

Article

“Firefly” of the Submarine Mountains: New Data on *Physiculus cynodon* (Moridae, Teleostei) from Emperor Seamounts and Northwestern Hawaiian Ridge

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Abstract: *Physiculus cynodon* is a member of the Moridae family and possesses a ventral bioluminescent organ. Although it has been captured by commercial vessels for decades, our understanding of its biology and ecology remains fragmented. This paper provides data on the species’ spatial and vertical distributions; age and growth; size, age, sex compositions; and sex ratio in the waters around the Emperor Seamounts and the northwestern Hawaiian Ridge. This information is based on the analysis of multi-year Russian data obtained from scientific surveys and observations on commercial fishing vessels. The northernmost capture of this species has been recorded at Nintoku Seamount. Additionally, this species was regularly encountered at depths ranging from 53 to 900 m on seamounts such as Lira (Annei), Koko, Milwaukee (Yuryaku and Kammu), Colahan, and C-H of the Emperor Seamounts and Hancock, Zapadnaya, and Academician Berg of the northwestern Hawaiian Ridge. Catch rates of *P. cynodon* gradually decreased in a southeastern direction. Notably, the relative abundance of this species in bottom trawl catches significantly surpasses that in pelagic catches. The age of the fish in the catch varied from 9 to 37 years, and its growth is described by the VBGF equation with the following coefficients: $L_{\infty} = 858.6$, $k = 0.030$, $t_0 = 3.5$. While the growth patterns for males and females were similar, it is worth mentioning that males rarely survive beyond the age of 25 years.

Keywords: spatial and depth distributions; length–weight relationship; age and growth; otoliths; size–age and size–sex compositions; sex ratio; Lira (Annei) Seamount; Koko Seamount; Milwaukee Seamounts; Yuryaku Seamount; Kammu Seamount; Colahan Seamount; C-H Seamount; Hancock Seamount; northwestern Pacific



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1. Introduction

The family Moridae is the second most species-rich family in the order Gadiformes, following Macrouridae, with 19 genera and 112 species being valid [1]. The most diverse

genus within Moridae is *Physiculus*, represented by 31–43 species, widely distributed in tropical and temperate waters of all oceans, including seamounts, submarine ridges, and island chains in the Pacific Ocean [2–6]. In the North Pacific, 5 to 7 species of this genus are registered [2,7]. One of the most abundant species in the northwestern Pacific is the subtropical West Pacific endemic *Physiculus japonicus* [7–10]. This species ranges from waters of the southern Sea of Japan, the Pacific coast of Japan, and the East China Sea to the seamounts east of the Japanese Archipelago [11–15].

Information on the species composition of the genus *Physiculus* on seamounts in the northwestern Pacific remains somewhat contradictory. *Physiculus japonicus* has been recorded on seamounts Shoho and Shotoku near the coast of Japan but is absent on the more southern seamounts Ritto and Nikko, where it is replaced by *P. rhodopinnis* and *P. yoshidae* [15]. On the Hancock Seamount (northwestern part of the Hawaiian Ridge), previous reports [16,17] mentioned the occurrence of *P. grinnelli* and *P. edelmanni* (the latter species is currently considered in the genus *Gadella* with a range in the western Indian Ocean [6]). In a recent publication [18], *P. grinnelli* and *P. nigripinnis* are reported for the waters off Necker Island (central part of the Hawaiian Islands). Some Russian authors [9,19,20] recorded that the Emperor Seamounts and northwestern Hawaiian Ridge are inhabited by *P. japonicus*. However, a new species, *Physiculus cynodon*, was described from this region in 1986 [21]. Despite this, some Russian authors [19,20] continued to list *P. japonicus* for the waters of the Emperor Seamounts and the northwestern part of the Hawaiian Ridge, ignoring Sazonov [21] and Prokofiev [22]. *P. japonicus* was also included in the databases of the Pacific Branch of the Russian Federal Research Institute of Fisheries and Oceanography (TINRO) for the waters of Japan, the Emperor Seamounts, and the northwestern part of the Hawaiian Ridge [23,24]. Judging by the above-mentioned distribution of *Physiculus* species in the northwestern Pacific, it can be confidently stated that all records in the waters of the Emperor Seamounts and the vast majority of records in the waters of the northwestern Hawaiian Ridge are *P. cynodon*. It is likely that in the waters of the northwestern part of the Hawaiian Ridge (Hancock Seamount), catches could contain *P. grinnelli* [16,17]. However, the occurrence of this species, according to the mentioned publications, was insignificant. It should be borne in mind that these papers were published prior to the description of *P. cynodon*, and the identification may be questionable. In addition, on the distribution map of Pacific *Physiculus* (Figure 17, page 130), Paulin [2] did not record the presence of *P. grinnelli* from the northwesternmost part of the Hawaiian Ridge.

Species of *Physiculus* in the northwestern Pacific have some commercial significance. *P. japonicus* is caught as bycatch in bottom trawl, trap, and gillnet fisheries in some north-eastern areas of Japan and Taiwan, is used for human consumption, and is also a promising raw material source for surimi production [4,8,10]. *P. cynodon* is considered a promising target for fishing in the waters of the Emperor Seamounts [19,20].

The biology of this species, like that of other morids, is poorly understood [25]. Among the North Pacific *Physiculus*, *P. japonicus* in the coastal waters of Japan is the most well-studied one [8,26,27]. Researchers are particularly interested in questions related to symbiotic bacteria that facilitate the functioning of the ventral luminous organ (e.g., [28–31]), a characteristic feature of all species of the genus *Physiculus* [2,32]. However, the distribution and biology of *P. cynodon*, inhabiting seamounts in the northwestern Pacific, remain completely unstudied. The lack of information on the current level of bycatch of non-target species and the status of bycatch species populations in bottom fisheries in the high seas, including waters of seamounts, remains a global problem [33].

This paper presents, for the first time, data on the spatial and vertical distribution; age and growth; size, age, and sex compositions; and sex ratio of *P. cynodon* in the waters around the Emperor Seamounts and the northwestern Hawaiian Ridge based on the analysis of long-term Russian data obtained during scientific surveys and observations aboard commercial fishing vessels.

2. Materials and Methods

Species identification was conducted via examination of five specimens caught in 2019 on the Koko Seamount [20] and deposited in the fish collection of the Shirshov Institute of Oceanology, Russian Academy of Sciences (IO RAS, uncatalogued). All specimens had canine teeth on the jaws (Figure 1), about 180 scales in the lateral line, and 59–61 vertebrae (calculations were made from radiographs). These key external morphological characters correspond well to the description of *P. cynodon* presented by Sazonov [20], Okamoto et al. [7], and Prokofiev [22].

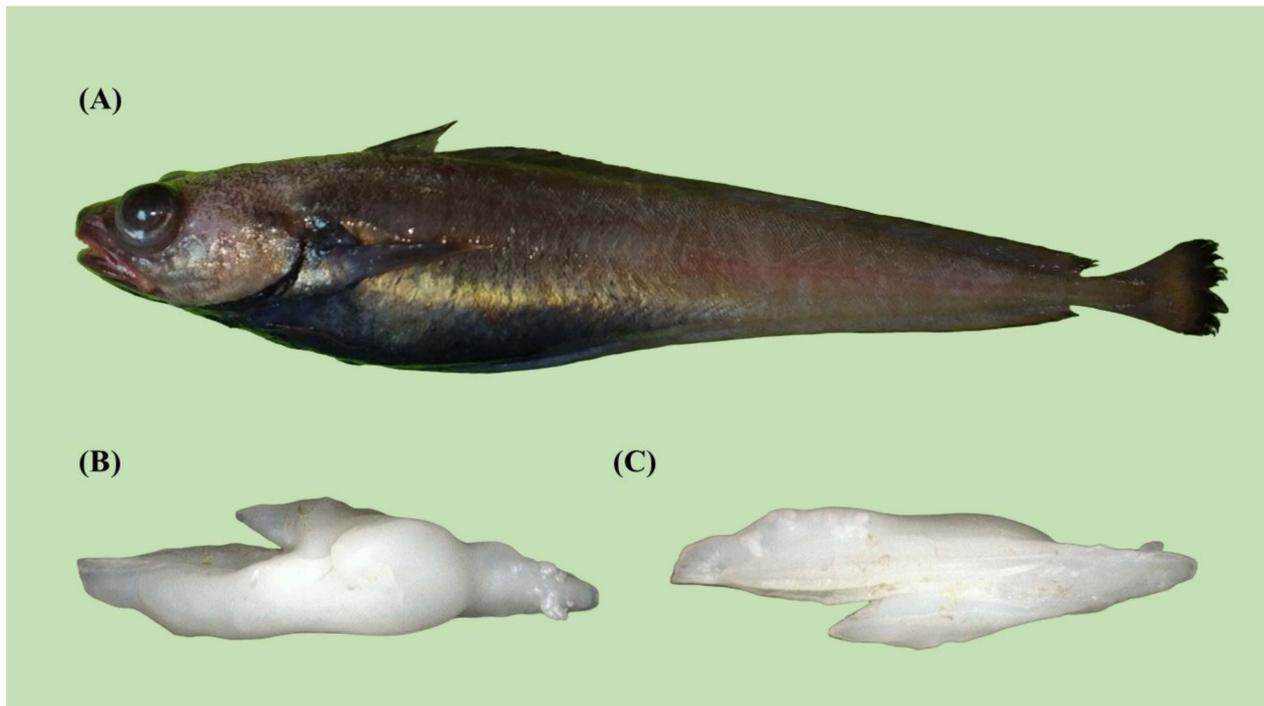


Figure 1. (A) *Physiculus cynodon* from waters around the Emperor Seamounts (TL = 25.3 cm); (B,C) sagittal otoliths (photos by the authors).

