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Article

Reproductive Behavior and Sexual Patterns in Two Cales, *Heteroscarus acroptilus* and *Olisthops cyanomelas* (Odacidae) at Rocky Reefs in Temperate Australia

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Abstract: We investigated reproductive behavior and sexual patterns in two odacid fish—Rainbow cale *Heteroscarus acroptilus* and Herring cale *Olisthops cyanomelas*—inhabiting temperate reefs in Australia on the basis of underwater observations and histological studies. The males of both species established a territory and continuously courted females they encountered in the territory. The males and females went up in the water column to release gametes in pairs. We found ovarian cavities in the gonadal tissue of *H. acroptilus* males, suggesting that protogynous sex change occurred in this species. Dichromatism is reported in *O. cyanomelas*, with males having a dark blue body color while females have a brown body color; however, we found small mature males also included among brown individuals. Furthermore, we diagnosed *O. cyanomelas* with gonochorism, which is rare in closely related labrids. We compared the similarities and differences in reproductive behavior and sexual patterns between the two species and with labrids.

Keywords: spawning ecology; reproductive tactics; sex reversal; protogyny; gonochorism; monoandry; hermaphroditism; gonadal tissue; southern hemisphere; Tasman Sea

Key Contribution: We revealed the reproductive behavior of odacid fish through underwater observations for the first time. We found two sexual patterns of protogyny and gonochorism in two odacid species.

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1. Introduction

Odacidae is one of three families in Labriformes [1], in which six genera with 12 species are reported [2]. All odacid species are distributed along the southern coast of Australia or New Zealand, inhabiting seaweed beds on temperate shallow rocky reefs. Labridae is also a family in Labriformes, in which some 71 genera with more than 500 species are recorded from tropical to temperate regions of the Atlantic, Indian and Pacific Oceans [1]. Recent molecular phylogenetic studies have reported that odacids are deeply nested within the labrid tribe Hypsigenyini [3,4]. Studying the reproductive behavior and sexual patterns of odacids that have evolved in isolated areas is crucial not only for understanding the diversity and uniqueness observed in those regions, but also for elucidating the evolution of reproductive behavior and sexual patterns of labrids that have diversified in the oceans around the world.

Ecological studies on odacids have included butterfish *Odax pullus* inhabiting rocky reefs in New Zealand, with reports on the influence of season, ontogeny, and tide on diet [5], otolith-based age estimation, sex-specific growth, longevity, and age-based reproductive events [6], and temperature-related variations in growth rate, size, maturation, and life span [7]. Furthermore, a histological study revealed that the sexual ontogeny of *O. pullus* is monandric protogyny, with all males developing from mature females after female-to-male sex reversal [8]. On the other hand, the reproductive behavior of the odacids has been reported only sporadically. Males are territorial and spawning occurs from winter to summer in *O. pullus* [8,9]. Herring cale *Olisthops cyanomelas* males established territories on the reefs covered with kelp forest and mated with females on the edge of the forest [10].

Herein, we have conducted underwater SCUBA observations and specimen collection of two odacids, Rainbow cale *Heteroscarus acroptilus* and *O. cyanomelas*, at rocky reefs in the suburbs of Sydney, Australia from 2005 to 2014. Due to the intermittent nature of the research and limited time and periods of the study, we cannot provide a comprehensive report on the reproductive behavior and sexual patterns of odacids. Nevertheless, we made remarkable discoveries during our investigation. For the first time reported in the literature, we observed and documented the fundamental reproductive behaviors, such as courtship, aggression, mating, and spawning, of odacids through underwater observations. In addition, a histological study of their gonadal tissues revealed that *H. acroptilus* exhibits protogynous hermaphroditism, whereas *O. cyanomelas* exhibits gonochorism, which is rare in closely related labrids. Moreover, we evaluated the fit of the sexual pattern and mating behavior of the odacids to the size-advantage (SA) model, which predicts the evolution of sex change [11,12]. Additionally, we compared the reproductive behavior and sexual pattern between the two odacids and with closely related labrids, identifying both similarities and differences.

