Hermaphroditism in fishes: an annotated list of species, phylogeny, and mating system

Tetsuo Kuwamura1,2 · Tomoki Sunobe3 · Yoichi Sakai4 · Tatsuru Kadota5 · Kota Sawada6

Abstract
Fewer than 1% of vertebrate species are hermaphroditic, and essentially all of these are fishes. Four types of hermaphroditism are known in fishes: simultaneous (or synchronous) hermaphroditism (SH), protandry (male-to-female sex change; PA), protogyny (female-to-male sex change; PG), and bidirectional sex change (BS or reversed sex change in protogynous species). Here we present an annotated list of hermaphroditic fish species from a comprehensive review and careful re-examination of all primary literature. We confirmed functional hermaphroditism in more than 450 species in 41 families of 17 teleost orders. PG is the most abundant type (305 species of 20 families), and the others are much less abundant, BS in 66 species of seven families, SH in 55 species of 13 families, and PA in 54 species of 14 families. The recently proposed phylogenetic tree indicated that SH and PA have evolved several times in not-closely related lineages of Teleostei but that PG (and BS) has evolved only in four lineages of Percomorpha. Examination of the relation between hermaphroditism type and mating system in each species mostly supported the size-advantage model that predicts the evolution of sequential hermaphroditism. Finally, intraspecific variations in sexual pattern are discussed in relation to population density, which may cause variation in mating system.

Keywords Bidirectional · Protandry · Protogyny · Sex change · Simultaneous hermaphroditism

Introduction
Over one-half of the world’s living vertebrates (> 60,000 species) are fishes (> 32,000 species; Nelson et al. 2016). Approximately 99% of all vertebrate species consist of separate-sex individuals (gonochorists), i.e., pure males and pure females. The other 1% of vertebrate species are hermaphroditic, and almost all of them are fishes (Avise 2011; Ashman et al. 2014). Among hermaphroditic fishes, four major types of hermaphroditism are known (Sadovy de Mitcheson and Liu 2008; Munday et al. 2010): simultaneous (or synchronous) hermaphroditism (SH), protandry (PA), protogyny (PG), and bidirectional sex change (BS or reversed sex change in protogynous species; Kuwamura et al. 2014). Simultaneous hermaphrodites produce both mature eggs and sperm in their gonads at the same time, but self-fertilization rarely occurs in fishes (Avise 2011). In sequential hermaphrodites, either male-to-female sex change (PA) or female-to-male sex change (PG) occurs during the lifetime of an individual. Reports on bidirectional sex change within a species have increased since the 1990s (Kuwamura and Nakashima 1998; Munday et al. 2010), mostly as reversed sex change in

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* Tetsuo Kuwamura
kuwamura@lets.chukyo-u.ac.jp

1 School of International Liberal Studies, Chukyo University, Yagoto-honmachi, Nagoya 466-8666, Japan
2 Present Address: Faculty of Liberal Arts and Sciences, Chukyo University, Yagoto-honmachi, Nagoya 466-8666, Japan
3 Laboratory of Fish Behavioral Ecology, Tateyama Station, Field Science Center, Tokyo University of Marine Science and Technology, Banda, Tateyama 294-0308, Japan
4 Graduate School of Integrated Sciences for Life, Hiroshima University, Kagamiyama, Higashi-Hiroshima 739-8528, Japan
5 Seikai National Fisheries Research Institute, Japan Fisheries Research and Education Agency, Taira-machi, Nagasaki 851-2213, Japan
6 Oceanic Ecosystem Group, National Research Institute of Far Seas Fisheries, Japan Fisheries Research and Education Agency, Fukuura, Kanagawa 236-8648, Japan
The evolution of hermaphroditism among animals has been explained by two major hypotheses: the low-density model for simultaneous hermaphroditism and the size-advantage model for sequential hermaphroditism (Ghiselin 1969, 1974). In low-density conditions, few mating opportunities are expected, and mating success will be much higher in simultaneous hermaphrodites than that in gonochorists if random mating occurs (Tomlinson 1966), although hermaphrodites suffer the energetic cost of maintaining two reproductive systems (Heath 1977). Self-fertilization further increases the benefits of simultaneous hermaphroditism under extreme low density with little opportunity to find conspecifics (Tomlinson 1966). In addition, simultaneous hermaphroditism is presumably favored by diminishing fitness return for the investment to one sexual function, e.g., owing to small mating groups or brood space limitation (Charnov 1982).

For sequential hermaphroditism, the size-advantage model (SA model) predicts that the occurrence and direction of sex change are determined by mating system, because the relation between reproductive success and body size of males depends on mating system, while reproductive success of females increases with growth irrespective of mating system (Warner 1975, 1984). For example, in species with random mating regardless of male body size, in which females do not have preference for large males and accept small ones, male reproductive success is not related to body size, and male-to-female sex change (PA) will be favored, because the reproductive success of small males is higher than that of females of the same size, and vice versa in large males and females. By contrast, in species with polygynous mating systems, in which large males monopolize females, male reproductive success sharply increases with growth, and female-to-male sex change (PG) will be favored, because large females can increase reproductive success by changing sex to male. Contrastingly, in species with size-associative mating or group spawning by one female with multiple males (i.e., intense scramble-type sperm competition), in which reproductive success of males and females increases with growth in a similar fashion, gonochorism will evolve because of the cost of sex change (Warner 1975, 1984). Some mating systems with extensive sperm competition and size–fecundity skew will also reduce or eliminate the size advantage and result in a reduction or even a lack of sex change (Muñoz and Warner 2003, 2004). Bidirectional sex change has recently been regarded as a tactic to secure mating opportunities when mate-search (finding an opposite-sex individual) after the loss of partners is difficult or costly because of low density, and it is suggested to have derived from either protogynous (Kuwamura et al. 2014, 2016a) or gonochoristic ancestors (Sunobe et al. 2017). Large amounts of evidence supporting the SA model have been reported, especially from coral reef fishes (Nakazono and Kuwamura 1987; Warner 1988; Munday et al. 2006; Sadovy de Mitcheson and Liu 2008; Kazancioglu and Alonzo 2010; Erisman et al. 2013). However, the mating systems of many other hermaphroditic fishes are still unknown.

Sadovy de Mitcheson and Liu (2008) published a comprehensive review of functional hermaphroditism in teleost fishes, providing family accounts with a genus-level list of 94 genera in 27 families of seven teleost orders (based on the classification of Nelson 2006) with confirmed functional hermaphroditism. They also listed 31 genera in 21 teleost families that have been suggested as hermaphroditic but not confirmed. Hermaphroditism has evolved in many different fish lineages, predominantly among tropical marine perciforms, in which hermaphroditism expression diversity is the greatest. However, because the sexual pattern and mating system are often highly variable even within a single genus or species (Munday et al. 2006), the genus-level list provided by Sadovy de Mitcheson and Liu (2008) is not sufficient to estimate the evolutionary patterns of sexuality. Although Devlin and Nagahama (2002) provided a list of 259 species in 25 teleost families, they did not make such a clear distinction between functional and non-functional hermaphroditism which is essential to evolutionary/ecological analyses.

The purpose of this study is to present an annotated species-level list of functional hermaphroditism in fishes, which will enable a wide range of interesting analyses, after a comprehensive review and careful re-examination of all primary literature. Frequencies of hermaphroditism in each family and order were summed up, and its distribution on the recently proposed phylogenetic tree (Betancur-R et al. 2017) was examined. Mating systems of hermaphroditic fish species were also reviewed, and the relation between the type of hermaphroditism in each species and its mating system was investigated to test the SA model. Finally, intraspecific variations in sexual pattern are discussed in relation to population density, which may cause variation in mating system.

Materials and methods

Construction of the database of hermaphroditic fishes. We searched original papers on hermaphroditic fish species using references of review papers (e.g., Nakazono and Kuwamura 1987; Devlin and Nagahama 2002; Sadovy de Mitcheson and Liu 2008) and by Internet searches (mainly by Google Scholar) entering keywords such as hermaphroditism, sex change, protogyny, and protandry along with names of known hermaphroditic taxa (orders/families/genera). For each species, we recorded type of hermaphroditism (SH, PA, PG, and BS), methods of confirmation (histology, aquarium or field observations, see below), mating system...
(see below), habitat (e.g., deep sea, coral reef), reference, and remarks. Species name and habitat are based on FishBase (https://www.fishbase.in). The results were compiled into the list based on the fish classification system of Nelson et al. (2016). Then, to avoid overlooking any species, we conducted similar Internet searches for papers reporting hermaphroditism in each of the remaining families of fishes without known cases of hermaphroditism.

Table 1 is a simplified table in which only the type of hermaphroditism and mating system is shown, and detailed records and references are shown in Electronic supplementary material, Table S1 and S2, respectively. In each table, families and orders are arranged following the order of Nelson et al. (2016), and genera and species in alphabetical order within each family and genus, respectively.

To determine if hermaphroditism was confirmed or not in each species, we applied the criteria for functional hermaphroditism following Sadovy and Shapiro (1987) and Sadovy de Mitcheson and Liu (2008), i.e., detailed gonadal histological series ideally illustrated with photomicrographs that show various stages of sexual transition (as examples), simultaneous occurrence of mature testicular and ovarian tissues in gonads, or field or aquarium observations of gamete release and/or sexual characteristics (e.g., shape of urogenital papilla) in identified individuals. Moreover, histological observation on transition of gonad-associated structures could be used to determine the occurrence of sex change (Cole and Shapiro 1990; Sunobe et al. 2017), and microscopic observation of eggs and sperm is also useful to confirm sexual maturation. Species with suggested, but not confirmed functional hermaphroditism were also recorded (Table S1 with remarks, "?” indicates weak evidence), but excluded from Table 1.

