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Growing knowledge and understanding of dichromatism and sex reversal in Labridae

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Abstract

A brief survey is given of current literature in comparison with former studies. Since the 18th century phenotypic diversity of Labridae is a matter of argument. At first in dribs and drabs, yet last decades at a rapid rate, dichromatic adult morphs are synonymized. There are few monochromatic species.

Wrasses are protogynous hermaphrodites. Most species are described as monandric, but a minority (of slightly or extremely dichromatic) species is diandric, with both primary and secondary males. Terminal males reproduce with single females, but initial phase males spawn in aggregations. Some species are haremic, and large males are permanently or temporarily territorial. Last decades insight in the various social factors has greatly increased, resulting in theoretic models to explain the evolution of the typical, diverse modes of labrid reproductive biology.

Résumé

On passe brièvement en revue la littérature récente, en comparaison avec les études plus anciennes. Depuis le XVIIIème siècle, la diversité phénotypique des Labridae est un sujet de discussion. D'abord de façon sporadique, mais ces dernières décennies à un rythme rapide, les morphes dichromatiques adultes sont synonymisées. Il y a peu d'espèces monochromatiques.

Les Labridae sont des hermaphrodites protogynes. La plupart des espèces sont décrites comme étant monandriques, mais il y a une minorité d'espèces diandriques (faiblement ou extrêmement dichromatiques), aux mâles aussi bien primaires que secondaires. Les mâles terminaux se reproduisent avec des femelles seules, mais ceux de phase initiale fraient en aggrégations. Certaines espèces ont des harems, et les mâles de grande taille sont territoriaux, de façon permanente ou temporaire. Pendant ces dernières décennies, la connaissance de facteurs sociaux divers a beaucoup progressé, ce qui a abouti à des modèles théoriques pour l'explication de l'évolution des divers modes typiques de la biologie reproductive des Labridae.

Introduction

My introduction to the marine world was during a student field trip to southern France with Jan Stock as one of the leaders. Later, during fieldwork on the "girelle" in Banyuls-sur-Mer and PhD-work on Caribbean wrasses, Jan happened to be passing by. Finally, he succeeded the late professor Engel as my promotor. Just while preparing a contribution to Stock's farewell, Charnov's analysis of sex reversal in labroid fish (1982) was brought to my notice. I refrained from an intended paper on present day work, and became wrapped up once more in the fascinating world of "my" wrasses, that I left a quarter of a century ago.

When my labrid work was published (1966–1975) there was hardly any response. Conform to the "ignoration of hermaphroditic fish by comparative endocrinologists, behaviorists, and ecologists – all of whom should find among these unusual fish exceptions to prove their rules" (Atz, 1965)? or an illustration of the drawback of the attitude as scientist to stick to the facts and nothing but the facts, according to Hull's observation (1989) that "Those scientists who have attempted to produce theory-free descriptions of natural phenomena have had pitifully little impact on the course of science"?

Later, several ichthyologists extended both the empiric and theoretic knowledge about the swift, agile fish. Yet, except for the world-topic harem of *Labroides dimidiatus* (cf. Robertson, 1972) and the Science coverstory of *Thalassoma bifasciatum* (cf. Warner et al., 1975), the wrasses stayed mainly a field of interest for a relatively small in-crowd.

However, in view of the models labrids offer population biologists, and the interest of e.g. partial and total outsiders as sociobiologists and feminists for the evolution of sex and of sexual behavior in general, the Labridae certainly deserve more general recognition.

The speciose family of Labridae is most diverse in terms of size and form. Closely related species often cannot be separated on basis of meristic characters. Color pattern offers a relevant identification mark, though complicated by the fact that numerous species display a striking phenotypic diversity during life. Juveniles may differ from the adults, and there may be a smaller, plainly colored as well as a larger, brightly colored adult phase. The latter may exhibit an elongation of parts of the dorsal fin or of the pelvic fins, a strongly forked caudal fin, or a prominent hump on the forehead.