All records from the TINRO database related to *P. japonicus* from the waters around the Emperor Seamounts and northwestern Hawaiian Ridge were referred by us to *P. cynodon* based on the following considerations: *P. japonicus* is not found in this area since its range is limited to the waters of the southern Sea of Japan, the Pacific coast of Japan, the East China Sea, and the seamounts east of the Japanese Archipelago [11–15]. The occurrence of other congeners (*P. rhodopinnis*, *P. grinnelli*, *P. nigripinnis*, *P. yoshidae*) in the waters of the Emperor Seamounts and northwestern Hawaiian Ridge is unlikely since there are no confirmed records of these species in the area [2,6,13,15,18].

Two datasets were used for this work (see Figure 2 and Table 1). Raw data (1) were extracted from the extensive TINRO database “Marine Biology” [34,35]. These are compiled data from all scientific, exploratory, and commercial fishing cruises in the region. Many of them are not suitable for quantitative assessments of fish abundance since they do not contain information on trawling speed, opening of trawl mouth, or even the type of trawl used. Based on these data, a general map of the occurrence of the species with catch points (Figure 2) and catches per hour of trawling (Figure 3) was constructed. Cleaned and verified data (2) were taken from two databases [36,37] supplemented with the data from recent trawl surveys conducted by TINRO through 2019 (there were no surveys thereafter). These databases contain only carefully checked and edited data from selected scientific cruises and all technical parameters of fishing gear necessary for calculating fish abundance in specimens or kilograms per square kilometer. Based on these data, calculations, comparisons, tables, and graphs were made. The data from trawl stations

located relatively far from the tops of seamounts beyond the 4500 m isobaths, as well as single catches, indicated by asterisks in Figure 2, were removed from both samples. The results of the samples are presented in Table 1.

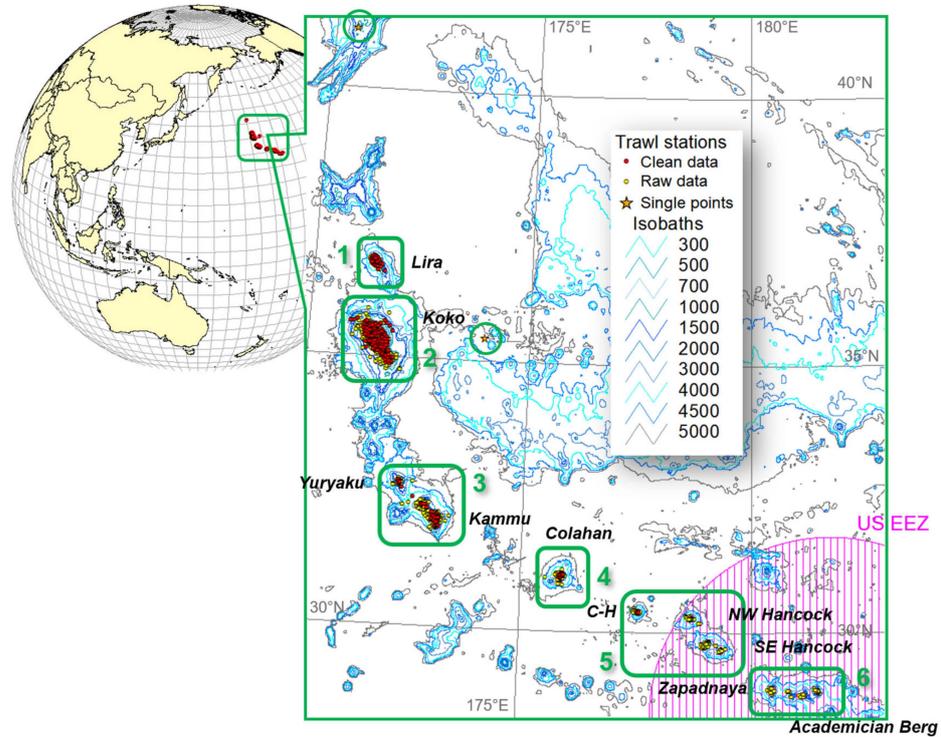


Figure 2. Locations of *Physiculus cynodon* captures (upper left corner, red circles) and their distribution off Emperor Seamounts and northwestern Hawaiian Ridge, 1968–2019 (numbers indicate separate seamounts or groups of seamounts).

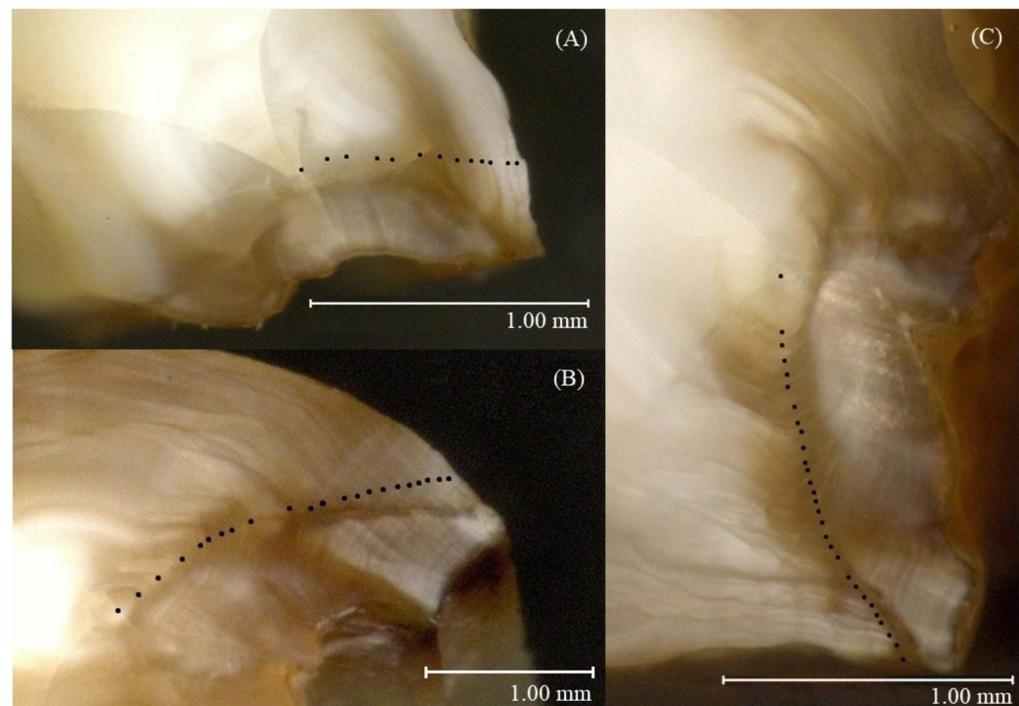


Figure 3. Cross-sections of otoliths of *Physiculus cynodon* from waters of the Emperor Seamounts: (A) TL 18.5 cm, 13 years; (B) TL 35.1 cm, 21 years; (C) TL 42.5 cm, 29 years (dots indicate annual growth zones; TL—total length).

Table 1. Characteristics of raw and cleaned datasets by area, years, depths, and numbers of bottom trawl (BT) and midwater trawl (MT) hauls used in the analysis of *Physiculus cynodon* catch data (for designations of areas, see Figure 2).

Area	Raw Data, 58 Cruises					Clean Data, 19 Cruises				
	Years	Depth Range, m	BT	MT	Total	Years	Depth Range, m	BT	MT	Total
1	1971–2019	0–770	21	188	209	1979–2019	0–770	6	349	355
2	1969–2019	0–1500	659	457	1116	1979–2019	0–550	69	172	241
3	1969–2013	0–800	324	788	1112	1979–2011	5–459	13	92	105
4	1969–2013	0–2000	655	45	700	1979–1982	40–500	19	11	30
5	1969–1976	0–999	498	76	574	1982–1982	120–260	0	5	5
6	1968–1976	0–700	79	158	237	-	-	0	0	0
Total	1968–2019	0–2000	2236	1712	3948	1979–2019	0–770	107	629	736

Analysis of Biological Data

To investigate the growth and age of fish, it is imperative to have representative samples that include all size classes. Therefore, the dataset from trawl catches in 2019 was complemented with larger specimens from the same region captured during longline fishing in 2016.

During the 2019 bottom trawl survey on the R/V “Professor Kaganovsky” in waters of the Lira and Koko seamounts, 406 *P. cynodon* specimens were captured, and otoliths were extracted from 58 of these for age determination. In 2016, during commercial longline operations on the F/V “Palmer,” 33 *P. cynodon* inds. were taken as bycatch, and otoliths were collected from all of them for age determination.