**Taxonomic, phylogenetic, and ecological distributions of hermaphroditism.** Frequencies of each type of hermaphroditism, i.e., SH, PA, PG, and BS (reversed sex change), in each family and order were summed up and compared between marine and freshwater families. The phylogenetic tree of Betancur-R et al. (2017), which shows the relationship of major groups (ordinal or supraordinal taxa), was used to examine the distribution of each type of hermaphroditism.

**Mating systems in hermaphroditic fishes.** To test the SA model (Warner 1975), the relation between the type of hermaphroditism and mating system of each species was investigated. Based on the data cited in Table S1, we classified the mating systems into the following seven types (modified from Kuwamura 1997; Table 1).

1) Random mating: Females mate with males regardless of their body size, without continuing pair bond (i.e., close and lasting association between a male and female).

2) Non-size-assortative monogamy: Pair bonding of a male and a female, which has no preference for male size and accepts a smaller male.

3) Size-assortative monogamy: Pair bonding of a male and a female, in which both prefer larger mates, resulting in pairing of similar-sized mates.

4) Harem polygyny: A large male monopolizes a harem of females.

5) Male-territory-visiting polygamy: Females visit male territories to mate. Males may establish small territories during spawning time even within a multi-male group.

6) Group spawning: Spawning of a single female with multiple males occurs without continuous bonding usually in a spawning aggregation.

7) Spawning aggregation: We used this category when spawning aggregation has been reported, but the detailed mating system is unknown (e.g., neither male territory nor group spawning has been reported).

Facultative monogamy in polygamous species, which may frequently occur in low-density condition (Barlow 1984), is not shown in Table 1.

**Results and discussion**

**Phylogeny and hermaphroditism.** We confirmed functional hermaphroditism in more than 450 species of 156 genera in 41 families of 17 teleost orders (based on the classification of Nelson et al. 2016). In Table 1, species with confirmed functional hermaphroditism were listed, indicating the type of hermaphroditism (SH, PA, PG, and BS). A detailed and annotated list of hermaphroditic fish species including additional information and unconfirmed species is provided as Electronic supplementary material Table S1 with a complete reference list of more than 500 papers (S2). We found functional hermaphroditism in 461 species and all of them are teleosts (Infraclasse Teleostei). Two types of hermaphroditism, i.e., PG and BS, are reported within a single species in 18 species (Table 1).

We found at least one hermaphroditic species in 41 families (9% of 470 families of Teleostei; Table 2). Percentage of hermaphroditic species in a family widely varied from 0.1% (2 of 1762 species in Cichlidae) to 100% (in both species of Giganturidae and Eleginopsidae). Among fish families including over 30 species, the percentage was relatively high in Sparidae (84%), Scaridae (35%), Ipnopidae (28%), Lethrinidae (26%), Pomacanthidae (26%), Labridae (19%), Cirrhitidae (18%), and Serranidae (17%), although these percentages represented the lower limits because sexual patterns of all species have not always been investigated in each family.

PG was the most abundant hermaphroditism type (305 species, 66% of 461 hermaphroditic species), while other types were much less abundant, i.e., BS in 66 species (14%), SH in 55 species (12%), and PA in 54 species (12%) (Table 2). SH, PA, PG, and BS were the most abundant in...
Table 1 List of hermaphroditic fish species and their mating systems. Order and family names are arranged following Nelson et al. (2016), and genus and species in alphabetical order within each family and genus, respectively.

| Order          | Family                  | Species                        | Sexual pattern | Mating system   |
|---------------|-------------------------|--------------------------------|----------------|-----------------|
| Anguilliformes| Muraenidae              | Gymnothorax griseus            | SH             |                 |
|               | Muraenidae              | Gymnothorax pictus             | SH             |                 |
|               | Muraenidae              | Gymnothorax thyroideus         | SH             |                 |
|               | Muraenidae              | Rhinomuraena quaesita          | PA             |                 |
| Clupeiformes  | Clupeidae               | Tenualosa macrura              | PA             |                 |
|               | Clupeidae               | Tenualosa toli                 | PA             |                 |
| Cypriniformes | Cobitidae               | Cobitis taenia                 | PA, G          |                 |
| Stomiiformes  | Gonostomatidae          | Cyclothone atraria             | PA             |                 |
|               | Gonostomatidae          | Cyclothone microdon            | PA             |                 |
|               | Gonostomatidae          | Gonostoma elongatum            | PA             |                 |
|               | Gonostomatidae          | Sigmops bathyphilum            | PA             |                 |
|               | Gonostomatidae          | Sigmops gracile                | PA             |                 |
| Aulopiformes  | Ipnopidae               | Bathymicrops brevianalis       | SH             |                 |
|               | Ipnopidae               | Bathymicrops regis             | SH             |                 |
|               | Ipnopidae               | Bathyperois grullator          | SH             |                 |
|               | Ipnopidae               | Bathyperois viridensis         | SH, G          |                 |
|               | Ipnopidae               | Bathyperois quadrifilis        | SH             |                 |
|               | Ipnopidae               | Bathyperois mediterraneus      | SH             |                 |
|               | Ipnopidae               | Bathypholops marionae          | SH             |                 |
|               | Ipnopidae               | Ipnops agassizii               | SH             |                 |
|               | Ipnopidae               | Ipnops meadi                   | SH             |                 |
|               | Giganturidae            | Gigantura chuni                | SH             |                 |
|               | Giganturidae            | Gigantura indica               | SH, G          |                 |
|               | Bathysauridae           | Bathysaurus ferox              | SH             |                 |
|               | Chlorophthalmidae       | Chlorophthalmus agassizii      | SH             |                 |
|               | Chlorophthalmidae       | Chlorophthalmus brasiliensis   | SH             |                 |
|               | Chlorophthalmidae       | Parasudis truculenta          | SH             |                 |
|               | Notosudidae             | Ahliesaurus brevis             | SH             |                 |
|               | Scopelarchidae          | Benthalbella infans            | SH             |                 |
|               | Scopelarchidae          | Scopelarchus guentheri         | SH             |                 |
|               | Paralepididae           | Antopterus pharao              | SH             |                 |
|               | Paralepididae           | Lestidium pseudophyraenoides   | SH             |                 |
|               | Alepisauridae           | Omosudis lowii                 | SH             |                 |
| Gobiiformes   | Gobiidae                | Coryphopterus alloides         | PG             |                 |
|               | Gobiidae                | Coryphopterus dicus            | PG             |                 |
|               | Gobiidae                | Coryphopterus eidolon          | PG             |                 |
|               | Gobiidae                | Coryphopterus glaucofraenum    | PG             | MTV polygamy    |
|               | Gobiidae                | Coryphopterus hyalinus         | PG             |                 |
|               | Gobiidae                | Coryphopterus lipernes         | PG             |                 |
|               | Gobiidae                | Coryphopterus personatus       | PG             |                 |
|               | Gobiidae                | Coryphopterus thrix            | PG             |                 |
|               | Gobiidae                | Coryphopterus aroplius         | PG             |                 |
|               | Gobiidae                | Eviota epiphanes               | PG, BS         |                 |
Table 1 (continued)