Since Linnaeus, roughly speaking, five steps in the approach of this dimorphism can be distinguished. At first, the adult forms were separated into different species. Secondly, they were considered to be females and males of one protogynous species. This concept was unsettled when among the "female" morph functional males were found. The first indications in this direction date back to the end of the 19th century but these findings were certainly not generally taken up. Skin- and scuba-diving expanded underwater observations on labrid social systems, including territorial and sexual behavior. This knowledge formed the base for hypotheses to explain labrid dichromatism and reproductive biology in the framework of evolutionary theories; at first, by field researchers (various papers by Warner and Robertson c.s.), later also by mere theoretic analysis (Charnov, 1982).

Around 1960/1963 – when for some European species color and sex were a matter of argument, and for the majority of Caribbean wrasses change of color was not or only vaguely described, not to mention its relation to sex – a first comparative, demographic labrid study (data on abundance, color-, size- and sex-composition of the populations) was performed. Investigations of 5800 specimens belonging to one Mediterranean and seven Caribbean species conclusively proved reversal of sex in all eight species studied, and quantified an interspecific variability with in some species a strict, in others a more loose relation between color, size, and sex (Roede, 1966, 1972, 1975).

The present paper intends to check the universality of this variability by a brief survey of current literature, including theoretical explanations concerning the evolution of dichromatism and sex reversal.

Labridae

General information. – (If no specific reference is given, the information is from Roede, 1972.)

Labrid fishes are (sub)tropical and temperate marine species of clear coastal waters. Typically, they have thick lips and protruding teeth.

Most wrasses are reef-dwellers, active during daytime, but with approach of sunset or danger rapidly seeking shelter among the rocks or dense layers of algae, or digging into the sand. Tropical species can be observed the whole year through but in colder areas in autumn and winter the fishes either move to deeper water or hibernate burrowed under the sand.

Various species form abundant aggregations, mingling with the crowds of other labroid species. Less common are less numerous, homospecific species staying at rockless sand cays or in seagrass beds. In general the greedy Labridae are benthophagic carnivores, not overparticular in the choice of their food. Though some interspecific differences in diet occur, there is a great overlap. According to size the diet changes from copepods to mainly crustaceans and molluscs. Robertson & Polunin (1981) and Robertson (1984) experimentally refuted the traditional view of a food resource partition among reef fishes. (The young of) some species are cleaner fishes, feeding on ectoparasites of other fishes.

Color patterns and dichromatism

Two categories of color changes can be distinguished:
a. Fast, reversible shadings of color – due to aggregations and dispersions of the pigment within the chromatophores. These are related to affective behavior.
b. Morphological color changes – in which the number of chromatophores may alter as well as the amount of pigment they contain. These are relatively slowly developing processes of a rather irreversible character.

The following refers to the morphological, adult color changes. Roede found in relation to increasing size a variety of: (a) no striking changes of color (*Halichoeres poeyi*), (b) only a shading from dark, contrasting colors towards soft, pastel hues with no actual changing of the basic pattern (*H. bivittatus*), (c) conspicuous color changes, varying from local alterations (*Hemipteronotus splendens*) to more radical ones involving all parts of the body (*Coris julis*, *Thalassoma bifasciatum*, *Halichoeres maculipinna* and *H. garnoti*).

Detailed descriptions were given of the smaller, more drab (be it in *Th. bifasciatum* on peak moments dazzlingly yellow) *first adult* or *initial phase*, intermediate color phases and the gaudy *terminal phase*. Due to reversible shadings the differences between the phases may in- or decrease temporarily.

At first, the two forms were indicated as either "drab and terminal", "drab and gaudy" or "female and male" phases. Roede preferred to denote the adulthood of also the smaller ones by using "first adult and terminal phase". This terminology has not been generally adopted and "initial phase" (IP) and "terminal phase" (TP) became common use. Be aware that "initial" is not equivalent to "juvenile". For a detailed survey, including courtship alterations, see Robertson et al., 1977.

Numerous reports on labrids have been presented by Randall, a Flying Dutchman moving from one sea to the other, generating new species on the moment he dives down; easily to be listed in the Guinness Record Book on basis of the hours spent under water, often at considerable depths, the number of species described, or the number of his color pictures of fish, showing the fins erected and the essential "life" colors.

Besides, Randall and others described:
(a) A few monochromatic species: *Coris venusta* (Randall, 1976), *Labroides dimidiatus* (Robertson & Hoffman, 1977), *Pseudolabrus semifasciatus*, *P. torotai* and *P. gayi* (but *P. fuentesi* is sexually dichromatic) (Russell & Randall, 1980) and *Labroides phthirophagus* (Randall, 1985).

