Behavioral ecology of coral reef fishes studied at Sesoko Station since 1992

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Abstract  This review provides a brief summary of our field research on the behavioral ecology of coral reef fishes conducted at Sesoko Station, University of the Ryukyus, Okinawa, Japan. We have continued observations and experiments on fish behavior using SCUBA or by snorkeling on the fringing reefs of Sesoko Island since 1982. The results of our four main research subjects, that is, mimicry, parental care and mating systems, bidirectional sex change, and mate choice and alternative mating tactics, all of which have been major subjects of behavioral ecology, are summarized with references and historical information. The titles and speakers of papers, presented at two international meetings organized by the author and held at the Sesoko Station in 1991 and 2004, and field studies conducted on fishes in Sesoko Island by other researchers, including graduate students from various universities, are introduced. The Sesoko Station has been providing excellent facilities for field studies of coral reef fishes and has contributed greatly to the development of the behavioral ecology of fishes.

Keywords  Mimicry, Parental care, Mating system, Sex change, Mate choice, Alternative mating tactics

Introduction  Behavioral ecology, which examines the survival value of behavior and individual fitness based on the theory of natural selection, was established in the 1970s (Wilson 1975; Dawkins 1976; Krebs and Davies 1978, 1981). It had not been introduced into Japan when I started research on fish behavior and ecology as a graduate student in 1973; however, by reading the books mentioned above, I gradually came to understand the concepts of behavioral ecology. The Japan Ethological Society and International Society for Behavioral Biology were founded in 1982 and 1986, respectively, and the paradigm of behavioral ecology was rapidly accepted by Japanese ecologists and ethologists, including ichthyologists, during the 1980s (Kuwamura 2013).

It was October 1974 when I first visited Sesoko Station (then the Sesoko Marine Science Laboratory), one year prior to the publication of the first edition of a picture book “Coastal Fishes of Southern Japan” (Masuda et al. 1975); one of the editors was Tetsuo Yoshino, with whom I stayed for a week. I worked with Yasunobu Yanagisawa, Ryuzo Fukao, and Kosaku Yamaoka, all of whom were graduate students of Kyoto University as I was, along with Nobuhiro Oshiro (University of the Ryukyus) to record and collect fishes on the coral reefs around Sesoko Island (for the list of fishes on the island, see Yoshino and Nishijima 1981). Moreover, I counted the number of individuals of the bluestreak cleaner wrasse, Labroides dimidiatus (Labridae), and its mimic, Aspidontus taeniatus (Blenniidae) (Fig. 1). Why did I do so?

I started my research as a graduate student on the cleaning symbiosis and social structure of L. dimidiatus (Kuwamura 1976, 1984) at the Seto Marine Biological Laboratory of Kyoto University in Shirahama, Wakayama Prefecture. During my stay in Shirahama, I also observed the feeding behavior of the false cleanerfish, A. taeniatus
that sometimes appeared there. The function of aggressive mimicry has been suggested based on the observation that *A. taeniatus* bit the fin of deceived fish (Wickler 1968); however, it rarely bit fish fins and mainly bit tentacles of tubeworms in the study site of Shirahama (Kuwamura 1981). Therefore, I was interested in investigating the actual function of the mimicry on the coral reefs of Okinawa. In addition to Sesoko Island, I visited the Yaeyama Islands (Ishigaki, Kuroshima, Taketomi, and Hateruma Islands) to conduct preliminary research on the mimicry and fish fauna for a few weeks in 1973, 1974, and 1978. In 1982, I decided to choose Sesoko Island as my main study site because it provided excellent research facilities for conducting field observations and experiments on fish behavior by snorkeling or using SCUBA.

In this review, I briefly summarize our research on the behavioral ecology of coral reef fishes conducted at Sesoko Station since 1982. I introduce four categories of research: mimicry, parental care and mating systems, bidirectional sex change, and mate choice and male alternative mating tactics, all of which have been major subjects of fish behavioral ecology.

**Mimicry of the cleaner fish**

After I decided to choose Sesoko Island as my main field, I conducted the first main research on the cleaner’s mimic, during the summer vacation of Chukyo University from 21 July to 30 August, 1982 (Kuwamura 1983). I observed *A. taeniatus* and its related species, the non-mimic *Aspidontus dussumieri*, and the skin-biting specialist *Plagiotremus rhinorhynchos*, for their feeding behavior and examined their gut contents. As in Shirahama (Kuwamura 1981), *A. taeniatus* rarely bit fish fins but mainly bit tentacles of tubeworms not exerting the effect of aggressive mimicry. Therefore, I concluded that the principal function of mimicry is immunity from predation (protective mimicry) rather than aggressive mimicry (Kuwamura 1983). I was satisfied with the results and changed my research subject from the next year (see the next section).

I expected that someone would follow up on my conclusion of mimicry in other localities; however, no response appeared for more than 30 years. Finally, in 2014, Cheney, Grutter, and Bshary published a paper on the geographical variation in the frequency of fin biting by *A. taeniatus* but could not determine the cause of the variation. Therefore, I decided to resume my research on the cleaner’s mimicry with Yoichi Sakai (Hiroshima University) and his student Misaki Fujisawa. We found that the frequency of fin biting by *A. taeniatus* decreased with growth, whereas that of eating demersal eggs of damselfishes increased with growth (Fujisawa et al. 2018). Moreover, we have revealed that small *A. taeniatus* relied on fin biting on Ishigaki Island of the Yaeyama Islands, where benthic foods such as tubeworms are scarce (Fujisawa et al. 2020).