| Order    | Family          | Species                        | Sexual pattern | Mating system       |
|----------|-----------------|--------------------------------|----------------|---------------------|
| Gobiidae | Gobiidae        | Fusigobius neophytus           | PG             | MTV polygamy        |
| Gobiidae | Gobiidae        | Gobiodon erythrosplas          | BS             | SA monogamy         |
| Gobiidae | Gobiidae        | Gobiodon histrio               | PG, BS         | SA monogamy         |
| Gobiidae | Gobiidae        | Gobiodon micropus              | BS             | SA monogamy         |
| Gobiidae | Gobiidae        | Gobiodon oculolinealus         | BS             | SA monogamy         |
| Gobiidae | Gobiidae        | Gobiodon okinawae              | PG             | SA monogamy         |
| Gobiidae | Gobiidae        | Gobiodon quinquestrigatus      | PG, BS         | SA monogamy         |
| Gobiidae | Gobiidae        | Lythrypnus dalli               | PG, BS         | MTV polygamy        |
| Gobiidae | Gobiidae        | Lythrypnus nesiotes            | PG             |                    |
| Gobiidae | Gobiidae        | Lythrypnus phorellus           | PG             |                    |
| Gobiidae | Gobiidae        | Lythrypnus pulchellus          | BS             |                    |
| Gobiidae | Gobiidae        | Lythrypnus spilus              | PG             |                    |
| Gobiidae | Gobiidae        | Lythrypnus zebra               | BS             | MTV polygamy        |
| Gobiidae | Gobiidae        | Paragobiodon echinocephalus    | PG, BS         | SA monogamy         |
| Gobiidae | Gobiidae        | Paragobiodon xanthosomus       | PG             | SA monogamy         |
| Gobiidae | Gobiidae        | Priolepis akihitoi             | BS             |                    |
| Gobiidae | Gobiidae        | Priolepis borea                | BS             |                    |
| Gobiidae | Gobiidae        | Priolepis cincta               | BS             | SA monogamy         |
| Gobiidae | Gobiidae        | Priolepis eugenius             | PG, BS         |                    |
| Gobiidae | Gobiidae        | Priolepis fallacincta          | BS             |                    |
| Gobiidae | Gobiidae        | Priolepis hipoili              | PG, BS         |                    |
| Gobiidae | Gobiidae        | Priolepis inhaca               | BS             |                    |
| Gobiidae | Gobiidae        | Priolepis latifascima          | BS             |                    |
| Gobiidae | Gobiidae        | Priolepis semidoliata          | BS             | SA monogamy         |
| Gobiidae | Gobiidae        | Rhinogobiops nicholsii         | PG             |                    |
| Gobiidae | Gobiidae        | Trimma annosum                | BS             |                    |
| Gobiidae | Gobiidae        | Trimma benjamini               | BS             |                    |
| Gobiidae | Gobiidae        | Trimma caesiura                | BS             |                    |
| Gobiidae | Gobiidae        | Trimma cana                    | BS             |                    |
| Gobiidae | Gobiidae        | Trimma caudomaculatum          | BS             | MTV polygamy        |
| Gobiidae | Gobiidae        | Trimma emeryi                  | BS             |                    |
| Gobiidae | Gobiidae        | Trimma fangi                   | BS             |                    |
| Gobiidae | Gobiidae        | Trimma flammeneum              | BS             |                    |
| Gobiidae | Gobiidae        | Trimma flavatram               | BS             |                    |
| Gobiidae | Gobiidae        | Trimma fucatum                 | BS             |                    |
| Gobiidae | Gobiidae        | Trimma gigantum                | BS             |                    |
| Gobiidae | Gobiidae        | Trimma grammistes              | BS             | Harem              |
| Gobiidae | Gobiidae        | Trimma kudoi                   | BS             |                    |
| Gobiidae | Gobiidae        | Trimma lantana                 | BS             |                    |
| Gobiidae | Gobiidae        | Trimma macrophthalma           | BS             |                    |
| Gobiidae | Gobiidae        | Trimma maiandros               | BS             |                    |
| Gobiidae | Gobiidae        | Trimma marinae                 | BS             |                    |
| Gobiidae | Gobiidae        | Trimma mila                    | BS             |                    |
| Gobiidae | Gobiidae        | Trimma nasa                    | BS             |                    |
| Gobiidae | Gobiidae        | Trimma naudei                  | BS             |                    |
| Gobiidae | Gobiidae        | Trimma necopinum               | BS             |                    |
| Gobiidae | Gobiidae        | Trimma okinawae                | PG, BS         | Harem              |
| Gobiidae | Gobiidae        | Trimma preclarum               | BS             |                    |
| Gobiidae | Gobiidae        | Trimma rubromaculatum          | BS             |                    |
| Gobiidae | Gobiidae        | Trimma sheppardi               | BS             |                    |
| Order            | Family        | Species                | Sexual pattern | Mating system  |
|------------------|---------------|------------------------|----------------|----------------|
| Gobiidae         | Gobiidae      | *Trimma stobbsi*       | BS             |                |
| Gobiidae         | Gobiidae      | *Trimma striatum*      | BS             |                |
| Gobiidae         | Gobiidae      | *Trimma taurocalum*    | BS             |                |
| Gobiidae         | Gobiidae      | *Trimma taylori*       | BS             |                |
| Gobiidae         | Gobiidae      | *Trimma unisquamis*    | BS             |                |
| Gobiidae         | Gobiidae      | *Trimma yanagitai*     | BS             |                |
|                  | Uncertain in ovalentaria |               |                |                |
| Pomacentridae    | Pomacentridae | *Amphiprion akallopisos* | PA             | NSA monogamy   |
| Pomacentridae    | Pomacentridae | *Amphiprion bicinctus* | PA             | NSA monogamy   |
| Pomacentridae    | Pomacentridae | *Amphiprion clarkii*   | PA             | NSA monogamy   |
| Pomacentridae    | Pomacentridae | *Amphiprion frenatus*  | PA             | NSA monogamy   |
| Pomacentridae    | Pomacentridae | *Amphiprion melanopus* | PA             | NSA monogamy   |
| Pomacentridae    | Pomacentridae | *Amphiprion ocellaris* | PA             | NSA monogamy   |
| Pomacentridae    | Pomacentridae | *Amphiprion perideraion* | PA         | NSA monogamy   |
| Pomacentridae    | Pomacentridae | *Amphiprion polynnus*  | PA             | NSA monogamy   |
| Pomacentridae    | Pomacentridae | *Amphiprion sandaracinos* | PA         | NSA monogamy   |
| Pomacentridae    | Pomacentridae | *Dascyllus aruanus*    | PG, BS, G      | Harem, MTV polygamy |
| Pomacentridae    | Pomacentridae | *Dascyllus carneus*    | PG             | Harem, MTV polygamy |
| Pomacentridae    | Pomacentridae | *Dascyllus flavicaudus* | PG, G         | Harem, MTV polygamy |
| Pomacentridae    | Pomacentridae | *Dascyllus marginatus* | PG             | Harem, MTV polygamy |
| Pomacentridae    | Pomacentridae | *Dascyllus melanarus*  | PG, G         | Harem, MTV polygamy |
| Pseudochromidae  | Pseudochromidae | *Pictichromis porphyrea* | BS         |                |
| Cichliformes     | Cichlidae     | *Satanoperca jurupari* | SH             |                |
| Cichliformes     | Cichlidae     | *Metriaclima cf. livingstoni* | PG       | MTV polygamy   |
| Cyprinodontiformes | Rivulidae    | *Kryptolebias hermaphroditus* | SH, G      |                |
| Cyprinodontiformes | Rivulidae    | *Kryptolebias marmoratus* | SH, G      |                |
| Cyprinodontiformes | Rivulidae    | *Kryptolebias ocellatus* | SH, G      |                |
| Poeciliidae      | Poeciliidae   | *Xiphophorus helleri*  | PG, G         |                |
| Synbranchiformes | Synbranchidae | *Monopterus albus*     | PG             | MTV polygamy   |
| Synbranchiformes | Synbranchidae | *Monopterus boueti*    | PG             |                |
| Synbranchiformes | Synbranchidae | *Ophisternon bengalense* | PG       |                |
| Synbranchiformes | Synbranchidae | *Synbranchus marmoratus* | PG       |                |
| Trachiniformes   | Pinguipedidae | *Parapercis clathrata* | PG             |                |
| Trachiniformes   | Pinguipedidae | *Parapercis colias*    | PG             |                |
| Trachiniformes   | Pinguipedidae | *Parapercis cylindrica* | PG             | Harem          |
| Trachiniformes   | Pinguipedidae | *Parapercis hexophthalma* | PG         | Harem          |
| Trachiniformes   | Pinguipedidae | *Parapercis nebulosa*  | PG             |                |
| Trachiniformes   | Pinguipedidae | *Parapercis snyderi*   | PG             | Harem          |
| Trachiniformes   | Pinguipedidae | *Parapercis xanthozona* | PG       |                |
### Table 1 (continued)

