STUDIES ON THE FAUNA OF CURAÇAO AND OTHER CARIBBEAN ISLANDS: No. 138.

COLOR AS RELATED TO SIZE, SEX, AND BEHAVIOR IN SEVEN CARIBBEAN LABRID FISH SPECIES

(genera *Thalassoma, Halichoeres* and *Hemipteronotus*)

by

MACHTELD J. ROEDE

(Universiteit van Amsterdam)

CONTENTS

Present addres of author: Institute of Human Biology, Utrecht.

ABSTRACT

Approximately 5500 Caribbean labrid fishes belonging to seven species were caught, transported, partly on ice, to the laboratory and subsequently studied. The major portion was examined immediately; some 20 per cent were stored briefly (less than three days) at minus 20°C.

Color pattern (and shape of fins) may change during adult life, varying from slightly (*Halichoeres poeyi*) to drastically (*Thalassoma bifasciatum*). Per species a classification into successive color phases has been introduced; these color phases are strongly related to body length.

In *Halichoeres maculipinna*, *Hemipteronotus splendens* and *Hemipteronotus martinicensis* females are restricted to the small, first adult color phase; males have exclusively been found in the larger intermediate and terminal color phases. This confirms the prevailing opinion that labrid dichromatism represents a sexual dimorphism. In *Halichoeres poeyi* females are also significantly smaller than males.

In the most abundant species, however, sex and color/size are not clearly related. In *Thalassoma bifasciatum* and *Halichoeres bivittatus* two types of males occur, as functional males are present in both the small, first adult color phase and in the large, terminal color phase. Functional females have been found in all sizes and colors in *Halichoeres bivittatus* and *Halichoeres garnoti*.

Sex reversal from female towards male sex – a common process in all species – occurs more or less coincidental to color change. As distinct from the Sparidae, Scaridae or Serranidae the reversal proceeds via a total decline of the transforming ovary. Consequently, temporary stages of functional hermaphroditism do not occur in Labridae.

ACKNOWLEDGEMENTS

With sincere gratitude I wish to express my thanks to Prof. Dr. H. ENGEL and Mrs. Dr. M. S. J. ENGEL-LEDEBOER who always found time to discuss my text. Dr. JACK E. RANDALL's interest in my doings has been encouraging; only a man of his talents could make it possible to realize an experimental study with unmanageable huge underwater cages. Dr. INGVAR KRISTENSEN, director of the CARMABI and his staff made the period on Curaçao unforgettable. Mr. PAPY RAMRATTAN MARTINEZ has been an excellent assistant in collecting labrids.

I am greatly indebted to Dr. J. HUIZINGA, who permitted me to continue this study notwithstanding my "reversal" from a marine to a human biologist. The frank and stimulating criticism of my work offered by Dr. G. W. F. EDGAR is greatly appreciated. Many members of the staff of the Institute of Human Biology, Utrecht, have given their valuable help to my effort to write this thesis, particularly Mrs. ANNE TOL.

JOS RUTING, VINUS VAN BAALEN and the technical staff of the Zoological Laboratory, Utrecht, made the drawings; special thanks are due to Mr. H. VAN KOOTEN for his expert contribution to the plates. I am grateful to Dr. P. WAGENAAR HUMMELINCK and Drs. LOUISE J. VAN DER STEEN for their patience and their conscientious treatment of my manuscript. Mrs. L. W. GEBHARDT-THURBER was so kind as to clear the final text of a number of language inaccuracies.

Part of the statistical work has been performed by the Afdeling Waarnemingsuitkomsten, T.N.O. The present study was supported by a grant of the Netherlands Foundation for the Advancement of Research in Suriname and the Netherlands Antillen (WOSUNA).

I. INTRODUCTION

Labrid dichromatism has been subjected to numerous investigations leading to controversial and sometimes confusing results. In an attempt to clarify the inconsistencies outlined below, the interrelationship between color, size, sex, and gonadal activity was studied in approximately 5500 specimens belonging to seven labrid species from the Caribbean waters. The sex distribution in different color phases and the possibility of sex reversal have been the main points of investigation.

The phenomenon of color dimorphism

The family of the wrasses – the Labridae – is a group of fishes showing a most diversified variation of beautiful and bright colors. Color differences within a species may be more striking than color differences between species. Juveniles may differ from the adults of the same species, which in turn may show two distinct color patterns (dichromatism).

In some species dichromatism is so pronounced that the color variants were considered to be two different species. Thus, the species pairs *Thalassoma nitidum* and *Th. bifasciatum*, *Labrus ossifagus* and *L. mixtus*, *Coris giofredi* and *C. julis*, *Stethojulis renardi* and *S. strigiventer* as well as *Gomphosus varius* and *G. tricolor* were only

recently recognized as belonging each to one single species, viz. *Thalassoma bifasciatum, Labrus bimaculatus, Coris julis, Stethojulis strigiventer* and *Gomphosus varius* respectively (LONGLEY, 1914; LÖNNBERG & GUSTAFSON, 1937; BACCI & RAZZAUTI, 1957; RANDALL, 1955a; STRASSBURG & HIATT, 1957).

Probably, this list is far from complete because dichromatism may not have been recognized as such in other species. For instance, this may be pertinent to wrasses enlisted for the Indo-Australian archipelago (DE BEAUFORT, 1940) in which no dichromatic species have been described. Recent studies in the area of the Indo-Pacific by RANDALL (MS) could pinpoint a dozen incorrectly classified dichromatic pairs of wrasses. He, e.g. proposes to unite *Anampses rubrocaudatus* and *A. chrysocephalus* into one species under the last name.

Color dimorphism is not present in every labrid species. For instance, it does not occur in *Ctenolabrus rupestris* (QUIGNARD, 1966).

In dichromatic labrid species dull colors are found often in small individuals, whereas large specimens display a gaudy pigmentation. In a few cases the exact relation between color and size has been analyzed (LÖNNBERG & GUSTAFSON, 1937; REINBOTH, 1957). Also the shape of the fins may alter when larger sizes are attained. In some species the caudal fin changes from a truncate towards a lunate form. In various cases either elongate dorsal spines get lost with growth (young razor fishes) or develop (*Coris julis*). Some razor fish species are characterized by a strongly increased first ventral ray when they are bigger. How far changes in color and shape run parallel, has hardly been investigated.

COLOR, SEX, AND SEX REVERSAL

Labrid dichromatism has been interpreted as a sexual dimorphism. The small, more drab specimens were simply thought to be females and immatures, and the large, colorful specimens males.

In other marine families of the Perciformes simultaneous hermaphroditism (Serranidae), proterandry (Sparidae) or protogyny (Ser-

ranidae, Sparidae, Maenidae) have been reported as common processes (REINBOTH, 1962; ATZ, 1964). In Labridae inversion of sex also turns out to be a basic theme in explaining changes in sex ratio during growth. Yet, until now proof for sex reversal in wrasses has been given only as the exception. In a few specimens histological investigations revealed intersexual characteristics, most probably transitional stages of a transformation from ovary into testis (REINBOTH, 1957, 1962a; OKADA, 1962, 1965).

An independence of color and sex was reported for *Bodianus rufus*, a labrid in which colors change very gradually during growth (FEDDERN, 1963). *Labrus merula* and *L. turdus* do not have an extreme dichromatic adult life cycle either. Yet, SORDI (1962) found that all specimens of *turdus* and about half the individuals of *merula* change with growth from female into male. These cases upset the alleged relation between color and sex.

TWO TYPES OF MALES

In other labrid species the sex-size-color relation proved to be even more controversial, since functional testes were found both in small, dull colored individuals, and in large colorful fish. The intriguing fact that males may occur either with "female" colors or with the bright "male" pattern resulted in varying explanations.

SOLJAN (1930a, b) reported for the two types of males of *Symphodus ocellatus* two strikingly distinct types of behavior. The large, bright males build nests, then court the females. The small males of similar morphology as these females, rush forward at the supreme moment and fertilize at least part of the eggs. SOLJAN traces the differences to a difference in genesis; the large nestbuilders should develop out of eggs hatched at the end of the spawning season, while the less colorful males should be born in the first months of the spawning season. Due to a faster growth rate the nestbuilders are larger than the older, small drab males when in the next spring the new period of reproduction starts. These conclusions have never been affirmed by other scientists.

According to LÖNNBERG & GUSTAFSON (1937) – discussing the red

and the blue-striped color patterns of *Labrus bimaculatus* – part of the males becomes ripe while still in the red stage; but their reproduction should take place chiefly when they have attained the blue stage. On the contrary, all females mature while retaining the red colors. Only a few females later transmute into the blue colors. These specimens may partly remain reproductive females and partly become intersexual. Whether these intersexuals are stages of a transition from female into male sex is as yet uncertain.

LOUISE STOLL (1955) suggested that *Thalassoma bifasciatum* – of which she found mature males in the small yellow stage as well as in the large bluehead stage – "is possibly a progynous species in which all individuals start life as female and later become male." Proof for reversal of sex has not yet been given.

Coris julis also shows a marked dichromatism, being dull brown-red at small size but a bright turquoise when larger. BACCI & RAZZAUTI (1957, 1958), finding a minority of about 16 to 18 per cent of the brown-red fish to be males, considered it as a protogynous species in which sex reversal from female to male takes place, roughly parallel to changes of color pattern. REINBOTH (1957, 1961) and MACHTELD ROEDE (1966) even found about 30 per cent of the small size group to be real functional males. Consequently, it would be erroneous to consider *C. julis* as strictly protogynous or to consider the dichromatism as a simple sexual dimorphism. REINBOTH denotes the two different types of males as "primary" and "secondary" males. The first should retain their dull colors and are of male sex from the beginning. Secondary males should originate by a spontaneous color and sex inversion of old females. He found proof for this in the shape of the gonoducts, the vas deferens of the secondary males showing characteristics of the former oviduct. REINBOTH (1962a) could not succeed, however, in finding histological proof of sex reversal or of the existence of two types of gonoducts in the males in *Thalassoma pavo*, a wrasse with a less pronounced dichromatism, yet two types of morphologically different males.

Senescense

Another aspect of labrid reproduction that requires further study has been mentioned by Machteld Roede (1966). Her investigations indicated that the large, most colorful *Coris julis* males had small, non-functional testes. The attainment of large size seemed to be accompanied by a reduction in gonadal function. Support for her suggestion of senescence is a remark of Lönnberg e.a. that very old specimens of *Labrus bimaculatus* "appear to become sterile with degenerated gonads" and the observation by Louise Stoll that in *Thalassoma bifasciatum* testes of small, yellow colored males were full of sperm and twice as large as the mature sperm-poor testes of large, bluehead colored males. In the discussion on the evolution of two types of males this phenomenon might be important.

Reviewing only part of the varying data and conclusions quoted above, Atz (1964) already remarked: "The study of sexual development in the wrasses and its relation to secondary sex characters and to reproduction is at present in a most puzzling state, but the data on hand are so tantalizing and challenging that further contributions should not be long in appearing."

Scope of present study

So far the labrids in the Caribbean area have been subjected mainly to taxonomical investigations. At first, dichromatism in two species, *Thalassoma bifasciatum* and *Halichoeres maculipinna* caused taxonomic confusion, but these two species were the first of which the dimorphic character was recognized. Yet, information on the degrees of color changes of Caribbean labrids or the moment of onset of the development of different colors is scarce. The relation of sex and color and the possibility of sex reversal has hardly been an object of attention. Moreover, some controversies in the data on body proportions and meristic data exist in the literature.

Consequently, the study of the wrasses in this paper has been based on the broadest possible spectrum of diverse characteristics.

Ecology, distribution, and especially behavior were studied in addition to life colors and meristic and morphometric traits.

More precisely the aim was to study for each species:
- The color pattern and possible successive color phases during life.
- The length of the body at which each pattern is displayed.
- The sex distribution of the successive color phases.
- The meristic traits and morphometry of the various sex and color groups.
- The sexual activity of the gonads in relation to size and color, with special attention to the possible occurrence of sex reversal and intersexuality.
- The behavior of the fish.
- The abundance, environment and the geographical and bathymetrical distribution.

Further:
- Some growth and hormone experiments were carried out to study the mechanism of color change. This proved to be difficult because labrid fish do not thrive in captivity.
- Information was obtained on the relation between gonadal activity and the lunar cycle.
- Histological observation of the gonads revealed some interesting aspects of ovulation.

Material

The Labridae, popularly known as wrasses, are a large family (up to 400 species) of marine fishes inhabiting (sub)tropical and temperate coastal waters. In most species the body is oblong or elongate, covered with cycloid scales; the lateral line is well-developed, continuous or interrupted, and often angulated. The lips are thick and fleshy, longitudinally plicate, hence the name of Labridae (*labrus* = lip). The lower pharyngeal bones, which are situated on the floor of the gullet, are completely united into one bone, having a T- or Y-shape, bearing conical or tuberculate teeth. The anterior teeth in the jaws are usually strong canines while the lateral teeth are more or less coalesced at their bases; there are no teeth on vomer or palatines. The nostrils are round, with two openings on each side. The dorsal fin is continuous, the spinous portion usually long; the anal similar to soft dorsal, and the dorsal and anal spines are not very strong. Ventral fins thoracic, each with one spine and five rays. Gills $3\frac{1}{2}$, the slit behind the last arch small or obsolete. Air bladder present. Most

wrasses are reef-dwellers, inhabiting shallow waters among coral reefs and rocks. Many of them are brilliantly colored. Wrasses are usually small or medium sized, but some species may weigh as much as 27 kg. In general, the commercial importance is limited and of a localized nature.

The following seven species were caught in sufficient numbers to be used for our studies:
Thalassoma bifasciatum (Bloch, 1791)
Halichoeres bivittatus (Bloch, 1791)
Halichoeres garnoti (Cuvier & Valenciennes, 1839)
Halichoeres maculipinna (Müller & Troschel, 1848)
Halichoeres poeyi (Steindachner, 1867)
Hemipteronotus splendens (Castelnau, 1855)
Hemipteronotus martinicensis (Cuvier & Valenciennes, 1839).

Other Caribbean labrid species were disregarded, because the numbers of individuals caught were too small to permit significant conclusions.

A total of 4474 individuals was dissected and the morphological results presented here were based on these specimens. Additional specimens were used for hormonal, growth and behavioral studies. A representative part of the material has been deposited in the collections of the Zoological Museum of the University of Amsterdam (ZMA 104.010–104.112).

II. TAXONOMY

Variation in color has given rise to much confusion and controversy in the literature on the taxonomy of Labridae. This is exemplified by the discrepancies in some of the following synopses. See also Table 1.

Thalassoma Swainson, 1839

Thalassoma SWAINSON, 1839, Nat. Hist. Fishes *2*: 224.
(Θαλλός = a green branch; σωμα = body)

Diagnosis: Oblong or elongate, snout not produced; head without scales; mouth rather small, scarcely protractile; pointed teeth in a single series in the jaws; two canines anteriorly in each jaw, no posterior canine; gill membrane attached to isthmus; lateral line continuous, with a sharp bent below soft dorsal; eight spines in the dorsal fin.

Species mostly in the Pacific and Indian Oceans, only few in the Atlantic. In the Caribbean only one species occurs.

TABLE 1

DESCRIPTIVE INFORMATION ABOUT THE VARIOUS SPECIES IN LITERATURE

Authors	*Thalassoma bifasciatum*			*Halichoeres*				*Hemipteronotus*	
	yellow phase	blue-head phase	both phases	*bivittatus*	*garnoti*	*maculipinna*	*poeyi*	*splendens*	*martinicensis*
1781 GRONOVIUS		+							
1791 BLOCH		+		+					
1802 LACÉPÈDE				+					
1839 SWAINSON		+							
1839 CUVIER & VALENCIENNES		+		+	+		+		+
1848 MÜLLER & TROSCHEL						+			
1855 CASTELNAU								+	
1860 POEY		+		+	+				
1862 GÜNTHER	+	+		+	+	+	+		+
1863 GILL				+					
1867 STEINDACHNER				+			+		
1868 POEY		+		+	+	+			
1871 COPE				+	+				
1875 POEY		+		+	+	+			+
1877 GOODE	+	+							
1882 GOODE & BEAN				+					
1886 JORDAN	+	+		+	+	+			+
1886 JORDAN & HUGHES	+	+		+	+	+			
1890 BEAN	+							+	+
1890 JORDAN	+	+		+	+	+	+	+	
1898 JORDAN & EVERMANN	+	+		+	+	+	+	+	+
1905 BARBOUR		+			+				
1906 BEAN	+	+		+	+	+			
1913 STARKS						+	+		
1915 LONGLEY			+	+		+			
1919 METZELAAR	+	+		+	+	+		+	
1927 BREDER	+	+			+		+	+	
1928 BEEBE & TEE-VAN	+	+	?		+				
1928 MEEK & HILDEBRAND				+			+		
1928 FOWLER	+	+		+	+	+			
1930 NICHOLS	+	+		+	+		+		
1930 PARR			+		+			+	
1933 BEEBE & TEE-VAN			+	+	+	+		+	
1941 LONGLEY & HILDEBRAND			+	+	+	+	+	+	
1948 BREDER			+	+					
1965 RANDALL & BÖHLKE				+	+	+	+		
1965 RANDALL								+	+
1966 CERVIGÓN			+	+	+	+			
1968 RANDALL			+	+	+	+	+	+	+
1968 BÖHLKE & CHAPLIN			+	+	+	+	+	+	+

16

Thalassoma bifasciatum (Bloch, 1791)

(Fig. 2)

"Blue Head." *bifasciatum* = two-banded.

Thalassoma bifasciatum is one of the wellknown examples of labrid species with a marked dichromatism. The differences between the two color patterns (Fig. 4/1 and 4) are so extreme, that many authors considered them to be two different species. LONGLEY (1914, 1915) already suggested that both color patterns belonged to one species, but this was not generally accepted at first.