Yet, prudence is called for when uniform coloration is recorded, because this can be due to the fact that the relatively more rare TP specimens were just not included in collected samples. As illustrated by *Thalassoma cupido*, an abundant Japanese wrasse that became listed as dichromatic when Katherine Meyer (1977) bothered to collect a 220 specimens.
(b) Some species showing just a fading of colors in relation to increase in size, in some combined with alteration of particular spots, e.g. *Halichoeres podostigma* (Randall, 1980), *H. hortulanus* and *H. trispilus* (Randall & Smith, 1982), *H. ornatissimus* and *Thalassoma ballieui* (Randall, 1985).
(c) Yet, dozens of species show either a partial dichromatism, e.g. *Halichoeres dussumieri* and *H. stigmaticus* (Randall et al., 1982), or are completely dimorph, e.g. *Anampses chrysocephalus*, *A. neoguinaicus* and *A. femininus* (exceptionally IP more colorful than TP) (Randall, 1972), *Coris gaimard* (Randall, 1976), *C. aygula*, *Stethojulis albovittata*, *Halichoeres marginatus*, *Anampses meleagrides* (Randall, 1983) and *A. cuvier*, *Coris ballieui*, *C. flavovitta*, *Stethojulis balteata*, *Thalassoma duperrey*, *Th. purpureum*, *Th. trilobatum*, *Pseudojulis cerasinus* and *Gomphodus varius* (Randall, 1985).

Later publications thus subscribe to the conclusion that Labridae are mutually divergent in their phenotypic diversity, even to be found within one genus.

The relationship of color to size, and sex

At first, the distinct phenotypes were a source of confusion and – especially in the 18th and 19th century – of extreme controversy. They received different vernacular and scientific names, e.g. *Coris giofredi/C. julis* and *Thalassoma nitidus/Th bifasciatum*.

As early as 1800 Retzius synonymized morphs of *Labrus bimaculatus*. Steindachner (1868) was the first to unite the brownish and the orange banded turquoise forms of *Coris julis*, but his revision of systematics was not generally accepted up to 1955. Longley's uniting (1914, 1915) of the yellow and bluehead-green morphs of *Thalassoma bifasciatum* became generally accepted after 1930. (Detailed survey and references in Roede, 1972.)

The last decades frequently, and now noiselessly, incorrectly classified dichromatic pairs are linked, such as (IP and TP, respectively) *Stethojulis strigiventer/S. renardi* (cf. Randall, 1955), *Anampses caeruleopunctatus/A. diadematus* (Randall, 1972), *Coris rosea/C. ballieui* (Randall, 1976), *Halichoeres gymnocephalus/H. chloropterus* and *H. timorensis/H. kawarin* (Randall, 1980), *Lepidaplois albomaculatus/Bodianus axillaris*, *Julis kalosoma/Stethojulis interrupta*, *Julis notopsis/Halichoeres marginatus*, *Macropharyngodon varialvus/M. bipartitus*, and *Julis umbrystygma/Thalassoma purpureum* (survey in: Randall, 1983) or *Anampses rubrocaudatus/A. chrysocephalus* and *Gomphodus varius/G. tricolor* (Randall, 1985). Sometimes also intermediates and juveniles have received separate scientific names. Of the now linked pair *Halichoeres leparensis* and *H. argus* the intermediate *H. fijiensis* was even considered as their hybrid (Weber, 1913 and De Beaufort, 1940 in: Randall, 1980), while the adult forms *Coris eydouxii* (IP) and *C. lepomis* (TP) now are synonymized under the juvenile name *Coris flavovittata* (cf. Randall, 1976, 1985).

A second step was to regard labrid adult dimorphism as a sexual dichromatism, the smaller morph being females, the more conspicuous one males. Also in monochromatic species females are smaller, whereas most large fish are males. This implies a reversal of sex as a common phenomenon.