2. Materials and Methods

2.1. Study Species and Site

Rainbow cale *Heteroscarus acroptilus* and Herring cale *Olisthops cyanomelas* are Australian endemic species restricted to the temperate areas of southern Australia from New South Wales to Western Australia. They inhabit waters near the surface along exposed rocky coasts, usually with brown macroalgae. Females of *H. acroptilus* are variably green to reddish brown; dark brown and white blotches variously develop and align horizontally and vertically to form a camouflage pattern, males are yellowish orange with two blackish-brown intermittent bands on the side. The first and second dorsal fin spines are longer than the other dorsal fin spines. Their total length reaches 25 cm [13,14]. The body color of *O. cyanomelas* females is brown, with narrow blue wavy lines on the head, while that of males is pale blue to nearly black with bright blue lines along the margins of the caudal fin, along the leading edge of the pectoral fins, and on each side of the snout. Their total length reaches 40 cm [13,14].

We conducted underwater scuba observations and specimen collection of *O. cyanomelas* and *H. acroptilus* at three sites of Sydney suburbs: Fairlight Beach (33.8002° S, 151.2749° E) and Shelly Beach (33.8006° S, 151.2955° E), situated at the side of North Harbor and Tasman Sea of Manly, respectively, and Sutherland Point (34.0008° S, 151.2227° E) situated at the entrance of Botany Bay, Kurnell, NSW, Australia (Figure 1).

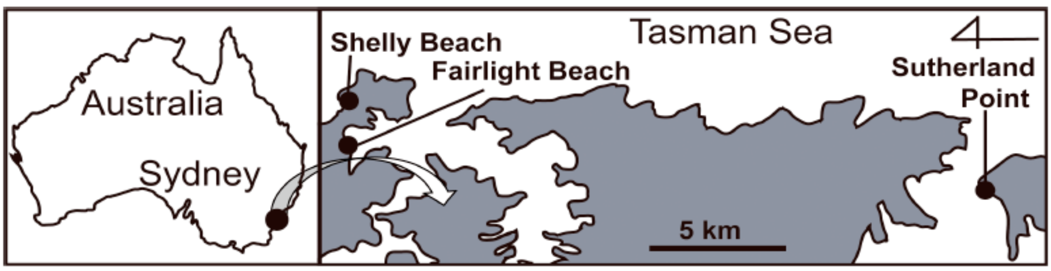

Figure 1. The location of study sites in the Sydney suburbs, New South Wales, Australia.

2.2. Underwater Observations

We conducted this research while being dispatched from Japan to Australia; therefore, the research period and the season for underwater observations were limited. All the observations were performed during the period from sunrise to sunset.

We made underwater scuba observations of *H. acroptilus* at the rocky reefs in about 5 m water depth at Shelly Beach on 18, 19, 21, 25, 26, and 27 February, and at Fairlight Beach on 24 February 2005. In the survey from 26 November to 12 December 2008, we set an observation area of 20 m × 20 m on a reef with kelp forest of *Ecklonia radiata* at a depth of 3–8 m, about 70 m offshore from Sutherland Point, with numbered buoys on the reef or kelp at intervals of about 5 m. In the observation area, we identified one male based on the presence of a split in its fins. We recorded aggressive, courtship and spawning behavior of the males on waterproof paper, photographed using an underwater camera (Sony DSC-PC9 digital camera with Sony Marine Pack housing, Sony Corporation, Tokyo, Japan), and recorded on video (Sony DCR-PC1 digital video camera with SEA&SEA VX-1D housing. SEA&SEA Co., Ltd., Tokyo, Japan). In the survey from 12 to 22 September 2014, we set a 40 m × 10 m observation area on the reef at Shelly Beach at a depth of 4–6 m. We identified and observed one male in the same way and recorded his behavior with an underwater camera (Olympus TG-1 digital camera with Olympus PT-53 housing, Olympus Corporation, Tokyo, Japan). We also recorded water temperatures using the temperature measurement function of a waterproof wristwatch (Casio 4707, CASIO COMPUTER Co., Ltd., Tokyo, Japan) during the underwater observations.

We made underwater scuba observations of *O. cyanomelas* at Sutherland Point. We tracked the individuals encountered on rocky reefs covered with kelp at a water depth of approximately 10 m, about 100 m offshore and observed their behavior on 23 and 28 February 2005. We observed the individuals encountered in the observation area for *H. acroptilus* from 26 November to 12 December 2008. We recorded the behavior of the individuals on waterproof paper, photographed with an underwater camera and recorded on video.