A. – Synonymy for the yellow color pattern
(*i.e.* color phase 1; Fig. 2/1a, b, c)

Julis nitida GÜNTHER, 1862, *4*: 190; METZELAAR, 1919: 106; BEEBE & TEE-VAN, 1928: 205.
Julis nitidissima GOODE, 1877: 293.
Thalassoma nitidum; JORDAN & HUGHES, 1886: 68; JORDAN, 1886d: 590; 1890: 653; BEAN, 1890: 198; JORDAN & THOMPSON, 1905: 246; FOWLER, 1928: 454; NICHOLS, 1915: 144; 1921: 23; 1930: 316.
Chlorichthys nitidus; JORDAN & EVERMANN, 1896: 414; 1898: 1608; BEAN, 1906b: 68; BLOSSER, 1909: 298; ROSÉN, 1911: 60.
Chlorichthys nitidissimus; JORDAN & EVERMANN, 1898: 1608.
Thalassoma nitida; BEEBE & TEE-VAN, 1928: 205.

B. – Synonymy for the bluehead pattern
(*i.e.* color phase 4; Fig. 2/4)

Labrus capite obtuso GRONOVIUS, 1781: 71.
Labrus bifasciatus BLOCH, 1791: 131, pl. 283; BLOCH & SCHNEIDER, 1801: 243.
Labrus bifasciatus var. *torquatus* BLOCH & SCHNEIDER, 1801: 243.
Julis detersor CUVIER & VALENCIENNES, 1839, *13*: 408; STORER, 1846: 141; GÜNTHER, 1862, *4*: 186; JORDAN, 1886c: 540 (reidentification of the type of *J. detersor*).
Chloricthys bifasciatus; SWAINSON, 1839, *2*: 232; SWAIN, 1882: 275.
Chlorichthys bifasciatus; JORDAN & RUTTER, 1897: 119; JORDAN & EVERMANN, 1898: 1609; BEAN, 1906b: 68; FOWLER, 1919: 144; ROSÉN, 1911: 24, 60.
Labrus ornatus GRAY, 1854: 83.
Julis gillianus POEY, 1860: 214; 1868: 332.
Julis bifasciata; GÜNTHER, 1862, *4*: 186; METZELAAR, 1919: 107.
Julis bifasciatus; POEY, 1875: 107; GOODE, 1877: 291.
Thalassoma bifasciatum; JORDAN & HUGHES, 1886: 68; JORDAN, 1886d: 590; JORDAN, 1890: 652, 654, 691; JORDAN & THOMPSON, 1905: 246; NICHOLS, 1915: 144; 1921: 23; FOWLER, 1928: 454; NICHOLS, 1930: 317.

Thalassoma bifasciatus; JORDAN, 1890: 56; BREDER, 1927: 60; BEEBE & TEE-VAN, 1928: 205.
Iridio cyanochephalus BARBOUR, 1905: 125; BEAN, 1906b: 68.
Bermudichthys subfurcatus NICHOLS, 1920: 62.

C. – Synonymy of authors considering both color patterns belonging to one species
(*i.e.* color phase 1–4; Fig. 2/1–4)

Chloricthys bifasciatus; LONGLEY, 1914: 208.
Thalassoma bifasciatus; LONGLEY, 1915: 208; BEEBE & TEE-VAN, 1928: 205 (under reserve); BREDER, 1948: 206; CERVIGÓN, 1966: 609.
Thalassoma bifasciatum; PARR, 1930: 87; TEE-VAN, 1932: 42; BEEBE & TEE-VAN, 1933a: 151; 1933b: 201, 305; BEEBE & HOLLISTER, 1935: 219; LONGLEY & HILDEBRAND 1941: 196; FOWLER, 1942: 12; 1950: 89; 1952: 102; 1953: 65; STOLL, 1955: 125; RANDALL, 1955: 237; RANDALL & RANDALL, 1960: 444, 449; 1963: 50, 54; ZUMPE, 1963: 86; FEDDERN, 1965: 899; STARCK & DAVIS, 1966: 337; RANDALL, 1968: 210; BÖHLKE & CHAPLIN, 1968: 453.
Thallasoma bifasciatum; CALDWELL, 1959: 72.

Vernacular names:
For the yellow color phase: *Pietchie Pienta* (i.e. variegated) (Leeward Isl., METZELAAR, 1919); *Shining Wrasse* (BEEBE e.a., 1928; NICHOLS, 1930); *Scotch Slippery Dick* (Bermuda, BEAN 1906b; TEE-VAN, 1932); *Peepchi Pinta, Gevlekt Pikkertje* (Neth. Antilles, ZANEVELD, 1959).
For the bluehead color phase: *Pietchie Blauw* (Leeward Isl., METZELAAR); *Bicolored Wrasse* (BEEBE e.a.; NICHOLS); *King Slippery Dick* (Bermuda, TEE-VAN); *Peepchi Docto*; *Docto, Stropdas* (Neth. Antilles, ZANEVELD).

Diagnosis: D VIII-13; A III-11; V I-5; P I-13.
Body slender, compressed; cheeks and opercles scaleless; a slight sheath of scales along base of dorsal; anterior canines 2/2; in the small ones the caudal fin is strongly convex; tail first truncate, with growth becoming concave; small specimens yellow; large specimens bicolored, anteriorly half deep blue, posteriorly half bottle green.

Halichoeres Rüppell, 1835

Halichoeres RÜPPELL, 1835, Neue Wirbelth. Abyssinien: 10.

(ἁλς = sea; χοῖρος = hog)

Diagnosis: Head naked, compressed, conic; lateral line not interrupted, bent abruptly behind; caudal rounded; gill membranes

united to each other and isthmus; large conical teeth in front of jaws; a posterior canine tooth directed forward on each side of the upper jaw. Species with canines 4/4 all belonging to the East Indies and Polynesia, those with canines 2/4 all American.

For a key to the Atlantic species of *Halichoeres* see RANDALL & BÖHLKE, 1965: 237–238, and BÖHLKE & CHAPLIN, 1968: 447–448.

Halichoeres bivittatus (Bloch, 1791)

(Fig. 3)

"Slippery Dick." *bivittatus* = two-banded.

Labrus bivittatus BLOCH, 1791: 133 (from a painting by PLUMIER); BLOCH, 1792, pl. 284 fig. 1.
Labrus psittaculus LACÉPÈDE, 1802, *3*: 523 (from a copy of PLUMIER's painting).
Julis psittaculus; CUVIER & VALENCIENNES, 1839, *13*: 387; JORDAN, 1886c: 540 (reidentification of the type of *J. psittaculus*).
Julis humeralis POEY, 1860: 212.
Choerojulis grandisquamis GILL, 1863: 206.
Choerojulis bivittatus; POEY, 1868: 335.
Choerojulis arangoi POEY, 1875: 109, pl. 4 fig. 1.
Platyglossus florealis JORDAN & GILBERT, 1882a: 287; GOODE & BEAN, 1882: 236.
Platyglossus bivittatus; GÜNTHER, 1862, *4*: 164; STEINDACHNER, 1867: 355; COPE, 1870: 463; GOODE & BEAN, 1882: 236; JORDAN, 1884: 136; BEAN & DRESEL, 1884: 153; JORDAN, 1885: 98; JORDAN, 1886a, b, c, d: 28, 45, 540, 590; JORDAN & HUGHES, 1886: 63; METZELAAR, 1919: 105.
Platyglossus humeralis; GÜNTHER, 1862, *4*: 165; GOODE & BEAN, 1882: 236; JORDAN & GILBERT, 1883: 603.
Choerojulis humeralis; POEY, 1868: 335; GOODE & BEAN, 1879: 338.
Platyglossus radiatus JORDAN & GILBERT, 1882b: 608.
Platyglossus grandisquamis; JORDAN & GILBERT, 1883: 603.
Halichoeres bivittatus; JORDAN, 1890: 645; FOWLER, 1928: 454; NICHOLS, 1930: 315; LONGLEY & HILDEBRAND, 1941: 191; FOWLER, 1950: 82; RANDALL & RANDALL, 1963: 56; RANDALL & BÖHLKE, 1965: 246; CERVIGÓN, 1966: 606; RANDALL, 1968: 202; BÖHLKE & CHAPLIN, 1968: 456.
Iridio bivittatus; JORDAN & EVERMANN, 1898: 1595; BEAN, 1906b: 63; MOWBRAY, 1931: 1.
Halichoeres radiatus; MEEK & HILDEBRAND, 1928: 717 (*non* Jordan, 1887 (1891)).
Halichoeres bivitata; BREDER, 1948: 206.

Vernacular names: *Petit perroquet* (perroquet = parrot) (CUVIER e.a., 1839); *Doncella* (JORDAN e.a., 1898); *Pietch pompuna* (Leeward Isl., METZELAAR); *Pietsj pompoena* (Neth. Antilles, METZELAAR); *Slippery Dick* (BEAN, 1906b; NICHOLS, 1930; BREDER, 1948); *Peepchi pompuna, Pompoen Pikkertje* (Neth. Antilles, ZANEVELD, 1959).

Diagnosis: D IX-11; A III-12; V I-5; P I-11.
Two pairs of enlarged canine teeth anteriorly in lower jaw; gill rakers 15 to 20; anterior lateral line scales with more than one pore; two lengthwise dark brown or blackish stripes.

Halichoeres garnoti (Cuvier & Valenciennes, 1839)

(Fig. 4)

"Yellow-head Wrasse." Named after GARNOT, collector at Martinique.

Julis garnoti Valenciennes, in CUVIER & VALENCIENNES, 1839, *13*: 390.
Julis cinctus POEY, 1860: 211, pl. 13 fig. 19.
Julis ruptus POEY, 1860: 212, pl. 13 fig. 20.
Choerojulis ruptus; POEY, 1868: 334.
Platyglossus ruptus; COPE, 1871: 464.
Platyglossus garnoti; GÜNTHER, 1862, *4*: 162; JORDAN, 1886b, c, d: 45, 541, 590; JORDAN & HUGHES, 1886: 61; METZELAAR, 1919: 104.
Choerojulis cinctus; POEY, 1875: 108.
Halichoeres garnoti; JORDAN, 1890: 643; BREDER, 1927: 59; FOWLER, 1928: 461; BEEBE & TEE-VAN, 1928: 204; PARR, 1930: 86; NICHOLS, 1930: 313; LONGLEY & HILDEBRAND, 1941: 193; RANDALL & RANDALL 1963: 56; RANDALL & BÖHLKE, 1965: 250; CERVIGÓN, 1966: 605; RANDALL, 1968: 206; BÖHLKE & CHAPLIN, 1968: 458.
Iridio garnoti; JORDAN & EVERMANN, 1898: 1953; BARBOUR, 1905: 126; BEAN, 1906b: 68; BEEBE & TEE-VAN, 1933a: 151.
Iridio decoratus BEAN, 1906a: 29; BEAN, 1906b: 64, fig. 5.

Vernacular names: *Pietche Blauw* (Leeward Isl., METZELAAR); *Doncelle, Peepchi Blauw, Blauw Pikkertje* (Neth. Antilles, ZANEVELD).

Diagnosis: D IX-11; A III-12; V I-5; P I-11.
Two pairs of enlarged canine teeth anteriorly in lower jaw; gill rakers 15 to 20; anterior lateral line scales with more than one pore; scales before dorsal large; head olive-black and base of dorsal violet; in larger specimens a vertical dark bar; the very small orange with a midlateral blue stripe.

Halichoeres maculipinna (Müller & Troschel, 1848)

(Fig. 5)

"Clown Wrasse." *macula* = spot, *pinna* = fin.

Also in *H. maculipinna* color differences gave rise to descriptions of different species. In 1906 BEAN created two synonyms, *Iridio microstomus* and *I. meyeri*; NICHOLS (1920) two more, *I. similis* and *I. frenatus*, but the confusion never became as persistent and great as in *Thalassoma bifasciatum* or in the *Hemipteronotus* genus and species.

Julis maculipinna Müller & Troschel, 1848, in SCHOMBURGK: 674.
Platyglossus maculipinna; GÜNTHER, 1862, *4*: 165; JORDAN, 1885: 99; JORDAN, 1886a, d: 28, 590; METZELAAR, 1919: 105.
Choerojulis maculipinna; POEY, 1868: 336.
Halichoeres maculipinna; JORDAN, 1890: 644; FOWLER, 1928: 80; LONGLEY & HILDEBRAND, 1941: 190; RANDALL & RANDALL, 1963: 56; RANDALL & BÖHLKE, 1965: 238; CERVIGÓN, 1966: 604; RANDALL, 1968: 206; BÖHLKE & CHAPLIN, 1968: 454.
Iridio maculipinna; JORDAN & EVERMANN, 1898: 1594; BEAN, 1912: 122; BEEBE & TEE-VAN, 1933a: 150.
Iridio meyeri BEAN, 1906a: 29; BEAN, 1906b: 65, fig. 7.
Iridio microstomus BEAN, 1906a: 30; BEAN, 1906b: 67, fig. 8.
Platyglossus microstomus; METZELAAR, 1919: 106.
Halichoeres penrosi STARKS, 1913: 59, pl. 7.
Iridio frenatus NICHOLS, 1920: 61.
Iridio similis NICHOLS, 1920: 61.

On account of the color description *Pusa radiata* JORDAN & GILBERT, 1878: 374, and *Platyglossus maculipinna* JORDAN & HUGHES, 1886: 62, were not included. JORDAN & GILBERT described only one specimen, from Beaufort, N.C. (unfortunately lost); this was quoted by JORDAN & HUGHES, who sunk the erroneously used genus name *Pusa*. RANDALL (*in litt.*) suggests that this lost specimen may have been a juvenile *H. radiatus*. The present author is inclined to assume it may have been a *H. bivittatus* individual, among others because only this species has been reported by others as well from such northern regions as North Carolina.

Diagnosis: IX-11; A III-11; V I-5; P I-12.
One pair of enlarged canine teeth anteriorly in lower jaw; gill rakers 13 to 15; a single pore on each lateral line scale; a lengthwise dark band just above the midline of the body; a small dark spot at rear base of dorsal fin and another at upper edge of pectoral base; a black spot on dorsal fin between fifth and seventh dorsal spines.

Halichoeres poeyi (Steindachner, 1867)

(Fig. 6)

"Black-Ear Wrasse." Named after FÉLIPE POEY.

Julis crotaphus CUVIER & VALENCIENNES, 1839, *13*: 390.
Platyglossus crotaphus; GÜNTER, 1862, *4*: 162.
Platyglossus poeyi STEINDACHNER, 1867: 355, 356.
Halichoeres poeyi; JORDAN, 1890: 646; LONGLEY & HILDEBRAND, 1941: 194; RANDALL & BÖHLKE, 1965: 24; RANDALL, 1968: 209; BÖHLKE & CHAPLIN, 1968: 455.
Iridio kirchii JORDAN & EVERMANN, 1896: 413; JORDAN & EVERMANN 1898: 1598 EVERMANN & MARSH, 1902: 232.
Iridio poeyi; JORDAN & EVERMANN, 1898: 1599.
Halichoeres kirchii; BREDER, 1927: 60; MEEK & HILDEBRAND, 1928: 720; NICHOLS 1930: 315.

Diagnosis: D IX-11; A III-12; V I-5; P I-11
Two pairs of enlarged canine teeth anteriorly in lower jaw; gill rakers 15 to 20; anterior lateral line scales with more than one pore; a single dark vertically oval spot behind the eye; a small black spot at rear base of dorsal fin.

Hemipteronotus Lacépède, 1802

Hemipteronotus LACÉPÈDE, 1802, Hist. nat. Poissons *3*: 214.

(ἡμι = half; πτερόν = wing; νῶτος = back)

Diagnosis: Body oblong, rather steep, strongly compressed; lateral line interrupted behind; dorsal with nine spines, first two dorsal spines may be more or less conspicuously removed, not entirely detached; head deep, the dorsal profile with a sharp edge, strongly curved, sloping almost vertically from before the eyes to snout; eye much nearer dorsal profile of head than mouth; head naked except for small scales on the cheeks; mouth small, low, jaws not highly protractile; two enlarged curved canine teeth anteriorly in jaws; no posterior canines, gill membranes attached to isthmus; gill rakers not long.

The classification of the Razor fishes has been very confused, both at the generic and the specific level. Already GÜNTER (1862) and JORDAN (1890) discussed the necessity to unite some Razor fish species. DE BEAUFORT (1940: 54) remarked: "The genera *Hemipteronotus, Iniistius, Novacula* and *Novaculichthys* have been united by several authors into one. They are certainly very near to each other and species are known which form transitions from one genus to the other. It is greatly for convenience sake that I have kept these genera apart ... *Hemipteronotus* Lac. is the oldest name, and has to be used in case one considers these genera as one." RANDALL (1965) united the four genera together with the genus *Xyrichthys* under *Hemipteronotus*. For detailed information including a key to the Atlantic species of *Hemipteronotus* we refer to the same publication.

Hemipteronotus splendens (Castelnau, 1855)

(Fig. 7)

"Green Razorfish." *splendens* = glowing.

Xyrichthys splendens CASTELNAU, 1855: 28, pl. 5 fig. 2 (picture of the holotype in RANDALL, 1965, Copeia *4*: 494); PARR, 1930: 95; BEEBE & TEE-VAN, 1933b: 202.

Xyrichthys ventralis BEAN, 1890: 198; JORDAN, 1890: 659; LONGLEY & HILDEBRAND, 1941: 201.

Novaculichthys ventralis; JORDAN & EVERMANN, 1898: 1615.

Xyrichthys martinicensis METZELAAR, 1919: 109 (*non* Cuvier e.a., 1839); LONGLEY & HILDEBRAND, 1941: 203 (*non* Cuvier e.a.).

Xyrichthys argentimaculata BREDER, 1927: 66 (*non* Steindachner, 1861).

Novaculichthys rosepes BREDER, 1927: 67.

Xyrichthys rosipes PARR, 1930: 96 (*non* Jordan & Gilbert, 1884); BEEBE & TEE-VAN, 1933b: 202.

Xyrichthys venustus; PARR, 1930: 93 (*non* Poey, 1875).

Hemipteronotus splendens; RANDALL, 1965: 494, fig. 5, 6, 7; RANDALL, 1968: 215; BÖHLKE & CHAPLIN, 1968: 462.

Diagnosis: D IX-12; A III-12; V I-5; P I-10.
Suborbital distance not great; pelvic fins of large specimens very elongate; four scales above first lateral line scale to origin of dorsal fin; five pored scales in posterior section of lateral line; caudal fin rounded; gill rakers 17 to 21 (6 or 7 on upper limb); profile of forehead not notably steep; large specimens with a black spot within a pale region on side of body.

Hemipteronotus martinicensis (Cuvier & Valenciennes, 1839)

(Fig. 8)

"Straight-Tail Razorfish." *martinicensis* = from Martinique.