| Order      | Family          | Species                      | Sexual pattern | Mating system         |
|------------|-----------------|------------------------------|----------------|-----------------------|
|            | Trichonotidae   | Trichonotus filamentosus     | PG             |                       |
|            | Creediidae      | Crystallodytes cookei        | PA             |                       |
|            | Creediidae      | Linnichthys fasciatus        | PA             |                       |
|            | Creediidae      | Linnichthys nitidus          | PA             |                       |
|            | Labriformes     |                              |                |                       |
| Labridae   | Labridae        | Achoerodus gouldii           | PG             |                       |
| Labridae   | Labridae        | Achoerodus viridis           | PG             |                       |
| Labridae   | Labridae        | Anampses geographicus       | PG             |                       |
| Labridae   | Labridae        | Bodianus axillaris           | PG             |                       |
| Labridae   | Labridae        | Bodianus diploetaenia       | PG             | MTV polygamy          |
| Labridae   | Labridae        | Bodianus echancheri         | PG             | GSP                   |
| Labridae   | Labridae        | Bodianus frenchii           | PG             |                       |
| Labridae   | Labridae        | Bodianus mesothorax         | PG             | SPA                   |
| Labridae   | Labridae        | Bodianus rufus              | PG             | Harem                 |
| Labridae   | Labridae        | Cheilinus chlorurus         | PG             |                       |
| Labridae   | Labridae        | Cheilinus diaphrurms        | PG             |                       |
| Labridae   | Labridae        | Cheilinus fasciatus         | PG             | Harem                 |
| Labridae   | Labridae        | Cheilinus trilobatus        | PG             | Harem, MTV polygamy   |
| Labridae   | Labridae        | Cheilinus undulatus         | PG             | MTV polygamy          |
| Labridae   | Labridae        | Cheilinus azurio            | PG             |                       |
| Labridae   | Labridae        | Cheilinus cauteroma         | PG             |                       |
| Labridae   | Labridae        | Cheilinus cyanodus          | PG             |                       |
| Labridae   | Labridae        | Cheilinus fasciatus         | PG             |                       |
| Labridae   | Labridae        | Cheilinus graphicus         | PG             |                       |
| Labridae   | Labridae        | Cheilinus rubescens         | PG             |                       |
| Labridae   | Labridae        | Cheirodon schoenleintii     | PG             |                       |
| Labridae   | Labridae        | Cheirodon venustus          | PG             |                       |
| Labridae   | Labridae        | Cirrhilabrus temmincki      | PG             | MTV polygamy          |
| Labridae   | Labridae        | Clepticus parrae            | PG             | SPA                   |
| Labridae   | Labridae        | Coris auricularis           | PG             |                       |
| Labridae   | Labridae        | Coris dorsomaculua          | PG             | Harem                 |
| Labridae   | Labridae        | Coris guimard              | PG             | MTV polygamy          |
| Labridae   | Labridae        | Coris julius                | PG             | MTV polygamy          |
| Labridae   | Labridae        | Coris variegata             | PG             |                       |
| Labridae   | Labridae        | Decodon melasma             | PG             |                       |
| Labridae   | Labridae        | Epibulus insidator          | PG             | Harem, MTV polygamy   |
| Labridae   | Labridae        | Gomphosus varius            | PG             | MTV polygamy          |
| Labridae   | Labridae        | Halichoeres bivittatus      | PG             | MTV polygamy, GSP     |
| Labridae   | Labridae        | Halichoeres garnoti         | PG             | MTV polygamy          |
| Labridae   | Labridae        | Halichoeres maculpinna      | PG             | MTV polygamy          |
| Labridae   | Labridae        | Halichoeres margaritaceus    | PG             | Harem                 |
| Labridae   | Labridae        | Halichoeres marginatus      | PG             | MTV polygamy, GSP     |
| Labridae   | Labridae        | Halichoeres melanochir      | PG             | MTV polygamy          |
| Labridae   | Labridae        | Halichoeres melanurus       | PG             | MTV polygamy          |
| Labridae   | Labridae        | Halichoeres miniatus        | PG             | Harem                 |
| Labridae   | Labridae        | Halichoeres nebulosus       | PG             |                       |
| Labridae   | Labridae        | Halichoeres picus           | PG             |                       |
| Labridae   | Labridae        | Halichoeres poeyi           | PG             |                       |
| Labridae   | Labridae        | Halichoeres radiatus        | PG             |                       |
| Labridae   | Labridae        | Halichoeres scapularis      | PG             |                       |
| Order  | Family | Species                          | Sexual pattern | Mating system          |
|--------|--------|----------------------------------|----------------|------------------------|
| 1      | Labridae | Halichoeres semicinctus          | PG             | MTV polygamy, GSP      |
| 1      | Labridae | Halichoeres tenaspinnis          | PG             | MTV polygamy           |
| 1      | Labridae | Halichoeres trimaculatus         | PG, BS         | MTV polygamy, GSP      |
| 1      | Labridae | Hemigymnus melapterus           | PG             |                        |
| 1      | Labridae | Hologymnus annulatus            | PG             |                        |
| 1      | Labridae | Inistius dea                    | PG             |                        |
| 1      | Labridae | Inistius geisha                  | PG             |                        |
| 1      | Labridae | Inistius pentadactylus          | PG             | Harem                  |
| 1      | Labridae | Labrichthys unilineatus          | PG             | Harem                  |
| 1      | Labridae | Labroides diminutus             | PG, BS         | Harem                  |
| 1      | Labridae | Labrus bergylta                  | PG             |                        |
| 1      | Labridae | Labrus merula                    | PG             |                        |
| 1      | Labridae | Labrus mixtus                   | PG             |                        |
| 1      | Labridae | Labrus viridis                   | PG             |                        |
| 1      | Labridae | Lachnolaimus maximus            | PG             | Harem                  |
| 1      | Labridae | Macropharyngodon moyeri         | PG             | Harem                  |
| 1      | Labridae | Notolabrus celiotus              | PG             | MTV polygamy           |
| 1      | Labridae | Notolabrus gymnogenis           | PG             |                        |
| 1      | Labridae | Notolabrus parilus               | PG             |                        |
| 1      | Labridae | Notolabrus tetricus             | PG             | MTV polygamy           |
| 1      | Labridae | Ophthalmochirus lineolatus       | PG             |                        |
| 1      | Labridae | Parajulis poecilepterus          | PG             | GSP                    |
| 1      | Labridae | Pictilabrus laticlavius          | PG             | MTV polygamy           |
| 1      | Labridae | Pseudocheilinus ataenia          | PG             |                        |
| 1      | Labridae | Pseudocheilinus evanidus         | PG             |                        |
| 1      | Labridae | Pseudocheilinus hexataenia       | PG             | Harem                  |
| 1      | Labridae | Pseudolabrus guentheri           | PG             |                        |
| 1      | Labridae | Pseudolabrus rubricans           | PG             | MTV polygamy           |
| 1      | Labridae | Pseudolabrus sieboldi            | PG             | MTV polygamy           |
| 1      | Labridae | Pteragonus aurigas              | PG             | MTV polygamy           |
| 1      | Labridae | Semicossyphus darwini            | PG             |                        |
| 1      | Labridae | Semicossyphus pulcher           | PG             | MTV polygamy           |
| 1      | Labridae | Semicossyphus reticulatus        | PG             |                        |
| 1      | Labridae | Stethojulis balteata             | PG             |                        |
| 1      | Labridae | Stethojulis interrupta           | PG             | MTV polygamy           |
| 1      | Labridae | Stethojulis strigiventer         | PG             |                        |
| 1      | Labridae | Stethojulis trilineata           | PG             | MTV polygamy           |
| 1      | Labridae | Suzeichthys ornatus              | PG             | MTV polygamy           |
| 1      | Labridae | Symphodus melanocercus           | PG             | MTV polygamy           |
| 1      | Labridae | Symphodus tinca                  | PG, G          | MTV polygamy           |
| 1      | Labridae | Thalassoma bifasciatum           | PG             | MTV polygamy, GSP      |
| 1      | Labridae | Thalassoma capido                | PG             | MTV polygamy, GSP      |
| 1      | Labridae | Thalassoma duperrey              | PG             | MTV polygamy, GSP      |
| 1      | Labridae | Thalassoma hardwicki             | PG             | MTV polygamy, GSP      |
| 1      | Labridae | Thalassoma janseni               | PG             | MTV polygamy, GSP      |
| 1      | Labridae | Thalassoma lucasanum             | PG             | MTV polygamy, GSP      |
| 1      | Labridae | Thalassoma lunare                | PG             | MTV polygamy, GSP      |
| 1      | Labridae | Thalassoma laticeps              | PG             | MTV polygamy, GSP      |
| 1      | Labridae | Thalassoma pavo                  | PG             | MTV polygamy, GSP      |
| 1      | Labridae | Thalassoma purpureum             | PG             |                        |
Table 1 (continued)