2.3. Specimen Collection

We collected a total of 22 fish specimens from the observation area using a fence net or spear: 1 specimen in February 2005 at Fairlight Beach, 1 specimen in December 2005 and 2 specimens in December 2008 at Sutherland Point for *H. acroptilus* (Table S1); 8 specimens in December 2005 and 10 specimens in December 2008 at Sutherland Point for *O. cyanomelas* (Table S2).

We sacrificed the collected specimens in ice water, photographed them with a digital camera immediately thereafter, and fixed them in 10% formalin. We also fixed mature eggs that leaked out of the peritoneal cavity of the *O. cyanomelas* during the fixing process separately with formalin. We collected fertilized eggs of *H. acroptilus* using a hand net in the water immediately after spawning at Sutherland Point on 7 December 2008, and fixed the eggs in formalin.

The fish specimens and fertilized eggs obtained in this study have been registered and are currently held by the Coastal Branch of National History Museum and Institute, Chiba. We collected the fish specimens under a scientific collection permit of the NSW Fisheries P03/0101.

2.4. Gonad Histology

We measured total length and body weight, and then extracted the gonads from the fish and weighed them for the collected specimen. We excised part of the gonad for the gonad samples and we embedded them in paraffin wax, sectioned them at 5–10 µm, mounted them on glass slides, and stained them with Mayer's hematoxylin and eosin stain. However, we did not prepare gonadal tissue sections of the ovaries with ovulated eggs in the peritoneal cavity.

We observed completed gonad preparations with a biological microscope Nikon E800 with an objective lens of 10×–40× and photographed them with a digital photography device and cameras attached to the lens barrel (Nikon Digital Sight DS-L5 & DS-5M, Nikon Corporation, Tokyo, Japan). Additionally, we classified phases of gonadal development based on previous studies [8,15]. The gonad preparations, remnants of gonad samples, and paraffin-embedded gonads have been preserved in the museum as part of the fish specimens, with the gonadal tissue photos as attachment to the fish specimens. The photos are also available on figshare [16].

3. Results

3.1. Reproductive Behavior of *Heteroscarus acroptilus*

The identified male individuals maintained a territory of 55.3 m^2 and 193 m^2 in the observation area and mated with females within the territory in 2008 and 2014, respectively. When the male patrolled the territory, aggressive behavior was observed toward conspecific males in adjacent territories on the boundary. The two males faced each other with their mouths open, and their body color changed: the black block pattern seen on the side of the body disappeared; and the margins of the dorsal fin and anal fin became whitish (Figure 2A, Video S1). No interspecific aggressive behavior was observed between *H. acroptilus* and *O. cyanomelas* males cohabiting at Sutherland Point in the 2008 observations.