A comprehensive biological analysis was conducted following standard protocols [38,39]. The analysis involved measurements of total length (TL) and body weight (W), as well as the determination of sex and gonadal maturity stage. Otoliths (sagittae) were extracted from freshly caught fish during the onboard biological analysis. Otolith measurements, weighing, and age determination were carried out in the laboratory. Otolith length (Lo) was measured using a digital caliper (Kraftool GmbH, Böblingen, Germany), with an accuracy of 0.01 mm, and weight (Wo) was determined using electronic scales (Sartorius GmbH, Goettingen, Germany), with an accuracy of 0.001 g.

To compare the length–weight relationships (LWRs) of males and females, coefficients of the LWR equation were calculated for both sexes. Given that the distribution of the obtained data was not normal (tested for normality using Shapiro–Wilk tests, with significance set at $p \leq 0.05$; males $W = 0.95$, $p = 0.216$; females $W = 0.96$, $p = 0.084$), we employed the Mann–Whitney U test for comparison.

To compare the growth rates of males and females, age–TL relationships were employed. As these relationships displayed a normal distribution for both sexes (tested for normality using Shapiro–Wilk tests, with significance set at $p \leq 0.05$; males $W = 0.93$, $p = 0.931$; females $W = 0.96$, $p = 0.064$), the comparison was conducted using a Student’s *t*-test.

A widely employed method for estimating the age of fish using otoliths, which has demonstrated success in demersal (including deep-water) species inhabiting the waters along the west coast of the USA and Canada [40], is the “break and burn” technique. This method has also proven effective in studying the age of some morid species [41–49].

The otoliths were broken transversely using a lancet and then subjected to the flame of an alcohol burner. In cases where it was necessary, some otoliths were polished using abrasive discs coated with aluminum oxide or silicon carbide, with grit sizes ranging from 0.1 to 0.9 μm (Buehler, Chicago, IL, USA). The suitability of each otolith for further analysis depended on the results of visual inspections. Otolith surfaces were examined at $1\times$ magnification using a trinocular microscope, Motic SMZ-143 (Motic, Hong Kong, China). To aid in examination, otolith surfaces were coated with glycerine and illuminated with reflected light, and photographs were captured using a Toupcam UCMOS14000KPA camera (Toupcam Photonics, Hangzhou, China) (Figure 3).

The average percent error (APE) index was calculated according to the methods proposed by Beamish and Fournier [50], based on a comparison of age estimations by three different readers. The age of each individual fish was determined as the mean age derived from three independent readings. The consistency of age estimations among readers was assessed through pairwise comparisons and considered reliable if the APE values were less than 10% [51].

The selection of the most appropriate growth function to describe *P. cynodon* growth was carried out using the Akaike information criterion (AIC) [52]. This involved a comparison of linear, power, and logistic relationships; the Gompertz curve; and the von Bertalanffy equation.

The mean specific rate of growth was estimated using the following formula [53,54]:

$$C = \frac{\ln(L_{n+1}) - \ln(L_n)}{t_{n+1} - t_n}$$

where L_{n+1} and L_n are the mean lengths of fish at the ages of t_{n+1} and t_n , respectively.

Statistical analysis of the results was performed using MS Excel and PAST ver. 3.14 software [55].

Based on the results of the age determination of *P. cynodon*, a length–age key was developed [56], which was used to calculate the age composition of the sample collected from the waters of the Lira and Koko seamounts in 2019.

3. Results

3.1. Catch Rate and Distribution

Data from Russian bottom and midwater trawl surveys conducted between 1968 and 2019 reveal that the northernmost record of Japanese codling was on Nintoku Seamount. However, this species was consistently found in trawl catches on the Lira (Annei), Koko, Milwaukee (Yuryaku and Kammu), Colahan, and C-H seamounts of the Emperor Seamounts. It was also encountered on Hancock, Zapadnaya, and Academician Berg seamounts situated in the northwestern part of the Hawaiian Ridge (see Figure 2). Notably, both the maximum and average catches of the studied species displayed a gradual decrease trend in the southeastern direction (Table 2). Maximum and average catches were highest on Lira Seamount (>7.0 and 3.3–4.4 thousand inds. per hour, respectively), while on the southernmost seamounts, these figures were only 195–220 and 15.6–34.3 inds. per hour, respectively. The fishing effort numbers (numbers of hauls) on Lira and the southernmost seamounts were similar (209 and 237, respectively), with the highest number of hauls conducted on Koko and Milwaukee (Yuryaku and Kammu) seamounts, reaching 1116 and 1112, respectively.

Table 2. Depths of captures and catch rates of *Physiculus cynodon* off Emperor Seamounts and northwestern Hawaiian Ridge, 1968–2019.

Area	Capture Depths, m			Highest CPUEs		Highest Mean CPUEs	
	Min.	Max.	Mean	Depth Range, m	Inds. Caught per h	Depth Range, m	Inds. Caught per h
1	120	700	373.9	400–450	7013.3–7627.8	275–430	3320.0–4380.0
2	53	550	303.8	290–383	3258.0–4140.0	278–383	657.1–3528.0
3	285	500	373.6	330–385	384.0–432.0	354–392	192.0–232.0
4	250	900	345.4	275–280	248.6–466.7	224–350	20.3–28.8
5	260	400	296.8	270–300	72.0–96.0	270–295	2.5–8.0
6	190	280	240.0	195–220	34.3–109.1	195–220	15.6–34.3

On Lira Seamount (Figure 4A), all trawl catches of *P. cynodon* were primarily concentrated in the north, mainly within the 1500 m isobath. Maximum catches exceeded 7000 inds. per hour were recorded in a wide area spanning almost entire northern part of the seamount.

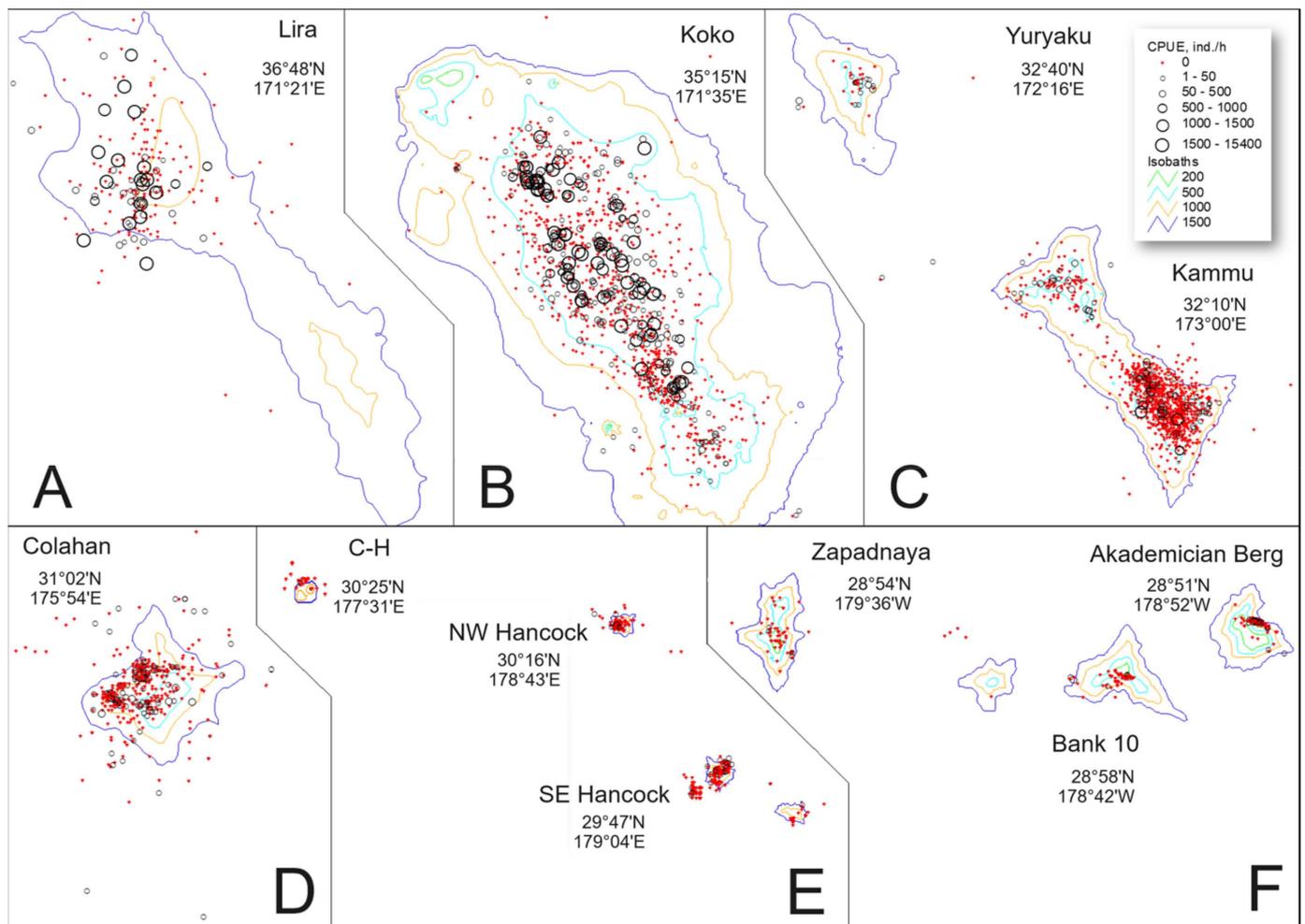


Figure 4. CPUEs of *Physiculus cynodon* off Emperor Seamounts and northwestern Hawaiian Ridge, 1968–2019 (capital letters (A–F) correspond to areas 1–6 in Figure 2 and Table 1). Coordinates of seamount peaks are provided below their names according to <https://earthref.p/org/SC> (accessed on 24 August 2023) and [57].