Hajime Sato, a student of Sakai’s laboratory, joined our team and found a color variant of *A. taeniatus* on the Sesoko reef in 2019 for the first time from the Indo-West Pacific (Sato et al. 2020a). The variant had a brownish color pattern, instead of a bluish mimic pattern. We compared feeding behavior between the different color patterns, but found no significant difference in the frequency of fin biting, probably because the frequency was very low due to the abundance of benthic foods such as tubeworms (Sato et al. 2020b). We are continuing our research focusing on group formation to eat eggs to elucidate the cleaner’s mimicry in Sesoko and other localities.

**Parental care and mating systems**

While I was conducting field research for my doctoral thesis on the social structure of *L. dimidiatus* in
Shirahama, I was also interested in parental care in fishes, especially paternal mouthbrooding of cardinalfishes (Apogonidae). I compared the mating systems of three species of cardinalfishes in Shirahama (Kuwamura 1985): the solitary species *Apogon doederleini* and *A. niger* bred in transient pairs, whereas the gregarious species *Apogon notatus* formed territorial monogamous pairs. I planned to develop this work in Sesoko, where many species of Apogonidae were reported (Yoshino and Nishijima 1981), and conducted preliminary observations from the summer of 1982. Discouragingly, spawning was not observed during daytime in most species in Sesoko, although the above three species spawned during daytime in Shirahama (Kuwamura 1985). Therefore, I concluded the research, and only reported night spawning of *Cheilodipterus quinquelineatus* that was observed for the first time (Kuwamura 1987).

In 1984, I began research on maternal egg care of triggerfishes (Balistidae) because paternal egg care is common and maternal care is rare among marine fishes. I found that each individual of *Rhinecanthus aculeatus* maintained a territory for several years. Furthermore, a male’s territory usually overlapped with two or three territories of females (polygynous mating system); females spawned demersal eggs within their territories early in the morning and took care of the eggs by themselves until sunset of the spawning day (Fig. 2; Kuwamura 1997a). Males did not participate in egg care but defended females from other males (Kuwamura 1997a; Ziadi-Künzli and Tachihara 2016). Maternal egg care and female-defense polygyny have also been confirmed in another triggerfish, *Sufflamen cryopecterus* (Ishihara and Kuwamura 1996; Seki et al. 2009).

I was interested in the relationship between the sex of the caretaker and the mating system not only in marine fishes but also in freshwater fishes; hence, I visited Lake Tanganyika in East Africa to conduct underwater observations of cichlid fishes in late 1983 (six months) and the summers of 1986 and 1989 (three months each). Both mouthbrooders and substrate-brooders were found among the Tanganyikan cichlids. Mouthbrooders were usually male-territory-visiting polygamous with maternal mouthbrooding and exceptionally monogamous with biparental mouthbrooding. In contrast, the mating system of substrate-brooders was usually monogamous with biparental guarding and exceptionally polygynous with maternal guarding (Kuwamura 1986, 1997b). The breeding habits of cichlids in Lake Tanganyika are fascinating; however, I decided to concentrate on the research at Sesoko Island after 1990 because it was difficult to continue field research at both sites due to time constraints. To summarize my interest in parental care and mating systems in fish, I wrote a Japanese book including both cichlids and marine fishes (Kuwamura 1988, revised in 2007).

**Bidirectional sex change and behavioral process of sex change**

In 1987, we published a Japanese book on sex change in fish (Nakazono and Kuwamura 1987). While editing the book chapters, I was interested in a paper (Lassig 1977) that suggested monogamy and protogyny in a coral-dwelling goby *Paragobiodon echinocephalus* (Fig. 3) because the size-advantage model that explains the evolution of sex change predicts protogyny in polygynous species and protandry in monogamous species (Warner 1975, 1984). To confirm whether *P. echinocephalus* is an exception to the size-advantage model, I decided to conduct a thorough investigation of the species on Sesoko Island with two of the eight authors of the above book: Yutaka Yogo (postdoctoral of Kyushu University) who had studied the reproductive behavior of a protogynous fish, *Pseudanthias squamipinnis*, on Miyake-jima Island (Yogo 1985), and Yasuhiro Nakashima (postdoctoral of Kyoto University) who had studied protandrous sex change in a...
shrimp *Athanas kominatoensis* in Shirahama (Nakashima 1987). First, we confirmed size-assortative monogamy in each coral head: small pairs bred in small corals and large pairs in large corals (Kuwamura et al. 1993, 1996). We found bidirectional sex change for the first time in fish in the field (Kuwamura et al. 1994; Nakashima et al. 1995). Tracking tagged individuals revealed protogyny was the basis of the growth-rate advantage in females, and the reversed sex change (male to female) was relatively rare (Kuwamura et al. 1994). We also confirmed size-assortative monogamy and bidirectional sex change in other coral-dwelling gobies *Gobiodon* spp. (Nakashima et al. 1996).

Based on these findings, I hypothesized that reversed sex change should occur in hitherto known protogynous species such as the polygynous wrasse, *L. dimidiatus* and protandrous species such as the monogamous anemonefish, *Amphiprion* spp., and we conducted aquarium experiments to keep two individuals of the same sex and mate-removal experiments in the field. First, by the aquarium experiments of keeping two males together, we confirmed the reversed (male to female) sex change in the protogynous wrasse, *L. dimidiatus* (Kuwamura et al. 2002). In 1996, Yoichi Sakai, a postdoctoral of Osaka City University, who had studied the sexually dichromatic polygynous and protogynous angelfish *Centropyge ferrugata* (Pomacanthidae) in Sesoko (Sakai 1997), joined our team and confirmed the reversed sex and color change of *C. ferrugata* in the aquarium experiments (Sakai et al. 2003a).