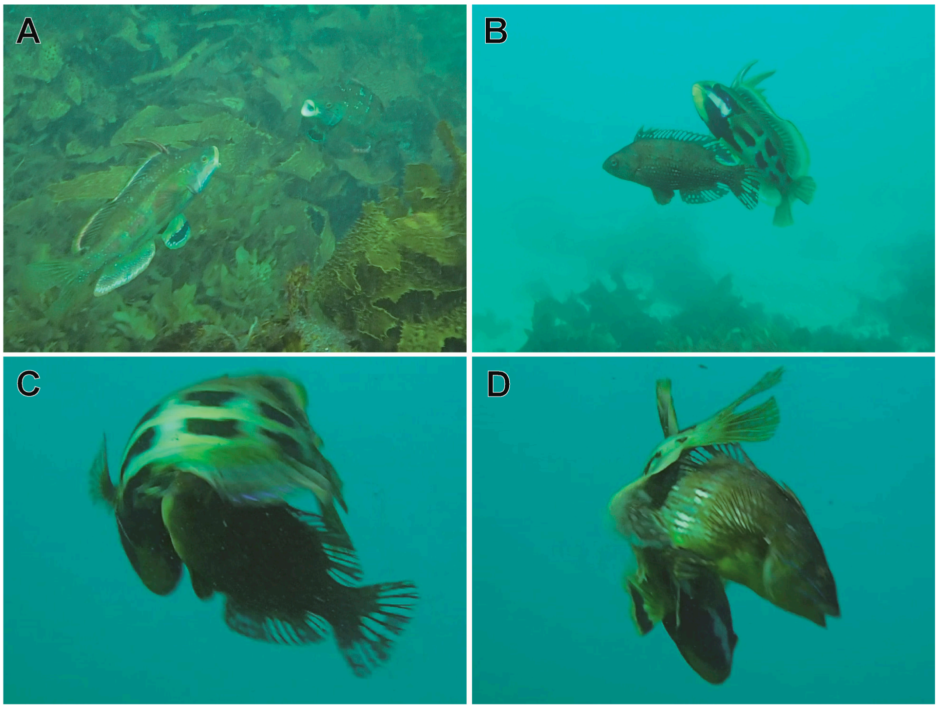

Figure 2. Male–male aggressive behavior (**A**), spawning ascent (male: light, **B**), flexion of the body at the top of the ascent (**C**) and releasing of gametes (**D**) of Rainbow cale *Heteroscarus acroptilus*. Each image is one frame of the movies shown as Videos S1 and S2.

When a male found a female in the kelp during territorial patrols, he courted her by spreading all his fins in front of the female. When the male courtship was successful, the male and female left the kelp together, and the male began to slowly ascend behind the female with his head slightly raised (Figure 2B). However, the females often returned to the kelp during the ascent. The male then either repeated the courtship of the female or abandoned her to find another female. The male and female ascended approximately 0.5–2 m above the kelp and, crossing their bodies in opposite directions with their bodies bending (Figure 2C), released gametes at the timing of their genital pores overlapping (Figure 2D), and then quickly returned to the kelp (Video S2).

The territorial males went to find another female soon after spawning and mated with up to five females during 60 min observations. A total of 23 spawnings of *H. acroptilus* were observed from 14:44 to 17:30, 2 h 6 min to 3 h 21 min before sunset, at a water temperature of 17.9 °C–22.5 °C (Table S3). We classified eggs of *H. acroptilus* as isolated pelagic eggs. Fertilized eggs collected during the underwater observation (Table S3, no. 5) were nearly spherical in shape and 0.84 (0.81–0.86) mm (n = 10) in diameter.

3.2. Reproductive Behavior of Olisthops cyanomelas

Male *O. cyanomelas* established a territory of approximately 15 m × 15 m. Male–male aggressive behavior was observed near the boundary of the territories. Two males swam parallel near the boundary, after which one male chased the other, whereupon bright blue lines along the fins and snout became prominent (Figure 3A, Video S3). When the male found a female, he pursued her and courted her by vigorously swinging his caudal fin left and right, occasionally with his body tilting horizontally. In many cases, however, the females left without accepting the courtship of the male, and he began to look for other females (Video S4). When the male courtship was successful, the males and females left the kelp, ascended side by side by approximately 2 m, and released gametes at the point when they turned their bodies at the top (Figure 3B, Video S5). The female soon returned to the kelp, while the male resumed the search for another female. The male repeatedly mated with two females at 11:54 and 11:59 on 28 February 2005 at a water temperature of 23.3 °C. During the 2008 observations, although male aggressive and courtship behavior were observed, no spawning behavior was observed.

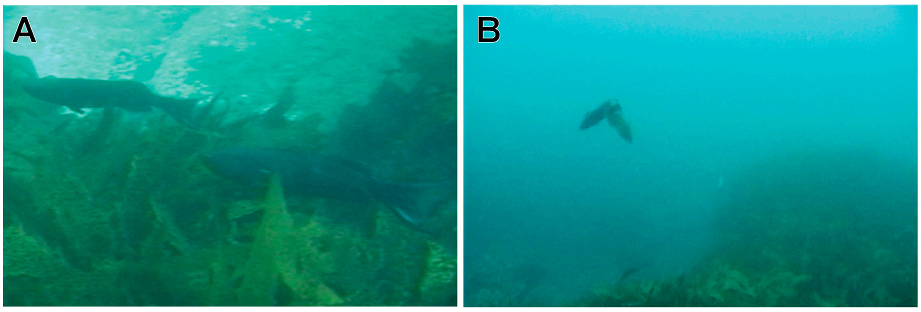

Figure 3. Male–male aggressive behavior (**A**) and pair spawning (male: left, **B**) of Herring cale *Olisthops cyanomelas*. Each image is one frame of the footage shown as Videos S3 and S5.