On Koko Seamount (Figure 4B), the majority of catches were within the 500 m isobath. Maximum catches were significantly lower compared to Lira Seamount (3.3–4.1 thousand inds. per hour) and observed across the entire surface of the seamount from northwest to southeast.

On the Milwaukee Seamounts (Figure 4C), the majority of catches were associated with Kammu Seamount. On Yuryaku, catches were scarce, not exceeding 50 inds. per hour, and were within the 1000 m isobath. On Kammu, nearly all catches were within the 1000 m isobath, with maximum catches occurring in its southern section. Overall, for this area, despite the nearly equal number of hauls conducted on Koko Seamount, the maximum catches of Japanese codling were an order of magnitude lower (384–432 inds. per hour).

On the Colahan Seamount (Figure 4D), maximum catches did not exceed 500 inds. per hour, with an average of 20–29 inds. per hour. In contrast to seamounts farther north, the studied species was observed well beyond the 1500 m isobath and was also found in deeper waters.

On the C-H Seamount, only a few catches, not exceeding 50 inds. per hour, were in its northern part within the 1500 m isobath (Figure 4E). The main catches in the fifth area were recorded on SE Hancock Seamount and spanned its summit, mainly within the 1500 m isobath. Catches of *P. cynodon* on NW Hancock were significantly rarer and smaller

in size. Overall, the maximum catches reached 72–96 inds. per hour with an average of 2.5–8.0 inds. per hour, making it the lowest among all surveyed seamounts.

On the southernmost seamounts (Figure 4F), the number of trawls conducted was low (237). Maximum catches were similar to those in the adjacent area (34–109 inds. per hour), but on average, they were three to four times higher (16–34 inds. per hour). Zapadnaya and Bank 10 seamounts were characterized by rare and low catches. On Academician Berg Seamount, the catch size was higher, with the majority concentrated in the central-eastern part of the seamount.

The results of the analysis of *P. cynodon* abundance on different seamounts, based on clean data, slightly differ from the raw data presented above. Overall, they indicate that catches in areas 3 and 4 are significantly lower (averaging 73–169 inds./km²) than those on the northernmost seamounts in areas 1 and 2 (averaging 654–951 inds./km²). The maximum density was observed on Koko Seamount, while Lira Seamount ranked second (Figure 5A). Nevertheless, a statistical test of these results revealed no significant differences in densities across these four areas (ANOVA, $F = 1.0504$, $p = 0.3802$).

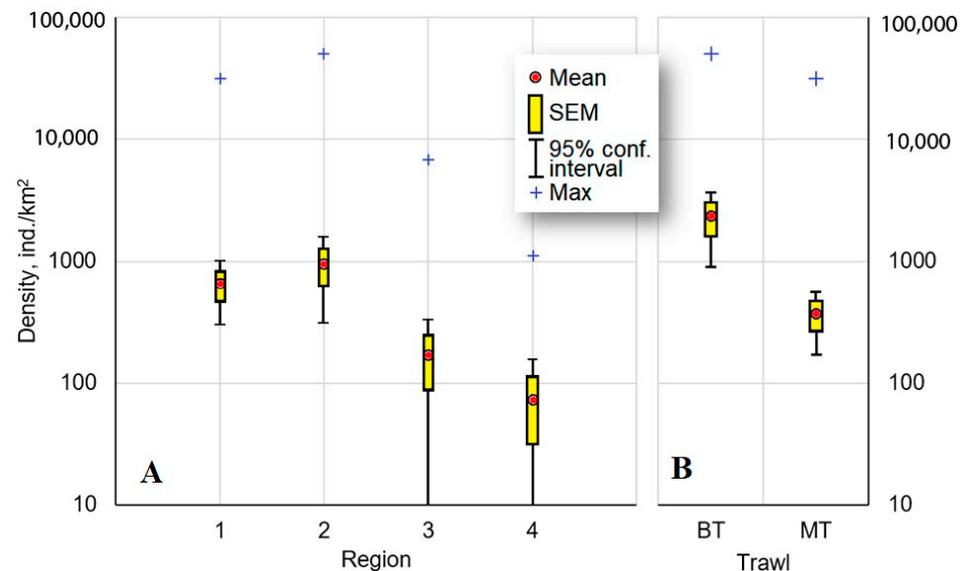


Figure 5. Relative abundance of *Physiculus cynodon* off Emperor Seamounts and northwestern Hawaiian Ridge, 1968–2019, depending on area (A) and gear type (B) (for designations of areas, see Figure 2; BT—bottom trawl; MT—midwater trawl; SEM—standard error of mean).

Comparing the catch size between bottom and midwater trawl hauls using clean data, showed statistically significant differences for different trawl types (ANOVA, $F = 25.9307$, $p < 0.0001$). The catch size of bottom trawls (on average, 2319 inds./km²) was almost an order of magnitude higher compared to that of midwater trawls (371 inds./km²) (Figure 5B).

The relative abundance statistically differed across time (ANOVA, $F = 6.1669$, $p < 0.0001$). In the 2010s, there were significantly fewer hauls, especially by midwater trawls, compared to the 1970s–1980s, but high catches were still occasionally taken (Figure 6A). High catches were just as frequent in the water column as on the bottom, although, generally, the highest catches were by bottom trawls.

The catch size statistically significantly differed across depth ranges (ANOVA, $F = 2.0992$, $p < 0.0001$). Maximum catches in both bottom and midwater trawls were recorded around 400 m (Figure 6B). At these depths, catches could be either insignificant or zero.

Depths at which *P. cynodon* catches were recorded on different seamounts varied significantly (Table 2). On average, catch depths generally decreased from the northwest to the southeast. While the average catch depth on Lira Seamount was 374 m, it was 240 m on the southernmost seamounts. Similar patterns were observed for maximum catches (400–450 m vs. 195–220 m) and average catches (275–430 m vs. 195–220 m).

Catch size exhibited significant variation throughout the day (Figure 6C). High catches were observed both on the bottom and in water column from the evening (17:00) to early morning (06:00). The disparity in fish density between these time periods was statistically significant (ANOVA, $F = 8.6267$, $p = 0.0033$). Maximum and average catches during nighttime were nearly an order of magnitude higher compared to those during daylight hours (976 vs. 156 inds./km² and 50,450 vs. 5587 inds./km², respectively).

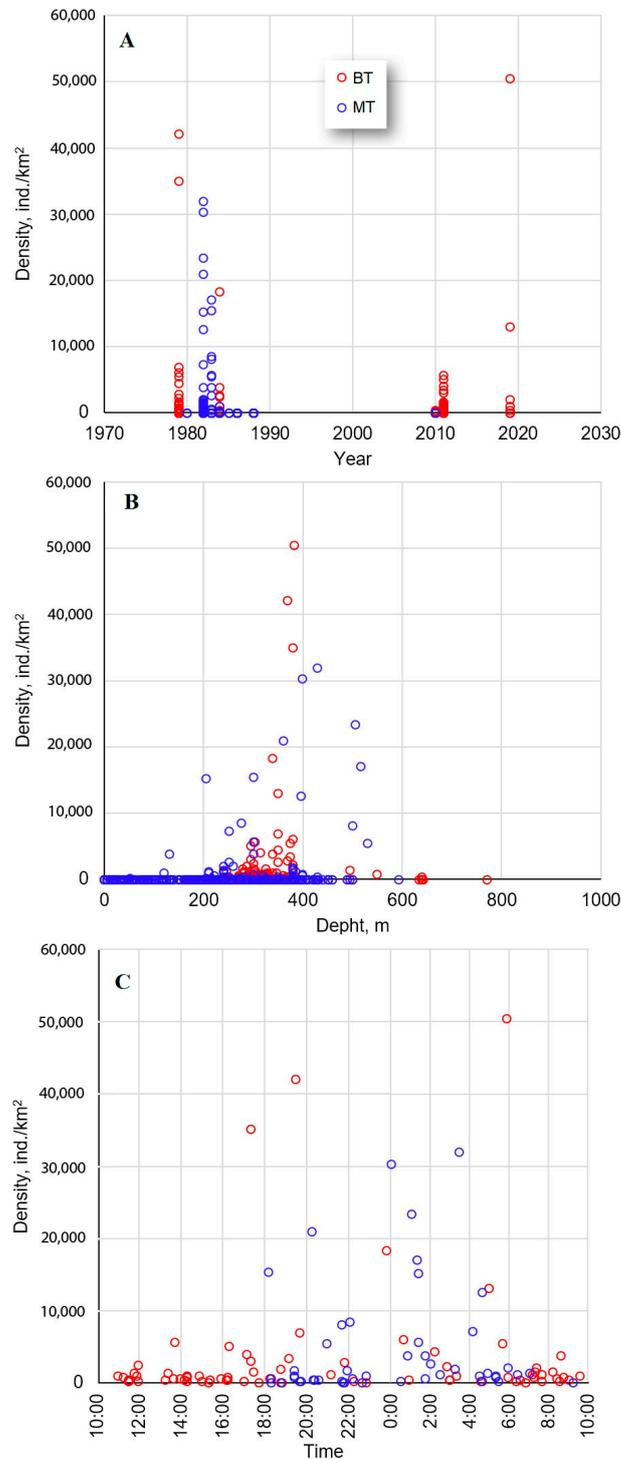


Figure 6. Relative abundance of *Physiculus cynodon* off Emperor Seamounts and northwestern Hawaiian Ridge, 1968–2019, depending on year (A), depth (B), and time of the day (C) (BT—bottom trawl; MT—midwater trawl).