Subsequently, I proposed the low-density hypothesis for the evolution of reversed sex change in protogynous species, and it was confirmed in *L. dimidiatus* and *C. ferrugata* in the field, by mate-removal experiments (Kuwamura et al. 2011, 2014), which were conducted with Shohei Suzuki (see next section), and Tatsuru Kadota, a newly joined postdoctoral at Hiroshima University, who had studied reversed sex change in the harem protogynous hawkfish, *Cirrhitichthys falco*, on Kuchierabu-jima Island (Kadota et al. 2012). We also confirmed reversed sex change in the magenta dottyback, *Pictichromis porphyria* (Kuwamura et al. 2015) and the humbug damselfish, *Dascyllus aruanus* (Kuwamura et al. 2016a).

However, in protandrous anemonefishes *Amphiprion* spp., which were studied by Hattori (1994) in Sesoko, we could not confirm the reversed (female to male) sex change either in the aquarium experiments or in the field (Kuwamura and Nakashima 1998; Kuwamura unpublished data). We confirmed that reversed sex change has not been reported in any protandrous species by preparing a database of approximately 500 hermaphroditic fish species (Kuwamura et al. 2020).

In addition to bidirectional sex change, we examined detailed behavioral processes during protogynous sex changes by male-removal experiments. Within an hour after male removal, the largest female of a harem of *L. dimidiatus* started male courtship behavior and conducted pair spawning with a smaller female, and female-female spawning continued for a few weeks until the completion of gonadal change (Nakashima et al. 2000). The largest female subsequently spawned in the female role when the male was returned immediately after female-female spawning. Similar female-female spawning was also confirmed in another protogynous wrasse, *Halichoeres melanurus* (Sakai et al. 2002) and a harem angelfish, *Centropyge vroliki* (Sakai et al. 2003b). We suggest that the largest female would readily adopt male sexual behavior to retain smaller females as future mates.

Gosuke Takamoto (an undergraduate student at Kyushu University) and Satoko Seki (a graduate student at Osaka City University) who joined our team in 2001 and 2000, respectively, conducted male-removal experi-
ments in the haremic triggerfish *S. cryopterus* and confirmed sex change from female to male (Takamoto et al. 2003), which was the first report of protogyny from Tetradontiformes. Similar male-removal experiment was performed by Saki Murayama (a graduate student at the University of the Ryukyus) in another haremic triggerfish *R. aculeatus*; however, sex change did not occur, and small primary males were found (Murayama 2009). We have yet to find the reason why polygynous *R. aculeatus* does not follow the prediction of the size-advantage model.

**Mate choice and alternative male mating tactics**

In 1992, Nozomi Mizushima, a graduate student at Kyoto University, joined our team as the first coworking student to conduct research on sex change and mate choice in a coral-dwelling damselfish, *D. aruanus* (Pomacentridae; Fig. 4). Females spawned demersal eggs on the coral branch in semilunar cycles, and males guarded the eggs until hatching (Mizushima et al. 2000). When corals were abundant, females visited multiple males before spawning days to choose their preferred mates (Mizushima 2002). Male-removal experiments resulted in temporal female egg care instead of sex change (Mizushima 2002). Later, under low-density conditions, we confirmed protogynous sex change by removing males and reversed sex change by removing females (Kuwamura et al. 2016a).

In 1993, inspired by the research performed by Warner and Schultz (1992), I started a research project on mate choice and sexual selection in a protogynous wrasse, *H. melanurus*, with Kenji Karino, a graduate student at Kyushu University, who had studied mate choice in a territorial damselfish, *Stegastes nigricans* in Sesoko (Karino 1995; Karino and Kuwamura 1997). Large terminal phase (TP) males of *H. melanurus* established mating territories during spawning time at dusk, and females visited the male territories to pair-spawn (Kuwamura et al. 2000). Small initial phase (IP: similar to female color) males could not defend territories and tried streaking into a spawning pair to release sperm as an alternative mating tactic. Females preferred TP males with large yellow spot at the pectoral fin base (Kuwamura et al. 2000). However, females under high predation risk had less opportunity to choose preferable mates and had to mate with the nearest males in most cases (Karino et al. 2000).

In 2001, Teppei Sagawa and Shohei Suzuki, undergraduate students at the University of the Ryukyus, joined our team to study mate choice and alternative male mating tactics of other damselfish and wrasses. Sagawa and Tsutomu Hanahara (who joined in 2003 as a graduate student at the University of the Ryukyus), studied nest-visiting behavior by territorial males and female-like behavior by sneaking males, in the staghorn damselfish, *Amblyglyphidodon curacao* (Hanahara and Sagawa 2008). Nest-visiting behavior was observed in both the breeding and non-breeding seasons, suggesting that it may be a search for a better nest to which to move. Suzuki studied the reproductive behavior of IP and TP males in the threespot wrasse, *Halichoeres trimaculatus*. When multiple IP males gathered, they conducted group spawning (Fig. 5), which was revealed to have resulted from the streaking of small IP males into a pair spawning of a larger IP male (Suzuki et al. 2008, 2010). As IP males were recognized as primary males, this was surprising (Kuwamura 2004); however, Suzuki found that one of the IP males who participated in spawning changed sex and pair-spawned with a TP male in the female role next year when the population density decreased (Kuwamura et al. 2007). Later, reversed sex change in both IP and TP males
were confirmed by aquarium experiments conducted at Okinawa Churaumi Aquarium (Kuwamura et al. 2007) with the cooperation of Naomi Tanaka, who studied the pair territory of the vagabond butterflyfish, Chaetodon vagabundus, in Sesoko when she was a graduate student at the University of the Ryukyus.