3.3. Gonadal Tissue and Sexual Systems of Heteroscarus acroptilus

The body colors of the collected *H. acroptilus* specimens were yellowish-orange (Table S1 nos. 1 and 2, 200–215 mm TL), and brown (Table S1 nos. 3 and 4, 145–152 mm TL). Spermatids (St) and spermatocytes (Sc) were observed in the gonadal tissue of the two yellowish-orange specimens, and also spermatozoa (Sz) in smaller specimens. Furthermore, the ovarian cavity (OC) was observed in both specimens (Figure 4A,B). We therefore diagnosed the two specimens as developing or spawning-capable males.

Primary growth oocytes (PG) were noted in the gonadal tissue of two brown specimens, and oocytes undergoing germinal vesicle breakdown (GVBD) in larger individuals (Figure 4C,D); we therefore diagnosed that the larger specimen is a spawning-capable female, while smaller specimen is an immature female.

3.4. Gonadal Tissue and Sexual Patterns of Olisthops cyanomelas

The body colors of collected *O. cyanomelas* specimens were blue (225–350 mm TL, n = 6) and brown (61–380 mm TL, n = 12) (Figure 5). Sz, St, and Sc were observed in the gonadal tissue of all blue specimens (Table S2 nos. 1–6). Furthermore, the same stages of spermatogenic tissues were found in relatively smaller brown specimens (Figure 6A, Table S2 nos. 7 and 8, 245–250 mm TL). We therefore diagnosed all blue and some brown specimens as mature, spawning-capable males. No ovarian cavities were observed in the gonadal tissue (Figure 6B).

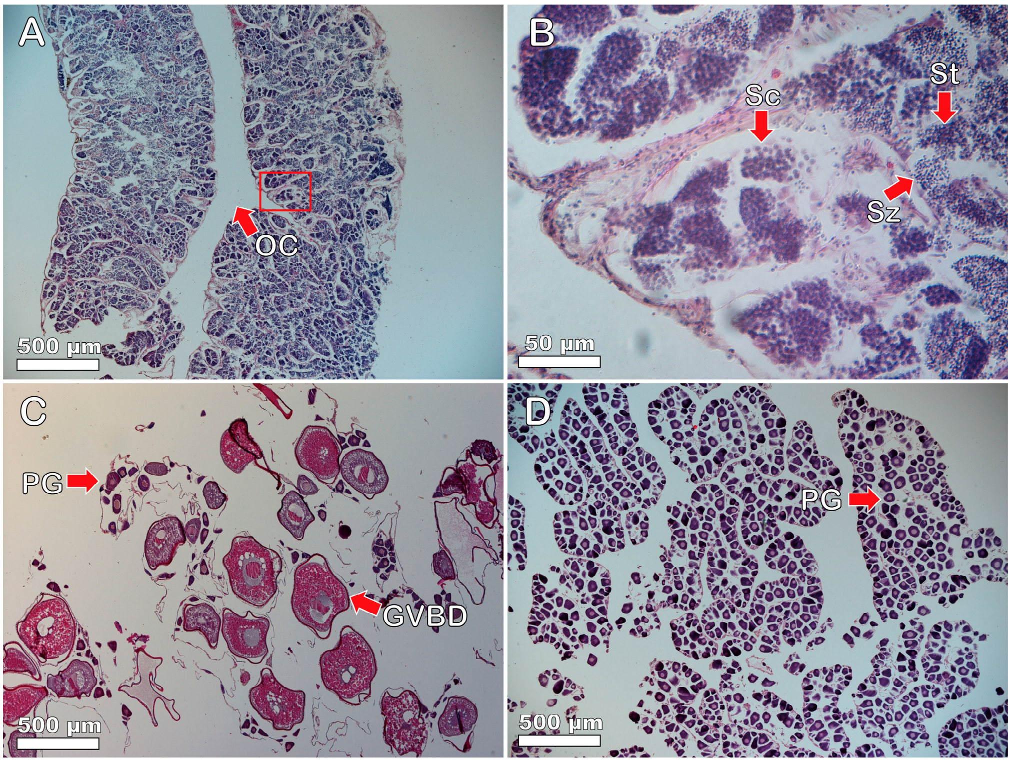

Figure 4. Photomicrographs of transverse histological sections of the male (**A**) (Table S1 no. 2) and its enlargement of the area surrounded by the red frame (**B**), and the females (**C**, Table S1 no. 3; **D**, Table S1 no. 4) of Rainbow cale *Heteroscarus acroptilus*. See text for abbreviations.