3.2. Biological Features

3.2.1. Size Composition of Catches

The samples collected displayed diverse size compositions due to the varying selectivity of bottom trawls and longlines (Figure 7). The body length of individuals caught by trawls in 2019 ranged from 97 to 524 mm, with an average of 258.6 ± 3.3 mm. In this sample, males had total lengths ranging from 150 to 390 mm, with an average of 285 ± 4.9 mm, while females had TLs ranging from 140 to 524 mm, averaging 251.2 ± 3.9 mm, and juveniles were from 97 to 120 mm, on average 112 ± 2.7 mm long. The most abundant size class in the catch consisted of individuals with TL between 210 and 250 mm, accounting for 34.3% of the catch. Slightly fewer fish fell within the TL range of 260 to 300 mm (20.0% of the catch), 310 to 350 mm (17.0%), and 160 to 200 mm (16.5%), while fishes from other size classes in the trawl catches were encountered infrequently (Figure 7).

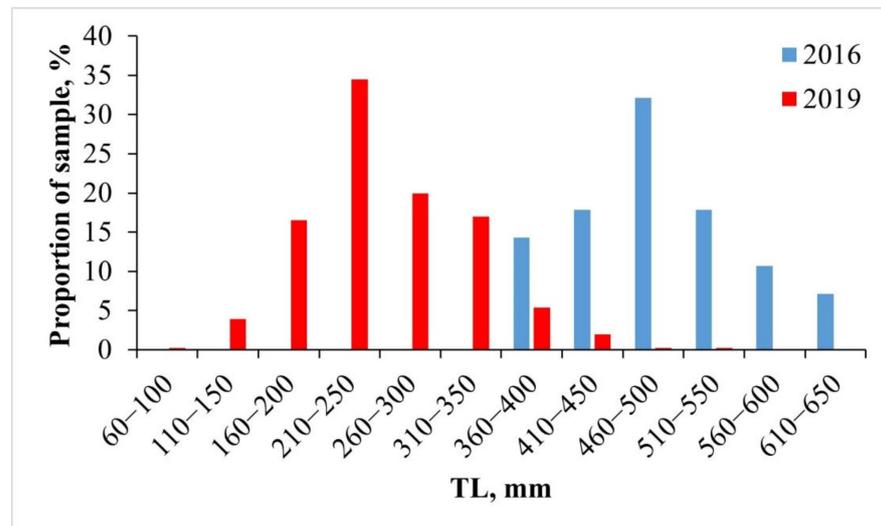


Figure 7. Size composition of *Physiculus cynodon* in longline (2016) and bottom trawl (2019) catches from off the Emperor Seamounts.

In 2016, fish in the longline catches were significantly large; their total lengths varied from 370 to 622 mm, with an average of 488.8 ± 11.7 mm. The males had TLs ranging from 370 to 550 mm, with an average of 436 ± 39.6 mm, and the females had TLs ranging from 370 to 622 mm, with an average of 499.4 ± 13.3 mm. The most abundant size class consisted of fish with TL between 460 mm and 500 mm, accounting for 32.1% of the catch. The least numerous size class consisted of larger specimens with TLs ranging from 610 to 650 mm, representing 7.1% of the catch, while other size classes in the catches ranged from 10% to 20% (Figure 7).

The body weight from trawl catches varied from 7 to 1068 g, with an average of 230.0 ± 19.3 g. The males had a body weight of 30 to 410 g, with an average of 213.8 ± 19.4 g, the females had a body weight of 42 to 1068 g, with an average of 246.7 ± 27.8 g. Juveniles had a body weight of 7 to 10 g, with an average of 8.5 ± 0.9 g. The body weight of fish captured by longlines ranged from 300 to 1880 g, with an average of 881.2 ± 74.6 g. The males in these catches weighed 300 to 1320 g, with an average of 657.5 ± 227 g; the females weighed 300 to 1880 g, with an average of 947.9 ± 85.4 g.

In the 2019 trawl catches, females dominated, comprising 70.9%; males made up 27.1%, and juveniles made up 2.0%. In the longline catches of 2016, the sex ratio was different, with a more significant predominance of females over males (85.7%), and juveniles were not recorded in the longline catches.

The sex ratio varied among different size groups. Among fish less than 250 mm long, females were predominant. Among fish between 260 and 400 mm TL, the sex ratio was

close to 1:1, while among larger individuals, females still dominated. Among fish larger than 450 mm, males were not encountered (Figure 8).

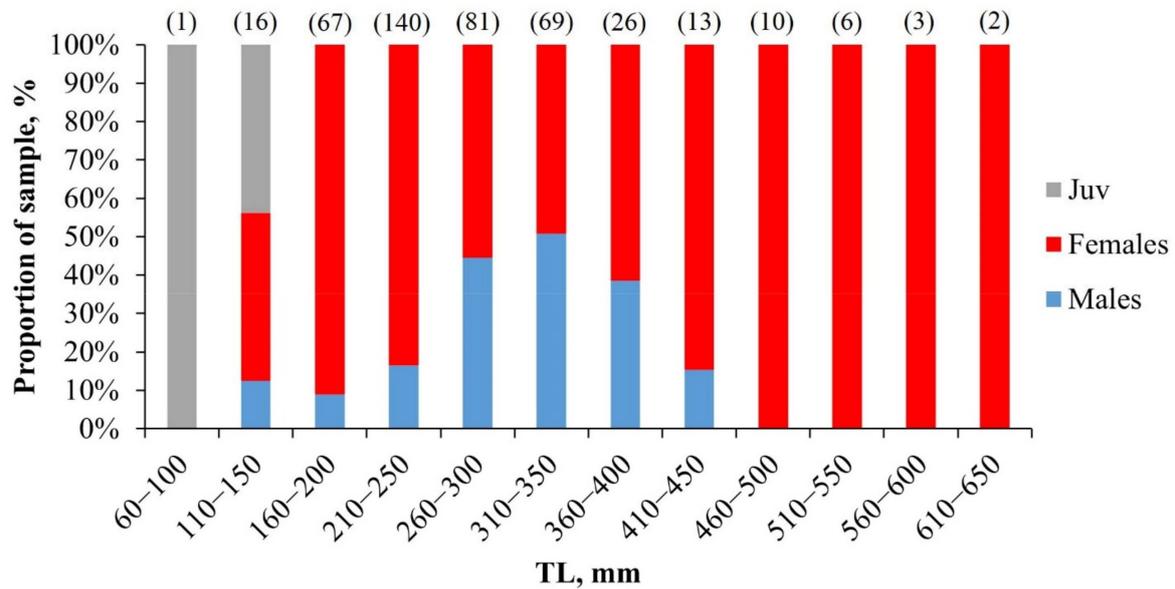


Figure 8. Sex ratio of *Physiculus cynodon* from off the Emperor Seamounts in different size classes (number of specimens is shown in brackets).

The combined data also showed that the sex ratio at different depths varied (Figure 9). Males predominated in catches at around 280 m; females began to dominate at depths exceeding 360 m, with their proportion at depths approaching 400 m exceeding 90%. In 280 m to 360 m, there was no clear dominance of one sex.

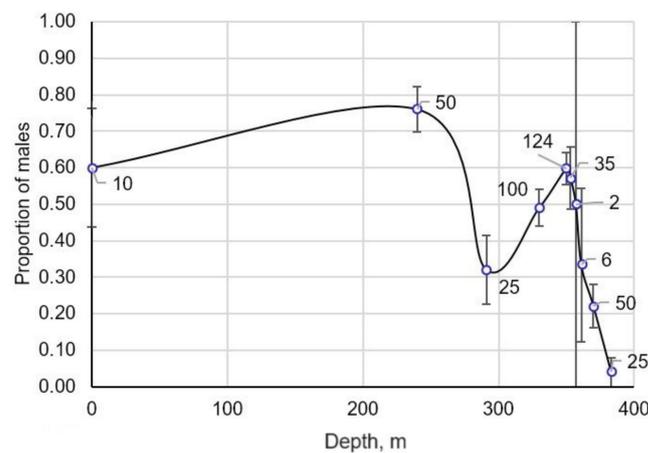


Figure 9. Sex ratio of *Physiculus cynodon* off Emperor Seamounts and northwestern Hawaiian Ridge, 1968–2019, by depth ranges (numbers on the graph are sample sizes, bars are standard errors).