Effects of the 1998 massive coral bleaching and subsequent recovery

In the summer of 1998, massive coral bleaching occurred because of high water temperature in Sesoko and other islands of Okinawa. We continued the research as mentioned previously; however, the number of individuals and species of fishes gradually decreased with the destruction of coral skeletons (e.g., Kokita and Nakazono 2001a). Therefore, I changed my main field to the north coast of Iriomote Island of the Yaeyama Islands, where massive coral bleaching did not occur in 1998. From 2005 to 2009, I studied alternative male mating tactics and interspecific variations in spawning time among scarids and labrids at the reef edge of Uehara on Iriomote Island (Kuwamura et al. 2009, 2016b).

Corals and fishes gradually recovered in Sesoko, and I returned in 2009. While preparing a review on bidirectional sex change in fishes with Philip Munday (Munday et al. 2010), who studied bidirectional sex change in Gobiodon histrio (Munday et al. 1998) at James Cook University following our papers on Paragobiodon and Gobiodon, I reckoned that field experiments were needed to test the low-density hypothesis for the evolution of reversed sex change in protogynous fishes. I conducted the experiments with Suzuki and Kadota, as mentioned above (Kuwamura et al. 2011, 2014, 2015, 2016b). Thereafter, I resumed research on the cleaner’s mimicry with Fujisawa, Sato, and Sakai, as mentioned previously (Fujisawa et al. 2018, 2020; Sato et al. 2020a, b).

International meetings held at Sesoko Station and other studies by graduate students

To provide graduate students with opportunities for presentation in English, I organized two international meetings at Sesoko Station with Yasuhiro Nakashima and Kazuhiko Sakai, as the Joint-Use Research Meeting of Tropical Biosphere Research Center, University of the Ryukyus. From August 30 to September 2, 1991, a satellite meeting of the 22nd International Ethological Conference (IEC) on “Reproductive behavior and ecology of marine fishes and other animals” was attended by 47 participants from six countries, and 25 papers were presented in oral sessions (Kuwamura et al. 1992; Appendix 1). A satellite meeting of the 10th International Coral Reef Symposium (ICRS) on “Sex allocation and sexual conflict in coral reef organisms” was held on July 3–5, 2004: 33 participants from five countries attended it, and 21 papers were presented in oral sessions (Appendix 2). About half of the speakers in the two meetings were graduate students.

In addition to our research and those cited above, a number of graduate students from various universities conducted field research on the behavioral ecology of fish on the reefs of Sesoko Island and nearby Okinawa Island using Sesoko Station. From 1982, Yuji Hirose (University of the Ryukyus) studied patterns of pair formation in protandrous anemonefish Amphiprion spp. (Hirose 1995). Hiroko Sakashita (University of the Ryukyus) investigated the sexual dimorphism and food habits of the polygynous clingfish, Diademichthys lineatus (Sakashita 1992). Takeshi Takegaki (Kyushu University) examined the role of mounds and division of labor in the monogamous goby, Valenciennea longipinnis, in relation to burrowing behavior (Takegaki and Nakazono 1999, 2000). Tomoyuki Kokita (Kyushu University) investigated pair territory and sexual conflict in the longnose filefish, Oxymonacanthus longirostris (Kokita and Nakazono 1999,

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**Fig. 5** Just before group spawning of IP males of the threespot wrasse, Halichoeres trimaculatus (taken by Tetsuo Kuwamura on the reef edge of Tokashiki Island)
After 2000, Hiroki Hata (Kyoto University) discovered weeding by the territorial herbivorous damselfish, _Stegastes nigricans_ and a novel obligate cultivation mutualism with _Polysiphonia_ algae (Hata and Kato 2002, 2006). Yuko Sekiya (Osaka City University) studied female mate preferences in the goby, _Eviota prasina_ (Sekiya and Karino 2004). Lori Hosaka LaPlante (University of Connecticut) revealed the function of female belly color advertising sexual receptivity in the pink-belly wrasse, _Halichoeres margaritaceus_ (LaPlante 2015).

Satoshi Awata (Osaka City University) studied seasonal changes in reproductive and physical conditions and sexual dimorphism in the blenny, _Salarias fasciatus_ (Awata et al. 2010).

In conclusion, the Sesoko Station has been providing facilities for field studies of coral reef fishes and has contributed greatly to the development of behavioral ecology of fishes, apart from coral biology. The Sesoko Station will continue to be available for research on all topics related to the behavioral ecology of coral reef fishes.

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**References**

Awata S, Miura S, Seki S, Sagawa T, Sato N, Sakai K (2010) Seasonal changes in reproductive and physical condition, sexual dimorphism, and male mating tactics in the jewelled blenny _Salarias fasciatus_. Ichthyol Res 57: 161–168

Cheney KL, Grutter AS, Bshary R (2014) Geographical variation in the benefits obtained by a coral reef fish mimic. Anim Behav 88: 85–90

Dawkins R (1976) The selfish gene. Oxford University Press

Fujisawa M, Sakai Y, Kuwamura T (2018) Aggressive mimicry of the cleaner wrasse by _Aspidontus taeniatus_ functions mainly for small blennies. Ethology 124: 432–439

Fujisawa M, Sakai Y, Kuwamura T (2020) The false cleanerfish relies on aggressive mimicry to bite fish fins when benthic foods are scarce in their local habitat. Sci Rep 10: 8652