| Order            | Species                     | Sexual pattern | Mating system                  |
|------------------|-----------------------------|----------------|---------------------------------|
| Labridae         | Thalassoma quinquevittatum  | PG             | MTV polygamy, GSP              |
| Labridae         | Xyrichtys martinicensis     | PG             | Harem                          |
| Labridae         | Xyrichtys novacula          | PG             | Harem                          |
| Odacidae         | Odax pullus                 | PG             |                                |
| Scaridae         | Calotomus carolinus         | PG             | MTV polygamy                   |
| Scaridae         | Calotomus japonicus         | PG             | MTV polygamy                   |
| Scaridae         | Calotomus spinidens         | PG             | MTV polygamy                   |
| Scaridae         | Cetoscarus bicolor          | PG             |                                |
| Scaridae         | Chlorurus sordidus          | PG             | MTV polygamy                   |
| Scaridae         | Chlorurus spilatus          | PG             |                                |
| Scaridae         | Cryptotomus roseus          | PG             | MTV polygamy                   |
| Scaridae         | Hipposcarus harid           | PG             |                                |
| Scaridae         | Scarus ferrugineus          | PG             |                                |
| Scaridae         | Scarus festivus             | PG             |                                |
| Scaridae         | Scarus forsteni             | PG             | MTV polygamy                   |
| Scaridae         | Scarus frenatus             | PG             | Harem                          |
| Scaridae         | Scarus ghobban              | PG             |                                |
| Scaridae         | Scarus globiceps            | PG             | MTV polygamy, GSP              |
| Scaridae         | Scarus iseri                | PG             | Harem, GSP                     |
| Scaridae         | Scarus niger                | PG             | MTV polygamy, GSP              |
| Scaridae         | Scarus oviceps              | PG             | MTV polygamy                   |
| Scaridae         | Scarus psittacus            | PG             | MTV polygamy                   |
| Scaridae         | Scarus rivulatus            | PG             | MTV polygamy                   |
| Scaridae         | Scarus rubrovioaceus        | PG             |                                |
| Scaridae         | Scarus russellii            | PG             |                                |
| Scaridae         | Scarus scaber               | PG             |                                |
| Scaridae         | Scarus schlegeli            | PG             | MTV polygamy                   |
| Scaridae         | Scarus spinus               | PG             |                                |
| Scaridae         | Scarus taeniopterus         | PG             |                                |
| Scaridae         | Scarus tricolor             | PG             |                                |
| Scaridae         | Scarus vetula               | PG             | Harem, MTV polygamy            |
| Scaridae         | Scarus viridifascatus       | PG             |                                |
| Scaridae         | Sparisoma atomarium         | PG             | Harem                          |
| Scaridae         | Sparisoma aurorufrenatum    | PG             | Harem                          |
| Scaridae         | Sparisoma chrysopterum      | PG             | MTV polygamy                   |
| Scaridae         | Sparisoma cretense          | PG, G          | Harem                          |
| Scaridae         | Sparisoma radians           | PG             | Harem, MTV polygamy, GSP       |
| Scaridae         | Sparisoma rubripinne        | PG             | MTV polygamy, GSP              |
| Scaridae         | Sparisoma viride            | PG             | MTV polygamy                   |
| Perciformes      | Centropomus undecimalis     | PA             |                                |
| Latidae          | Lates calcarifer            | PA             |                                |
| Polynemidae      | Galeoides decadaecytus      | PA, G          |                                |
| Polynemidae      | Filimonus heptadactyla      | SH, G          |                                |
| Polynemidae      | Polydactylus macrochir      | PA             |                                |
| Polynemidae      | Polydactylus microstomus    | SH, G          |                                |
| Polynemidae      | Polydactylus quadripilis    | PA             |                                |
| Terapontidae     | Bidyanus bidyanus           | PA             |                                |
| Terapontidae     | Mesopristes cancellatus     | PA             |                                |
| Serranidae (Epinephelinae) | Cephalopholis argus | PG         | Harem                          |
| Family | Species | Sexual pattern | Mating system |
|--------|---------|----------------|---------------|
| Serranidae (Epinephelinae) | Cephalopholis boenak | PG, BS | |
| Serranidae (Epinephelinae) | Cephalopholis cruentata | PG | Harem |
| Serranidae (Epinephelinae) | Cephalopholis cyanostigma | PG | Harem |
| Serranidae (Epinephelinae) | Cephalopholis fulva | PG | Harem |
| Serranidae (Epinephelinae) | Cephalopholis hemistiktos | PG | Harem |
| Serranidae (Epinephelinae) | Cephalopholis miniata | PG | Harem |
| Serranidae (Epinephelinae) | Cephalopholis panamensis | PG | Harem |
| Serranidae (Epinephelinae) | Cephalopholis taeniops | PG | |
| Serranidae (Epinephelinae) | Cephalopholis urodeta | PG | |
| Serranidae (Epinephelinae) | Epinephelus adscensionis | PG | Harem |
| Serranidae (Epinephelinae) | Epinephelus aeneus | PG | |
| Serranidae (Epinephelinae) | Epinephelus aequipinnatus | PG, BS | |
| Serranidae (Epinephelinae) | Epinephelus andersoni | PG | |
| Serranidae (Epinephelinae) | Epinephelus bruneus | PG, BS | |
| Serranidae (Epinephelinae) | Epinephelus chlorostigma | PG | |
| Serranidae (Epinephelinae) | Epinephelus coioides | PG | |
| Serranidae (Epinephelinae) | Epinephelus diacanthus | PG | |
| Serranidae (Epinephelinae) | Epinephelus drummondhayi | PG | |
| Serranidae (Epinephelinae) | Epinephelus fasciatus | PG | |
| Serranidae (Epinephelinae) | Epinephelus fuscoguttatus | PG | SPA |
| Serranidae (Epinephelinae) | Epinephelus guttatus | PG | SPA |
| Serranidae (Epinephelinae) | Epinephelus iatralis | PG, G | GSP |
| Serranidae (Epinephelinae) | Epinephelus labriformis | PG | |
| Serranidae (Epinephelinae) | Epinephelus malabaricus | PG | |
| Serranidae (Epinephelinae) | Epinephelus marginatus | PG | MTV polygamy |
| Serranidae (Epinephelinae) | Epinephelus merra | PG | SPA |
| Serranidae (Epinephelinae) | Epinephelus morio | PG | |
| Serranidae (Epinephelinae) | Epinephelus ongus | PG | SPA |
| Serranidae (Epinephelinae) | Epinephelus rivalis | PG | |
| Serranidae (Epinephelinae) | Epinephelus striatus | PG, G | GSP |
| Serranidae (Epinephelinae) | Epinephelus taurina | PG | |
| Serranidae (Epinephelinae) | Hyporthodus flavolimbatus | PG | |
| Serranidae (Epinephelinae) | Hyporthodus niveatus | PG | |
| Serranidae (Epinephelinae) | Hyporthodus quernus | PG | |
| Serranidae (Epinephelinae) | Mycteroperca bonaci | PG | |
| Serranidae (Epinephelinae) | Mycteroperca interstitialis | PG | |
| Serranidae (Epinephelinae) | Mycteroperca microlepis | PG | SPA |
| Serranidae (Epinephelinae) | Mycteroperca olfax | PG | SPA |
| Serranidae (Epinephelinae) | Mycteroperca phenax | PG | SPA |
| Serranidae (Epinephelinae) | Mycteroperca rubra | PG | SPA |
| Serranidae (Epinephelinae) | Mycteroperca venenosa | PG | GSP |
| Serranidae (Epinephelinae) | Plectropomus laevis | PG | |
| Serranidae (Epinephelinae) | Plectropomus leopardus | PG | SPA |
| Serranidae (Epinephelinae) | Plectropomus maculatus | PG | |
| Serranidae (Serraninae) | Bullisichthys caribbaeus | SH | |
| Serranidae (Serraninae) | Centropristis striata | PG | |
| Serranidae (Serraninae) | Centropristis ocyurus | PG | |
| Serranidae (Serraninae) | Chelidoperca hirundinacea | PG | |
| Serranidae (Serraninae) | Diplectrum bivittatum | PG | |
| Serranidae (Serraninae) | Diplectrum formosum | SH | |
### Table 1 (continued)

| Family                     | Species                   | Sexual pattern | Mating system               |
|----------------------------|---------------------------|----------------|-----------------------------|
| Serranidae (Serraninae)    | Diplectrum macropoma      | SH             | SA monogamy                 |
| Serranidae (Serraninae)    | Diplectrum pacificum      | SH             |                             |
| Serranidae (Serraninae)    | Diplectrum rostrum        | SH             |                             |
| Serranidae (Serraninae)    | Hypoplectrus aberrans     | SH             | SA monogamy                 |
| Serranidae (Serraninae)    | Hypoplectrus chlorurus    | SH             | SA monogamy                 |
| Serranidae (Serraninae)    | Hypoplectrus nigricans    | SH             | SA monogamy                 |
| Serranidae (Serraninae)    | Hypoplectrus puella       | SH             | SA monogamy                 |
| Serranidae (Serraninae)    | Hypoplectrus unicolor     | SH             | SA monogamy                 |
| Serranidae (Serraninae)    | Paralabrax maculatofasciatus | PG, G          |                             |
| Serranidae (Serraninae)    | Serranichthys pumilio     | SH             |                             |
| Serranidae (Serraninae)    | Serranus annadaris        | SH             |                             |
| Serranidae (Serraninae)    | Serranus atricauda        | SH             |                             |
| Serranidae (Serraninae)    | Serranus auriga           | SH             |                             |
| Serranidae (Serraninae)    | Serranus baldwini         | SH             | Harem                       |
| Serranidae (Serraninae)    | Serranus cabrilla         | SH             |                             |
| Serranidae (Serraninae)    | Serranus hepatus          | SH             |                             |
| Serranidae (Serraninae)    | Serranus phoebe           | SH             |                             |
| Serranidae (Serraninae)    | Serranus psittacinus      | SH             | Harem                       |
| Serranidae (Serraninae)    | Serranus scriba           | SH             |                             |
| Serranidae (Serraninae)    | Serranus subligarius      | SH             | SA monogamy                 |
| Serranidae (Serraninae)    | Serranus tabacarius       | SH             | SA monogamy                 |
| Serranidae (Serraninae)    | Serranus tigrinus         | SH             | SA monogamy                 |
| Serranidae (Serraninae)    | Serranus tortugurum       | SH             | SA monogamy                 |
| Serranidae (Grammistini)   | Pseudogramma gregoryi     | SH             |                             |
| Serranidae (Grammistini)   | Rhypticus saponaceus      | PG             |                             |
| Serranidae (Grammistini)   | Rhypticus subbifrenatus   | PG             |                             |
| Serranidae (Anthiinae)     | Anthias anthias           | PG             |                             |
| Serranidae (Anthiinae)     | Anthias nicholsi          | PG             |                             |
| Serranidae (Anthiinae)     | Anthias noeli             | PG             |                             |
| Serranidae (Anthiinae)     | Baldwinella vivans        | PG             |                             |
| Serranidae (Anthiinae)     | Hemanthias leptus         | PG             |                             |
| Serranidae (Anthiinae)     | Hemanthias persuans       | PG             |                             |
| Serranidae (Anthiinae)     | Hypoplectrodes huntii     | PG             |                             |
| Serranidae (Anthiinae)     | Hypoplectrodes maculochi  | PG             |                             |
| Serranidae (Anthiinae)     | Pronotogrammus martincensis | PG          |                             |
| Serranidae (Anthiinae)     | Pseudanthias conspicuous   | PG             |                             |
| Serranidae (Anthiinae)     | Pseudanthias elongatus    | PG             |                             |
| Serranidae (Anthiinae)     | Pseudanthias pleurotinaea | PG             |                             |
| Serranidae (Anthiinae)     | Pseudanthias rubrizonatus | PG             |                             |
| Serranidae (Anthiinae)     | Pseudanthias squamipinnis | PG          | MTV polygamy                |
| Serranidae (Anthiinae)     | Sacura margaritacea       | PG             |                             |
| Pomacanthidae              | Centropyge acanthops      | PG, BS         |                             |
| Pomacanthidae              | Centropyge bicolor        | PG             | Harem                       |
| Pomacanthidae              | Centropyge ferrugata      | PG, BS         | Harem                       |
| Pomacanthidae              | Centropyge fisheri        | PG, BS         | Harem                       |
| Pomacanthidae              | Centropyge flavissimus    | BS             | Harem                       |
| Pomacanthidae              | Centropyge heraldi        | PG             | Harem                       |
| Pomacanthidae              | Centropyge interruptus    | PG             | Harem                       |
| Pomacanthidae              | Centropyge multiplinclus  | PG             |                             |
| Pomacanthidae              | Centropyge poteri         | PG             | Harem                       |
| Order | Family | Species | Sexual pattern | Mating system |
|-------|--------|---------|----------------|---------------|
|       | Pomacanthidae | Centropyge tibicen | PG | Harem |
|       | Pomacanthidae | Centropyge vrolicki | PG | Harem |
|       | Pomacanthidae | Chaetodontoplus septentrionalis | PG | Harem |
|       | Pomacanthidae | Genicanthus bellus | PG | |
|       | Pomacanthidae | Genicanthus caudovittatus | PG | Harem |
|       | Pomacanthidae | Genicanthus lamarck | PG | Harem |
|       | Pomacanthidae | Genicanthus melanospilos | PG | Harem |
|       | Pomacanthidae | Genicanthus personatus | PG | Harem |
|       | Pomacanthidae | Genicanthus semifasciatus | PG | Harem |
|       | Pomacanthidae | Genicanthus watanabei | PG | |
|       | Pomacanthidae | Holacanthus passer | PG, G | Harem |
|       | Pomacanthidae | Holacanthus tricolor | PG | Harem |
|       | Pomacanthidae | Pomacanthus zonipectus | PG | |
|       | Pomacanthidae | Apolemichthys trimaculatus | PG | |
|       | Malacanthidae | Malacanthus plumieri | PG | Harem |
|       | Cirrhitidae | Amblycirrhitus pinos | PG | |
|       | Cirrhitidae | Cirrhitichthys aprinus | PG | Harem |
|       | Cirrhitidae | Cirrhitichthys aureus | PG, BS | |
|       | Cirrhitidae | Cirrhitichthys falco | PG, BS | Harem |
|       | Cirrhitidae | Cirrhitichthys oxycapillus | PG | Harem |
|       | Cirrhitidae | Neocirrhites armatus | PG | Harem |
|       | Eleginopsidae | Eleginops maclinira | PA | |
| (continued) | Scorpaeformes | Platycephalidae | Cociella crocodila | PA | |
|       | Scorpaeformes | Platycephalidae | Inegocia japonica | PA | Random mating |
|       | Scorpaeformes | Platycephalidae | Kumoocia rodericensis | PA | |
|       | Scorpaeformes | Platycephalidae | Onigocia macrolepis | PA | |
|       | Scorpaeformes | Platycephalidae | Platycephalus sp. | PA | Random mating |
|       | Scorpaeformes | Platycephalidae | Saggundus meerdervoorti | PA | |
|       | Scorpaeformes | Platycephalidae | Thysanophrys celebica | PA | Random mating |
|       | Moroniformes | Moronidae | Morone saxatilis | PA | |
|       | Spariformes | Nemipteridae | Scolopsis monogramma | PG | |
|       | Spariformes | Nemipteridae | Scolopsis taenioptera | PG | |
|       | Spariformes | Lethrinidae | Lethrinus nebulosus | PG, G | |
|       | Spariformes | Lethrinidae | Lethrinus genivittatus | PG | |
|       | Spariformes | Lethrinidae | Lethrinus lentjan | PG | |
|       | Spariformes | Lethrinidae | Lethrinus variegatus | PG | |
|       | Spariformes | Lethrinidae | Lethrinus miniatus | PG | |
|       | Spariformes | Lethrinidae | Lethrinus rubricerulatus | PG | |
|       | Spariformes | Lethrinidae | Lethrinus atkinsoni | PG | |
|       | Spariformes | Lethrinidae | Lethrinus harak | PG | |
|       | Spariformes | Lethrinidae | Lethrinus ornatus | PG | |
|       | Spariformes | Lethrinidae | Lethrinus rarus | PG | |
|       | Spariformes | Acanthopagrus australis | PA | |
|       | Spariformes | Acanthopagrus berda | PA | SPA |
|       | Spariformes | Acanthopagrus schlegelli | PA | |
|       | Spariformes | Acanthopagrus latus | PA | |
Serranidae, Sparidae, Labridae, and Gobiidae, respectively (26, 16, 98, and 50 spp., respectively). Most cases of BS in Gobiidae have been determined by gonad histology or aquarium experiments (e.g., Sunobe et al. 2017; Table S1), and the frequency of each sex change direction in the field is known only in a few species (Kuwamura et al. 1994; Manabe et al. 2007).