3.2.2. Relationships between Body and Otolith Sizes

For comparing the relationships between body weight (W, g) and total length (TL, mm) in males and females, the coefficients of the W to TL ratio were calculated for both sexes. The comparison did not reveal any significant differences between them ($U = 1108.5$, $Z = -1.55464$, with $p = 0.120$).

The relationship between body weight (W, g) and total body length (TL, mm) of *P. japonicus* from the Emperor Ridge waters is best described by the power function $W = 1.2 \times 10^{-5} TL^{2.92}$ with $R^2 = 0.92$ (Figure 10a).

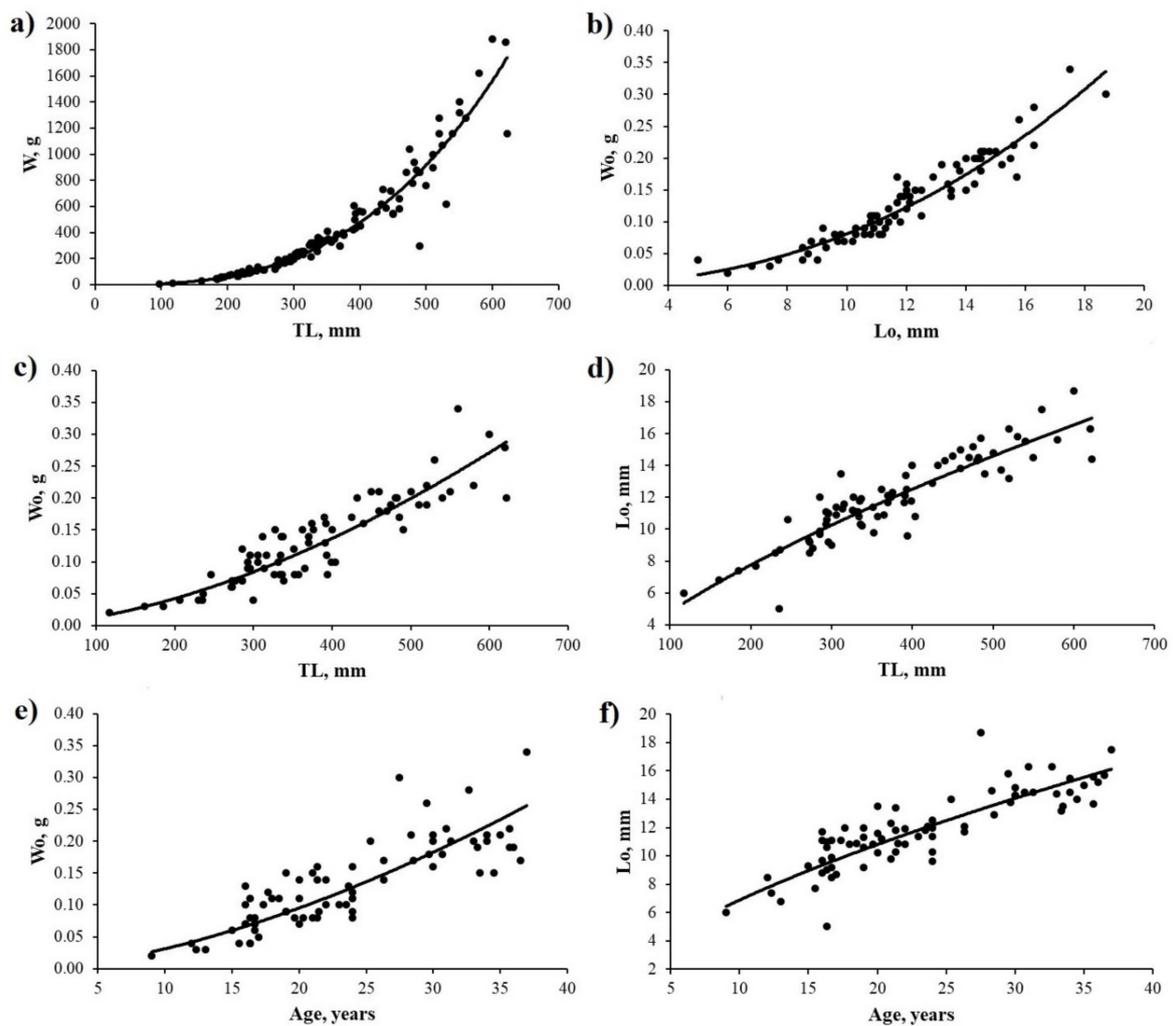


Figure 10. Relationships between (a) body weight (W) and total length (TL), (b) otolith weight (Wo) and otolith length (Lo), (c) otolith weight (Wo) and total length (TL), (d) otolith length (Lo) and total length (TL), (e) otolith weight (Wo) and age, and (f) otolith length (Lo) and age of *Physiculus cynodon* from waters of the Emperor Seamounts.

The length of otoliths of *P. cynodon* in the combined sample varied from 5 to 18.7 mm, with an average of 11.9 ± 0.31 mm, and weight ranged from 0.02 to 0.34 g, with an average of 0.13 ± 0.01 g. The relationship between otolith weight (Wo) and otolith length (Lo) is described as $Wo = 4.4 \times 10^{-4} Lo^{2.27}$ with $R^2 = 0.91$ (Figure 10b). The relationship between otolith weight and TL described by the formula $Wo = 5.4 \times 10^{-6} TL^{1.69}$ with $R^2 = 0.81$ (Figure 10c). The relationship between otolith length and TL is described by the equation $Lo = 0.2 TL^{0.69}$ with $R^2 = 0.82$ (Figure 10d).

The APE indexes for readers 1, 2, and 3 were 6.5%, 5.0%, and 4.3%, respectively, indicating that our age estimations can be considered relatively reproducible.

Out of the 8.8% of fish selected for otolith age analysis, some were found unsuitable for age estimation due to poorly defined boundaries between annual zones and cracking upon heating. As a result, age could be determined for only 83 individuals. Their ages in the sample ranged from 9 to 37 years, with an average of 23.2 ± 0.76 years. Male ages ranged from 9 to 35 years, with an average of 19.8 ± 1.34 years, while female ages ranged from 12 to 37 years, with an average of 24.8 ± 0.90 years.

Among fish older than 25 years, males were rarely observed (Figure 11). Nonetheless, a comparison of the age and body length ratios for males and females in the study sample

did not reveal significant differences ($t = 0.402, p = 0.689$), indicating similar growth rates for fishes of both sexes.

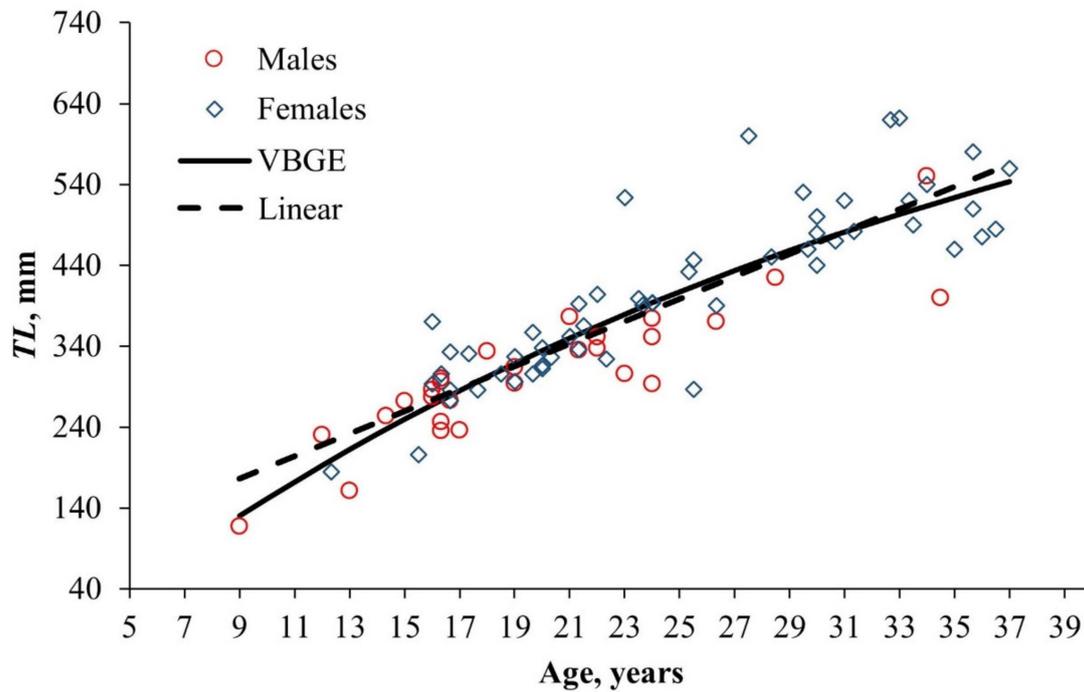


Figure 11. Growth curves of *Physiculus cynodon* from waters of the Emperor Seamounts calculated based on the VBGE and linear function.