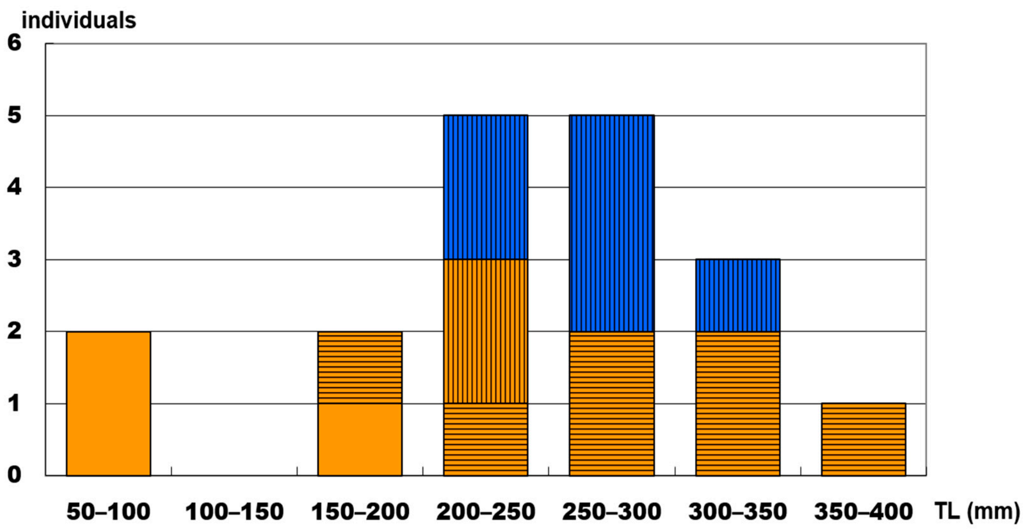

Figure 5. Total length, body color, and sexuality of Herring cale *Olisthops cyanomelas*. Vertically striped blue columns depict blue males, vertically striped brown columns depict brown males, horizontally striped brown columns depict brown females and brown columns without stripes depict sex-unknown individuals.

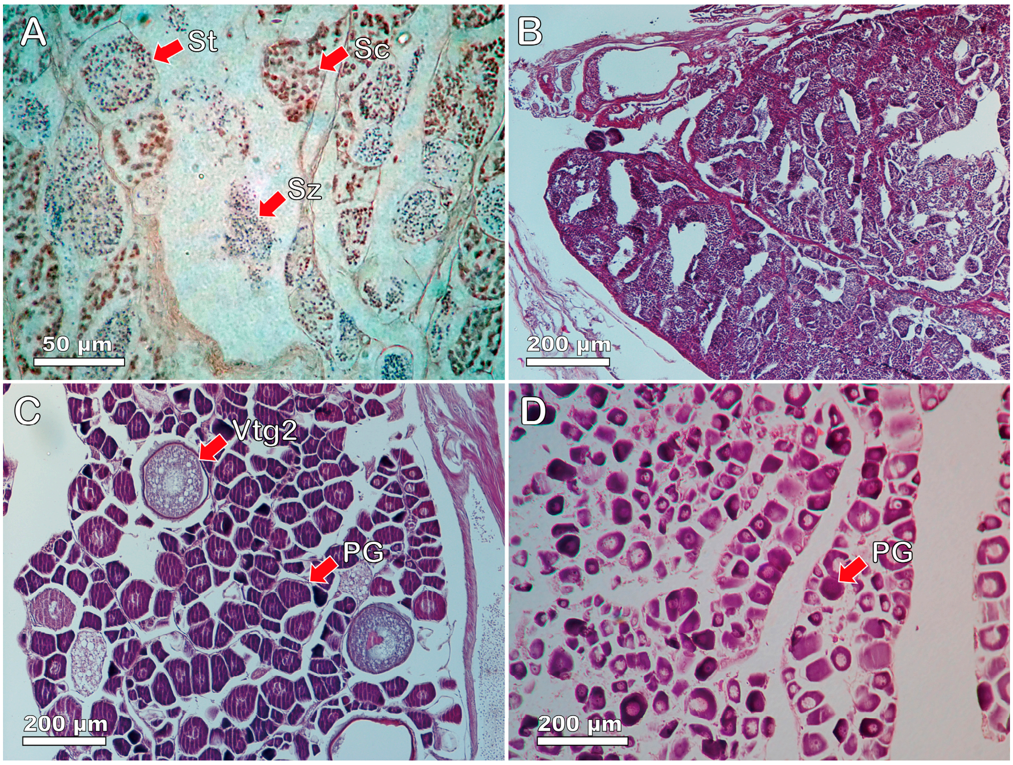

Figure 6. Photomicrographs of the transverse histological sections of the males (**A**, Table S2 no. 8; **B**, Table S2 no. 2), the developing female (**C**, Table S2 no. 12), and the immature female (**D**, Table S2 no. 14) of Herring cale *Olisthops cyanomelas*. See text for abbreviations.