The great differences in color and shape of the fins made CUVIER & VALENCIENNES separate *Xyrichthys martinicensis* and *X. lineatus*, GÜNTHER *Novacula martinicensis* and *N. lineata* and POEY *Xyrichthys modestus* and *X. venustus*. RANDALL (1965: 499) stated: "The author suspected that the 2 were the same only after noting that they lived together in the same habitat and that the larger form, which was less frequently seen, is always male."

JORDAN (1886c) was mistaken in regarding *X. vitta* C. & V. as a synonym of *martinicensis* (RANDALL, 1965: 493).

The present author after examining the original specimen (Z.M.A. 108.362) considers METZELAAR's *Xyrichthys martinicensis* as belonging to *Hemipteronotus splendens*. This conclusion was confirmed by RANDALL (*in litt.*). There is also no doubt that the *X. martinicensis* described by LONGLEY & HILDEBRAND (1941: 203–205) is *He. splendens*.

Xyrichthys martinicensis CUVIER & VALENCIENNES, 1839, *14*: 49; JORDAN, 1886c, d: 541, 598.
Xyrichthys lineatus CUVIER & VALENCIENNES, 1839, *14*: 50 (*non* Gmelin).
Novacula martinicensis; GÜNTHER, 1862, *4*: 171.
Novacula lineata; GÜNTHER, 1862, *4*: 171.
Xyrichthys modestus POEY, 1867: 238; JORDAN & EVERMANN, 1898: 1619.
Xyrichthys venustus POEY, 1875: 110.
Xyrichthys infirmus BEAN, 1890: 199, pl. 29.
Novaculichthys martinicensis; JORDAN & EVERMANN, 1898: 1616.
Novaculichthys infirmus; JORDAN & EVERMANN, 1898: 1616.
Hemipteronotus martinicensis; RANDALL, 1965: 497; RANDALL, 1968: 216; BÖHLKE & CHAPLIN, 1968: 463.

Diagnosis: D IX-12; A III-12; V I-5; P I-10.
Suborbital distance not great; pelvic fins of large specimens moderately long; four scales above lateral line scale to origin of dorsal fin; five pored scales in posterior section of lateral line; caudal fin truncate or very slightly rounded; gill rakers 21 to 25 (7 or 8, usually 8, on upper limb); all dorsal spines about equally flexible; no black spot on side of the body; axil of pectoral fin dusky to dark brown.

III. GENERAL INFORMATION

The investigations were carried out in Curaçao (N.A.) at the Caribbean Marine Biological Institute (Caraïbisch Marien-Biologisch Instituut), the CARMABI, from June 1962–December 1963, with a break from February–April 1963, when comparative studies were done in Puerto Rico on Isla Magueyes, off La Parguera, in the field station of the Institute of Marine Biology, Mayagüez, University of Puerto Rico.

Because of the great conformity of the coastal areas of investigation in Curaçao and Puerto Rico, the data may well be compared. The only difference in the collecting procedure was that in Puerto Rico a boat had to be used to visit the reefs, while in Curaçao collecting could be done starting directly from the shore.

Curaçao

Curaçao, the largest island of the Netherlands Antilles, is located in the southern part of the Caribbean Sea (12°15′ N, 69° 00′ W), only 64 km from the Venezuelan mainland coast but out of reach of the mud-laden coastal waters.

The climate of Curaçao is characterized by high temperatures, a low erratic rainfall and strong tradewinds, the averages being about 27°C, 50 cm and 5 m/sec. respectively. Most of the rain comes down in short, heavy showers. The rainwater hardly penetrates the rocky surface and for the greater part runs off straight to sea. Rivers are absent and the coastal water is crystal clear which favors coral growth.

The tide is predominantly diurnal with a semidiurnal tide superimposed, resulting in an irregular rhythm. Even at spring tide the range is less than 30–40 cm.

Nevertheless, these differences may cause strong currents, particularly in the narrow natural canals that connect several large inland bays with the sea (e.g. Piscadera Bay). Here, the local coastal water may remain turbid by the tidal current for one to two hours.

Surface coastal water temperatures have a fairly small range, averaging 27°C in January–February, 26°C in March–April, 27°C in May–September and 28°C in October–December.

The salinity has an annual mean average of 36.1‰.

Since the longitudinal axis of Curaçao runs NW-SE, the prevailing easterly trade-winds strike the island at an oblique angle. This accounts for the marked difference between the N-E and the S-W coasts.

The N(E) coast is subjected to strong wind and wave action. There are almost no bays; along this whole north coast waves lash the steep coral limestone cliffs. As a consequence, only experienced swimmers manage to explore this northern coastal area.

On the contrary at the S(W) coast, there is much less wave action. Drowned valley systems turned into several handshaped bays. The S coast is also cliff-lined with in many places ridges and beaches of coral debris and coral sand.

Along the north as well as the south coasts rather strong currents run in a western direction.

The littoral margin of Curaçao is very narrow: at only 10–100 m from shore the bottom slopes down steeply at the so-called "blue edge." Generally, between the shore line and this blue edge there is a flat, sandy plateau. Where beaches occur, the depth increases more gradually whereas in front of cliffs and ridges the increase in depth is sudden and great.

The clear coastal water, proper temperature, the availability of oxygen and food (as a result of constant motion) and suitable sites (slightly raised above the bottom) gave coral reefs an opportunity to develop in the shallow water, which renders the area appropriate for studying coral fishes.

Some of the most common coral species in the shallow are explored are *Montastrea annularis, M. cavernosa, Diploria strigosa* and *Siderastrea siderea*, forming the most conspicuous massive coral heads. Between these corals smaller protuberances of *Agaricia agaricites, Porites astreoides* and *Meandrina meandrites* are to be found together with the small branched *Eusmilia fastigiata*, while *Madracis asperula* covers large parts with an ostensible fluffy layer. Gorgonids are frequently found. In shallow waters mostly *Acropora palmata* occurs. The walls of coral shingle are generally derived from more fragile species such as *Acropora cervicornis* which usually occurs in somewhat deeper water.

More detailed information about the coast, respectively the corals of Curaçao is given in the publications of the Buisonjé & Zonneveld (1960) and Roos (1964, 1967, 1971).

Puerto Rico

Puerto Rico, one of the Greater Antilles (18°00′ N, 66°–67° W), has forest-capped mountains. The arid climate of the southwestern part of the island, however, is quite similar to that of Curaçao. In this area – where part of the studies was done – the

annual rainfall is low (76 cm) while the evaporation rate is high; no rivers are present and the coastal water is usually very clear.

The tide is mainly diurnal with a range of less than one foot. Surface water temperatures range from about 25.5°C to 32.0°C. The salinity averages 35.4‰.

Winds and waves from the Atlantic strike Puerto Rico from the E and N-E almost constantly. The S and W coasts, however, are subjected to much less heavy surf and winds. In the area of La Parguera the winds blow from the SE or ESE. Oceanic currents run along the N and S coasts in a western direction.

Except at the eastern and southern parts of the W coast, the shallow coastal belt of Puerto Rico is at most places only a few km wide. Off La Parguera after approximately 9 km the bottom drops from 22 m to 1300 m.

Along the south coast of Puerto Rico conditions favor coral growth. In front of the coast at La Parguera numerous well-developed coral reefs occur as far as 10 km offshore. The "inner reefs" are situated close to the shore forming an arc, convex to the south. Some 3 km off shore there is a second line of elongate "outer reefs." Between the inner and outer reefs the depth ranges from 15 to 20 m. The bottom here consists of fine to medium-grained calcareous sand. South of the outer reefs to the edge of the "shelf" the depth also varies from 15 to 20 m.

Detailed information about the shape and history of the reefs off La Parguera and their coral growth is given in the publication of ALMY & CARRIÓN-TORRES (1963).

IV. ABUNDANCE, ENVIRONMENT, AND DISTRIBUTION

Abundance and environment

Various places were visited in order to get an impression of the distribution and abundance of the species studied and to find out where collection would yield the best results. Finally ten localities on Curaçao and seven localities in Puerto Rico were selected for fishing (Table 2). In Chapter III is explained why on Curaçao only the S-W coast was suitable for our purpose; in Puerto Rico the study had to be confined to a small area near La Parguera, situated in the S-W part of the island.

The collecting localities were: soft sloping sandy plateaus scattered with numerous coral formations (Playa Kalki, center of Porto Marie, west part of Boca San Michiel); coral reefs (Piscadera Bay, Puerto Rico); exposed rocks and corals along the cliff coast (Westpunt, east of Porto Marie, westward of Piscadera Bay, coast between Pietermaai and Marie Pompoen). On beachrock terraces in very shallow waters along the shore line, constantly exposed to the surf (west parts of Vaersen Bay and Boca San Michiel) collecting was less easy.

Because of the advantage of quick transport most collecting was done at Piscadera Bay and the Boca San Michiel. Seventeen trips were made to the coastal area of Porto Marie when it appeared that this was the spot to find *Hemipteronotus martinicensis*. In Puerto Rico the outer reef Cayo Turrumote was both rich in number of

species and in specimens. Its great distance from the shore, however, gave difficulties in rough sea – which often was the case – so most collecting had to be done at the fringing reefs of San Laurel.

TABLE 2

DISTRIBUTION AND ABUNDANCE ON THE VARIOUS LOCALITIES of *Thalassoma, Halichoeres* and *Hemipteronotus* species

– not found
\+ present (1–5 observed)
++ abundant (5–15 observed)
+++ very abundant (> 15 observed)

Locality	*Thalassoma bifasciatum*	*Halichoeres*				*Hemipteronotus*	
		bivit.	*garnoti*	*maculi.*	*poeyi*	*splendens*	*martini.*
CURAÇAO							
Playa Kalki	++	++	–	–	–	–	–
Westpunt Baai	+++	+++	+	+	–	–	–
Santa Cruz Baai	++	++	+	+	–	–	–
Boca Santa Marta	+++	++	–	–	–	–	–
Porto Marie Baai	+++	+++	++	++	+	+	++
Daaibooi Baai	++	++	+	+	–	–	–
Vaersen Baai	+++	+++	–	–	–	–	–
Boca San Michiel	+++	+++	++	++	+	+	–
Piscadera Baai	+++	+++	++	+	+	–	–
Coast at Penstraat	+++	++	+	+	–	–	–
Total collected	2411	1319	383	149	62	85	151
PUERTO RICO							
Cayo San Christóbal	++	++	–	–	–	–	–
El Laurel	+++	+++	–	+	–	–	–
La India	+++	+++	–	+	+	–	–
Cayo Májimo	++	++	–	+	–	–	–
Isla La Gata	–	++	–	+	–	–	–
Palo	++	++	–	–	–	–	–
Cayo Turrumote	+++	+++	–	+	+	–	–
Total collected	356	595	–	19	4	–	–
Grand total	*2767*	*1914*	*383*	*168*	*66*	*85*	*151*

The number of specimens present at a given moment on a certain spot, depends on a number of uncontrollable variables, e.g. meteorological circumstances and the time of the day. Places where wrasses were exceedingly abundant proved to be devoid of labrids early in the morning and around and after sunset. Cloudy weather or turbidity due to hurricane influences made the numbers present also decrease. Studies of distribution based on field observations have to take into account these facts and are in a way unreliable. Poisoning the whole population in a certain area provides a small chance that animals escape observation. It does not, however, completely rule out the said variables of weather and time of the day. Moreover, even then labrid fish are capable of escaping because of their well-developed hiding mechanisms.

As I had the opportunity of visiting the localities at many different times, the final conclusions are based on observations under various circumstances. Moreover, the hoopnet ensured catches of representative samples of the wrasses present at the moment of collecting. Thus, taking into account the restrictions discussed above, it was felt justified to consider the observations under discussion as giving a not too distorted idea of the whole population living at a certain spot.

The distribution of the seven species is given in Table 2. The relative abundance has been indicated by +++, ++, + or — (i.e. "exceedingly abundant" up to "not present"). Exact figures have only been listed for the total numbers per species. (Exact numbers for the different localities would be incomparable, some having been visited more frequently than others).

Thalassoma bifasciatum and *Halichoeres bivittatus* are approximately evenly distributed in all localities and are present in large numbers wherever they occur. *H. garnoti* and *H. maculipinna* were found in considerable numbers in some localities only, whereas *H. poeyi* and *Hemipteronotus splendens* occurred here and there and always in small numbers. *He. martinicensis* has exclusively been found at one strictly located spot, but there in relative abundance.

It is remarkable that in Puerto Rico nearly no wrasses were found on several beautiful inner reefs near La Parguera, though they were abundant in variety of species and in number of specimens on the outer reefs.

No consistent differences in salinities between the inner reefs and the more open waters were reported (ALMY & CARRIÓN-TORRES, 1963). Rapid growth of red mangroves and still developing mud flats covering dead colonies of *Porites porites* were found in the inner reefs due to less intensive wave action. Oxygen and temperature may vary to a greater extent in the inner lagoons of the inner reefs than in the same areas of the outer reefs. These factors may well have influenced the presence of the labrid fishes. It is worth mentioning that for stony coral species as well ALMY e.a. found the greatest variety of species on the outer reef of Cayo Turrumote.

Next to the localities listed in Table 2 other habitats were also visited. It was apparent that labrids prefer clear water. For instance, no labrid fish were found in muddy parts close to mangrove vegetations where collecting with a special trait-net was tried, nor in the prairies of *Zostera* such as to be found close to the field station at La Parguera, P.R., or Awa di Oostpunt and large parts of Fuik Bay, Curaçao. Only *H. poeyi* and *He. splendens* are said to frequent seagrass beds but not many of them were encountered here.

Another condition for the occurrence of labrids seems to be the presence of rocks and corals. On the extensive, bare sand cays between the reefs off La Parguera no fish were seen. Neither was any wrasse noticed on patches of bare sand along the shallow westcoast of Aruba or at San Nicolas Bay. But at the clear and rocky coast around the small island of Klein Curaçao and at many parts of the rocky coast of Bonaire similar variations in species and abundance have been observed as on Curaçao.

The species *Hemipteronotus martinicensis* differs from the other six species in some salient features. They form more close, homospecific colonies and were found consistently at one spot only. During each visit only about twenty to thirty specimens were seen, but on each following visit they were present in about the same quantity. Collecting apparently did not affect their number.

The area they frequented was a soft sloping sand cay at a depth of about eight meters, without large rocks or coral formations in the middle of Porto Marie Bay, at some distance of the more rocky areas where other wrasses occurred.

This species stayed close to the bottom, generally not higher than two to three meters above the sand. On the bottom many tiny hills could be seen. These, about 50 to 100 cm apart, consisted of the same

material as the rest of the bottom, not of detritus or small stones. Often, specimens were hovering perpendicularly close above such a hillock. At the slightest disturbance they dashed away into the sand. No specimens were straggling at more than a few meters' distance from the colony. Though at distances of about twenty meters other labrid species were found, *He. martinicensis* did not mingle with these.

Juveniles

Among aggregations of adult labrids no specimens smaller than about three cm have been found. Of all seven species studied the very young – in which gonads are not yet developed – were dwelling somewhere else.

Juvenile *Th. bifasciatum* and *H. bivittatus* have been found occasionally in rather shallow water at different times of the year, on Curaçao as well as in Puerto Rico. They were found in small shoals of about 7–15 individuals among the long spines of *Diadema antillarum*, where also clouds of copepods were observed, or they formed small schools around projecting pieces of coral or beach rock in areas also frequented by the larger wrasses. The juveniles stayed completely separate from these gregarious adults, even when being at no more than a few meters distance. They did not show any interest in sea urchin bait. On most revisits, the shoals of juveniles were not encountered again, but several times larger juveniles, of about 3–4 cm, were refound on the flat terraces in shallow water of Santa Cruz Bay. Here, collection with a small thrownet was possible.

Juveniles of *H. garnoti* occur more solitarily on bare sand banks. On rare occasions, a few of these orange-colored fishes were observed, staying close to the bottom of a flat cay along the eastern margin of Piscadera Bay. On the slightest disturbance they dashed off into the sand; only a small spot of broken ground gave away their hiding-place. By running a stick through this area the small fish could be forced to leave the sand. Usually, they managed to escape.

Juveniles of the other species have not been observed and collected.

Bathymetrical distribution

For various fish species a size-depth relation has been mentioned. Moe (1966, 1967) suggested that red groupers may move offshore as their size increases. According to Quignard (1966) the juveniles of

some Mediterranean *Labrus*, *Symphodus*, *Ctenolabrus* and *Coris* species live very close to the shore, in a depth range of only a few centimeters to three meters. Individuals of one year and older frequent areas of three to six meters deep.

The present author also noticed that in shallow waters small labrids were often found, and large, terminal phase fish only occasionally, but she considers this separation as not definite. (The actual age of the wrasses was not determined, as she could find neither in the scales nor in the otoliths sufficient indications, a consequence of the absence of distinct seasons in the Caribbean region.)

Juveniles of *Th. bifasciatum* and *H. bivittatus* occurred in shallow waters of one to a few meters deep, while juveniles of *H. garnoti* were found on a sand bank at a depth of about three to five meters. Small individuals of the first adult phase – about 3 to 5 cm length – of the former two species were often encountered in shallow waters of only 20 to 100 cm deep, dancing up and down, moving along with the turbulence of the water.

These small individuals, however, were also seen playing around in choppy water around emerging rocks that went steep down several meters, or moving along close to the bottom some meters deep. Moreover, small *bifasciatum* and *bivittatus* individuals were noticed while cleaning ectoparasites from other species which never come close to shore but frequent the area around the blue edge.

On the other hand, larger individuals sometimes joined the small ones in the shallow areas. Yet, large, terminal phase fishes clearly prefer water of more than two, three meters deep.

It may be concluded that both *Th. bifasciatum* and *H. bivittatus* not only have a wide geographical distribution but also cover a large range in depth, from very shallow water to the areas along the blue edge. This agrees with the data reported by LONGLEY e.a. (1941).

Halichoeres garnoti was never observed in shallow waters close to the shore nor in deeper water of deeply landlocked bays. This species showed preference for more turbulent places in the open sea.