Comparisons using the Akaike criterion showed that the linear function best describes the growth (Table 3), with the following coefficients: $a = 13.9, b = 51.6$, and $R^2 = 0.8$. Despite the lower Akaike criterion values for the von Bertalanffy growth equation (VBGE) compared to other functions, given its widespread use in describing the growth of long-lived, deep-sea fish species, it was also calculated based on the data from this study. Its parameters were $L_\infty = 858.6, k = 0.030$, and $t_0 = 3.5$, with $R^2 = 0.8$ (Figure 11).

Table 3. Akaike information criterion (AIC) values for different growth functions of *Physiculus cynodon* from waters of the Emperor Seamounts (maximum AIC value is given in bold).

Function	AIC
Linear: $TL = at + b$	2.0542
Power: $TL = at^b + c$	2.0213
VBGE: $TL = L_\infty(1 - e^{-k(t-t_0)})$	1.9664
Logistic: $TL = \frac{a}{1 + be^{ct}}$	1.9735
Gompertz: $TL = ae^{be^{ct}}$	1.9694

The specific growth rate of *P. cynodon* noticeably decreases over the studied lifespan range. Between the ages of 10 and 15 years, the specific growth rate of the fish decreases markedly compared to the period from 15 to 35 years (Figure 12).

The relationship between otolith weight and age (A) is described by the function $W_o = 7.7 \times 10^{-4} A^{1.61}$ with $R^2 = 0.69$ (Figure 10e). The relationship between otolith length (Lo) and age (A) is $Lo = 1.54 A^{0.65}$ with $R^2 = 0.73$ (Figure 10f).

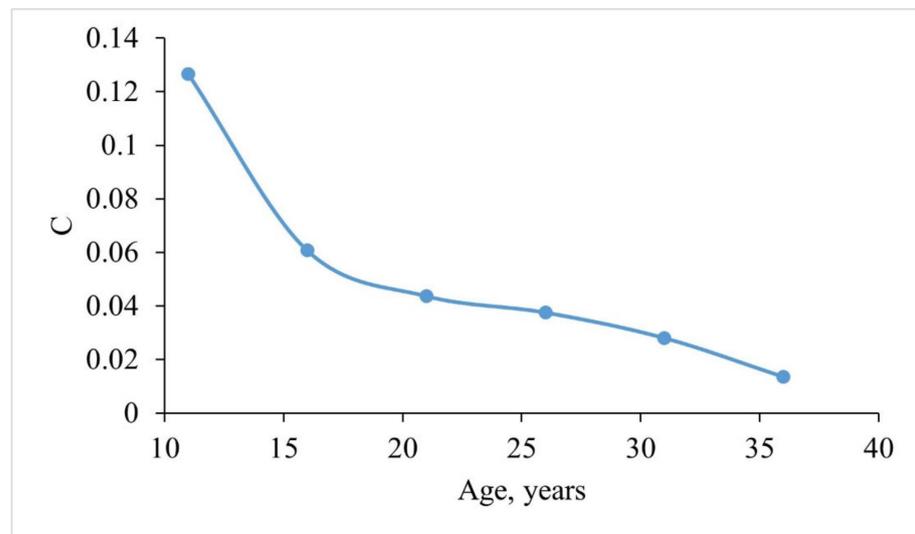


Figure 12. Specific growth rate of *Physiculus cynodon* from waters of the Emperor Seamounts.

According to the age structure calculated using the size–age key, in the trawl catches of 2019, fish aged 16 years predominated, constituting 28.4% of the catch. There were significantly fewer individuals aged 12 years (13.9%) and 17 years (12.9%). Fish older than 20 years were rare (Figure 13). The age structure of longline catches was significantly different. In this sample, fish younger than 28 years were rare, with a prevalence of 30-year-old (14.3%), 31-year-old (10.7%), and 36-year-old (10.7%) fishes.

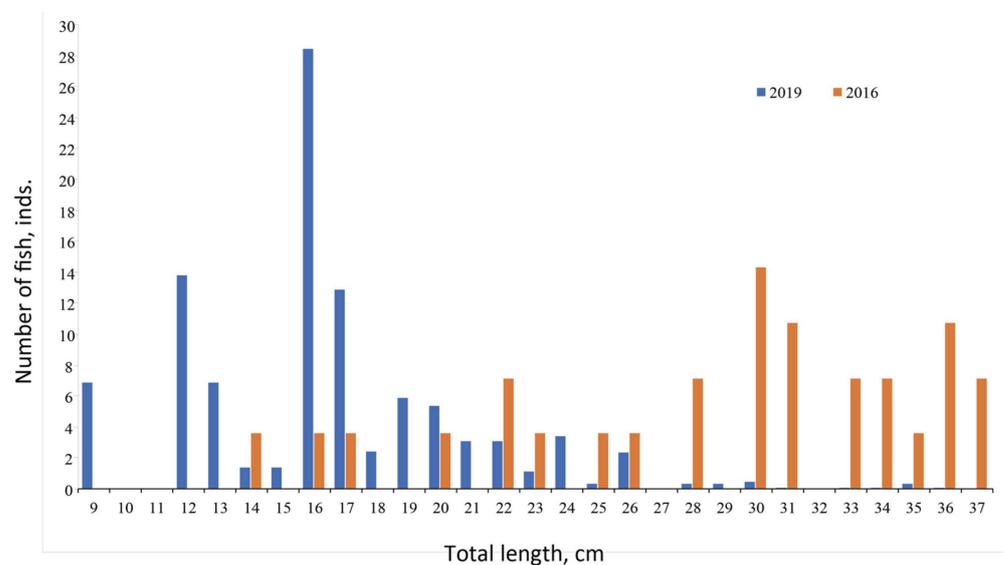


Figure 13. Unweighted age composition of *Physiculus cynodon* from waters of the Emperor Seamounts in 2016 (longline catches) and 2019 (bottom trawl catches).

4. Discussion

4.1. Catch Rate and Distribution

Borets [9] reported (as *P. japonicus*) that *P. cynodon* is found throughout the study area from Lira Seamount in the northwest to Academician Berg Seamount in the southeast. There are no confirmed records of this species in northernmost locations in published literature [20,57,58]. *Physiculus cynodon* has never been a targeted species on the seamounts under study. It has primarily been bycatch associated with the main commercial species *Pentaceros wheeleri* and *Beryx splendens* [33,57,59]. The maximum trawl fishing efforts on the

Emperor Seamounts were concentrated on Jingu, Lira, Koko, Yuryaku, Kammu, Colahan, and C-H seamounts [19,60–62].

Commercial fishing by Russian and Japanese fishing vessels began in the late 1960s. After ten years of intensive fishing, the resources of the primary target species, *P. wheeleri*, were significantly depleted, leading to the cessation of widespread trawl fishing on the Emperor Seamounts [17,19]. Following the 1977 US ban on fishing in the EEZ around the Hawaii, trawl fishing was prohibited on seamounts in the northwestern part of the Hawaiian Ridge. Trawling shifted outside the US EEZ, but catches were low, resulting in a substantial reduction in fishing efforts [33,62]. From 2012 to 2018, Koko, Kammu, and Colahan seamounts were intensively exploited by Japanese and South Korean trawlers [61]. Recently, the North Pacific Fisheries Commission introduced small-scale closures for bottom fishing on Koko and C-H seamounts, but it is believed that fishing is still ongoing on Koko, Yuryaku, and Kammu seamounts [60,62].

The spatial distribution of fishing efforts is described in the literature for 2012 to 2018 based on Japanese and South Korean data [61]; it can be compared with Russian data from 1968 to 2019. For Lira Seamount, the distribution of Russian catches of *P. cynodon* corresponds to the distribution of trawl efforts by Japanese and South Korean vessels. In both cases, catches of *P. cynodon* and the primary fishing efforts were concentrated in the northern part of the seamount within the 1500 m isobath. The distribution pattern of Russian catches of *P. cynodon* on Koko Seamount closely matches the distribution of efforts in 2012–2018. Both catches and efforts were predominantly located in the central part of the seamount within the 500 m isobath, from its northwestern boundary to its southeast. On Yuryaku Seamount, maximum efforts 2012 to 2018 were observed in the central part of the seamount, while Russian catches of *P. cynodon* were recorded in the central-eastern part. There is no apparent correlation between catches of the species in Russian catches and the efforts of Japanese and South Korean vessels. The latter were almost evenly distributed across the seamount's summit within the 1500 m isobath, while the maximum catches by Russian vessels were in the southern part, bounded by the 1000 m isobath.

On Colahan Seamount, the maximum fishing efforts in 2012–2018 were concentrated in the central part of the summit in a narrow strip from the northeast to the southwest. Russian catches were across the entire surface of the seamount and in the surrounding waters. There are no published data available on the distribution of fishing efforts on seamounts in the northwestern Hawaiian Ridge. Summarizing the results, in most cases, the distribution pattern of *P. cynodon* catches from 1968 to 2019 on the Emperor Seamounts corresponds to fishing by Japanese and South Korean trawlers from 2012 to 2018. This suggests that *P. cynodon* is a common bycatch species. Instances where the distribution pattern of *P. cynodon* catches slightly differed from that of fishing efforts might be correlated with changes in fishing tactics employed by Japan and South Korea, such as upgrading their vessels with advanced technical equipment and improved fishing gear.