Ovaries of larger brown specimens (Table S2 nos. 9–11, 310–380 mm TL) were filled with ovulated eggs; thus, they were diagnosed as mature, spawning-capable females. The eggs were spherical in shape and measured 0.99 (0.96–1.02) mm (n = 10) in diameter. Secondary vitellogenic oocytes (Vtg2) and PG were observed in the gonadal tissue of two brown specimens (Figure 6C, Table S2 no. 12 and 13, 253–270 mm TL); we therefore diagnosed them as developing females not ready to spawn. PG was noted; however, no other later-stage oocytes were found in the gonadal tissue of two brown specimens (Figure 6D, Table S2 nos. 14 and 15, 162–240 mm TL); we therefore diagnosed them as immature females. Three smaller brown individuals we encountered (Table S2 nos. 16–18, 61–156 mm TL) were sex-unknown immature individuals. The total length of males and females did not differ significantly (Mann–Whitney U-test, p = 0.48).

4. Discussion

4.1. Reproductive Behavior

Here, we revealed the reproductive behavior of two odacid fishes—*Heteroscarus acroptilus* and *Olisthops cyanomelas*—for the first time through underwater observations. Comparing the reproductive behavior with that of the labrids closely related to the odacids, the spawning behavior is common in both families in that they both release separated pelagic eggs in the water column. The mean egg diameters of the two odacids measured 0.84–0.99 mm, while that of the 23 other closely related species of labrids measured 0.45–1.08 mm [17].

Spawning events were observed in September (early spring), December (early summer), and February (late summer) in *H. acroptilus*, and in December in *O. cyanomelas* in our study; however, the full duration of spawning season of the two odacids remains unknown due to our limited observations. On the other hand, histological studies of the gonads of *Odax pullus* indicated that the spawning season is from July to January—that is, from mid-winter to mid-summer in New Zealand [8]. Although it is not common in labrids to have a spawning season in winter, *Notolabrus gymnogenis*, a temperate species inhabiting southern Australia, has been reported to breed from April to October [18]. On the other hand, the spawning season of most temperate wrasses in the northern hemisphere is from spring to summer, and a few species spawn in autumn [19], but none in winter. Some species are known to burrow into the sand and hibernate in the winter [20].

Comparing the reproductive behavior of *H. acroptilus* and *O. cyanomelas*, both odacids inhabit kelp forests on shallow coastal reefs and males establish a territory and mate polygynously with multiple females in a day. Because of the short observation period and failure to identify female individuals, the exact mating system of the two odaids remains unknown.

4.2. Sexual Pattern

The present histological study revealed an ovarian cavity in the gonads of male *H. acroptilus*; we therefore deduced that this species is a protogynous hermaphrodite that functions as a female first and then changes sex to become a male. Protogynous hermaphrodism was reported in the confamilial *Odax pullus* [2]. The sexual ontogeny of *O. pullus* was monandric protogyny, with all males developing from mature females after female-to-male sex reversal. All individuals underwent an immature female phase before maturing as functional females aged 1.1–1.5 years, and sex change was estimated to occur in females aged 2–3 years [8]. Our underwater observations showed that predominant males established territories and mated polygynously, and no sneaking or group spawning were observed in *H. acroptilus*. Considering this, primary males, if they exist, might be rare in the population of the present study.

Protogynous sex change, which is strongly related to a polygynous mating system [21], is most commonly observed in hermaphroditic fishes. When large males monopolize mating to the detriment of small males, male fertility rises dramatically at a certain point in growth, and an individual that remains a female when small and changes to a male at a large size will be selectively favored [11,12]. Our underwater observations and collected specimens clearly showed that males were larger than females in *H. acroptilus*. Furthermore, the male established a territory and mated with females polygynously. These features seem to fit the scenario of the SA model that evolves protogynous hermaphroditism.