Hanahara T, Sagawa T (2008) Nest visiting behavior and nest change by male staghorn damselfish, _Amblyglyphidodon curacao_. Japan J Ichthyol 55: 27–35

Hata H, Kato M (2002) Weeding by the herbivorous damselfish _Stegastes nigricans_ in nearly monocultural algae farms.
Mar Ecol Prog Ser 237: 227–231
Hata H, Kato M (2006) A novel obligate cultivation mutualism between damselfish and Polysiphonia algae. Biol Lett 2: 593–596
Hattori A (1994) Inter-group movement and mate acquisition tactics of the protandrous anemonefish, Amphiprion clarkii, on a coral reef, Okinawa. Japan J Ichthyol 41: 159–165
Hirose Y (1995) Patterns of pair formation in protandrous anemonefishes, Amphiprion clarkii, A. frenatus and A. perideraion, on coral reefs of Okinawa, Japan. Environ Biol Fishes 43: 153–161
Ishihara T, Osato J, Nagata K, Sakai Y (2012) Reversed sex change in Stegastes nigricans: effect of distance to mates. Behav Ecol Sociobiol 68: 55–59
Karino K (1995) Male-male competition and female mate choice through courtship display in the territorial damselfish Stegastes nigrican. Ethology 118: 226–234
Karino K, Kuwamura T (1997) Plasticity in spawning visits of female damselfish, Stegastes nigrican: effect of distance to mates. Behav Ecol Sociobiol 41: 55–59
Karino K, Kuwamura T, Nakashima Y, Sakai Y (2000) Predation risk and the opportunity for female mate choice in a coral reef fish. J Ethol 18: 109–114
Kokita T, Nakazono A (1999) Pair territoriality in the longnose filefish, Oxymonacanthus longirostris. Ichthyol Res 46: 297–302
Kokita T, Nakazono A (2001a). Rapid response of an obligately corallivorous filefish Oxymonacanthus longirostris (Monacanthidae) to a mass coral bleaching event. Coral Reefs 20: 155–158
Kokita T, Nakazono A (2001b) Sexual conflict over mating system: the case of a pair-territorial filefish without parental care. Anim Behav 62: 147–155
Krebs JR, Davies NB (eds) (1978) Behavioural ecology. Blackwell
Krebs JR, Davies NB (1981) An introduction to behavioural ecology. Blackwell
Kuwamura T (1976) Different responses of inshore fishes to the cleaning wrasse, Labroides dimidiatus, as observed inSirahama. Publ Seto Mar Biol Lab 23: 119–144
Kuwamura T (1983) Reexamination on the aggressive mimicry of the cleaner wrasse Labroides dimidiatus by the blenny Aspidontus taeniatus (Pisces: Perciformes). J Ethol 1: 22–33
Kuwamura T (1984) Social structure of the protogynous fish Labroides dimidiatus. Publ Seto Mar Biol Lab 29: 117–177
Kuwamura T (1985) Social and reproductive behavior of three mouthbrooding cardinalfishes, Apoγon doederleini, A. niger and A. notatus. Environ Biol Fishes 13: 17–24
Kuwamura T (1986) Parental care and mating systems of cichlid fishes in Lake Tanganyika: a preliminary field survey. J Ethol 4: 129–146
Kuwamura T (1987) Night spawning and paternal mouthbrooding of the cardinalfish Cheilodipterus quinquelineatus. Japan J Ichthyol 33: 431–434
Kuwamura T (1988) Parental care and social systems in fish. Kaimisha, Tokyo
Kuwamura T (1997a) Evolution of female egg care in haremic triggerfish, Rhinecanthus aculeatus. Ethology 103: 1015–1023
Kuwamura T (1997b) The evolution of parental care and mating systems among Tanganyikan cichlids. In: Kawanabe H, Hori M, Nagoshi M (eds). Fish Communities in Lake Tanganyika, Kyoto University Press, pp 57–86
Kuwamura T (2004) Sex changing fishes on coral reefs. Iwanami, Tokyo
Kuwamura T (2007) Parental care in fishes: origin of sexual roles. Kaityusha, Tokyo
Kuwamura T (2013) History and mission of behavioral ecology. In: Kuwamura T, Awata S (eds) An Introduction to Behavioral Ecology of Fishes. Tokai University Press, pp 240–253
Kuwamura T, Kadota T, Suzuki S (2014) Testing the low-density hypothesis for reversed sex change in polygynous fish: experiments in Labroides dimidiatus. Sci Rep 4: 4369
Kuwamura T, Kadota T, Suzuki S (2015) Bidirectional sex change in the magenta dottyback Pictichromis porphyrea: first evidence from the field in Pseudochromidae. Environ Biol Fishes 98: 201–207
Kuwamura T, Karino K, Nakashima Y (2000) Male morphological characteristics and mating success in a protogynous coral reef fish, Halichoeres melanurus. J Ethol 18: 17–23
Kuwamura T, Nakashima Y (1998) New aspects of sex change among reef fishes: recent studies in Japan. Environ Biol Fishes 52: 125–135
Kuwamura T, Nakashima Y, Sakai K (1992) Meeting report:
Reproductive behavior and ecology of marine fishes and other animals. Galaxea, Publ Sesoko Mar Sci Cent 11: 57–71
Kuwamura T, Nakashima Y, Yogo Y (1994) Sex change in either direction by growth-rate advantage in the monogamous coral goby, Paragobidon echinocephalus. Behav Ecol 5: 434–438
Kuwamura T, Nakashima Y, Yogo Y (1996) Plasticity in size and age at maturity in a monogamous fish: effect of host coral size and frequency dependence. Behav Ecol Sociobiol 38: 365–370
Kuwamura T, Sagawa T, Suzuki S (2009) Interspecific variation in spawning time and male mating tactics of the parrot-fishes on a fringing coral reef at Iriomote Island, Okinawa. Ichthyol Res 56: 354–362
Kuwamura T, Sunobe T, Sakai Y, Kadota T, Sawada K (2020) Behav Ecol 38: 365–370
Kuwamura T, Suzuki S, Kadota T (2011) Reversed sex change in protogynous damselfish, Dascyllus aruanus. J Ethol 34: 725–733
Kuwamura T, Suzuki S, Kadota T (2016a) Male-to-female sex change in widowed males of the protogynous damselfish Dascyllus aruanus. J Ethol 34: 85–88
Kuwamura T, Suzuki S, Kadota T (2016b) Interspecific variation in the spawning time of labrid fish on a fringing reef at Iriomote Island, Okinawa. Ichthyol Res 63: 460–469
Kuwamura T, Suzuki S, Tanaka N, Ouchi E, Karino K, Nakashima Y (2007) Sex change of primary males in a diandric labrid Halichoeres tricolor: coexistence of protandry and protogyne within a species. J Fish Biol 70: 1898–1906