Sex reversal

In the dioecious higher vertebrates, reproducing by internal fertilization, spontaneous reversal of sex occurs most rarely. It is due to a tumor or sex chromosomal aberrations. But in the higher bony fishes *hermaphroditism* (the presence of recognizable ovarian and testicular tissue in a single individual; Atz, 1964) is the rule rather than the exception, especially among Cyprinodontiformes and Perciformes. Often this hermaphroditism takes the *sequential* form, i.e. the individual changes sex somewhere during its life.

In the Serranidae both synchronous and protogynous hermaphroditism are well represented. In a number of species the gonads stay functional during the transition from female towards male; yet, self-fertilization is not frequent. In Sparidae protogynous, protandrous as well as simultaneous hermaphroditism occur. But unlike the serranid ovotestis, the ovarian and the testicular parts are clearly separated by connective tissue. In Labridae protogynous reversal of sex proceeds via a total decline of the transforming ovary. Consequently, a temporary functional hermaphroditism does not occur in this family (Atz, 1964; Roede, 1973). In ancient times sex of labrids already caused confusion; Pliny correctly observed that in the "girelle" (*Coris julis*) there are more females than males, and sometimes no males at all.

Macro- and micro-inspection of gonads gave conclusively proof of sex reversal. Generally regression of ovaries takes place in wrasses of intermediate sizes; areas of spermiogenesis amid ovarian structure in regression are found in fish in initial colors (Reinboth, 1961, 1975; Roede, 1966, 1972; Meyer, 1977). Randall (1980) reported (gross inspection) intersexual gonads in intermediate fish of *Halichoeres melanurus*, *H. chloropterus* and *H. timorensis.*

The idea of a sex-specific dichromatism proved to be an over-simplification because in some species among the initial morph up to 15–30% were found to be functional males, with often very mature testes.

This was signalized for *Coris julis* (Lo Bianco, 1909; Bacci & Razzanti, 1957, 1958; Reinboth, 1957; Roede, 1966), *Crenilabrus ocellatus* and *C. quinquemaculatus* (Soljan, 1930, 1931), *Labrus bimaculatus* (Lönnberg & Gustafson, 1937), *Thalassoma bifasciatum* (Longley et al., 1941; Stoll, 1955; Roede, 1972), *Halichoeres bivittatus* (Roede, 1972) and *Stethojulis strigiventer* (Randall, 1955).

Diandry

Reinboth (1961) distinguished *primary males*, (male at birth and throughout life; externally to be distinguished from IP females by genital papillae) and *secondary males* (formerly females), differing in vas deferens and structure of the gonad. By now diandry is amply studied, especially in *Thalassoma bifasciatum* (various publications by Warner and Robertson c.s., Drew, 1986) and *Th. cupido* (Meyer, 1977).

Yet, in the numerous taxonomic descriptions of the last decades only incidentally the occurrence of males among the initial phase is reported, e.g. for *Halichoeres scapularis* and *H. marginatus* (Randall et al., 1982) and *Thalassoma trilobatum* (Randall, 1985).

Gonadal activity

Testes of IP males are markedly more developed than those of TP males. The mature testes of the former occupy great part of the abdominal cavity, whereas TP testes, also in the minority with ripe gonads, are relatively small strings. Most of the largest terminal males have nonfunctional gonads, with local forms of senescence (quantified in Roede; confirmed, also for diandric parrotfishes, by Robertson & Choat, 1975; Warner & Robertson, 1978).

It seems paradoxical that the larger, often territorial and aggressive part of the population has absolutely and relatively smaller gonads. This in contrast to observations by various authors that TP males (at least of *Thalassoma bifasciatum*) may spawn 40–100 times, but IP males just once or twice a day.

Monandry

In the major part of at least 90 species they described, Randall and co-authors stick to a strict color- and size-specific separation of females and males. E.g. for *Halichoeres margaritaceus*, *H. nebulosus* and *H. miniatus* (Kuiter & Randall, 1981), the *Anampses*, *Pseudolabrus* and most of the *Halichoeres* species mentioned above, eight species of *Pseudojuloides* (Randall & Randall, 1981) and various *Paracheilinus* species (Randall & Lubbock, 1981).

Indeed, next to diandry monandric species (all males being reversed females) exist, as shown by demographic studies for *Halichoeres garnoti*, *Hemipteronotus splendens*, *Hemipteronotus martinicensis*, *Bodianus rufus* and *Clepticus parrae* (Roede, 1972; Warner et al., 1978).