Three types of hermaphroditism were found in Pomacentridae (PA, PG, and BS) and Serranidae (SH, PG, and BS) (Table 2), while two types were found in Muraenidae and Polynemidae (SH and PA), Cichlidae (SH and PG), Sparidae (PA and PG), and Gobiidae, Pseudochromidae, Labridae, Pomacanthidae, and Cirrhitidae (PG and BS). This indicated that different types of hermaphroditism have appeared in different lineages repeatedly (see Mank et al. 2006), and the sexual pattern is often highly variable in expression within a single family.

The frequency of hermaphroditic fish families in each order is presented in Table 3. We found hermaphrodites in 17 orders (27% of 63 orders of Teleostei). Two families in Series Ovalentaria, Pomacentridae and Pseudochromidae, are not classified into orders by Nelson et al. (2016), but were counted as belonging to the same order here, for convenience. Among 17 orders, PG was the most abundant (20 families, 49% of 41 hermaphroditic families), BS the least abundant (7 families, 17%), and SH and PA had similar abundances (13 and 14 families, 32% and 34%, respectively). The tendency was somewhat different from that of

### Table 1 (continued)

| Order | Species                  | Sexual pattern | Mating system |
|-------|--------------------------|----------------|---------------|
| Sparidae | Calamus leucosteus | PG             |               |
| Sparidae | Chrysolephas cristiceps | PG             |               |
| Sparidae | Chrysolephas punicus | PG             |               |
| Sparidae | Chrysolephas laticeps | PG             |               |
| Sparidae | Dentex gibbosus         | PG             |               |
| Sparidae | Dentex tamifrons        | PG             |               |
| Sparidae | Diplodus annularis      | PA, G          |               |
| Sparidae | Diplodus capensis       | PA, G          |               |
| Sparidae | Diplodus puntazzo       | PA, G          |               |
| Sparidae | Diplodus sargus         | PA, G          |               |
| Sparidae | Diplodus vulgaris       | PA, G          |               |
| Sparidae | Lithognathus morrurus   | PA, G          |               |
| Sparidae | Pagellus acarne         | PA, G          |               |
| Sparidae | Pagellus bavarveo       | PA, G          |               |
| Sparidae | Pagellus erythrinus     | PG             |               |
| Sparidae | Pagrus auriga           | PG             |               |
| Sparidae | Pagrus caeruleosticis   | PG             |               |
| Sparidae | Pagrus ehrenbergii      | PG, G          |               |
| Sparidae | Pagrus major            | PG, G          |               |
| Sparidae | Pagrus pagrus           | PG             |               |
| Sparidae | Rhabdosargus sarba      | PA, G          |               |
| Sparidae | Sarpa salpa             | PA, G          | SPA           |
| Sparidae | Sparidentex hasta       | PA             |               |
| Sparidae | Sparus aurata           | PA             | GSP           |
| Sparidae | Spicara chryseis        | PG             |               |
| Sparidae | Spicara smaris          | PG             |               |
| Sparidae | Spicara maena           | PG             |               |
| Sparidae | Spondyliosoma cantharus | PG             |               |
| Tetraodontiformes | Sufflamen chrysopterus | PG             | Harem         |

SH simultaneous hermaphroditism, PA protandry, PG protogyny, BS bidirectional sex change or reversed sex change in protogynous species, G gonochorism, SA monogamy size-assortative monogamy, NSA monogamy non-size-assortative monogamy, Harem harem polygyny, MTV male-territory-visiting polygamy, GSP group spawning, SPA spawning aggregation unknown detailed mating system, blank unknown. Facultative monogamy in polygamous species is not shown. If intraspecific variation has been reported in sexual pattern or mating system, two or more types are shown. Detailed data of each species and references are given in Table S1 and S2, respectively.
Table 2 Frequency of hermaphroditic fish species in each family. Order and family names are arranged following Nelson et al. (2016). Summed up from Table 1.