Kuwamura T, Tanaka N, Nakashima Y, Karino K, Sakai Y (2002) Reversed sex-change in the protogynous reef fish Labroides dimidiatus. Ethology 108: 443–450
Kuwamura T, Yogo Y, Nakashima Y (1993) Size-assortative monogamy and paternal egg care in a coral goby Paragobidon echinocephalus. Ethology 95: 65–75
LaPlante LH (2015) Female belly colour and bobbing behaviour advertise sexual receptivity in a pelagic-spawning coral reef fish. Behaviour 152: 705–725
Lassig BR (1977) Socioecological strategies adopted by obligate coral-dwelling fishes. Proc 3rd Int Coral Reef Symp 1: 565–570
Masuda H, Araga C, Yoshino T (1975) Coastal fishes of southwestern Japan. Tokai University Press, Tokyo
Mizushima N (2002) Reproductive strategy of the female humbug damselfish, Dascyllus aruanus. PhD Thesis (Kyoto University)
Mizushima N, Nakashima Y, Kuwamura T (2000) Semilunar spawning cycle of the humbug damselfish Dascyllus aruanus. J Ethol 18: 105–108
Munday PL, Caley MJ, Jones GP (1998) Bi-directional sex change in a coral-dwelling goby. Behav Ecol Sociobiol 43: 371–377
Munday PL, Kuwamura T, Kroon FJ (2010) Bidirectional sex change in marine fishes. In: Cole KS (eds) Reproduction and Sexuality in Marine Fishes: Patterns and Processes. pp. 241–271. University of California Press
Murayama S (2009) The possibility of sex change in the black-bar triggerfish Rhinecanthus aculeatus. Master thesis (University of the Ryukyus)
Nakashima Y (2007) Sex change of primary males in a diandric labrid Halichoeres trimaculatus: coexistence of protandry and protogyne within a species. J Fish Biol 70: 1898–1906
Nakahama T, Nakashima Y, Yogo Y (1996) Both-ways sex change in monogamous coral gobies, Gobiodon spp. Environ Biol Fishes 46: 281–288
Nakashima Y, Sakai Y, Karino K, Kuwamura T (2000) Female-female spawning and sex change in a haremic coral-reef fish, Labroides dimidiatus. Zool Sci 17: 967–970
Nakazono A, Kuwamura T (eds) (1987) Sex change in fishes. Tokai University Press, Tokyo
Nanami A, Nishihira M (1999) Nest construction by the labrid fish Choerodon jordani (Snyder 1908). Coral Reefs 18: 292
Sakai Y (1997) Alternative spawning tactics of female angelfish according to two different contexts of sex change. Behav Ecol 8: 372–377
Sakai Y, Karino K, Nakashima Y, Kuwamura T (2002) Status-dependent behavioural sex change in a polygynous coral-reef fish, Halichoeres melamurus. J Ethol 20: 101–105
Sakai Y, Karino K, Kuwamura T, Nakashima Y, Maruo Y (2003a) Sexually dichromatic protogynous angelfish Centropyge ferrugata (Pomacanthidae) males can change back to females. Zool Sci 20: 627–633
Sakai Y, Tsujiura C, Nakata Y, Tanabe H, Maejima G (2003b) Rapid transition in sexual behaviors during protogynous sex change in the haremic angelfish Centropyge vroliki
(Pomacanthidae). Ichthyol Res 50: 30–35
Sakashita H (1992) Sexual dimorphism and food habits of the clingfish, Diademichthys lineatus, and its dependence on host sea urchin. Environ Biol Fishes 34: 95–101
Sato H, Sakai Y, Kuwamura T (2020a) Non-mimic color variant of the false cleanerfish Aspidontus taeniatus found in Okinawa, Japan. Galaxea, J Coral Reef Studies 22: 1–2
Sato H, Sakai Y, Kuwamura T (2020b) Testing the effect of mimicry using a color variant of the false cleanerfish Aspidontus taeniatus. Japan J Ichthyol 67: 253–258
Seki S, Kohda M, Takamoto G, Karino K, Nakashima Y, Kuwamura T (2009) Female defense polygyny in the territorial triggerfish Sufflamen chrysopterus. J Ethol 27: 215–220
Sekiya Y, Karino K (2004) Female mate preference in goby Eviota prasina: do secondary sexual traits influence female choice? Zool Sci 21: 859–863
Suzuki S, Kuwamura T, Nakashima Y, Karino K, Kohda M (2010) Social factors of group spawning as an alternative mating tactic in the territorial males of the three-spot wrasse Halichoeres trimaculatus. Environ Biol Fishes 89: 71–77
Suzuki S, Toguchi K, Makino Y, Kuwamura T, Nakashima Y, Karino K (2008) Group spawning results from the streaking of small males into a sneaking pair: male alternative reproductive tactics in the threespot wrasse Halichoeres trimaculatus. J Ethol 26: 397–404
Takamoto G, Seki S, Nakashima Y, Karino K, Kuwamura T (2003) Protogynous sex change in the haremic triggerfish Sufflamen chrysopterus (Tetraodontiformes). Ichthyol Res 50: 281–283
Takegaki T, Nakazono A (1999) Division of labor in the monogamous goby, Valenciennea longipinnis, in relation to burrowing behavior. Ichthyol Res 46: 125–129
Takegaki T, Nakazono A (2000) The role of mounds in promoting water-exchange in the egg-tending burrows of monogamous goby, Valenciennea longipinnis (Lay et Bennett). J Exp Mar Biol Ecol 253: 149–163
Warner RR (1975) The adaptive significance of sequential hermaphroditism in animals. Am Nat 109: 61–82
Warner RR (1984) Mating behavior and hermaphroditism in coral reef fishes. Am Sci 72: 128–136
Warner RR, Schultz ET (1992) Sexual selection and male characteristics in the bluehead wrasse, Thalassoma bifasciatum: mating site acquisition, mating site defense, and female choice. Evolution 46: 1421–1442
Wickler W (1968) Mimicry in plants and animals. McGraw-Hill
Wilson EO (1975) Sociobiology: the new synthesis. Belknap Press of Harvard University Press
Yogo Y (1985) Studies on the sexual maturation and reproductive ecology in three protogynous fishes. Rep Fish Res Lab. Kyushu Univ 7: 37–83
Yoshino T, Nishijima S (1981) A list of fishes found around Sesoko Island, Okinawa. Sesoko Mar Sci Lab Tech Rep 8: 19–87
Ziadi-Künkli F, Tachihara K (2016) Female defence polygyny and plasticity in the mating system of the demersal triggerfish Rhinecanthus aculeatus (Pisces: Balistidae) from Okinawa Island. Mar Biol 163: 27