The author has strong doubts, though, whether all the species presented elsewhere as sexually dichromatic actually are monandric. Only studies of sufficiently large samples can give a decisive answer for each species concerned. This is not a negative criticism, since some of the discussed species are rare ones, or common, yet with a predilection for deep waters, or secretive in habits so it is praiseworthy that a few specimens have ever been collected.

Summarizing, there is no relation between diandry and degree of color change, diandry being reported for species with a great (*Coris julis*, *Thalassoma bifasciatum*, *Stethojulis strigiventer*, *Halichoeres marginatus*) or only a moderate (*Th. cupido*, *Halichoeres bivittatus*) contrast between initial and terminal phase. While the apparently much more common monandry is proven for species that are monochromatic (*Halichoeres poeyi*), monandric species show only slight or moderate (*Hemipteronotus splendens* and *He. martinicensis*), or striking differences between the adult morphs (*H. garnoti* and many others).

Labrid social systems

For an understanding of the basic causes that favor dichromatism and sequential hermaphroditism various aspects of labrid social systems are relevant. By now, population density and structure are being studied even by grid studies and observations of individual fish (Shapiro, Fitch in: Drew, 1986).

Sexual Behavior

Modes of reproduction are diverse. In tropical labrids gametes are released freely into the water, but temperate wrasses may lay demersal eggs and exhibit male brood-care (Robertson et al., 1977).

In all species pair-spawning occurs, a terminal male reproducing with single females. These males may defend either permanently or temporarily territories, and display courting behavior. (Such behavior gave Randall support for linking dichromatic pairs.) In diandric species, moreover, IP females and males spawn in aggregations. Both types of spawning are characterised by a rapid up and down rush to minimize reef-based predation on the spawners or the eggs. Often the fishes migrate from their feeding areas to special spawning sites, at specific times of the day.

Soljan (1930, 1931) reported that when large *Crenilabrus* males, after building nests, court the females, small males of similar hues as the females rush foreward at the supreme moment to fertilize at least part of the eggs. Such "sneaking" (stealing spawnings with a female waiting to spawn with a TP male) and "streaking" (joining TP male and female at the climax of spawning) by IP males is now reported for several other diandric species (Warner et al., 1978).

Either the fish form loosely organised mating systems, or males maintain harems (*Labroides dimidiatus*, Robertson et al., 1977; *Cirrhilabrus rubriventralis* and *Paracheilinus* species, Randall et al., 1981). The latter display a rigid hierarchy, with a permanently territorial male dominating males and a group of females.

Abundance and sex ratios

In all species females are in the majority; the initial phase strikingly outnumbers intermediates and terminal specimens. Either part of the fish stop growing, or there is a sudden size-specific mortality. In this respect the description of three types of Y chromosomes in *Coris julis* may matter (Duchâc et al., 1982, in: Drew, 1986). These could control intraspecific differences in the ability to change sex and colors (see below), but also lifespan.

Local differences are analysed in detail, mainly for *Thalassoma bifasciatum*. Over the day sex ratios may temporarily differ. Samples of clusters ready to spawn consist mainly of mature IP males, but in sexually inactive groups females strongly outnumber IP males. With increase of reef size population (deme) size increases, yet the proportion of bluehead (TP) males, thus the number of territories, decreases (Warner & Hoffman, 1980).

Determination of sex and sex reversal

The discussion is directed to the question whether sex determination is strictly controlled by genes, triggered by environmental events, or a combination of both (e.g. an environmentally induced shift in gene expression). In at least some species sex reversal is socially induced, as is shown by change of sex by the removal of a male in haremic species (Robertson, 1972), or by surpassing a threshhold number of females. Experimentally, thus even small females can be forced to reverse sex (Shapiro, 1984, in: Drew, 1986).

Theoretic models

Most theories to explain the complex labrid interrelations of dichromatism and modes of reproduction were formulated around the seventies.

The conflicting necessities of concealment for predators and of sexual recognition should influence the degree of dichromatism. Labrids of coral areas tend to be fully dichromatic, whereas for wrasses from seagrass beds cryptic coloration is more essential in view of a greater risk on predation. In a species with long-term stability and constant male–female interactions such as monochromatic *Labroides dimidiatus*, males – all maintaining harems and sexually active – have not to differentiate themselves from inactive or nonterritorial males. Here are no strong selection pressures towards difference in coloration (Robertson et al., 1977). This is contradicted, though, by other haremic species as *Paracheilinus* being sexually dichromatic.