| Order          | Family                      | Number of hermaphroditic species | Total number of species | Habitat** |
|----------------|-----------------------------|----------------------------------|-------------------------|-----------|
|                |                             | SH  | PA  | PG  | BS  | Total | %*  |                         | M | F | (M&)F |                     |
| Anguilliformes | Muraenidae                  | 3   | 0   | 0   | 4   | 100.0 | 2.0 | 200 | M                   |
| Clupeiformes   | Clupeidae                   | 0   | 2   | 0   | 2   | 100.0 | 0.9 | 218 | M                   |
| Cypriniformes  | Cobitidae                   | 0   | 1   | 0   | 1   | 100.0 | 0.5 | 195 | F                   |
| Stomiiformes   | Gonostomatidae              | 0   | 5   | 0   | 5   | 100.0 | 16.1| 31  | M                   |
| Aulopiformes   | Ipnopidae                   | 9   | 0   | 0   | 9   | 100.0 | 28.1| 32  | M                   |
|                | Giganturidae                | 2   | 0   | 0   | 2   | 100.0 | 0.9 | 218 | M                   |
|                | Bathysauridae               | 1   | 0   | 0   | 1   | 100.0 | 50.0| 2   | M                   |
|                | Chloropthalmidae            | 3   | 0   | 0   | 3   | 100.0 | 17.6| 17  | M                   |
|                | Notosudidae                 | 1   | 0   | 0   | 1   | 100.0 | 5.9 | 17  | M                   |
|                | Scopelarchidae              | 2   | 0   | 0   | 2   | 100.0 | 11.1| 18  | M                   |
|                | Paralepididae               | 1   | 0   | 0   | 1   | 100.0 | 3.7 | 27  | M                   |
|                | Alepisauridae               | 1   | 0   | 0   | 1   | 100.0 | 11.1| 9   | M                   |
| Gobiiformes    | Gobiidae                    | 0   | 0   | 24  | 50  | 74    | 4.9 | 1359 | M(F)                |
| Uncertain in ovalentaria | Pomacentridae | 0  | 10  | 6  | 1  | 16 | 4.1 | 387 | M                  |
|                | Pseudochromidae             | 0   | 2   | 4   | 6   | 100.0 | 3.9 | 152 | M                  |
| Cichliformes   | Cichlidae                   | 1   | 0   | 1   | 0   | 100.0 | 0.1 | 1762| F                  |
| Cyprinodontiformes | Rivulidae | 3   | 0   | 0   | 3   | 100.0 | 0.8 | 370 | F                  |
|                | Poeciliidae                 | 0   | 0   | 1   | 0   | 100.0 | 0.3 | 353 | F                  |
| Synbranchiformes | Synbranchidae | 0  | 0   | 4   | 4   | 100.0 | 17.4| 23  | F                  |
| Trachiniformes | Pinguipedidae               | 0   | 0   | 7   | 0   | 100.0 | 8.5 | 82  | M                  |
|                | Trichonotidae               | 0   | 0   | 1   | 0   | 100.0 | 10.0| 10  | M                  |
|                | Creediidae                  | 0   | 3   | 0   | 3   | 100.0 | 16.7| 18  | M                  |
| Labriiformes   | Labridae                    | 0   | 0   | 98  | 2   | 100.0 | 18.9| 519 | M                  |
|                | Odacidae                    | 0   | 0   | 1   | 0   | 100.0 | 8.3 | 12  | M                  |
|                | Scaridae                    | 0   | 0   | 35  | 0   | 100.0 | 35.4| 99  | M                  |
| Perciformes    | Centropomidae               | 0   | 1   | 0   | 1   | 100.0 | 8.3 | 12  | M&F                |
|                | Latidae                     | 0   | 1   | 0   | 0   | 100.0 | 7.7 | 13  | M&F                |
|                | Polynemidae                 | 2   | 3   | 0   | 5   | 100.0 | 11.9| 42  | M                  |
|                | Terapontidae                | 0   | 2   | 0   | 2   | 100.0 | 3.8 | 52  | (M&F)              |
|                | Serranidae                  | 26  | 0   | 66  | 3   | 100.0 | 17.1| 538 | M                  |
|                | Pomacanthidae               | 0   | 0   | 22  | 4   | 100.0 | 25.8| 89  | M                  |
|                | Malacanthidae               | 0   | 0   | 1   | 0   | 100.0 | 2.2 | 45  | M                  |
|                | Cirrhitidae                 | 0   | 0   | 6   | 2   | 100.0 | 18.2| 33  | M                  |
|                | Eleginopsidae               | 0   | 1   | 0   | 0   | 100.0 | 100.0| 1  | M                  |
| Scorpaeniformes | Platyccephalidae            | 0   | 7   | 0   | 0   | 100.0 | 8.8 | 80  | M                  |
|                | Scorpaenidae                | 0   | 0   | 1   | 0   | 100.0 | 0.2 | 454 | M                  |
| Moroniformes   | Moronidae                   | 0   | 1   | 0   | 0   | 100.0 | 25.0| 4   | M&F                |
| Spariformes    | Nemipteridae                | 0   | 0   | 2   | 0   | 100.0 | 3.0 | 67  | M                  |
|                | Lethrinidae                 | 0   | 0   | 10  | 0   | 100.0 | 26.3| 38  | M                  |
|                | Sparidae                    | 0   | 16  | 16  | 0   | 100.0 | 84.2| 38  | M                  |
| Tetraodontiformes | Balistidae | 0  | 0   | 1   | 0   | 100.0 | 2.4 | 42  | M                  |
| Total number of species | | 55  | 54  | 305 | 66  | 461 |      |                      | M | F | (M&F) |                     |

SH simultaneous hermaphroditism, PA protandry, PG protogyny, BS bidirectional sex change or reversed sex change in protogynous species. When two or more types are reported within a species, we counted them in each column.

*Percentage of hermaphroditic species in each family (total number of species after Nelson et al. 2016)

**M marine, F fresh water (after Nelson et al. 2016). In parentheses if no hermaphrodites have been reported from the habitat.
Hermaphroditism in fishes

the number of species. The number of species with BS was higher than that with SH or PA because of the extensive surveys on BS species of Gobiidae (Table 2, S1). The percentage of hermaphroditic families in an order varied widely from 4.9% (2 out of 41 families in Scorpaeniformes) to 100% (all three families in Labriformes) (Table 3). All four types were only found in Perciformes, and three types (PA, PG, and BS) in the tentative order (Pomacentridae–Pseudochromidae) in Ovalentaria.

By combining our list with the phylogenetic tree of Betancur-R et al. (2017), it was indicated that SH and PA have evolved several times in not-closely related lineages; SH in Elopomorpha, Aulopiformes, Ovalentaria, and Eupercaria, and PA in Elopomorphida, Clupeiformes, Cypriniformes, Stomiiformes, Aulopiformes, and Uncertain** in Ovalentaria. All four types of hermaphroditism were found in marine families, while three types (except BS) were found in freshwater families. In freshwater families, the number of species of each type was similar (SH, 4; PA, 3; PG, 6), and the total number of freshwater hermaphroditic species (13 spp., 3% of all hermaphroditic species) was much lower than that in marine families (445 spp., 97%). The percentage of freshwater species in hermaphroditic species (3%) was significantly lower than that of the freshwater species in all fishes (about 43%; Nelson et al. 2016) ($\chi^2 = 294, \ P < 0.001$), although phylogenetic distribution of marine and freshwater species should be considered for a sophisticated test of the different likelihood of hermaphroditism evolution between habitats.

Regarding this hermaphroditism absence from most freshwater habitats, it has been suggested that the relatively large eggs or young produced by many freshwater species tend to accentuate the physical differences in male

### Table 3: Frequency of hermaphroditic fish families in each order. Order names are arranged following Nelson et al. (2016). Summed up from Table 2

| Order                  | Number of families including hermaphrodites | Total number of families | Group names in Fig. 1 |
|------------------------|---------------------------------------------|--------------------------|-----------------------|
|                        | SH  | PA  | PG  | BS  | Total | %*          |
| Anguilliformes         | 1   | 0   | 0   | 0   | 1     | 5.3         | Elopomorpha |
| Clupeiformes           | 0   | 1   | 0   | 0   | 1     | 20.0        | Clupeiformes|
| Cypriniformes          | 0   | 1   | 0   | 0   | 1     | 7.7         | Cypriniformes|
| Stomiiformes           | 0   | 1   | 0   | 0   | 1     | 20.0        | Stomiiformes|
| Aulopiformes           | 8   | 0   | 0   | 0   | 8     | 53.3        | Aulopiformes|
| Gobiiformes            | 0   | 0   | 1   | 1   | 1     | 12.5        | Gobiaria     |
| Uncertain** in Ovalentaria | 0   | 1   | 2   | 2   | 2     | 25.0        | Ovalentaria  |
| Cichliformes           | 1   | 0   | 1   | 0   | 1     | 50.0        | Ovalentaria  |
| Cyprinodontiformes     | 1   | 0   | 1   | 0   | 2     | 20.0        | Ovalentaria  |
| Synbranchiformes       | 0   | 0   | 1   | 0   | 1     | 33.3        | Anabantia    |
| Trachiniformes         | 0   | 1   | 2   | 0   | 3     | 27.3        | Eupercaria   |
| Labriiformes           | 0   | 0   | 3   | 1   | 3     | 100.0       | Eupercaria   |
| Perciformes            | 2   | 5   | 4   | 3   | 9     | 14.5        | Eupercaria   |
| Scorpaeniformes        | 0   | 1   | 1   | 0   | 2     | 4.9         | Eupercaria   |
| Moroniformes           | 0   | 1   | 0   | 0   | 1     | 33.3        | Eupercaria   |
| Spariformes            | 0   | 1   | 3   | 0   | 3     | 50.0        | Eupercaria   |
| Tetraodontiformes      | 0   | 0   | 1   | 0   | 1     | 10.0        | Eupercaria   |
| Total number of families| 13 | 14  | 20  | 7   | 41    |             |

**SH** simultaneous hermaphroditism, **PA** protandry, **PG** protogyny, **BS** bidirectional sex change or reversed sex change in protogynous species. When two or more types are reported within a family, we counted them in each column.

*Percentage of hermaphroditic families in each order (total number of families after Nelson et al. 2016)

**Treated as one order for convenience
Fig. 1 Phylogeny of fishes and occurrence of hermaphroditism. The phylogenetic tree was processed from Fig. 1 of Betancur-R et al. (2017). SH simultaneous hermaphroditism, PA protandry, PG protogyny, BS bidirectional sex change or reversed sex change in protogynous species. For group names and orders, see Table 3
and female anatomy, possibly forming a barrier or physical constraint to hermaphroditism (Warner 1978) and that fewer and larger eggs and more parental care may reduce the size advantage (Sadovy de Mitcheson and Liu 2008). Moreover, mating systems of freshwater fish should also be taken into consideration.