Appendix 1 Speakers and titles in the 22nd International Ethological Conference (IEC) Satellite Meeting “Reproductive behavior and ecology of marine fishes and other animals” organized by Tetsuo Kuwamura, Yasuhiro Nakashima, and Kazuhiko Sakai, held from August 30 to September 2, 1991, at Sesoko Station. The abstracts of the presented papers have been published in a meeting report by Kuwamura et al. (1992). For speakers, affiliations are given in parentheses.

Tetsuo Kuwamura (Chukyo University): Opening address
Kazuhiko Sakai (University of the Ryukyus): Resource allocation plasticity in a massive coral, Goniastrea aspera, with special reference to onset of sexual reproduction
Ravenska T. Radjawane (University of the Ryukyus), Moritaka Nishihira: Reproductive ecology of the cluster wrinkle Planaxis sulcatus (Born) on an Okinawan reef flat
Janet L. Leonard (University of Oklahoma): Sexual conflict theory and opisthobranch mating systems (Gastropoda)
Eric A. Fischer (National Audubon Society): Life history trade-offs in harlequin bass
Robert A. Kinzie III (University of Hawaii): Reproductive biology of a threatened amphidromous goby Lentipes concolor
H. Jane Brockmann (University of Florida): The effects of age on male behavior in Limulus polyphemus
Hiroyuki Munehara (Hokkaido University), Yasunori Koya, et al.: Reproductive style of the marine sculpin Alcichthys alcicornis exhibiting copulation and paternal care
Masanori Kohda (Osaka City University): Filial cannibalism by paternal males in a damselfish Stegastes altus
Kenji Karino (Kyushu University): Male-male competition and female mate choice in a herbivorous damselfish, Stegastes
Takuro Shibuno (Hiroshima University): Female spawning migration of the protogynous wrasse *Halichoeres marginatus*

Robert R. Warner (University of California, Santa Barbara): Sexual selection and male characteristics in the bluehead wrasse: mating site acquisition, site defense, and female choice

Mart R. Gross (University of Toronto): Evolution of alternative reproductive strategies in fishes

Toshiaki Fuse (Kyoto University): Social and mating systems in a dragonet, *Neosynchyropus ocellatus*

Hisao Hamaguchi (Miyako High School): The factors that reduce feeding rate of territorial males in *Canthigaster valentini* (Tetraodontidae)

Izumi Akagawa (University of Tokyo), Munee Okiyama: Maternal behavior of *Rudarius ercodes*: what is the spawning parade?