In 1981 Robertson argued that the evolutionary development of dichromatism is rather a response to inter- than intrasexual interactions. The relative spatial distributions of feeding and spawning sites affect the chance of spawning with a TP male, and the ability of males to monopolize mates.

Lower vertebrates are strictly dioecious. This leads to the question how natural selection has favored hermaphroditism over dioecy in higher teleosts. Most discussions are based on Ghiselin's suggestion (1969) that reversal of sex was favored when the reproductive success is closely related to age or size, thus evolved since it was more advantageous for males to be larger. This is complicated, though, by the phenomenom of diandric species, where non-sex changing males co-exist with sequential hermaphrodites. Randall et al. (1963) already remarked that pair spawning is the basic reproductive pattern for parrot and labrid fishes and aggregate spawning a secondary development.

The existence of diandry depends upon opportunities for primary males to breed. Their frequency depends upon population density, a non-permanent territorial mating system, and their chances to interfere with the spawning of large, terminal males. When males, however, have a strong social control over the females, the species is monandric. These ideas are checked by Charnov (1982) who tested the ESS (Maynard Smith's "Evolutionary Stable Strategy" of 1976) allocation to male versus female function by subjecting labrid data to the Shaw-Mohler and derived equations.

Summarizing, social systems control mating opportunities, yet spatial distribution of food and shelter determine social systems. Accordingly, among the herbivore scarids with permanent territories haremic species are much more common than among the carnivorous labrids.

References

Atz, J.W., 1964. Intersexuality in fishes. In: C.N. Armstrong & A.J. Marshall (eds.), Intersexuality in vertebrates including man: 145–232 (Academic Press, London/New York).

Atz, J.W., 1965. Hermaphroditic fish. Science, 150 (3697): 789–797.

Charnov, E.L., 1982. The theory of sex allocation. Monographs in Population Biology, 18: 1–335 (Princeton University Press, Princeton, N.J.)

Drew, Catherine L., 1986. Dichromatism and diandry in Thalassoma bifasciatum (Labridae), the Bluehead Wrasse. Thesis Stat. Univ. New York at Stony brook: 134+25 pp.

Ghiselin, M.T., 1969. The evolution of hermaphroditism among animals. Quart. Rev. Biol., 44: 189–208.

Hull, D.I., 1989. Progress in ideas of progress. In: M.H. Matthew (ed.), Evolutionary progress: 27–48 (University of Chicago Press, Chicago).

Kuiter, R.H. & J.E. Randall, 1981. Three look-alike Indo-Pacific labrid fishes, Halichoeres margaritaceus, H. nebulosus and H. miniatus. Rev. fr. Aquariol., 8: 13–14.

Meyer, Katherine A., 1977. Reproductive behavior and patterns of sexuality in the Japanese labrid fish Thalassoma cupido. Japan. J. Ichthyology, 24: 101–112.

Randall, J.E., 1955. Stethojulis renardi, the adult male of the labrid fish Stethojulis strigiventer. Copeia, 3: 237.

Randall, J.E., 1972. A revision of the labrid fish genus Anampses. Micronesica, 8: 151–195.

Randall, J.E., 1976. A review of the Hawaiian labrid fishes of the genus Coris. Uo, Jap. Soc. Ichthyol., 26: 1–10.

Randall, J.E., 1980. Two new Indo-pacific labrid fishes of the genus Halichoeres, with notes on other species of the genus. Pacific Science, 34: 415–432.

Randall, J.E., 1983. Red Sea reef fishes: 1–192 (Immel Publ., London).

Randall, J.E., 1985. Guide to Hawaiian reef fishes: 1–79 (Harrowood Books, Newton Square PA).

Randall, J.E. & M. Dor, 1980. Description of a new genus and species of labrid fish from the Red Sea. Israel Journal of Zoology, 29: 153–162.

Randall, J.E. & R. Lubbock, 1981. Labrid fishes of the genus Paracheilinus, with descriptions of three new species from the Philippines. Japan. J. Ichthyology, 28: 19–30.