It was for instance rarely encountered in Piscadera Bay but large

groups of all sizes could be found just westwards of this bay in waters only a few meters deep, where there was more wave action. In the same way one had to go eastwards of Porto Marie Bay or around the corner of the steep cliffs that border the deep landlocked bay of Santa Cruz to find *H. garnoti*. Its preference for open water may account for the fact that this species has been mentioned relatively rarely and up to now was less well represented in collections, compared to the former two species (see Table 1).

Halichoeres garnoti is not restricted to a small range in depth. BÖHLKE e.a. (1968) reported that it has been collected down to a depth of 160 feet.

Small specimens of *H. maculipinna* were often observed playing around in very shallow waters among groups of small specimens of *Th. bifasciatum* and *H. bivittatus*. Large, terminal phase specimens prefer to stay more close to the bottom in waters of a few meters deep. This species has been collected down to a depth of 80 feet (RANDALL e.a., 1965).

H. poeyi and *He. splendens* were found in not too turbulent waters of a few meters deep. *He. martinicensis* has only been observed in water of a few meters deep, but RANDALL (1965) collected specimens from 20 to 70 feet.

MIGRATION AND HIBERNATION

Factors which may bias sampling include migration and hibernation.

In wrasses living in colder areas a seasonal disappearance has been suggested occasionally (GOURRET, 1893). LÖNNBERG e.a. (1937) report that European *Labrus ossifagus* (*bimaculatus*) is found in shallower waters in May and June during the spawning season. Later, when in autumn the water gets colder, the fish disappear from their summer haunts. It is suggested that the wrasses not really leave the coast but only move down to about 40 m depth. Here, the water stays some degrees above zero. Empirically, they found that the wrasses could not endure a temperature closer to the freezing point. For both Mediterranean *Coris julis* (TORTONESE, 1967) and *Xyrichthys novacula* (QUIGNARD, 1966) a migration towards deeper levels of more than 100 meters during winter has been reported.

Hibernation, burrowed under the sand, may also account for the absence during

the cold season. Fishermen at the Laboratoire Arago, Banyuls-sur-Mer (France) provided me the information that during the winter months repeatedly girelles had been invisible, hidden away in the sand of large aquaria.

In the Caribbean a seasonal disappearance can be excluded since the temperature of the water, at the depth the wrasses frequent, is high the whole year through. This is supported by the fact that both the number of specimens found during the 15 months of observation and collecting, and the numbers of specimens with functional gonads remained fairly constant.

GEOGRAPHICAL DISTRIBUTION

The following reviews the habitats and abundance for the species studied as apparent from the literature. Only those papers were included in which the diagnosis satisfied the criteria set for our own material.

Thalassoma bifasciatum has been described from many places in the West-Indies. The most northern areas in the south-west Atlantic are: Bermuda (GOODE, 1877; BARBOUR, 1905; BEAN, 1906a, b; NICHOLS, 1920; BEEBE e.a., 1933a, b) and the Bahamas (BEAN 1905 – Eleuthera, Nassau; ROSÉN, 1911 – Andros Isl.; FOWLER, 1919, 1947; NICHOLS, 1921 – Turk's Isl.; BREDER, 1927; PARR, 1930; STOLL, 1955 – Bimini; RANDALL e.a., 1963; BÖHLKE e.a., 1968). Along the coast of Florida: Tortugas (JORDAN e.a., 1905), Panama City (CALDWELL, 1959), Miami (FOWLER, 1923) and the Florida Keys (FOWLER, 1928 – Key West; FEDDERN, 1965).

The most westward data are from Cozumel Island, Yucatán (BEAN, 1890) and Honduras (FOWLER, 1942 – Sheen Cay), while many specimens have been reported for the Antilles (GRONOVIUS, 1781), Cuba (POEY, 1860, 1868; BREDER, 1927), Jamaica (GÜNTHER, 1862; POEY, 1875; JORDAN e.a., 1897), Haiti (FOWLER, 1928, 1937, 1952; BEEBE e.a., 1928), the Dominican Republic (CUVIER e.a., 1839), Puerto Rico (NICHOLS, 1915), the Virgin Islands (BLOSSER, 1909 and FOWLER, 1919 – St. Croix; RANDALL e.a., 1963; RANDALL, 1963 – St. John), St. Martin and St. Eustatius (METZELAAR, 1919), Martinique (CUVIER e.a.) and the Grenadines (BEEBE e.a., 1935). The most southern data are Colombia (FOWLER, 1953 – Courtown Keys), Venezuela (CERVIGÓN, 1966), and Curaçao and Bonaire (METZELAAR).

BLOCH's (1791 and 1801): "Habitat: Indicum mare" must be a mistake. OSORIO (1909) is the only author who reported *Julis nitida* for the Cape Verde Islands; BÖHLKE e.a. (1968) – without mentioning further references – gave as distribution for *Th. bifasciatum*: "recorded from both sides of the Atlantic." QUIGNARD (1966), however, did not include this wrasse in his detailed study on labrids from the Eastern Atlantic.

According to recent authors (e.g. FEDDERN, 1965) and our data *Thalassoma*

bifasciatum is a common West Indian species, widely distributed on the reefs. The yellow phase significantly outnumbers the larger, bluehead phase (Table 4).

In older quotations, however, the bluehead has been described as more common. GRONOVIUS, BLOCH, CUVIER & VALENCIENNES, SWAINSON and POEY (Table 1) exclusively described the bluehead form; JORDAN & EVERMANN entitled it as "not uncommon," but for description of the yellow specimens they had to quote GOODE, because they did not know this "species" themselves. METZELAAR mentioned "West Indies, not uncommon" for the bluehead, while he described the yellow "species" for Jamaica only. Similar discrepant information was given by BEEBE & TEE-VAN.

Coincidently as the homospecific character of the yellow and the bluehead specimens was realized, the reports on the abundance agreed more with recent observations.

A similar situation can be encountered when reviewing the literature on the Mediterranean *Coris julis*. The oldest descriptions of this Mediterranean labrid only concerned the larger, more gorgeous phase; then, for a long time, this "species" was considered as more numerous. Recently e.g. ROEDE (1966) proved that the smaller, sober specimens were significantly in the majority. As I then remarked "The preference of former days for putting large, remarkable individuals into museum collections apparently caused an extreme selection and hindered the proper conclusions about distribution and frequency."

Halichoeres bivittatus ranges further north and south than any of the other labrids studied.

It was reported as north as Beaufort, North Carolina (GILL, 1863; JORDAN e.a., 1878; JORDAN, 1886a; JORDAN e.a., 1886). For Bermuda (BEAN, 1906b; RANDALL e.a., 1965), the Bahamas (BÖHLKE e.a., 1968), Tortugas (LONGLEY e.a., 1941) and Key West, Florida (JORDAN e.a., 1882a; JORDAN e.a., 1898). Moreover for the Gulf of Mexico (GOODE e.a., 1882) and Panama (MEEK e.a., 1928).

In the Caribbean Sea – Cuba (POEY, 1860, 1868, 1875; GÜNTHER, 1862; JORDAN, 1885, 1886b; JORDAN e.a., 1898), Jamaica (GÜNTHER, 1862; BEAN e.a., 1894), Puerto Rico (RANDALL e.a., 1963), the Virgin Islands (RANDALL, 1963; RANDALL e.a., 1963), St. Martin (COPE, 1870; METZELAAR, 1919), Martinique (BLOCH, 1791; LACÉPÈDE, 1802), Barbados (STEINDACHNER, 1867), Aruba, Bonaire, Curaçao and Trinidad (METZELAAR) and Venezuela (CERVIGÓN, 1966). More southward localities are Suriname (CUVIER e.a., 1839, specimen bought in Amsterdam; STEINDACHNER) and Brazil (JORDAN e.a. 1898; METZELAAR; RANDALL e.a. 1965).

H. bivittatus, in former centuries mentioned more often than the other species (Table 1), was already in the earliest descriptions reported as exceedingly abundant (JORDAN & HUGHES, 1886). This was affirmed by e.g. NICHOLS (1930), LONGLEY & HILDEBRAND (1941) and RANDALL & BÖHLKE (1965).

H. bivittatus has been observed along rocky and weedy shores and reefs (JORDAN e.a.), interstices of the reefs and also a variety of localities in shallow waters (NICHOLS) and reef and reef-sand areas (RANDALL e.a.), while HILDEBRAND reported: "inhabits grassy bottoms and also is common about coral stacks and gorgonians and on alga-covered bottom."

Halichoeres garnoti also shows a wide distribution.

It was reported as north as Bermuda (BEAN, 1906a, b; BEEBE e.a., 1933a; RANDALL e.a., 1965), the Bahamas and Florida (BREDER, 1927; PARR, 1930; RANDALL e.a.;

BÖHLKE e.a. 1968). For the Caribbean Sea from Cuba (POEY, 1860; JORDAN 1886b; JORDAN e.a., 1886; JORDAN e.a. 1898; RANDALL e.a.) and from Jamaica, Haiti (RANDALL e.a.), Puerto Rico and the Virgin Islands (COPE, 1870 – St. Croix; NICHOLS, 1930; RANDALL e.a. – St. John), from Martinique (CUVIER e.a., 1839; JORDAN, 1886; JORDAN e.a. 1898), from Grenada, Barbados, Tobago (RANDALL e.a.), Venezuela (CERVIGÓN, 1966) and from Curaçao (METZELAAR, 1919; RANDALL e.a.) and Bonaire (METZELAAR).

BEEBE & TEE-VAN (1928) were among the first authors to give more information than just the occurrence when they reported "found on all coral reefs." RANDALL & BÖHLKE (1965: 252) wrote: "Although not well represented in collections, *H. garnoti* is a moderately common reef fish in the West Indies and Florida Keys."

Halichoeres maculipinna is neither limited in its distribution.

It has been reported from Bermuda (BEAN, 1906a, b; NICHOLS, 1920; BEEBE e.a., 1933a, b), the Bahamas (RANDALL e.a., 1965; BÖHLKE e.a., 1968), Florida (LONGLEY e.a. 1941 – Florida Keys; RANDALL e.a.) and in the Caribbean Sea: Puerto Rico Mona Island, Virgin Islands, Barbados, Tobago (RANDALL e.a.), Trinidad (GÜNTHER, 1862; RANDALL e.a.), Curaçao, N.A. (METZELAAR, 1919; RANDALL e.a.). CERVIGÓN (1966) reported it for Venezuela and STARKS (1913) for Natal, Brazil.

Only one specimen (no longer existent) has been reported from Beaufort N. C. (JORDAN e.a., 1878). [This was copied by JORDAN e.a. (1886), JORDAN e.a. (1898), METZELAAR (1919), RANDALL e.a. (1965) and CERVIGÓN (1966)]. As discussed in Chapter II, the present author considers this a case of misidentification; no further specimens of *H. maculipinna* have been reported from such northern areas.

H. maculipinna, not often mentioned in former days (Table 1), was considered as a moderately common species by LONGLEY & HILDEBRAND (1941), RANDALL & BÖHLKE (1965) and CERVIGÓN (1966).

STARKS (1913) collected *H. maculippinna* in tide pools. LONGLEY e.a. (: 190) reported: "Found occasionally along the rocky shore of Loggerhead Key, rather more abundant and larger in the coral and gorgonian belt west and north of this key and most numerous along the outer face of Bird Key reef, where the bottom is thickly threwn with small dead heads of massive coral, overgrown with *Sargassum* and the slit fronds of iridescent *Zonaria*."

Halichoeres poeyi was described from the Atlantic coast of tropical America northward to Florida.

More in detail: the Bahamas (RANDALL e.a., 1965; BÖHLKE e.a., 1968), Florida (BREDER, 1927; LONGLEY e.a., 1941 – Florida Keys; RANDALL e.a.), Cuba, Jamaica (JORDAN e.a., 1898; RANDALL e.a.), Hispaniola, Puerto Rico, the Virgin Islands, St. Martin, Martinique, Dominica, Grenada and Curaçao (RANDALL e.a.), Panama (MEEK e.a., 1928 – Colón); Surinam (STEINDACHNER, 1867; JORDAN e.a., 1898) and Brazil (CUVIER e.a., 1839 – Bahia; JORDAN e.a. 1898; STARKS, 1913 – Natal; NICHOLS, 1930; RANDALL e.a. – Bahia, Rio de Janeiro).

Concerning *H. poeyi*, only occasionally mentioned in former days, LONGLEY & HILDEBRAND (1941: 194) remarked: "This fish may be found singly, or by twos and threes, about Loggerhead Key, but it is more abundant on Long Key flats and inside Bird Key reef." RANDALL & BÖHLKE (1965: 249) wrote: "Occasionally it may be encountered on reefs."

Next to the presence in tidepools mentioned by STARKS (1913), LONGLEY e.a.

(: 194) write: "In spite of the fact that an occasional individual may be seen even on the isolated White Shoal, where no turtle grass occurs, its preferred habitat is in *Thalassia*." According to RANDALL e.a. (: 249) "*H. poeyi* is most commonly seen in seagrass beds, for which its green color is appropriate." This has been repeated in BÖHLKE e.a. 1968.

Hemipteronontus splendens does not essentially differ in its distribution from the other labrid species.

It has been reported from Bermuda (BEEBE e.a., 1933a; RANDALL, 1965), the Bahamas (BREDER, 1927 – Cay Sal Bank; PARR, 1930 – Turk's Islands; RANDALL; BÖHLKE e.a. 1968), Florida (BREDER, 1927 – Alligator Reef; LONGLEY e.a., 1941 – Tortugas, north of Loggerhead; RANDALL – Florida Keys), Cozumel Island, Yucatán (BEAN, 1890; JORDAN e.a., 1898; RANDALL), and many places in the Caribbean, such as Puerto Rico, the Virgin Islands, St. Eustatius, St. Lucia and the Grenadines and more southwards Curaçao, and Brazil (RANDALL).

He. splendens has only occasionally been mentioned formerly, but according to LONGLEY and RANDALL it is common in sandy regions and open water as well as in *Thalassia* and *Zonaria* areas.

Of *Hemipteronotus martinicensis* only few older data are extant.

It was reported from Martinique (CUVIER e.a., 1839; JORDAN e.a., 1898), Cuba (POEY, 1867; JORDAN e.a., 1898), and Cozumel Island, Yucatán (BEAN, 1890; JORDAN e.a., 1898). RANDALL (1965) collected specimens in the Bahamas, Puerto Rico, the Virgin Islands, Barbados and Curaçao; BÖHLKE e.a. (1968) describe the species from the Great Bahama Bank.

Their being bound to special habitats – at some distance of other labrids – may explain why *He. martinicensis* has not been reported very often.

RANDALL (1965: 500) describes the occurrence of a colony "in 30 ft. of water in sand and *Halophyla* bottom." In 1968 (: 216) he writes: "on sand bottom. Not uncommon at depths of about 20 to 70 feet." BÖHLKE & CHAPLIN (1968: 463) have taken this species only once but then in fair numbers, from a light marly sand bottom at a depth of 45 to 50 feet, from a bed of garden eels. They describe little pits in the sand into which the fish dive when approached but do not mention the obvious little hills, seen by the present author.

The enumeration of habitats makes it evident that the seven labrid species are restricted to the Atlantic coasts of tropical America.

V. METHODS

COLLECTING

Collecting of wrasses is a challenge, a game, because they are swift, dexterous and agile fish. Unexpectedly and rapidly they may vanish, slip into small holes and openings in the rocks, hide in the sand and apparently disappear from the scene. Accordingly, they were given names such as "Slippery Dick." Moreover, they are very handy in stealing bait without getting caught. Hence the argot name "dégraisseur," given on Martinique.

In antiquity the greedy character of Mediterranean wrasses was already known. One of the hunting hounds of the packs of Acteon was given the name *Labros* to indicate its voracity and impetuosity (Met. i. III., v 224). Their reputation of those days of being cunning, tricky, tantalizing and even wicked is well expressed and indicated in the greek proverb: "γύλος εἶμαι σὲ γελῶ καὶ χάνος εἶμαι χάνομαι" (I am γύλος, the mocker, and I laugh at you; I am χάνος the gaper, and I scoff at you)" (quoted by MAIR, in D'ARCY THOMPSON, 1947).

As their fast flight reaction may cause undesirable selection, the author screened several methods to decide which one would best approximate random sampling by yielding large catches.

In areas such as the Mediterranean where labrids are used as food,* various

* DIOSCORIDES (B 35) and PLINY (xxxii 94) already gave recipes for the use of wrasses in fish soups. More recently, the novelist SIMENON also mentions the girelle as a tasteful ingredient in soups.

procedures have been developed, among which the use of special baskets, called "girelliers" from the French name "girelle" for the wrasse *Coris julis*. These were not available nor appropriate for the purpose of catching large numbers of specimens such as required for the present study.

In the Caribbean the smaller labrid species are rarely used as food. Incidentally they are caught by the common methods such as spear, hook-and-line or glass jars, timetaking procedures with low output. Results are no better by the use of traps.

Traps or fish pots are in widespread use in the tropics ("canaster" Cur., "canasta" P.R.). Both cylindrical and polygonal shapes, of extra small mesh size, were tried. Most of the wrasses, however, seem to escape when the traps are left on the bottom for a longer period of time. If the traps are left in the sea overnight, as is generally done, no labrids will be found in them at all. Most fishes, once inside a trap, try to escape by probing the periphery rather than the center of the trap where the small opening is located. Labrids, however, professionals in slipping through small passages in coral and rocks, have no problems in finding their way out of the trap once they have lost interest for the bait inside. The only useful method was to stay with the trap and empty it after 10 to 30 minutes. Yet, even when the number caught was increased by diving down to chase surrounding wrasses into the trap, the yield was mostly low, too selective and time-consuming.

Poisoning with a solution of rotenone ($C_{23}H_{22}O_6$) causes a vasoconstriction of the capillaries of the gills (HAMILTON, 1941). This method used in studies on fish populations in particular locations, did not work with our labrids. In Puerto Rico the poison was released near the bottom, but the wrasses could even escape from this radical method. (Later, RANDALL, 1965, managed to capture *Hemipteronotus martinicensis* by forcing emulsified rotenone into the sand.)

An often used tool in the tropics is the thrownet, a circular net with lead weights around the periphery. For the purpose of catching small coral fishes a particular thrownet of about 100 cm diameter was used. It had a hole in the center, through which one hand could reach and move the coral and rocks used as a shelter by the fishes, whereas the other arm pressed down upon the net to keep it close to

the bottom. The roused fishes were removed by hand through the hole.