Conversely, in *O. cyanomelas*, we could not find any evidence suggesting protogyny in the histological study; there were no ovarian cavities or oocytes observed in the gonadal tissues of mature males. Furthermore, there was no difference in total length between males and females. Therefore, we deduced that this species is gonochoristic, with individuals remaining either male or female throughout their lives. Protogyny is reported in many closely related species of labrids [21]; however, gonochorism is reported only in limited species.

The SA model predicts that when males and females form monogamous pairs matched by size or when males compete with each other to fertilize eggs, and thus to produce the most sperm, both sexes show a similar increase in fertility with size, and no selection for sex change exists [12,22]. One possible reason for gonochorism in the present species is alternative tactics in small males. Our study revealed that brown-colored individuals include not only females but also mature small males. The small males could interrupt the pair of large males and females and participate in spawning as a sneaker. Although we observed no sneaking behavior in *O. cyanomelas*, the gonadosomatic index (GSI) of brown males was higher than that of blue males (Table S2), which would be advantageous for sperm competition in sneaking or streaking tactics. Sneaking tactics have also been reported in the gonochoristic wrasse *Symphodus ocellatus* [23].

5. Conclusions

We observed and documented the fundamental reproductive behaviors, such as courtship, aggression, mating and spawning, in two odacid species—*Heteroscarus acroptilus* and *Olisthops cyanomelas*—inhabiting temperate reefs in Australia through underwater observations. This marks the first instance of such observations. Both odacids were found in kelp forests on shallow coastal reefs. The males established a territory and mated polygynously with multiple females in a day. The males and females ascended the water column to release gametes in pairs. The mating system and spawning behavior of the odacids closely resembled those of their closely related labrids.

In addition, our histological study of the gonadal tissues revealed that *H. acroptilus* individuals initially function as females and later undergo a sex change to become males. The characteristics of larger males and polygynous mating of *H. acroptilus* align with the scenario proposed via the SA model, which describes the evolution of protogynous hermaphroditism. On the other hand, *O. cyanomelas* exhibit gonochorism, maintaining a consistent male or female sex throughout their lives, which is a rarity among closely related labrids. Dichromatism is reported in *O. cyanomelas*, with males displaying a dark blue body color and females presenting a brown body color; however, our observations identified small mature males within the brown individuals. The presence of the small brown males may contribute to the gonochorism observed in *O. cyanomelas*.

Due to the limited duration of the study, we are unable to present a comprehensive report on the reproductive behavior and sexual patterns of odacids. Nevertheless, we have made significant discoveries as summarized above. Further studies on the reproductive behavior of odacids are crucial for understanding the diversity and uniqueness of the endemic species. Additionally, these studies are essential for elucidating the evolution of reproductive behavior of closely related labrids that have diversified in the oceans around the world.

Supplementary Materials: The following supporting information can be downloaded at: https://www.mdpi.com/article/10.3390/fishes8100491/s1, Table S1: Information on collected specimens and their preparation of gonadal tissue sections of Rainbow cale *Heteroscarus acroptilus*; Table S2: Information on collected specimens and their preparation of gonadal tissue sections of Herring cale *Olisthops cyanomelas*; Table S3: Spawning date, time, site of Rainbow cale *Heteroscarus acroptilus*; Video S1: Aggressive behavior between two males of Rainbow cale *Heteroscarus acroptilus*; Video S2: Spawning behavior of Rainbow cale *Heteroscarus acroptilus*; Video S3: Aggressive behavior between two males of Herring cale *Olisthops cyanomelas*; Video S4: Courtship behavior of Herring cale *Olisthops cyanomelas*; Video S5: Spawning behavior of Herring cale *Olisthops cyanomelas*.

Author Contributions: H.K. planned and conducted underwater research and analyzed field observation data, photos, and videos. T.S. conducted histological studies and diagnosed the phases of gonadal development. All authors have read and agreed to the published version of the manuscript.

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Institutional Review Board Statement: The collection of fish specimens in this study was conducted under a scientific collection permit of the NSW Fisheries P03/0101. The handling of the caught fish was carried out according to "Guidelines for the use of fishes in research" established by the Ichthyological Society of Japan.

Data Availability Statement: The photos of the collected specimens and their gonadal tissues from the two odacid species used in this study are available on *figshare* [16].

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Conflicts of Interest: The authors declare no conflict of interest.

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