus berglax*, with recorded mean values dipping below 0.5% in immature fish. The low male GSI indicates a lack of sperm competition, which matches with the generally female-biased sex ratios.

The highest seasonal mean GSI values in mature females of both *C. braueri* and *C. simorhynchus* occurred in winter, while that of *M. laevis* occurred in summer. Phase 3 gonads occurred in every season in all three species (except spring and summer in *C. braueri*, as no samples from those seasons contained this species), and always constituted at least 20% of the total gonads taken during that season. This, together with the general lack of differences in female GSI across seasons, suggests that reproductive seasonality is weak.

This lack of seasonality in GSI contrasts with the findings of Eliassen and Falk-Petersen (1985) for *Macrourus berglax*, in which mean GSI in mature females in March to May lies between 3 and 5% but steadily increases to 14% by December. It is difficult to directly compare *M. berglax* to South African species, consider that Eliassen and Falk-Petersen's (1985) data were based on Norwegian fish. It is to be expected that a species in highly seasonal near-polar waters would show far greater reproductive seasonality than ones from lower latitudes. On the other hand, *M. berglax* occurs at a greater average depth of 700m, and seasonal effects on GSI could be reduced at that depth. Additionally, while the southernmost latitude on the Agulhas Bank does not reach beyond 37°S, the west coast and, to a lesser degree, parts of the south coast undergo seasonal upwelling in summer due to offshore winds (Schumann *et al*., 1982). The upwelling is known to increase productivity, producing a seasonal effect on fish stocks which is not reflected in the GSI of any of the macrourids.

The hepatosomatic index (HSI) did not show pronounced seasonal patterns. Mean HSI values peak in autumn or winter in both females and males, but without a consistent pattern (e.g. *M. laevis* females have their highest HSI in winter, but males in autumn). HSI in females was consistently higher than in males. The higher female HSI cannot be attributed to females being larger, as there is no relationship between HSI and body mass.

The liver functions as an energy storage organ in macrourids, allowing them to metabolise liver tissue during times of low food or when preparing to breed (Drazen, 2002). A decrease in liver mass during the energy-intensive reproductive period was documented in *Macrourus berglax* females, in which HSI decreased as GSI increased (Eliassen & Falk-Petersen, 1985). The lack of reproductive seasonality, as well as the lack of a relationship between GSI and HSI, and the absence of differences in HSI by gonad phase suggests that this is not the case in any of the three species observed in this study. Given the higher HSI in females compared to males, females of these macrourids likely do draw on energy stored in their liver for reproduction, but this effect is diminished due to the lack of a defined spawning season.

Two main ovarian organisational schemes have been documented in macrourids (D'onghia *et al*., 1999). Both *Macrourus berglax* (Murua *et al*., 2000) and *Trachyrinchus scabrus* (Fernandez-Arcaya *et al*., 2012) have been shown to be group-synchronous, while *Nezumia aequalis* and *Coelorinchus caelorinchus* (Fernandez-Arcaya et al., 2013) were asynchronous. Ovarian organisation does not necessarily depend on the environment, as while *M. berglax* is a polar species, the latter three all occur in the Mediterranean at comparable depths. The lack of strong seasonal patterns in *C. simorhynchus* is consistent with an asynchronous ovary that allows for continual spawning throughout the year. Spawning events in *M. laevis* can likely be assumed to take place in summer and winter, given that GSI values in females during those seasons are higher.

The absence of one gonad in some relatively undamaged specimens could not be explained, and possibly represents an extreme reduction of one gonad within the pair during development. This phenomenon was observed rarely, but was not a case of organ liquefaction as was recorded in some livers here.

Future studies should aim to obtain more gonad material for C. braueri, to characterise its ovarian organisation and publish representative micrographs of the various reproductive developmental phases. More comprehensive seasonal coverage in these species could help determine if there are seasonal effects that may have been missed in this study due to its incomplete temporal sampling coverage. Additionally, fecundity should be estimated for all three species.

4.7 Parasites

The sphyriid *Sphyrion quadricornis*, found here on *C. braueri* and *C. simorhynchus* is known to parasitise both species in South Africa (Sebone, 2023). *Sphyrion* is a small genus of copepods which is ectoparasitic on deepwater fishes. Females, following a metamorphosis, develop specialised mouthparts that burrow under the skin of their hosts, attached to the rounded trunk and abdomen via a long, thin tube. Attached to the abdomen are egg sacs and the much smaller males. A congener, *S. lumpi*, is known from these species in the southeast Atlantic but was never encountered here. Sebone (2023) also lists two sphyriids in the genus *Lophoura* as parasites of *C. fasciatus* (presumably also referring to *C. simorhynchus*) in South African waters, neither of which was found here. No *Shyrion* or *Lophoura* are known from *M. laevis*, despite these genera being generalists on many gadoids and even non-gadoid fishes that parasitise non-macrourids such as *Genypterus* and *Merluccius*.