Data on the abundance of *P. cynodon* within its range are limited. Published literature provides population densities for Koko Seamount in 2010 [19] and 2019 [20]. The minimum recorded catch in 1982 on Koko Seamount averaged 0.9 kg/km². On Koko Seamount itself, the relative biomass of *P. cynodon* averaged 17.6 kg/km² in 2010 [19] and increased to 597.6 kg/km² in 2019 [20]. Our data significantly deviate from the published figures, likely due to different calculation methods. For Koko Seamount, the relative biomass of *P. cynodon* in 2010 was 11.2 kg/km² (slightly lower than published data), while in 2019, it was 1366.3 kg/km² (more than twice the published figures). The highest average catches in this area (5241.4 kg/km²) were in 1979.

Significant differences (by an order of magnitude) in *P. cynodon* catches in bottom and midwater trawls on the surveyed seamounts substantiate the findings that this species, like other members of *Physiculus*, is benthopelagic [12,27,63]. Variations in catches on the surveyed seamounts in different years are attributed to the long-term dynamics of fishing for the primary target species and the subsequent alterations in fish community composition. The highest catches were in the late 1970s, coinciding with the cessation

of active Soviet fishing for *Pentaceros wheeleri* and *Beryx splendens*. Large midwater trawl catches were observed in Russian scientific surveys in the early 1980s. Another period of large bottom trawl catches of *P. cynodon* was recorded in the late 2010s. The increase in *P. cynodon* catches on Koko Seamount in 2019, exceeding those in 2010 [19,20], likely occurred due to changes in fish communities. In 1968–1976, catches on Koko Seamount were dominated by *P. wheeleri*, but by the late 1980s, *B. splendens* started to predominate [57]. Subsequently, it was replaced by *Epigonus denticulatus* and *P. cynodon* [20]. Similar changes in catch composition due to commercial fishing have also been observed on Yuryaku, Kammu, and Colahan seamounts. For instance, from 1968 to 1973, *P. wheeleri* dominated the catches on these seamounts, but after a decade of fishing activities, *B. splendens*, *Helicolenus avius*, *Zenopsis nebulosus*, *E. denticulatus*, and *P. cynodon* began to predominate [64].

The significant increase in *P. cynodon* catches during dark hours, both near the seafloor and the water column, is likely associated with vertical diurnal migrations. Vertical diurnal migrations are common among planktivorous fish [65,66]. *P. cynodon* seems to be a generalist predator, with a significant portion of its diet consisting of pelagic fish, since in Koko Seamount in 2019, we found remnants of small unidentifiable fish in its stomachs. The most numerous benthopelagic species in this area during the research period was *Maurolicus imperatorius*, known to undertake vertical diurnal migrations [67]. The elevated catches of *P. cynodon* with bottom trawls on seamounts at night can possibly be explained by that at the periphery of seamount summits, this species may feed on mesopelagic fish that ascend into the water column from the surrounding canyon waters, leading to higher concentrations of the species. Such feeding behavior has been described for Atka mackerel *Pleurogrammus monopterygius* on plateaus off the North Kuril Islands [68,69].

4.2. Biological Features

4.2.1. Size Composition

The size composition of *P. cynodon* catches is significantly influenced by the type of fishing gear. In longline catches, the fish are notably larger than those in trawl catches. A similar situation has been documented for another species in the Moridae family from the Emperor Seamount waters, *Antimora microlepis*, where a prevalence of large specimens in longline catches was also observed [47]. Very small fish are absent even in trawl catches, likely due to juveniles being pelagic. The average body length of *P. cynodon* in trawls from the Emperor Seamount waters in 2019 was smaller than that reported in the same area by the fishing vessel “Oryong 503” in 2011 (K.A. Karyakin, unpublished data). According to the latter data, the average TL in bottom trawl catches ranged from 32.6 to 37.4 cm. The reduction in average body length may be associated with the impact of fishing, where larger individuals are targeted. However, the presence of large specimens in longline catches indicates the existence of remnants in the population.

4.2.2. Sex Ratio

Our results and previous research have suggested possible seasonal movements of *P. cynodon*, its congener *P. japonicus*, and its relative *Antimora rostrata* [8,70], which may also contribute to variations in sex composition. The absence of males among larger specimens of *P. cynodon* has also been observed for other morids from the North Pacific, e.g., *P. japonicus*, *Antimora microlepis*, and *Lepidion schmidti* [8,47,49].

4.2.3. Size-Related Relationships

Relationships between otolith length and weight, otolith weight and body length, otolith length and body length, otolith weight and age, and otolith length and age are presented for the first time for *P. cynodons*. The relationship between body length and weight is known for some of its congeners. For *P. caboverdensis*, the LWR has the following coefficients: $a = 0.0015$, $b = 3.4899$, $R^2 = 0.976$; for *P. cyanostrophus*, $a = 0.0068$, $b = 2.9628$, $R^2 = 0.964$ [71]. Calculated LWR coefficients for *P. japonicus* are $a = 0.00407$ (0.00207–0.00802), and $b = 3.10$ (2.92–3.28) [72]. The coefficient a for *P. cynodons* from the Emperor Seamount

waters significantly deviates from that for other species of *Physiculus*, while the coefficient b closely aligns with that for *P. cyanostrophus*. Despite the practice of interpreting LWR coefficient values in describing the biology and ecology of fish, such procedures should be conducted with great care when working with *Physiculus* due to the tail regeneration ability in *P. cyanostrophus* [73]. In the event of detecting survival following severe tail injuries and regenerative capabilities in *P. cynodon*, relationships between otolith characteristics and age become particularly valuable, as this caudal fin and caudal peduncle loss does not affect the rate of otolith growth [73].

4.2.4. Age and Growth

The results of age determinations for *P. cynodon* from the Emperor Seamount waters indicate its long lifespan. Relationships between age and body length, age and body weight, age and otolith length, and age and otolith weight allow the use of body length, weight, and otolith measurements for describing the age and growth of *P. cynodon*.

A comparison of the growth of males and females did not reveal significant differences, despite the average age disparity and absence of males in the older age classes. Growth characteristics not differing between males and females are common among deep-sea fish, such as other Moridae from the Emperor Seamounts, *A. microlepis* and *L. schmidti* [47,49].

The von Bertalanffy growth equation, developed on bioenergetic principles [74], is one of the most commonly used models for describing the growth of long-lived fish. However, many authors [53,74–78] have pointed out that this equation cannot be considered a universal law of growth but rather a model suitable for describing specific cases. Selecting a model that best fits the growth description is necessary for each particular case [52]. In our sample from the Emperor Seamounts, the growth of *P. cynodon* is best described by a linear function (see Table 3). The linear function has also proven to be the most suitable for describing the growth of another morid from the same area, *L. schmidti* [49]. The linear growth of *P. cynodon* is supported by the values of the LWR equation coefficient b , which is close to 3 (where $b = 3$ represents isometric growth [79]). It is important to note that in the present study, there were no fish smaller than 97 mm long, and the relationships describe the growth of fish starting from 9 years of age. Extrapolating our data on *P. cynodon* growth for its entire lifecycle is inappropriate. The abrupt reduction in the specific growth rate at 10–15 years (see Figure 12) might be a consequence of sexual maturation.

Prior to this study, among *Physiculus*, there was only a single publication [80] dealing with lifespan and growth described by the von Bertalanffy equation, and it was on *P. cyanostrophus*. According to these data, this species can live up to 18 years with a body length of about 350 mm. Its growth was described by the VBGF with the following coefficients: $L_{\infty} = 491.762$, $t_0 = -3.03$, $k = 0.06$. Our study found that *P. cynodon* can reach a much greater age (up to 37 years) and much larger sizes (up to 622 mm). This results in a higher value of the asymptotic length (L_{∞}) in the VBGF. The values of the coefficient k calculated for *P. cyanostrophus* are twice as high as those for *P. cynodon*, indicating a faster growth rate for *P. cyanostrophus*.

Among the morids of the Emperor Seamount, age has been studied for *A. microlepis* and *L. schmidti*. Comparing the von Bertalanffy equations for these species with that for *P. cynodon* reveals the latter has a higher k coefficient (Table 4), showing this species grows faster than the former two species and has a shorter lifespan. A similar increase in lifespan and a decrease in growth rate among closely related species have also been demonstrated for some scorpaenids (Scorpaenidae), e.g., *Sebastes* spp. and *Sebastolobus* spp. [81].

The difference in the age composition of catches between 2019 and 2016 effectively illustrates the selectivity of the fishing gear used to collect the samples. The absence of older age groups in trawl catches and younger ones in longline ones indicates the problems of relying on a single method to establish a species' age structure.

Table 4. Habitat depth, maximum age, and von Bertalanffy parameters for Moridae from the Emperor Seamount waters.

Species	Habitat Depth, m	Age Max, Years	L_{∞}	k	t_0	R^2	Reference
<i>A. microlepis</i>	175–3048	46	1311.0	0.016	−0.90	0.7	[47]
<i>L. schmidti</i>	375–2404	49	2225.3	0.0007	−6.2	0.7	[49]
<i>P. cynodon</i>	139–1007	37	858.6	0.030	3.5	0.8	Present study

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