Naomi Tanaka (Okinawa Expo Aquarium): Pair territory and diurnal migration of the vagabond butterflyfish *Chaetodon vagabundus*

Shinji Yabuta (Kyoto University): Spawning migration of monogamous pairs in the butterflyfish *Chaetodon trifasciatus*

Ernst S. Reese (University of Hawaii): Behavior and ecology of reproduction in butterflyfishes, family Chaetodontidae: what we know and what we don’t know

Tetsu Sato (Tokyo Sea Life Park), Hiroshi Arai, Masaaki Komada: Attack toward pair mate, female role taking over and stopping of spawning in a simultaneously hermaphroditic fish in an aquarium

Terry J. Donaldson (Division of Fish and Wildlife, Saipan): Courtship and spawning behavior of the grouper *Cephalopholis spiloparaea*

Yuji Hirose (Shimakami-Ohkanmuri High School): Small sea-anemones stunt the growth of the anemonefishes

Douglas Y. Shapiro (University of Puerto Rico), Daphne G. Fautin: Gonad development in anemonefishes; a new interpretation of protandric hermaphroditism

Yoichi Sakai (Osaka City University): Early sex change of an angelfish *Centropyge ferrugatus* (Pomacanthidae)

Tomoki Sunobe (Natural History Museum and Institute, Chiba): Mating system and sex change for both directions in the gobid fish *Trimma okinawae*

Yutaka Yogo (Showa Women’s High School), Tetsuo Kuwamura, Yasuhiro Nakashima: Evolution of sex change among monogamous fishes: theories and facts

**Appendix 2** Speakers and titles in the 10th International Coral Reef Symposium (ICRS) Satellite Meeting “Sex allocation and sexual conflict in coral reef organisms” organized by Tetsuo Kuwamura and Kazuhiko Sakai, held on July 3–5, 2004 at Sesoko Station. For speakers, affiliations are given in parentheses.

Tetsuo Kuwamura (Chukyo University): Opening address

Robert Warner (University of California, Santa Barbara), Roldan C. Munoz: A new version of the size-advantage model for sex change

Stefan Walker (James Cook University), Mark I. McCormick: The effect of female density on the rate of behavioural and gonadal sex change and the acquisition of secondary sexual traits in a haremic protogynous reef fish

Satoko Seki (Kyoto University of Foreign Studies), Gousuke Takamoto, Masanori Kohda, Kenji Karino, Yasuhiro Nakashima, Tetsuo Kuwamura: Mating system of the triggerfish, *Sufflamen chrysopterum*: resource defense or female defense polygyny?

Tatsuru Kadota (Hiroshima University), Yoichi Sakai, Hiroaki Hashimoto, Kenji Gushima: Mating system of the blackside hawkfish *Paracirrhites forsteri* (Cirrhitidae) on reefs of Kuchierabu-jima Island, with notes on the sex allocation

Mark I. McCormick (James Cook University): Protogyny in the damselfish, *Pomacentrus amboinensis*: investment by females in their future

Tepepi Sagawa (University of the Ryukyus), Tsutomu Hanahara: Female-like behavior by sneaking males of the staghorn damselfish, *Amblyglyphidodon curacao*

Yuko Sekiya (Osaka City University), Kenji Karino, Masanori Kohda: Dorsal fin length is determined by social dominance in the male goby, *Eviota prasina*

Tomoko Kataoka (Hiroshima University), Norio Shimizu, Yoichi Sakai, Hiroaki Hashimoto, Kenji Gushima: Male mating tactics of the terrestrial spawning fish *Andamia tetradactyla* (Blenniidae)

Terry J. Donaldson (University of Guam): Are reef fish spawning aggregations leks?

Shohei Suzuki (Osaka City University), Kyoko Toguchi, Yoshimi Makino: The formation of group spawning of IP males in a protogynous wrasse, *Halichoeres trimaculatus*

Tomohiro Takeyama (Osaka City University), Noboru Okuda, Yasunobu Yanagisawa: Sexual conflict in paternal mouthbrooding cardinalfishes: female mating competition and
male brood cannibalism
Kazuhiko Sakai (University of the Ryukyus): Sex allocation in scleractinian corals
Sayaka Kai (University of the Ryukyus), Kazuhiko Sakai: Size or age: which has the larger effect on growth and reproduction in colonial scleractinian corals?
Tsutomu Hanahara (University of the Ryukyus), Teppei Sagawa: Sneaking and visiting behavior by the male staghorn damselfish, *Amblyglyphidodon curacao*
Masakazu Tokuzato (University of the Ryukyus), Yasuhiro Nakashima: Curious mating behavior in Chromodorid nudibranchs
Hisaya Manabe (Kagoshima University), Mami Ishimura, Akihiko Shinomiya, Tomoki Sunobe: Both-ways sex change in the polygynous gobiid fish *Trimma okinawae*: when do males change back to females?
Tomoki Sunobe (Natural History Museum and Institute, Chiba), Masaru Nakamura, Yasuhisa Kobayashi, Tohru Kobayashi, Yoshitaka Nagahama: Gonadal structure and P450scc-, 3ß-HSD- and Arom-like immunoreactivity in the gobiid fish *Trimma okinawae* during both ways sex change
Philip L. Munday (James Cook University), Frederieke J. Kroon, David A. Westcott, Jean-Paul Hobbs: Estradiol production regulates sex change in each direction in coral-dwelling gobies
Kohei Ohta (National Institute for Basic Biology), Mami Sakai, J.K. Sundaray, Akihiko Yamaguchi, Michiya Matsuyama: Induction of bi-directional sex change by steroid hormones in the protogynous wrasse *Pseudolabrus sieboldi*
Tetsuo Kuwamura (Chukyo University), Shohei Suzuki, Kyoko Toguchi, Yoshimi Makino, Kenji Karino, Yasuhiro Nakashima, Naomi Tanaka: Sex change of the primary male in the protogynous wrasse *Halichoeres trimaculatus*
Akira Nishikawa (University of the Ryukyus), Kazuhiko Sakai: The state of coral communities in the Kerama and Okinawa Islands after the 1998 coral bleaching

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