The Chondracanthidae are a diverse family of parasitic copepods that inhabit the branchial chamber of a diverse variety of fish species. The genus *Chondracanthus* alone consists of more than 40 described species. Together with sphyriids, chondracanthids are among the most commonly encountered copepod parasites on deepwater fishes (Boxshall, 1998). *C. braueri* and *M. laevis* were infested by chondracanthid copepods in the gills. These were in poor condition and could not be definitively identified to species level, but those on *M. laevis* closely resembled a parasite of the species, *Chondracanthus neali* known from Ireland (Leigh-Sharpe, 1930), Australia (Ho, 1994) and South Africa (Walter & Boxshall, 2021b). It is very unlikely that the chondracanthids in *C. braueri* were *C. neali*, given that this species is considered host-specific to *M. laevis* and its congener *M. nipponensis*. No parasites in this genus have been reported in *Coelorinchus* grenadiers, although *Chondracanthus* are known from macrourids and gadoids other than *Malacocephalus* (e.g. *Chondracanthus australis* is known from *Macrouronus* and *Merluccius* (Walter & Boxshall, 2021a)), so this may simply reflect insufficient taxonomic scrutiny among the South African macrourid parasites. The bomolochid gill parasite *Hamaticolax maleus*, although known from South African *M. laevis*, was not present in fish of this study.

The small nematodes which were relatively abundant in all three species were likely species of the family Anisakidae, which are extreme generalists among teleosts. Anisakid nematodes including the genus *Anisakis* are known to be diverse within macrourids, with Kumagai and Nishino (2023) finding seven species of this family infecting a single *Coelorinchus* in Japanese waters. While no concerted effort was made to identify the cestodes found in this study, species within the genus *Nybelinia*, a confirmed parasite of several South African grenadiers (Palm *et al*., 1997), are known to cause cysts similar to those observed here.

Notably, no parasitic isopods were observed in any of the target species, despite evidence to suggest that isopods (particularly in the family Gnathiidae) are among the most abundant diverse deep-sea ectoparasites in the North Atlantic (Quattrini & Demopoulos, 2016).

Future studies could aim to incorporate known parasites into models of population structure and connectivity, to determine, for example, if these species migrate between the west coast and Agulhas Bank. Additionally, nothing is known about the internal parasites of these species, despite their prevalence in this study.

4.8 Conclusion

The depth distribution of the three grenadier species in South Africa showed them to prefer shallower depth intervals than that recorded off Namibia. Abundance and biomass were typically higher on the south coast than on the west coast, with the exception of *M. laevis* biomass, which was similar but slightly higher in the west. Abundance and biomass patterns are thought to be influenced by a combination of productivity, predation, fishing pressure, and potentially migration of adults.

While both pre-anal fin length and head length correlate well with total length, PAFL is recommended as the superior metric. The equations for estimation of total length (in mm) in specimens with broken tails were as follows: TL = 2.22 * PAFL + 56.7 (*C. braueri*), TL = 2.84* PAFL + 66.0 (*C. simorhynchus*), and TL = 3.73 * PAFL + 136.0 (*M. laevis*). Females were larger than males and sexually indeterminate fish, although the high proportion of fish in poor conditions was thought to have partially obscured true differences between males and indeterminates. Patterns of PAFL and average mass with depth could not be adequately described with simple linear or logarithmic relationships, nor do they necessarily show single maxima.

Length-weight regression parameters were found as: Mass = $8.36\text{x}10^{-5}$ * $\text{PAFL}^{2.97}$ (*C. braueri*), Mass = $1.12\text{x}10^{-4}$ * $\text{PAFL}^{3.08}$ (*C. simorhynchus*), and Mass =$2.09\text{x}10^{-3}$ * $\text{PAFL}^{2.59}$ (*M. laevis*). Both *Coelorinchus* species showed isometric growth, while *M. laevis* was characterised as hypoallometric. Both *C. braueri* and *C. simorhynchus* were relatively large at maturity in comparison to most other grenadiers, with PAFL_{50} of 107 mm and 89 mm (*C. braueri* females and males respectively) and 71 mm and 32 mm (*C. simorhynchus* females and males) However, this may be partially attributed to difficulties in macroscopic maturity staging. Males were found to mature at smaller lengths than females.

Despite well-supported linear relationships between the otolith width and fish PAFL, aging fish by counting otolith annuli proved difficult in all species but *C. braueri*. A von Bertalanffy regression for this species was estimated as $\text{PAFL}_t = 169.13*(1 – e^{-0.10*(t - (-1.73))})$, and the maximum observed age of 17 years was roughly in line with what is known from this genus.

C. braueri preyed primarily on small crustaceans and teleost fish, *C. simorhynchus* on a mix of crustaceans, ophiuroids and teleosts, and *M. laevis* on teleosts and cephalopods, with some large prawns. These findings are generally consistent with those of two previous diet studies on these species, although the relative importance of these prey groups could vary considerably, some new prey taxa are recorded, and some taxa were not recorded here at all.

Sex ratios ranged from roughly equal in *M. laevis* to moderately favouring females in *C. simorhynchus*, with *C. braueri* favouring females slightly. Sex ratios did not consistently vary with depth, but were different on the west and south coasts. GSI was typically less than 1% in males, between 2 and 8% in females, with mean female GSI of 3.2% (*C. braueri*), 3.7% (*C. simorhynchus*), and 2.6% (*M. laevis*). No evidence for strong reproductive seasonality was found. The ovaries of *C. simorhynchus* and *M. laevis* were characterised as asynchronous and group synchronous respectively.

Both *Coelorinchus* species were found to be parasitised externally by copepod *Sphyrion quadricornis*, while *C. braueri* and *M. laevis* were beset by unknown chondracanthid gill copepods.

It is evident that much work remains to be done before these species, and other, less well-researched macrourids may be incorporated into ecosystem and fisheries models or before their stocks and vulnerability may be assessed. Furthermore, it is clear that these species of grenadiers differ in many of their life history characteristics. Future models and fisheries policies must not treat grenadiers interchangeably, but rather consider them on a species-by-species basis where possible.

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