Randall, J.E. & Helen A. Randall, 1963. The spawning and early development of the Atlantic parrot fish, Sparisoma rubripinna, with notes on other scarid and labrid fishes. Zoologica, 48: 49–60.

Randall, J.E. & Helen A. Randall, 1981. A revision of the labrid fish genus Pseudojuloides, with descriptions of five new species. Pacific Science, 35: 51–74.

Randall, J.E. & Margaret M. Smith, 1982. A review of the labrid fishes of the genus Halichoeres of the Western Indian Ocean, with descriptions of six new species. Ichthyol. Bull. J. L. B. Smith Inst. Rhodes, Univ. Grahamst., 45: 1–26.

Reinboth, R., 1961. Natürliche Geschlechtsumwandlung bei adulten Teleosteern. Zool. Anz., (Suppl.) 24: 259–262.

Reinboth, R. (ed.), 1975. Intersexuality in the animal kingdom: 1–450 (Springer-Verlag, Berlin).

Robertson, D.R., 1972. Social control of sex reversal in coral-reef fish. Science, 177: 1007–1009.

Robertson, D.R., 1981a. Coexistence: symbiotic sharing of feeding areas and algal food by some coral reef fishes from the Western Indian Ocean. Mar. Biol., 62: 185–195.

Robertson, D.R., 1981b. The social and mating systems of two labrid fishes, Halichoeres maculipinna and H. garnoti, off the Caribbean coast of Panama. Mar. Biol., 64: 327–340.

Robertson, D.R., 1984. Cohabitation of competing territorial damselfishes on a Caribbean coral reef. Ecology, 65: 1121–1135.

Robertson, D.R. & J.H. Choat, 1974. Protogynous hermaphroditism and social systems in labrid fishes. Proc. Second Int. Symp. Coral Reefs, 1: 217–225.

Robertson, D.R. & S.G. Hoffman, 1977. The roles of female mate choice and predation in the mating systems of some tropical labroid fishes. Zeitschr. Tierpsychologie, 45: 298–320.

Robertson, D.R. & N.V.C. Polunin, 1981. Coexistence: symbiotic sharing of feeding areas and algal food by some coral reef fishes from the Western Indian Ocean. Mar. Biol., 62: 185–195.

Roede, Machteld J., 1966. Notes on the labrid fish Coris julis (Linnaeus, 1758) with emphasis on dichromatism and sex. Vie Milieu, (A) 17 (3A): 1317–1333.

Roede, Machteld J., 1972. Color as related to size, sex, and behavior in seven Caribbean labrid fish species (genera Thalassoma, Hallichoeres and Hemipteronotus). Studies Fauna Curaçao, 42: 1–266.

Roede, Machteld J., 1973. Intersexuality and sex reversal in fishes. Intern. Res. Commun. Syst. Veterinary Medicine and comparative Physiology, (73-9)15-14-12.

Roede, Machteld J., 1975. Reversal of sex in several labrid fish species. Pubbl. Staz. zool. Napoli, 39 (Suppl.): 595–617.

Russell, B.C. & J.E. Randall, 1980. The labrid fish genus Pseudolabrus from islands of the Southeastern Pacific, with description of a new species from Rapa. Pacific Science, 34: 433–440.

Soljan, T., 1930. Die Fortpflanzung und das Wachstum von Crenilabrus ocellatus Forsk., einem Lippfisch des Mittelmeeres. Zeitschr. wiss. Zool., 137: 150–174.

Soljan, T., 1931. Brutpflege durch Nestbau bei Crenilabrus quinquemaculatus Risso, einem adriatischen Lippfisch. Zeitschr. Morph. Ekol. Tiere, 20: 132–135.

Warner, R.R. & S. Hoffman, 1980. Local population size as a determination of mating system and sexual composition in tropical marine fishes (Thalassoma). Evolution, 34: 508–518.

Warner, R.R. & D.R. Robertson, 1978. Sexual patterns in the labroid fishes of the western Caribbean, I: The Wrasses (Labridae). Smiths. Contrib. Zool., 254: 1–27.

Warner, R.R., D.R. Robertson & E.G. Leigh, 1975. Sex change and sexual selection. Science, 190: 633–638.

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