This proved to be the only successful method for catching the very small (< 3 cm) youngsters of *Thalassoma bifasciatum*, *Halichoeres bivittatus* and *H. garnoti* that do not mingle with the larger congeners nor show any interest in bait. For collecting juvenile *garnoti* one had to poke around in the sand to make them come out to be caught.

When throw-nets were used on the larger wrasses, most were able to hide or slip away, hence this method was abandoned for collecting adults.

The final method we chose was that with the hoop-net, a type of a lift net, commonly used to catch crabs (Fig. 1).

Special nets were made of light blue nylon petticoat gauze with a mesh size of 0.3 cm. The bag of the cylindrical net was made 1 m deep, the upper part being fixed around a plastic covered iron hoop of 90 cm diameter. Four lines attached to the hoop were bound together on a long rope. As the net is lowered on the bottom,

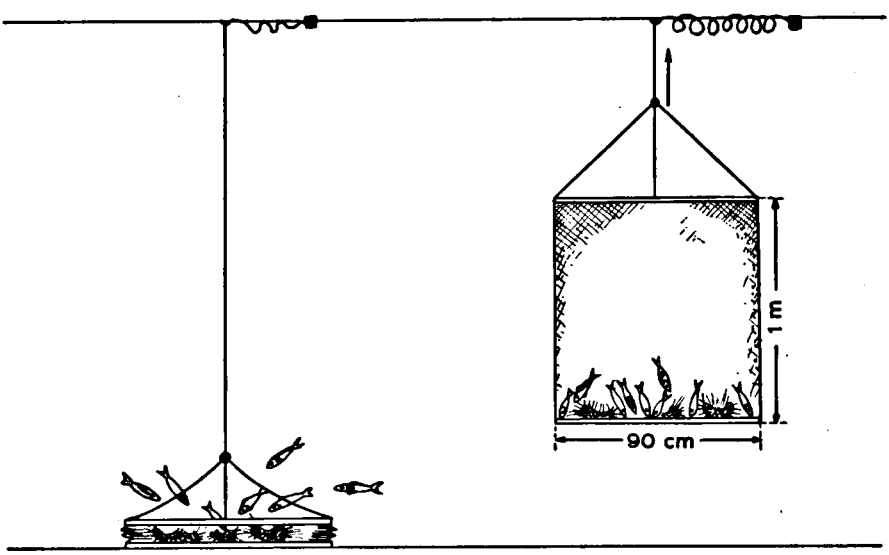


Fig. 1. Collecting with the hoop-net.

the gauze side walls fold together. It is important to place the net properly, so that the heavy hoop keeps the gauze down and prevents the sides of the net from moving to and fro with the water, which might frighten the wrasses.

Sea urchins were used as bait, the long spined *Diadema antillarum*, or if present, *Echinometra lucunter*, with smaller and less dangerous spines. The wrasses did not show any preference for either of the two species. When the echinoids are crushed the carnivorous labrids are readily attracted. The bait was crushed just above the net on the bottom of the sea. Although this requires diving down, disturbing the environment, it is preferable to crushing the sea urchins at the surface; portions of the bait might then attract fishes away from the net, while the concentration of bait on the net will be lower.

The collector swims at the surface observing the net through a face mask. When sufficient wrasses are over the surface of the net and in position to be caught, the long rope is rapidly pulled up. The fishes are disturbed by the movement and unfolding of the walls of the net which in this case is an advantage, as the labrids have a downward alarm reaction. They try to hide in the sand and thus congregate on the bottom of the net.

At the surface the captured fish are placed in a large potato or flour bag, fixed on a floating motor tube. After several hauls, when a sufficient number of individuals has been caught, the tube is pulled ashore. Thus the fish are kept alive for up to 30 minutes. In Puerto Rico, where collecting was done some miles offshore, every haul was pulled into the boat and the fish killed immediately.

As to the chance of getting random samples, the large number of specimens and the variety of species caught in this way seem to be encouraging. In many of the collecting stations various species were taken in the same haul. Moreover, the specimens collected in this manner are not selectively those that are hungry, but also bystanders, moving along with the group. This is one of the advantages over the use of a chicken wire trap, in which selection according to interest in food is predominant as the just curious ones stay outside and the slower ones keep on picking towards the unreachable bait from the outside. Yet, some selection may have been made by excluding individuals that are less interested in food, less bound by group behavior, or burrowed under the sand.

Usually, collection trips were made every second or third day to investigate a possible relation of gonad activity with time of the year and with the lunar cycle. Therefore, date and place of collecting were meticulously noted.

Preparation of samples

About 1100 fishes were kept alive for experiments. Attempts to study the fishes in captivity were at first hampered by the fact that they are difficult to transport alive. The most successful way was to carry only a few specimens in each tube or tank, having a thick layer of sand on the bottom with a relatively small quantity of water.

The other 4474 wrasses were put to death immediately after collecting. Right after the catch had been brought aboard or on shore, the fish were placed into a plastic container filled with ice cubes. Within 15 seconds the fishes are passive, within a minute completely unconscious and after a few minutes they are dead. This method is preferable to bringing the fish into water with a strong concentration of an anaestetic. This makes them overactive during their last minutes and the coloration considerably darker, which is undesirable as the examination of the different color patterns is an essential part of this study.

Occasionally, some specimens were examined immediately after collection aboard or ashore. The majority of fish, however, were transported on ice and examined at the laboratory as soon as possible. The usual time delay between collecting and arrival at the laboratory varied from five minutes to one hour.

Approximately 20 per cent of the catches that could not be dealt with immediately was stored briefly (usually a few hours utmost three days) on ice at minus 20°C. This material, however, was not used for body measurements or weight measurements as described in Chapter VII and XI.

Observations

Of each fish dissected, besides place and day of collecting, the following data were noted:

a. color
b. total and standard length
c. sex and the state of the gonads.

Ad *a.* Standards for color classification are defined in Chapter VI.

Ad *b*. Of part of the material also other body measurements and meristic features as fin counts were included; see Chapter VII.

Ad *c*. After dissection, the gonads were classified macroscopically as "female," "male" or "non-functional." The maturity of each gonad was coded I–VII, from "developing" to "very mature" or "spent." Length, breadth and weight of the gonads of a number of specimens were determined as well. Part of the gonads were fixed in Bouin's solution for histological studies.

Stomach contents were collected of a number of specimens while age determinations were attempted at by examination of otoliths and scales.

In the relevant chapters the methods of investigation will be further described.

VI. COLOR

Introduction

Formerly color (not seldom color in spirits) was often used as the most notable criterion for separating labrid species. This has caused much confusion. Color is a reliable characteristic only when one is aware of the fact that in some wrasses rather striking changes in pigmentation occur during one lifespan, so that color differences within even one species may, deceptively, be more impressive than the color differences between different species. Moreover, the phenomenon of dichromatism added to the controversies on sex in this family. To clarify these issues color study was made an essential part of our investigations.

Terminology

In view of the results the following terminology is proposed:

Color phase – In labrids there is a strong relation between color pattern and body length. It is not illogical that the existence of different color patterns in groups that differ in length, can be considered as following each other in time. Hence instead of color pattern, the term "color phase" has been used to denote distinct combi-

nations of body and fin colors. – Consequently in the present paper "color phases" refer to non-reversible, relatively long-lasting stages. Once a changing of colors has started, the process will slowly go on in only one direction towards the subsequent phase.

First adult phase – These are the smaller individuals, captured with the method set for adults. They are larger than the juveniles, have a slightly or strongly different color pattern and in most cases macroscopically visible gonads, often in very functional stages. Therefore, I consider them as being adult.

Intermediate phase(s) – This refers to fishes in which apparently the colors are in the process of alteration from the first adult phase towards the final terminal phase.

Terminal phase – This notation is used to indicate the final color phase that can develop during one life span.

These terms will also be used when refering to successive color patterns as described in the literature. There, the first adult phase is usually denoted as "female" phase or as "females and immatures," while the terminal phase is named "male phase." These have to be considered as incorrect simplifications for most labrid species (see Chapter X).

Color production

Though fish display a considerable variety in integumentary coloration, there are mainly two mechanisms involved in color production. Color stems either from special absorption characteristics of pigments (carotenoids, melanins, flavines and pterins) present in the chromatophores, or from scattering, diffraction and interference of light beams due to the physical configuration of purines, mostly crystalline guanine, inside the iridophores. In some species one of these factors may predominate, in others both pigmentary and structural effects take an equal and often complementary share in the phenomenon. For instance, the silvery reflection in many fishes is related to interference colors of iridescence, fortified by underlying dark pigment. Blue and green pigments are rare in fishes, yet wrasses and parrot fishes often show these colors. Generally, this blue color is due to interference by thin lamellae of guanine or to Tyndall scattering by submicroscopic particles of guanine backed by a

melanin screen. Green aspects often arise from the combined effects of structural blue and a yellow pigment (Fox, 1953).

Changes of color

It is important to separate *morphological* changes from the *physiological* changes in color such as can be related to changes in affective behavior (fright, excitement) and diurnal rhythm.

The majority of papers dealing with color changes in fishes mainly concern the *physiological changes*, in which two agencies are involved. The fast alterations in shades and general pattern may be due to shifts in position of the pigment present within the chromatophores of the skin. These aggregations or dispersions of the pigment are reversible processes, that may take place in even less than a few seconds or minutes. Physical color changes occur by means of alterations in the interference pattern in guanine crystals found in the iridophores. These changes can also be produced within a short interval and are completely reversible too. Both mechanisms easily produce noticeable effects.

Morphological color changes – a term coined by Sécerov (1909, in Brown, 1957) – are of a completely different nature. They are due to increase or decrease of either the number of chromatophores or the amount of pigment they contain. These color changes develop slowly and gradually and hence are often more inconspicuous, even though the final effect may be striking.

The present study is focused mainly on the latter type of color changes.

Only in a few cases have the basic histological and cellular structures of the pigmentation in labrids been analyzed. Physical colors form an essential component. In previous studies carotenoids have played an important part. No significant information, though, is available because techniques can be considered obsolete compared to present techniques of chemical analyses. It would be worth while to apply these to the exploration of the organic background of color differences and changes in wrasses.

Lönnberg e.a. (1937) found that the red and orange colors of both color phases of

Labrus ossifagus (*bimaculatus*) are produced by carotenoids, xanthophyll and an additional red carotenoid substance. GOODRICH (1939, fide NICOL, 1968) made a quantative analysis of chromatophores of terminal phase specimens of two *Thalassoma* species. The blue stripe of *Th. bifasciatum* proved to contain about three times as many xanthophores as the green areas; the yellow stripe of *Th. duperrey* (a wrasse from Hawaii) twice as much as the green parts. In both species melanophores were most numerous in the black stripe, while those of the green areas clearly surpass those of the blue, and yellow stripe respectively.

With obsolete methods of lipid extraction ABOLIN e.a. (1957a) found no difference in the total carotenoid content of the skin of both color phases of *Crenilabrus pavo*. The bright red of the terminal phase is due to high accumulation of astaxanthin ester in adequate chromatophores, while taraxanthin ester shows a more diffuse distribution over the entire integument in both phases. In *Labrus mixtus* (*bimaculatus*), however, they (1957b) found that the total of carotenoids of the first adult phase decidedly exceeds that of the terminal phase. In the former astaxanthin predominates strongly; in the terminal phase, conversely, xanthophyll prevails. PRISCILLA RASQUIN (1958) found in *Th. bifasciatum* more xanthophores in the first adult phase and fewer in the terminal bluehead phase.

As far as optical colors are concerned, the results correspond rather well. According to LÖNNBERG e.a. the black color of *L. bimaculatus* is due to melanin. As the optic color blue is produced by transparent iridocytes in connection with the melanophores, the paleness of the blue markings in the first adult red phase is explained by the scarcity of melanin, as compared to the blue-striped terminal phase. The alteration of the color in the spinuous dorsal is explained by intensified development of black pigment and consequently of blue color. Blue colors in the terminal phase of *Halichoeres poecilopterus* are also due to the existence of numerous guanophores and melanophores (KINOSHITA, 1935).

GOODRICH found that the number of iridocytes in the black, blue and green areas of *Th. bifasciatum* and the yellow and green of *Th. duperrey* are about the same. RASQUIN found fewer iridophores in the yellow phase, more in the terminal phase of *Th. bifasciatum*. GOODRICH & BIESINGER (1953) investigated the nature of the blue and black vertical bars of the terminal phase of *Th. bifasciatum* and the two longitudinal stripes of *H. bivittatus*, illustrating their results in stereograms. The general structure of the epithelial and dermal layers and the individual cellular elements of the two species were found to be essentially similar. In *H. bivittatus* the more ventral stripe is lighter because it carries fewer melanophores. In the blue zone of the Bluehead no blue pigment exists. The most distinctive characteristic is again clustering of groups of guanophores around individual melanophores.

Thus, morphological changes in color in general are characterized by a decrease in the number of xanthophores and an increase in the number of iridophores and in the amount of melanin. The latter accounts for increase of optical colors like blue, black and green, colors, typical of terminal phases of various labrid species.

DICHROMATISM IN LITERATURE

Labrid species in which extreme dimorphism caused duplication of names have already briefly been mentioned in the introduction. Here, more detailed references will be given. See also Table 21, in Chapter X.

In the Striped Wrasse, *Labrus bimaculatus* L., a labrid of the Mediterranean and Atlantic coasts, the first adult colors are mainly rose to red. Characteristic are two large black spots on the base of the soft part of the dorsal and a similar spot in the upper part of the caudal peduncle. Terminal colors are mainly dark olive, with four or five blue longitudinal bands. The vague blue bands that adorned head and sides of the red phase have in the blue-striped phase increased in number, intensity and size, while three dark spots are lacking. The big black blotch in the spinous portion of the dorsal of the first adult phase is substituted by a large blue space in the terminal phase.

According to LÖNNBERG & GUSTAFSON (1937) the red phase was described as *Labrus carneus* by YARRELL (1836) and as *trimaculatus* by VALENCIENNES (1839). The latter authors named the blue-striped phase *caeruleus, variegatus* and *mixtus*, respectively, though already in 1800 RETZIUS had argued that the two entirely different color patterns belonged to the same species. LÖNNBERG e.a. described both color phases under the name of *Labrus ossifagus*; QUIGNARD (1966) used *L. bimaculatus*.

The numerous publications on dichromatism in the Mediterranean "girelle" *Coris julis* (L.) demonstrate the evolution of opinions and interpretations of the complicated relation between color, size, and sex in labrid fishes.

In the first adult phase the body is plain reddish brown, uniform or broken into longitudinal bands; ventral along the sides a small yellow stripe may be visible; all dorsal spines are of equal length. The terminal phase is characterized by rich turquoise colors on the back of the body; there is a broad, dentate orange lateral band and a large, conspicuous black spot just behind the pectoral fin base. The turquoise phase is moreover associated with an elongation of the anterior first three spines of the dorsal fin; this part of the fin is strikingly black colored, bordered by bright red.

Among others, RISSO (1810, 1826), BONAPARTE (1832) and CUVIER e.a. (1839) looked upon the two very different color forms as different species. The reddish-brown fish was named *Julis giofredi*, the turquoise form *J. mediterranea* or *J. vulgaris*. Next to color and shape of the dorsal fin, other morphometric and meristic traits were used as evidence for a different specific identity, e.g. by MOREAU (1881), GOURRET (1839) and CAPORIACCO (1921). Though as early as 1868 STEINDACHNER had stated that both species should be considered as synonyms. Also CANESTRINI (1868) included in *J. mediterranea* the *giofredi* form, as he could not succeed in finding sufficient prevailing arguments for a separation into two different species. CANESTRINI is the first author who described an intermediate colored specimen. Nevertheless, in 1955 (ROSA DE STEFANI) both color forms were still subject to discussion as separate species.

FOWLER (1936), BACCI e.a. (1957, 1958), RENATA VANDINI (1965), QUIGNARD (1966) and TORTONESE (1967) support the existence of only one Mediterranean

species of *Coris*. REINBOTH (1957) gave definite proof for this when he induced an alteration from *giofredi* towards *julis* colors by injections of testosteron. MACHTELD ROEDE (1966) could not find any significant difference in the meristic traits, used by former authors to separate the two color forms; slight differences in body proportions could be explained as allometric changes.

Two Caribbean wrasses, not included in the present publication because they could not be collected in sufficiently large numbers, also display a strong dimorphism.

In *Halichoeres pictus* (Poey), the Painted Wrasse, the first adult color phase is white with two longitudinal yellowish brown stripes. Terminal colors are deep blue-green to yellowish green on the upper half of the body, shading to pale blue on lower half. Characteristic is a large black spot at the caudal base.

Halichoeres radiatus (L.), the Puddingwife, is first mainly yellow, with large quadrate blackish blotches along the base of the dorsal fin. Terminal colors are greenish with a dark-edged pale blue bar in the middle of the body (RANDALL & BÖHLKE, 1965; RANDALL, 1968).

Colors also vary extremely during one lifespan in the South Pacific wrasse *Stethojulis strigiventer* (Bennett) (RANDALL, 1955a). Here the first adult phase is brown. The terminal phase, earlier named *S. renardi*, is more colorful, with four dark-edged red lines on the head and body and posteriorly the eye, between the two lowermost red lines, a blue area.

Also somberly colored is the first adult phase of the Pacific labrid *Gomphosus varius* Lacépède, being plain black posteriorly and creamy white to light brown anteriorly (STRASBURG & HIATT, 1957). The terminal phase, at first referred to as *G. tricolor*, is rich blue-green with a vertical yellow-green cross bar near the pectoral base and blue on head and caudal fin.

OKADA (1955, 1962) described somberly reddish colors for the first adult phase of the Japanese *Halichoeres poecilopterus* (T. & Sch.) and *Duymaeria flagellifera* (C. & V.). Terminal colors here are dark blue with a large dark spot on the body below the end of the pectoral fin in the former, blackish purple with narrow yellowish green reticulations on the cheeks and opercles in the latter species.

Cases of more gradual and less striking transmutation of colors have also been given.