**Mating system and the evolution of hermaphroditism.**

In the field, mating systems have been reported in less than 40% of hermaphroditic species (Table 4), and most of them were shallow coral reef fishes (Table S1). Mating system is known only from 11 species with SH (20% of 55 spp.), i.e., small serranids living on coral reefs (Table 1, S1). Reciprocal pair spawning (i.e., egg trading) occurs in monogamous pairs (9 spp., e.g., Fischer 1981), or a large male (secondary male derived from hermaphrodite) controls a harem of simultaneous hermaphrodites (3 spp., e.g., Petersen and Fischer 1986). Mating systems of the other 80% of species with SH, including deep-sea species (e.g. Aulopiformes), remain unknown. SH in deep-sea fishes are often regarded as evidence for the low-density model (Tomlinson 1966; Ghiselin 1969), because population density is generally low in the deep sea. Although the study of mating behavior in deep-sea fishes is extremely difficult, underwater video tape recordings and the distribution of the number of fish caught have recently suggested pair bonding in two deep-sea SH species of Giganturidae (Kupchik et al. 2018). Another example of hermaphroditism is found in androdioecious (i.e., SH and males) killifish of genus *Kryptolebias*, in which hermaphrodites never mate with other hermaphrodites (Furness et al. 2015), but reproduce via selfing or mating with males.

The mating system has only been reported in 16 species with PA (30% of 54 spp.; Table 4). Non-size-assortative monogamy (i.e., females accept smaller males as in random mating) is known from 10 species of anemonefishes (Pomacentridae; Table 1; e.g., Fricke and Fricke 1977), and random mating from three species of Platyccephalidae (Table 1; e.g., Sunobe et al. 2016). These mating systems support the SA model prediction about PA being favored in species with random mating or non-size-assortative monogamy in which females accept smaller males (Warner 1975, 1984). Spawning aggregation and group spawning have also been reported (in two and one species, respectively, of Sparidae; Table 1; e.g., van der Walt and Mann 1998), but whether random mating occurs in the aggregation remains unknown.

Mating systems have been reported from 142 species with PG (47% of 305 spp.; Table 4). Harem polygyny and male-territory-visiting polygamy (62 and 69 spp., respectively) were the prevailing systems (adding up to 85% of 142 spp.; Table 4), e.g., Labridae, Scaridae, and Pomacentridae (Table 1). This supports the SA model prediction of PG being favored in polygynous species with large males monopolizing females (Warner 1975). Size-assortative monogamy has been reported from five species with PG (Table 4). All five species belong to Gobiidae, and BS was also confirmed in three of them (Table 1) and suggested in another one (Table S1). The tendency of PG with BS in the monogamous goby *Paragobiodon echinocephalus* has been explained by the growth-rate advantage in females (Kuwamura et al. 1994): the difference between sexes in growth rate favors the evolution of sex changer even if the size advantage is the same between the two sexes. For the other exceptional cases of group spawning in two labrid and three serranids, and spawning aggregation in one sparid, two labrds, and nine serranids (Table 1, 4), further observations

### Table 4  Relation between hermaphroditism and mating system. Summed up from Table 1

| Mating system* | Number of species in each type of sexual pattern** |
|----------------|-----------------------------------------------|
|                | SH   | SH, G | PA | PA, G | PG | PG, G | BS | PG, BS | BS | Total |
| Random mating  | 3    |       |    |       |    |       |    |         |    | 3     |
| Non-size-assortative monogamy | 10 |       |    |       |    |       |    |         |    | 10    |
| Size-assortative monogamy | 9   | 2     | 3  | 5     | 19 |       |    |         |    |       |
| Harem polygyny | 2    | 45    | 2  | 4     | 2  | 55    |    |         |    |       |
| Harem, GSP     | 1    |       |    |       |    |       |    |         |    | 1     |
| Harem, MTV polygamy | 5   | 3     | 1  | 9     |    |       |    |         |    |       |
| Harem, MTV polygamy, GSP | 1  |       |    |       |    |       |    |         |    | 1     |
| MTV polygamy   | 40   | 1     | 1  | 2     | 44 |       |    |         |    |       |
| MTV polygamy, GSP | 16  |       |    | 1     | 17 |       |    |         |    |       |
| Group spawning | 1    | 3     | 2  |       |    | 6     |    |         |    |       |
| Spawning aggregation | 1  | 1     | 11 | 5     | 0  | 8     | 38 | 283     |    |       |

*Harem harem polygyny, MTV polygamy male-territory-visiting polygamy, GSP group spawning

**SH simultaneous hermaphroditism, PA protandry, PG protogyny, BS bidirectional sex change or reversed sex change in protogynous species, G gonochorism

***Mating systems of hermaphroditic species are completely unknown in 26 families (see Table 1)
are needed because group spawning is also known in species with male-territory-visiting polygamy (Table 4; Warner and Hoffman 1980; Suzuki et al. 2010).

Mating system has been reported from 19 species with BS (29% of 66 spp.; Table 4). Size-assortative monogamy is known in eight species (Gobiidae), harem polygyny in seven species (Gobiidae, Pomacentridae, Labridae, Pomacanthidae, and Cirrhitidae), and male-territory-visiting polygamy in five species (Gobiidae, Pomacentridae, and Labridae) (Table 1). BS in the monogamous coral-dwelling gobies has been explained by the risk-of-movement hypothesis (Munday et al. 2010). BS in protogynous and polygynous species can be explained by the low-density hypothesis for the reversed sex change, because facultative monogamy occurs at low-density conditions in polygynous species (Kuwamura et al. 2014, 2016a). Contrastingly, the reversed (female-to-male) sex change does not occur even at very low density in the protandrous anemonefishes (Fricke and Fricke 1977; Kuwamura and Nakashima 1998; T. Kuwamura, unpublished data) or PA species with random mating (Table 1).

Mating system is only known in two of 13 freshwater hermaphroditic species, one in Cichlidae and the other in Synbranchidae (Table 2). Both species are PG with male-territory-visiting polygamy (Table 1), supporting the SA model. Although group spawning is common, mating systems of freshwater gonochorists are as various as in marine species (Taborsky 2008). For example, both monogamy and polygyny are known in cichlid fishes (Kuwamura 1997), but functional hermaphroditism is almost unknown, probably owing to biparental care or prolonged parental care of juveniles, which may reduce the difference in reproductive success between the sexes (Warner and Lejeune 1985).

**Effect of population density on mating system and sexual pattern.** Intraspecific variations in sexual pattern (including gonochorism) and mating system (excluding facultative monogamy in many polygamous species) have been reported in at least 50 and 28 species, respectively (Tables 1 and 4), which may be partly explained by differences in population density. It is well known that mating system may vary depending on population density (Fricke 1980; Warner and Hoffman 1980; Barlow 1984; Petersen 2006). Accordingly, the low-density hypothesis for the evolution of reversed sex change in polygynous and protogynous species has been proposed and tested (Kuwamura et al. 2002, 2011, 2014, 2016a), predicting that facultative monogamy and reversed sex change may occur under low-density condition in polygynous species. For example, in a coral-dwelling damselfish *Dascyllus aruanus* (Pomacentridae), female-to-male sex change (PG) occurs in harems on isolated corals as the SA model predicts, and reversed sex change (BS) occurs when widowed males meet under experimental low-density conditions at which facultative monogamy occurs (Kuwamura et al. 2016a). In contrast, sex change rarely occurs (i.e., gonochorism) in high-density populations living in continuous coral-covered habitats, where females can choose mates with low risk of movement (Kuwamura et al. 2016a). Moreover, in another pomacentrid, the monogamous and protandrous anemonefish *Amphiprion clarkii*, sex change rarely occurs in a high-density population with low risk of movement (Ochi 1989).

The effect of population density has also been reported from protogynous labrids. Two types of males (diandry) and alternative male mating tactics are well known in Labridae (Warner and Robertson 1978; Kuwamura et al. 2016b). Primary males mature and remain as males, i.e., gonochorists, and secondary males have changed sex from female (PG). Small IP (initial phase) males participate in group spawning or sneaking, and large TP (terminal phase) males establish mating territories and pair spawn with visiting females. The percentage of IP males (primary males) and the frequency of group spawning increase with population density (Warner and Hoffman 1980; Suzuki et al. 2010), and sex change rarely occurs under high densities (Warner 1982). Contrastingly, reversed (male-to-female) sex change has been reported in low-density populations of *Halichoeres trimaculatus* (Kuwamura et al. 2007). Reversed sex change in facultatively monogamous pairs in low-density conditions has also been confirmed in a haremic wrasse *Labroides dimidiatus* (Kuwamura et al. 2014).

These examples suggest that different population densities can cause intraspecific variation in sexual pattern through variations in the mating system. Protogynous species become gonochoristic in high-density conditions and reversed sex change may occur in low-density conditions. In protandrous species; however, reversed sex change has not been reported in low-density conditions and further investigations are needed. In Sparidae, for example, both hermaphroditism (PA or PG) and gonochorism are known in at least 12 species (Table 1, S1). Although their mating systems are almost unknown at present, they will be a good subject to examine the relationship between population density and sexual pattern.

There is much more work to be done to investigate the effects of population density and mating system on interspecific variations in sexual pattern, and we hope that the database presented here should allow for many future comparative tests. To further facilitate this work, we need to create a database of the mating systems of gonochoristic fish species similar to that presented here for hermaphroditic species. We can then proceed to make comparative tests with closely related groups that differ even more strongly in sexual pattern.

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