REINBOTH (1962a) discussed such dimorphism of the only *Thalassoma* species that frequents European coasts, *Th. pavo* (L.). The body is greenish; many scales show a vertical red line. At first, there are five green-blue cross bars on the sides and a blue-black spot between the second and third cross bars, close to the dorsal fin. Later, there is only one, but rather conspicuous, blue cross bar in the anterior part of the body. QUIGNARD (1966) briefly indicated slight color alterations for some other European wrasses, like *Symphodus* (*Crenilabrus*) *melops* (L.), *S.* (*C.*) *mediterraneus* (L.), *S.* (*C.*) *roissali* (Risso), *S.* (*C.*) *tinca* (L.), *S.* (*C.*) *bailloni* (C. & V.), *S.* (*C.*) *ocellatus* (F.) and *S.* (*C.*) *melanocercus* (Risso). These color discrepancies never caused taxonomic confusion.

FEDDERN (1963) described in Caribbean *Bodianus rufus* (L.) that no abrupt changes of color are noticeable at any time of its life history. Gradually the blue area that covers head and anterior part of the body is replaced by yellow and finally the

blue only occupies the upper portion of head and body and a portion of the dorsal and anal fins (the blue portions are red in specimens from deep water). In *B. pulchellus* (Poey), another Hogfish of the tropical western Atlantic, changes are more pronounced. After a pure yellow stage, red spreads over most parts of the body, leaving only the upper posterior part of the body and caudal fin and the posterior section of the dorsal fin yellow; the red is intersected by a broad white lateral band.

Dichromatism is not a common characteristic of all labrid species. In e.g. *Centrolabrus exoletus* (L.), *Ctenolabrus rupestris* (L.), *Symphodus* (*Crenilabrus*) *doderleini* Jordan or *Labrus viridis* L. no definite changes of color occur during life. Neither is *L. merula* L. an example of extreme dichromatism, though the largest specimens of this grey-green species are more deep blue (QUIGNARD, 1966).

A dichromatic life story is not limited to the Labridae. Different, successive color patterns also caused extreme taxonomic confusion in the family of the Scaridae (Parrot-fishes) (WINN & BARDACH, 1957; SCHULTZ, 1958; SMITH, 1959; RANDALL, 1963; RANDALL & RANDALL, 1963). LAVENDA (1949) discussed color dimorphism for the Atlantic Sea Bass *Centropristes striatus* (L.), REINBOTH (1963) for the Japanese serranid fish *Sacura margaritacea* (Hilgendorf).

PRESENT INVESTIGATIONS

Initial examination of the wrasses, both alive and freshly dead, resulted in the distinction of a number of color patterns, specific for each species. Our classification is essentially based on these distinctions.

It was not easy to keep wrasses alive for a period long enough to observe the slowly developing color changes per individual. So, we had to content ourselves mainly with the combination of observations made on a large number of specimens, all studied only once at the moment of collecting, assuming that they would represent the various phases which could be observed in a longitudinal study of one individual.

OBSERVATIONS ON COLOR CHANGE

Though about 500 individuals were kept alive for studying color per specimen, mostly for a couple of weeks or more, only few cases of actual color change can be reported. Further, progressing color change and even a complete color metamorphosis occurred among

fish kept for growth studies (see Chapter XIII). The stress of captivity to which labrids proved to be sensitive may have interfered with color change. Anyhow – in captivity – change of color is a gradual, time-consuming process.

Several times yellow phase *Th. bifasciatum* specimens were seen to adopt intermediate phase features in periods of three to four weeks or more. For instance, of six phase 1 specimens on July 14th having a mean TL of 7.4 cm, four were found back on August 21st, then having a mean TL of 7.8 cm. The two largest specimens, both TL 8.0 cm, showed characteristics of intermediate phase 2, such as bluish hues on the cheeks; the two other specimens were still in the first adult phase colors. – Of a group of eight yellow phase 1 specimens, kept in a concrete outdoor tank and having a mean TL of 6.3 cm on February 3rd, on April 24th only three were left. Two individuals, then TL 6.8 and 6.9 cm, showed intermediate features of color phase 2 to 3; the third one, TL 6.4 cm, now was in the terminal bluehead colors. – Also some *H. bivittatus* specimens were noticed changing towards slightly greener hues after three to four weeks.

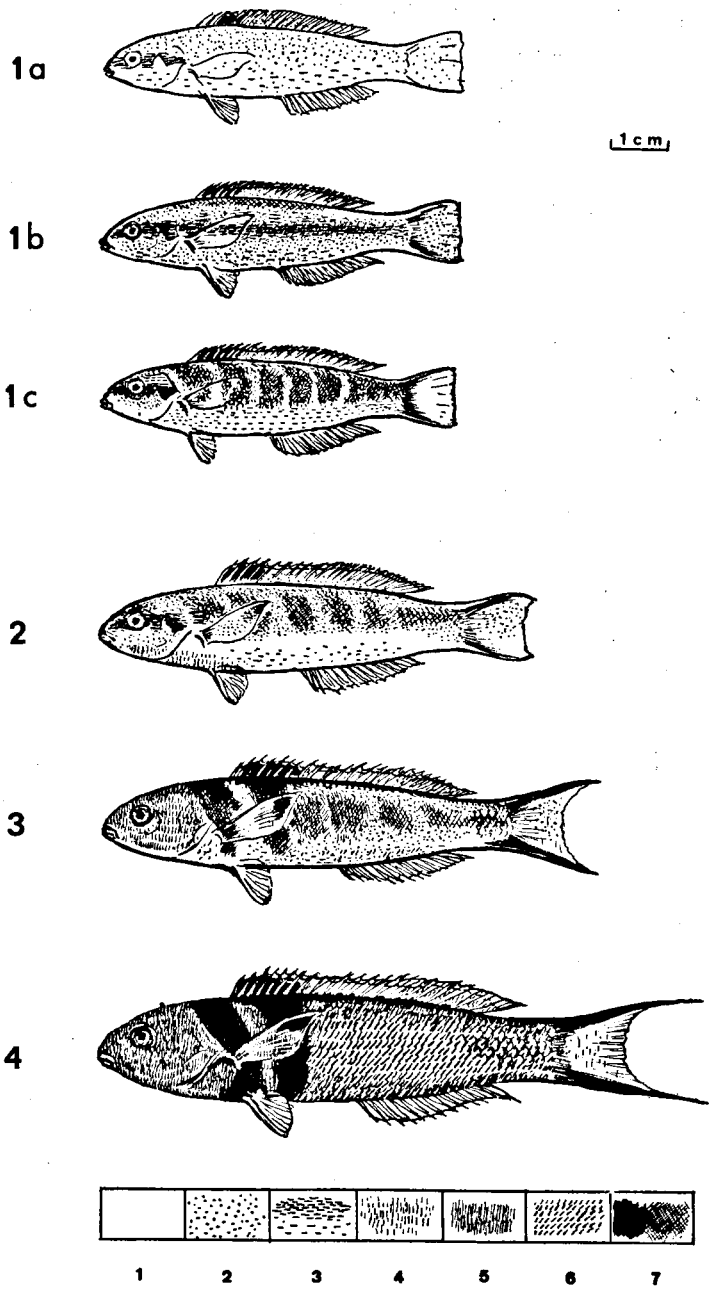
It took about eight months before the red colors of two specimens of *Labrus bimaculatus* had been transmuted into that of a terminal, blue striped fish (LÖNNBERG e.a., 1937). KAWAGUTI (in OKADA, 1962, 1965) observed how 30 out of 40 red specimens of *Halichoeres poecilopterus* turned into blue wrasses in the course of 40 days. LONGLEY e.a. (1941) shortly indicate actual observations on color change of *H. garnoti*, *He. splendens* and *Th. bifasciatum*. For the last species, similar records were given by TEE-VAN (1932). According to DORIS ZUMPE (1963) it took some weeks before two yellow *bifasciatum* specimens had changed spontaneously into bluehead colored fish.

These few cases from my own experience and those from the literature, indicate that when colors start to change, this transmutation slowly develops through the same gradual intermediate stages that can be distinguished on cross-sectional observations.

DESCRIPTION OF COLOR PHASES

The following descriptions refer to live colors, as in fixatives most of the small, often essential details disappear. Some characteristic features like black spots in the fins or on the sides can still be found in spirits.

When in a certain color phase pronounced forms of transitory hues occur, it is noted in the description. These swift physiological fluctuations are temporary; they can be seen to alter from one


1a
1 cm
1b
1c
2
3
4
1
2
3
4
5
6
7

moment to another and consequently differ essentially from the morphological alterations in pattern that develop more imperceptibly.

Because of the reversible fluctuations no use was made of standarized color cards. Putting the fishes on ice cubes is an advantage in studying colors. This procedure prevents the colors from getting considerably darker as happens when an anaesthetic like urethane is used, which causes a dispersion of melanin granules.

It goes without saying that the following color classification cannot be a rigid one, because marginal cases occur in which it is difficult to decide whether the colors observed have the relatively stable aspect of the first or the terminal adult phase, or that these should be classified as an intermediate phase.

Thalassoma bifasciatum (Fig. 2)

In this species the present author distinguishes a yellow phase and a terminal bluehead phase with two intermediate phases, hence four color phases in total. For the yellow phase some transitory stages are included.

Color phase 1 – *yellow* or *first adult phase* (Fig. 2/1a, b, c)

Juveniles of *Th. bifasciatum* are not essentially differently colored than the described yellow phase 1.

The main color of the body is yellow (brown), the belly rosy-white. From the lips, through the eye to the end of the operculum,

Fig. 2. Color phases in *Thalassoma bifasciatum*.
[Figs. 2–8: drawings by Jos Ruting]
1 = white; 2 = yellow; 3 = pink-violet; 4 = blue;
5 = dark blue; 6 = bottle green; 7 = black & brown
phase 1a–c: transitory variations of yellow or the first adult color phase
phase 2 : first intermediate color phase
phase 3 : second intermediate color phase
phase 4 : bluehead or terminal color phase

runs a rose-violet band interrupted half-way behind the eye by a small, yellow vertical stripe. The yellow (brown) dorsal fin is bordered by light blue and has a blue-back spot between the 2nd and 5th spine; caudal yellowish, its lobes darker-margined above and below; anal and ventrals bluish-white and the pectorals completely transparent. The shape of the caudal fin is not lunate, and ends straightly.

(ZMA 104.110; 104.013)

In phase 1 three transitory variations may occur of which phase 1a has formerly been classified as a separate species.

1a: Head and back brilliant yellow, this color extending on the sides, including the caudal fin.

1b: The horizontal band across the eye is continued on the sides into the caudal, from the operculum the color is rosy-brown or brownish. This mid-lateral band can become one to some millimeters broad.

1c: The lateral band can spread unto the base of the dorsal; it can even be broken into six large spots; the body is obliteratively shaded brown, not yellow.

The individuals may be seen to change from one variation into the other, very quickly even within seconds. The very brilliant yellow coloration (1a) was noticed on playful individuals in turbulent surf areas and in fish that were attracted to bait. Before and after, repeatedly the colors were seen to fade down again towards stage 1b and 1c, as the darker, more brownish variations occurred in resting or in disturbed fish.

By several authors the most yellow stage 1a is referred to as "reef fish," the more dull stage as "fish from inshore non-reef areas." The present author objects to indicating the different transitory stages as environmental forms. She considers the different stages of coloration to be induced by changes in behavior.

Color phase 2 – first intermediate phase (Fig. 2/2)

The first impression is that of phase 1c. There are, however, some minor differences.

The yellow is less bright. The ventral part of the head is bluish;

this blue can extend over the anterior part of the belly. The blue-black spot in the spinous dorsal is more obvious; the pectorals have slightly dusky tips.

The shape of the caudal is no longer straight, the outermost spines being a little elongated.

(ZMA 104.011; 104.012; 104.014; 104.017)

Color phase 3 – *second intermediate phase* (Fig. 2/3)

The head is blue; no pink-violet band across the eye. The two anterior-most of the six lateral spots are almost black; the four posterior lateral spots, on the contrary, are vague. The rest of the body, including the belly, is greenish yellow-brown.

The blue-black spot in the dorsal fin extends unto the 6th or 7th spine, the rest of the fin is greenish instead of yellow. Tips of pectorals dark. The shape of the caudal is lunate.

(ZMA 104.015; 104.018; 104.019; 104.020)

Color phase 4 – *bluehead* or *terminal phase* (Fig. 2/4)

Body remarkably bicolored: the head and throat up to the base of the pectorals deeply blue with some violet; the posterior part of the body, including the belly, is brilliant bottle green.

Two broad black vertical bars, extending from dorsal to belly. More exactly: the anterior starts between the head and the beginning of the dorsal fin and runs down across the base of the pectorals; the posterior black bar starts underneath the spinous dorsal and is covered by the top of the pectorals. The interspace is blue.

The blue-black spot covers the whole spinous dorsal fin; the soft dorsal is greenish. Caudal almost transparent, except for the dark blue outer lobes. Anal and ventrals bluish; the transparent pectorals have a large black spot at the tips.

The shape of the caudal fin is deeply forked, the outer rays being very elongated.

(ZMA 104.016; 104.021; 104.022; 104.023; 104.024)

History

The occurrence of several different transitory variations of phase 1 and the extreme difference between this yellow phase and the terminal bluehead phase have for long caused confusion, synonyms and double descriptions. In literature, however, *bifasciatum* never became a "fish of contention" as the Mediterranean wrasse *Coris julis*.

Gronovius, Bloch, Swainson, Cuvier & Valenciennes and Poey gave descriptions of only the terminal bluehead pattern. Günther, Goode, Jordan & Hughes, Jordan & Evermann, Bean, Metzelaar and Fowler described the yellow and the bluehead coloration separately as two different species.

Longley (1914) was the first author who considered the transitory forms of the yellow phase as well as the terminal forms to be synonyms and confirmed this view in 1915 and 1941.

Breder (1927) described for *Th. bifasciatus* great changes in the standard color pattern with age, which he illustrated in a diagram in which several characteristics as body length, shape of the tail and color phases are given, realising that for his broken banded phases the descriptions overlap those of *Th. nitidus*. Nevertheless, he did not unite them on the ground that (: 63): "It is quite conceivable that there may be existing in closely adjacent but different environments two such species in which one matures to a very different looking fish from its young, whereas the other almost or quite indistinguishable when small, matures without losing its juvenile characters." This demonstrates the great reserve felt in those days about the taxonomic place of these abundant reef fishes. In Breder's "Field Book" (1948) only one single species was described.

In 1928 Beebe & Tee-Van also considered the possibility of *nitida* and *bifasciatum* being the same species but postponed a final judgement; in 1933 they were convinced that only one species was involved. Nichols (1930: 316) wrote: "it has been claimed that they (*nitidum*) are the younger of that species (*bifasciatum*), but the proof advanced is not yet satisfactory to the present." In 1932, Tee-Van described and illustrated in an elucidative drawing the different yellow, intermediate and terminal forms, remarking: (: 43) "... and yet out of this apparent jumble, there can be shown progressive change of pigmentation from the smallest fish to the adults."

Louise Stoll (1955) injected methyl testosterone into yellow specimens and made these change into individuals with bluehead colors. These experiments proved the possibility of color change and thus of their belonging to the same species.

Older descriptions of the yellow phase

Günther described as *Julis nitida* the variations distinguished here as stage 1b and 1c. Goode, probably because he saw the animals alive or just dead, classified the bright yellow form 1a as *J. nitidissima*, though suggesting that it might be identical with *J. nitida*. Jordan & Hughes and Jordan & Evermann enlisted both *nitida* and *nitidissima* (after Günther and Goode) also remarking that both names most probably were synonyms. Longley (1914: 208) wrote: "The differences between *nitidus* and *nitidissimus* are transitory, the characteristic color of one at times replacing that of the other almost instantaneously."

METZELAAR briefly described stage 1c; BEEBE & TEE-VAN (1928) and NICHOLS gave characters resembling stage 1b and 1c. TEE-VAN mentioned all stages of this phase. The present author considers FEDDERN's "white phase" as one of the transitory forms of the yellow phase. The color picture in RANDALL (1968) shows a fish in my stage 1b. The colors he separated as a subsequent phase are comparable with my phases 1c and 2. BÖHLKE & CHAPLIN report how within seconds the various modifications of the yellow phase may be displayed.

Older descriptions of intermediate phase 2 and 3

Curious as it may seem, intermediates have seldom been included in the descriptions. LONGLEY (1914: 208) wrote: "Every appreciable degree of difference between the undifferentiated pattern of *nitidus* and the highly specialized pattern of *bifasciatus* may be seen in a single school of fishes." In 1941 he described some intermediates more in detail. BREDER (1927) mentions various intermediate forms. He remarked that the fact that at no place more than two phases overlap suggests that all individuals seem to pass through the various stages in a regular sequence, though at an irregular rate. His second phase agrees with my phases 1c and 2. TEE-VAN also gave intermediates. This in contrast to FEDDERN (1965: 902), who remarked: "All individuals on the reef other than those in the bluehead phase are in the yellow phase."

Older descriptions of the bluehead phase

Most authors (e.g. GRONOVIUS, 1781) mention the two dark cross bands as the most significant characteristic. These bars are said to be brown (BLOCH); black (BEEBE & TEE-VAN, 1928; LONGLEY e.a., FEDDERN) or dark blue (NICHOLS). BREDER (1948) described only one vertical bar. About this phenomenon LONGLEY e.a. (1941: 197) already remarked: "Rarely the pale bar [the interspace between the two bars] fails to develop and the body is then crossed by a solid black bar nearly as wide as the pectoral long."

The deeply forked caudal fin was also described by most authors, among them CUVIER e.a. and NICHOLS. A perfect color illustration of the notable bicolored terminal phase is given by RANDALL (1968).

Halichoeres bivittatus (Fig. 3)

In this species the differences between the specimens are not very conspicuous. Nevertheless, four subsequent color phases could be distinguished. In phase 1 transitory modifications occur.

Color phase 1 – *first adult phase* (Fig. 3/1)

In very small specimens the lower stripe may be faint, otherwise the juveniles are not essentially different from phase 1.

The main colors are white and brown; on the throat some vague pink oblique stripes. Striking are two longitudinal brown stripes on the sides. The broader and more intense brown dorsal band extends from snout, across the eye to the middle of the caudal base. The less dark brown anal band starting behind the opercles, runs just underneath the base of the pectorals to the caudal, three scales under the more dorsal band. The posterior half of the upper band is broken into

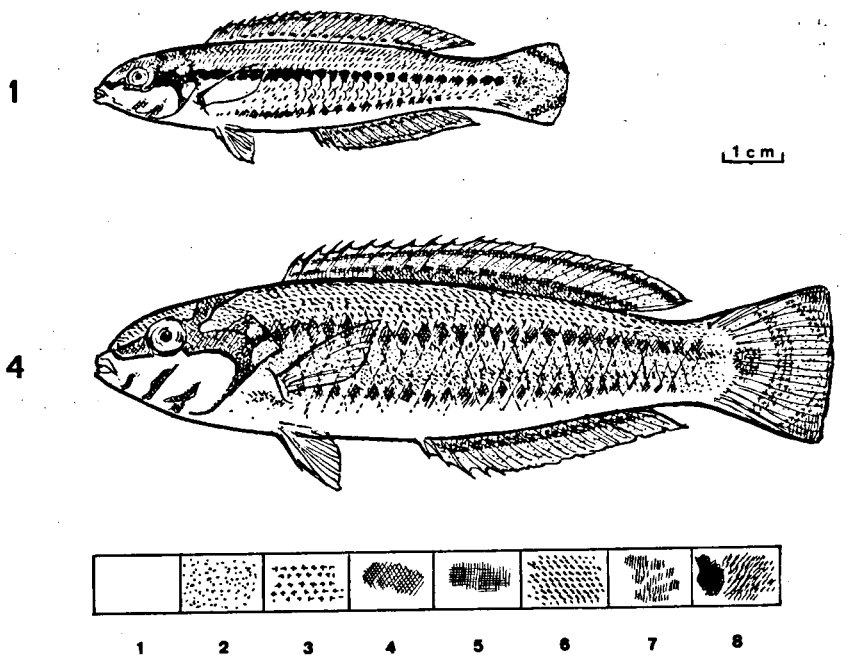


Fig. 3. Color phases in *Halichoeres bivittatus*.
1 = white; 2 = yellow; 3 = orange; 4 = pink;
5 = red; 6 = greenish; 7 = blue; 8 = black & brown
phase 1: first adult color phase
phase 4: pastel or terminal color phase

one-scale large spots; the lower stripe is totally dotted into scale large spots.

Dorsally of the uppermost band the body is beige-brown. The belly is cream-colored to white; the interspace between the two lateral bands is pale beige.

The opercles have two very pale yellow spots. One spot along the upper edge, with a small, but clear blue margin at its caudal side; the other spot at the top of the opercles.

The yellow dorsal fin is bluish-green at its base and bordered by a pale-blue. It has two longitudinal orange-red stripes; one near to the base, the other under the blue border. The caudal is yellow with a vague orange spot in the middle of its base and two oblique orange stripes more to the end. The ventrals are reddish, the pectorals transparent. A small, violet spot can be present at the base of the last ray of the dorsal fin.

(ZMA 104.025; 104.026; 104.027; 104.028; 104.029)

Transitory variations of phase 1 – The back dorsal of the uppermost band may vary from very pale beige to dark brown.

Color phase 2 – *first intermediate phase*

The first impression is that of color phase 1. However, there are some very pale pink stripes on the head. Underneath the most dorsal lateral band, the body is shaded with pink and pastel green. The orange spot-mid-base the caudal fin is clear, the oblique orange stripes are united into a cuneiform figure, the outer tops have a small blue tip.

(ZMA 104.030; 104.031; 104.032)

Color phase 3 – *second intermediate phase*

On the head there are clear pink stripes. The whole body shows pink and greenish dots. The upper lateral band is less intense brown, the lowest band is rosy colored and vague. Under the upper band some yellow. The two spots on the opercles are clear yellow, the blue

margin along the most anterior spot being rather broad. The caudal has a broad, curved orange band and orange in the corner above and below, with blue tips.

(ZMA 104.033)

Color phase 4 – *pastel terminal phase* (Fig. 3/4)

The general impression is a greenish, pastel colored fish. On the head, broad pink bands, bordered by small blue lines, e.g. one striking line running from snout through eye to link with upper lateral band. The two lateral bands, even the uppermost one, are not very striking, the colors being cerise-pink instead of brown. The back is greenish; under the most dorsal lateral band the body is yellow, changing gradually into greenish towards the lowest lateral band.

The two spots on the opercles are brilliant yellow; the blue margin behind the anterior one is broad and striking. In the dorsal fin the lowest orange-red lateral band is undulated, because of broad intrusions of this color on each interradial membrane. The caudal has a clear orange spot mid-base, a broad orange, curved band and broad, orange corners with large, blue tips.

(ZMA 104.034; 104.035)

History

Probably partly because in the beginning *H. bivittatus* was confused with *H. radiatus*, a species that goes through marked color changes (Randall e.a., 1965) and partly because of the indeed high frequency of transitory differences of color shades during the phase 1 stage, the Slippery Dicks got the reputation of displaying considerable variation in color (Jordan e.a., 1882a; Jordan e.a., 1889; Longley e.a., 1941). While in my opinion in this species the melting from phase 1 towards phase 4 is not so conspicuous at all.

Also the fact that *H. bivittatus* is one of the most abundant and widely distributed species and consequently has been observed more often, may explain why the relatively small color changes have been noticed more than those of species with more marked color changes like e.g. *H. garnoti*. Still in 1966 Cervigón remarked that the coloration of *H. bivittatus* is extremely variable and difficult to describe.

Most publications do not furnish evidence on the suggested color variations but merely describe one color pattern, mostly phase 1. E.g. Bloch's description (1791)

of a fish with two longitudinal brown stripes corresponds with my phase 1 as well as the color descriptions by CUVIER e.a. (1839), NICHOLS (1930) and FOWLER (1950). Also GÜNTHER (1862), both in describing *Platyglossus bivittatus* and *P. humeralis*, only gave specifications that correspond with my phase 1.

LACÉPÈDE (1802) who used a copy of a painting by Father PLUMIER to describe his *Labrus psittaculus*, pictures a Slippery Dick in the pastel phase 4 colors; the report of CUVIER e.a. of PLUMIER's painting also gives the impression of a phase 4 specimen.

Some of the gradual and lasting changing of the color pattern had already been reported by JORDAN & EVERMANN (1898: 1595): "these [longitudinal] bands growing fainter with age and sometimes disappearing, the lower one always wanting in the adult." For the rest, their endless color descriptions give contradictory and not relevant information.

Also confusing are the data given by MEEK & HILDEBRAND (1928). Because of their detailed color descriptions I am inclined to agree with RANDALL e.a. (1965) that instead of *H. radiatus* only *H. bivittatus* is reported, of which MEEK e.a. paint a correct picture of a color fading as occurs during the changing from phase 1 into 4. On the other hand, I do not subscribe to the remark of MEEK e.a. that with age the caudal fin changes from rounded towards emarginate, while also sizes of 340 mm and 420 mm length seem to me incompatible with this species.

LONGLEY & HILDEBRAND (1941: 191), who suggested: "the color is so variable and of so many shades," in my opinion only gave the reversible, transitory forms of phase 1. It is not clear if they realized the existence of lasting color changes. Their report on fin colors as in phase 3 and 4 does not agree with the rest of their phase 1-like description.

MOWBRAY (1931) objected to former reports on color changes and remarked: "There is but one known [of the genus *Iridio*] to me that is constant in pattern, this being *I. bivittatus* (Bloch). The pattern of this species is always the same, remarkably true to form. There may be, and there often is, a difference in the intensity of color, some being darker than others depending on bottom conditions ..." MOWBRAY supports his opinion by giving a clear picture on which 12 specimens of gradually increasing length, from 12 to 102 mm, are given. All clearly phase 1 individuals.

RANDALL & BÖHLKE (1965) are the first authors to distinguish the colors of the whitish and the larger more pastel colored specimens correctly and in detail. Their fig. 5 shows two specimens, with an appearance corresponding to my phases 1 and 4. A relation between size and color is suggested. RANDALL (1968) gives a color picture of a Slippery Dick in terminal colors. BÖHLKE & CHAPLIN (1968) emphasize the temporary, physiological fluctuations in coloration but hardly point out the lasting, morphological changes during life.

Halichoeres garnoti (Fig. 4)

A remarkable polychromatism occurs in this species. A completely deviating color pattern characterizes the juveniles; then during adult life various color stages are passed. The polymorphism of *H. garnoti*, however, never became as much-discussed as that of *Th. bifasciatum*

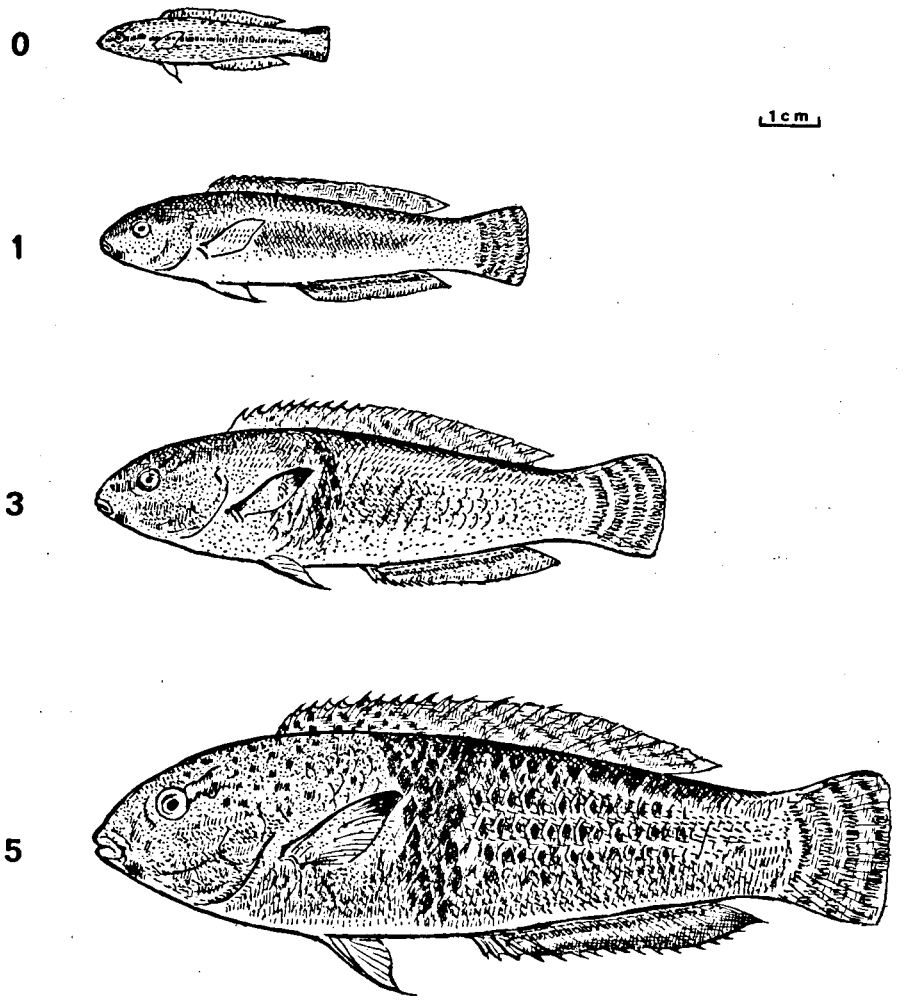


Fig. 4. Color phases in *Halichoeres garnoti*.

1 = white; 2 = yellow; 3 = orange; 4 = bluish gray;
5 = olive green; 6 = blue; 7 = maroon-violet; 8 = black & brown
phase 0: juvenile color phase
phase 1: first adult color phase
phase 3: second intermediate color phase
phase 5: yellow-head or terminal color phase

nor gave rise to taxonomic controversies. This may be because, in contrast to other species, the colors very gradually transmute from one phase into the other. Consequently, the adult fishes have been classified in five phases, a first adult phase and the yellow-head terminal phase, with three intermediate ones.

Color phase 0 – *juvenile phase* (Fig. 4/0)

The whole body is bright orange except for a small, bright turquoise-blue lateral stripe, running from the snout across the eye to caudal fin. Fins pale bluish with some orange.

(ZMA 104.046)

Color phase 1 – *first adult phase* (Fig. 4/1)

Dorsal part of head and back maroon-violet shading to a dull yellow-olive on sides and becoming pale yellow-white ventrally. From the eye small dark, reddish stripes obliquely backwards. On the jaw, just under the lips, a light blue circle around a dark blue spot.

The spinuous dorsal fin yellow-olive with blue dots; soft dorsal pale orange with small blue stripes, obliquely to the caudal. Caudal bluish-gray with sharply defined, slightly curved orange vertical bands. The anal is orange at its base, downwards becoming olive-yellow-violet-blue respectively. Ventrals pale pink; pectorals transparent.

(ZMA 104.036; 104.047; 104.048; 104.049; 104.050; 104.051)

Color phase 2 – *first intermediate phase*

As color phase 1, except for a very vague indication of a vertical band at the sides.

(ZMA 104.040; 104.041)

Color phase 3 – *second intermediate phase* (Fig. 4/3)

A vague vertical brown band at the sides, starting at the base of the dorsal where the spinous part becomes soft. Anterior of this band the body is yellowish. Pectorals with vague black tips.

(ZMA 104.037; 104.042)

Color phase 4 – *third intermediate phase*

The vertical brown band clear and extending unto the belly. Upper part of head and back anterior of the vertical band olive-yellow with vague residues of the maroon-violet. Flanks anterior of vertical bar clear yellow; sides posterior of the bar under the maroon-violet of the back more greenish. Belly bluish.

Pectorals clear black tips. Blue circle on lower jaw clear.

(ZMA 104.043)

Color phase 5 – *yellow-head terminal phase* (Fig. 4/5)

Strikingly bright colors; the vertical band dark brown and broad. Upper part of head and shoulders bright yellow with many tiny blue dots. Sides between head and vertical band also bright yellow. Posterior to the brown band the green sides show oval, brown lines in the middle of each scale. Belly blue. Pectorals have broad black tips.

(ZMA 104.038; 104.039; 104.044; 104.045)

Three specimens did not exactly fit in with the phases described. Characteristic of all three were the clear yellow sides, as in phase 4. There was, however, no, or only a very vague sign of the vertical bar. In two specimens the head was light as in phase 4; in one more dark as in phase 3. It was decided to place these three individuals (females) in phase 4.

History

Several authors did mention a considerable variability in general color and pattern, but only few were aware of the gradual change of one phase into the other.

A phase-1 pattern without the dark vertical band was pictured by Cuvier e.a. Other descriptions, including the cross bar, resemble my phases 3–5 (Jordan e.a., 1886, Jordan e.a., 1898, Longley e.a., 1941, Beebe e.a., 1928 and Nichols, 1930). As mentioned above, the connection between these patterns escaped the investigators. For instance, Poey (1860) assumed that the specimens of Cuvier could not be representatives of the same species.

Poey even distinguished between *Julis cinctus* and *J. ruptus*, based on size and color differences. In my opinion his first "species," a specimen of 16.5 cm length, was a phase-3 example, while his *ruptus*, 17.0 cm long and more yellow on the sides, agrees well with the yellowhead terminal phase-5.

Longley e.a. (1941) described a 9.3 cm specimen in phase 1 colors and a larger specimen in a phase 4 pattern. They also reported how a dark side bar started to appear in a fish of about 9.0 cm in captivity, but did not elaborate the feature of color changing.

Mowbray (in Breder) and Breder (1927) have set apart the very young individuals of small size and gave characteristics I reported for phase 0.

Randall & Böhlke (1965) and Randall (1968) are the only authors who explicitly described different successive color patterns; they distinguished three distinctive color phases. Their first phase for juveniles to about 6.0 cm corresponds to my phase 0, only in my opinion the body color should be described as bright orange, not yellow. (The color picture of a juvenile in Randall's fig. 229 shows a bright orange specimen as well). Their intermediate yellowish brown phase without any sign of the cross bar, has much in common with the fishes I considered as being in phase 1–2, while their "large adult males" are fishes that I should have classified as phase 3–4.

In Böhlke & Chaplin (1968) the gradual sequence of color patterns is not discussed.

Halichoeres maculipinna (Fig. 5)

There are two rather distinct phases, the first adult phase and the gorgeous terminal phase 4, with two intermediate phases. For both phase 1 and 4 transitory modifications are described.

Color phase 1 – *first adult phase* (Fig. 5/1)

Randall & Böhlke (1965: 239) gave a description and picture of a juvenile specimen, which chiefly differs from the first adult phase because spots in the spinuous portion of the dorsal fin are not yet developed.

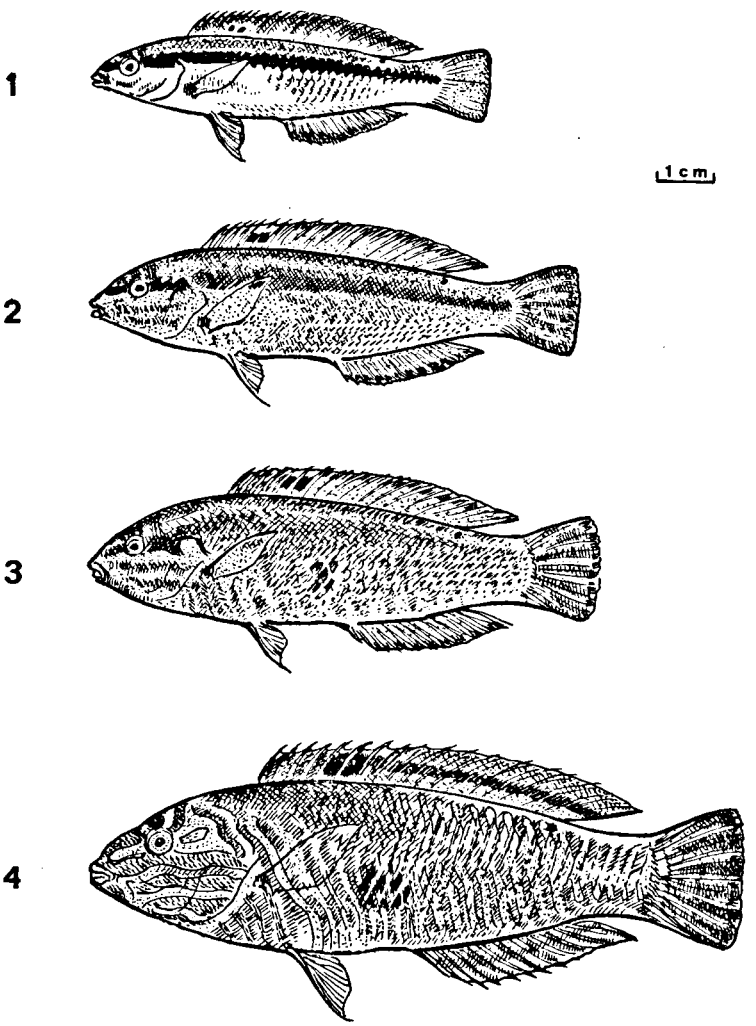


Fig. 5. Color phases in *Halichoeres maculipinna*.

1 = white; 2 = yellow; 3 = pink; 4 = green;
5 = red; 6 = blue; 7 = black & brown
phase 1: first adult color phase
phase 2: first intermediate color phase
phase 3: second intermediate color phase
phase 4: terminal color phase

A predominantly white fish with a characteristic dark longitudinal band. More in detail: a dark brown crenated lateral band running from the snout, across the eye towards the base of she caudal fin. Head and body ventral of this band white; the two rows of scales directly underneath the brown band often show pinkish edges. Dorsal to the lateral band the body is beige, being separated from the brown band by a small yellow stripe.

On top of the head three parallel small, pink bands, the most anterior one running from one eye to the other. Some pink around snout. On the lower part of the cheeks three vague pinkish lengthwise stripes may show. There is a small black spot at the base of the last dorsal ray.

Dorsal fin pale pink, more orange along the margin; in between the 5th and 7th dorsal spines two vague, blackish dots. Caudal dull yellow, the most outer upper and under parts pinkish-orange; anal pale pink, pectorals and ventrals transparent; a small light blue spot on top of base of the pectoral.

(ZMA 104.052/104.055; 104.061a; 104.064)

Transitory variations of phase 1:
1a – Back pale beige, but yellow stripe dorsal of the brown lateral band very bright.
1b – Back dark beige, yellow stripe nearly invisible.
1c – Back deeply brown, this color extending unto the brown lateral band; as a result the whole dorsal area shows as an even brown.

During observations of wrasses in their natural environment, phase 1a can be mistaken for phase 1b of *Th. bifasciatum* or phase 1b of *H. bivittatus*.

Color phase 2 – *first intermediate phase* (Fig. 5/2)

The lateral band less dark brown; body anterior to this band greenish-white with more pink-edged scales in ventral half of the body; just behind the head two vague, pink bands running obliquely

down and backwards. Pink on cheeks a little more clear; the two dots in spinous dorsal larger.

(ZMA 104.056; 104.057; 104.058)

Color phase 3 – *second intermediate phase* (Fig. 5/3)

General impression greenish. Lateral band present though vague. On the sides some scales above the anus are vaguely dark blue. The three lengthwise, slightly curved stripes on cheeks real pink.

The two dots in the dorsal, large; anterior to these dots fin greenish; caudal now at three sides bordered by orange; moreover a vague vertical, slightly curved pink band at its base and medio some pink-orange between the yellow rays. The pink-edged scales on the sides more fused.

(ZMA 104.059; 104.062; 104.063)

Color phase 4 – *terminal phase* (Fig. 5/4)

General impression green. Characteristic is the large inky area on the sides just above the anus. Besides the two pink, oblique bands before and behind the base of the pectorals running backwards, more pink oblique bands are formed on the sides because of completely fused pink.

Pink bands on top of the head and cheeks bright pink. The two dots in the dorsal fill up all the space between the 5th and 7th spines; anterior to these the dorsal is green, posteriorly pink with median green stripe. Nearly all space between the yellow rays of the caudal pinkish-orange.

(ZMA 104.060; 104.061; 104.065)

Transitory variations of phase 4:
4a – The green and the pink-orange very bright.
4b – All colors dark, dull; some indications of the browinsh lateral band; back beige-green.

Variation 4a was observed in very excited specimens, 4b in resting or frightened individuals.

History

The occurrence of lasting color changes is rarely mentioned in older publications. When specimens without and with the characteristic dark side spot were distinguished, the authors, Bean and Nichols, separated them in different species.

Günther (1862) described phases 1 and 2. He also mentioned: "sometimes a dark spot below the band on the middle of the body," a feature typical for phases 3 and 4, but he did not mention the size in which the spot was found nor the greenish shade of the body that goes with the occurrence of such a spot. Jordan & Evermann (1898) only described colors of a phase 1 individual.

Bean (1906a, b) gave detailed color descriptions of *Iridio microstomus* (one small specimen of 1½ inches SL) and *I. meyeri* (length of type specimen 4 inches SL), respectively. The former may be considered as an early form of phase 1 of *H. maculipinna*; the latter corresponds with my phase 2, though "the narrow oblique streaks on the pectoral region" tend towards phase 3. However, Bean did not describe the dark side spot, characteristic of the final phases. Hence, I do not agree with Randall e.a. (1965) when they consider Bean's *meyeri* a representative of the terminal phase. (We agree in identifying his *microstomus* and *meyeri* as *maculipinna*.)

Starks (1913), in describing the type and only specimen of his *H. penrosei*, paints in my opinion a perfect picture of the color details of phase 1 of *H. maculipinna*. E.g. "a broad, solid black band ... from ... snout to the base of the caudal. It is separated above from the color of the back – much lighter than the lateral band – by a narrow light band ..." His mentioning of "a black spot from the sixth to the seventh dorsal spine," very characteristic for *H. maculipinna* leaves no doubt about the identification, so I, without having examined Stark's type specimen, follow nevertheless Randall e.a. in considering Stark's *penrosei* as a *maculipinna* individual.

Nichols (1920) created two synonyms from two Bermuda specimens. The colors of his *Iridio similis* (90 mm SL) are similar to those described by the present author as phase 1; his *I. frenatus* corresponds with my phase 3–4. (Because of Nichols' morphometric and color information, I agree with Randall e.a. in considering both as *H. maculipinna* individuals).

Beebe & Tee-Van (1933a) realized that "the species is variable in coloration," though the dark terminal side spot is not mentioned. In the report of Longley & Hildebrand (1941) nothing about a phase 3 and 4 pattern is included either, nor in that of Cervigón (1966) who describes five specimen of 33–62 mm SL.

Randall & Böhlke (1965) described in detail colors corresponding with both my phases 1 and 4, of which their fig. 1 illustrates the essential differences. They also described juvenile colors of a specimen of 37 mm, different from phase 1 in the absence of the two blackish dots in the dorsal. Their two males of 109 and 129 mm are examples of the terminal phase; the former, caught "following the observation of its spawning" clearly corresponding to my stage 4a (transitory activity colors).

According to RANDALL & BÖHLKE, who consider the terminal phase to be equivalent with "male"-phase, the larger spot on the sides starts to develop at astandard length of about 75 mm. Color pictures of phase 1 and phase 4 can be found in RANDALL (1968). BÖHLKE & CHAPLIN (1968) mainly describe terminal colors; the occurrence of subsequent, different phases is hardly mentioned.

Halichoeres poeyi (Fig. 6)

No differences or only very small ones were found in the specimens collected; hence subdivision into different color phases was omitted, all specimens being united into color phase 1. One transitory variation can be distinguished.

Color phase 1 (Fig. 6)

Head and body olivaceous, ventrally shading to yellow-green anterior to the anus. Dark blue spot, anteriorly bordered by a light blue and distinct golden spot respectively, aslant above and behind the eye. A faint red spot on chin, just behind lower lip.

Dorsal of head and on cheeks some broad pink bands, e.g. one running from eye towards lips, forming a "V" with band from lips to

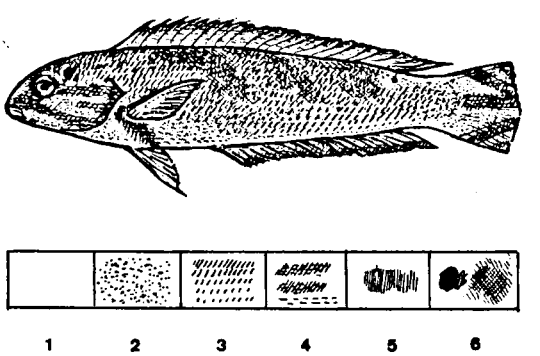


Fig. 6. Color in *Halichoeres poeyi*.
1 = golden; 2 = yellow; 3 = green;
4 = pink; 5 = blue; 6 = black & brown

lower edge of the opercles; a wavy pink band runs from the eye to the upper edge of the opercles; between the penultimate and ultimate bands a short band, from top of opercles to halfway the eye; these last three bands being united by a small, pink band along the edges of the opercle (forming a kind of "E" in mirror writing). All these bands may be lined by a small blue stripe.

On sides and dorsal part of the body, the scales may be bordered by pink-red.

A small, round inky spot at base of last dorsal ray; an oblique pink-orange band running from anterior of base of pectoral to midbelly, anteriorly edged by a small blue stripe.

Dorsal fin olivaceous, with narrow light blue margin and orange sub-marginal, median and basal stripes. Caudal dull yellow, the space in between the rays being orange. Yellow anal pink at base, with broad pink-orange margin. Ventrals pale beige; pectorals yellowish transparent; base of pectorals (impressing the oblique pink-orange band) is iridescent blue.

(ZMA 104.066; 104.073)

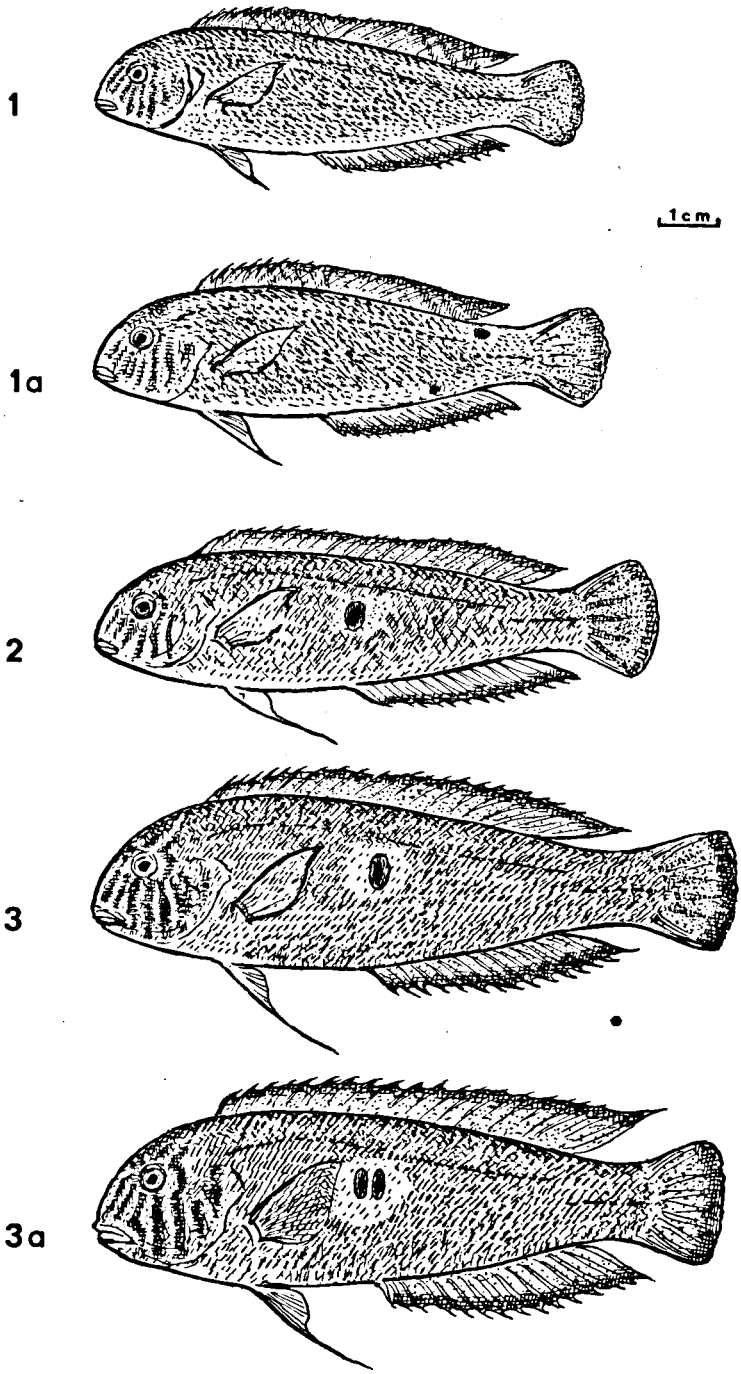
Transitory variation: On the dorsal part of the sides three very vague, pink-brownish bars may occur, running from the back obliquely down and backwards.

One variation was not of a temporary character. Being the only, and vague difference, it was not taken into account for distinguishing an other color phase.

In some larger specimens the caudal fin shows three red bands in the dull yellow; one horizontal band median in the fin and two oblique ones, converging towards the posterior margin of the caudal; all three bands lined by a narrow blue margin.

HISTORY

The descriptions by CUVIER e.a. (1839), GÜNTHER (1862), JORDAN e.a. (1898), BREDER (1927), MEEK e.a. (1928) and by LONGLEY e.a. (1941) are not essentially different from the present specification of colors. STEINDACHNER (1867) described in


1
1cm
1a
2
3
3a
1
2
3
4
5
6
7

his detailed report of one specimen of *Platyglossus poeyi* the for *Halichoeres poeyi* characteristic dark blue spot behind the eye as well as the convergent bands in the caudal fin; however, his manganese-red and reddish-brown for the under and upper half of the body are surprising. (JORDAN e.a. already discussed the fact that their *Iridio kirschii* and STEINDACHNER's *P. poeyi* were evidently closely related. According to RANDALL e.a. (1965) STEINDACHNER's species indeed is a synonym of *H. poeyi*).

The present author did not consider the slightly deviating pattern of the caudal fin in larger specimens sufficiently important to distinguish a terminal color phase. In her opinion, RANDALL e.a. are overestimating this feature when they remark (1965: 248): "the large male specimens are more complexly colored." Also BÖHLKE e.a. (1968) suggest more striking changes of coloration with growth than actually occur. The colors described by the present author are well-illustrated in a color picture by RANDALL (1968: 210). He gives also a description and color picture of a real yellow form of *H. poeyi*. The present author at no time observed such an extremely deviating color variation. It may be worthwhile to look into these discrepancies.

Hemipteronotus splendens (Fig. 7)

In this species no extreme dichromatism occurs, yet some differences between phase 1 and 3 are rather obvious; one intermediate phase is distinguished. Some slightly deviating patterns are described as phase 1a and phase 3a.

Color phase 1 – *first adult phase* (Fig. 7/1)

Body and head gray brownish-green. On sides of the head between snout and opercular margin vague, nearly vertical pink-orange stripes.

Spinous dorsal bluish with rose-orange margin, posteriorly more rosy-orange, with small bluish lines, more oblique and regular to the

Fig. 7. Color phases in *Hemipteronotus splendens*.
1 = white; 2 = yellow; 3 = pink-orange; 4 = green;
5 = brownish green; 6 = blue; 7 = black & brown
phase 1 : first adult color phase
phase 1a: variation of phase 1
phase 2 : intermediate color phase
phase 3 : terminal color phase
phase 3a: variation of phase 3

caudal. The dull yellow caudal nearly transparent, except for the posterior edge. Anal pale pinkish-red with small but rather dominant bluish lines situated as in the dorsal. Pectorals transparent; pale beige ventrals slighty elongated.

(ZMA 104.078; 104.079; 104.080; 104.082; 104.083)

Color phase 1a (Fig. 7/1a)

One specimen had a slightly deviating pattern: colors as described above. Moreover, two black spots on the body; one at the posterior base of the dorsal fin; one near to the ventral fin.

(ZMA 104.077)

Color phase 2 – *intermediate phase* (Fig. 7/2)

Body and head more greenish. Vertical stripes on cheeks deeper orange-brownish. In the middle of the sides, a few scales above the anus, a 3–4 scales broad grass-green area; generally containing a vague, blue-black spot in its center. Spinous dorsal colored like body and more greenish blue; edge of caudal pink, with small orange margin. Pectorals vaguely pinkish towards tip. Ventrals more elongated.

(ZMA 104.088)

Color phase 3 – *terminal phase* (Fig. 7/3)

Body and head green, shading to blue-green towards caudal and ventral part of the body. On the cheeks broad orange-brown bands, alternating with smaller (greenish) blue bands. An inky spot bordered by a very small, but obvious blue line, in the centre of the 5–6 scales long and 3 scales deep, brightly grass-green area.

Spinous dorsal greenish colored like body. Four-fifth of the caudal yellow, the posterior fifth pinkish-orange, separated from the yellow

by a small pink band. Last dorsal ray produced. Pectorals with rosy tips. First ray of pelvics very elongate, the tip may extend to the base of the 4th anal ray.

(ZMA 104.081; 104.084; 104.086)

Color phase 3a (Fig. 7/3a)

Colors as described for phase 3, except for the existence of two inky spots at the sides.

(ZMA 104.085)

This was found in three of the 42 terminal phase specimens studied. In a 113.6 mm TL male (ZMA 104.085) the two inky spots were located behind each other. In a 119.3 mm TL male the extra spot was less black, more brownish. At the left side its position was two scales lower, at the right side a few scales higher, both anterior to the normal side spot. In the third deviating male, a specimen of 113.1 mm TL the grass-green area at both sides extended on more scales; in the center right under each other were two inky spots, each surrounded by a small bright white area.

On account of the position of the inky spot either on the second or third row beneath the eleventh lateral line scale, LONGLEY e.a. (1941) distinguished two species *splendens* and *ventralis*. According to RANDALL (1965) *splendens* and *ventralis* should be regarded as southern and northern subspecies. In the majority of the terminal phase specimens examined by the present author, the spot was located on the second row beneath the eleventh lateral line scale. This would agree with LONGLEY's *splendens*. The three variants in which the spot deviates both in number and position, suggests that some polymorphic variation may occur, or that both northern and southern subspecies intermingle in the Curaçao area.

HISTORY

The characteristic side spot of the terminal phase was not mentioned by JORDAN e.a., METZELAAR or BREDER. Three *Xyrichthys* species formerly classified by PARR (1930) were identified by RANDALL (1965) as three stages of *splendens*. PARR's *rosipes* appears to be the juvenile; his *venustus* corresponds with my first adult phase, his *splendens* with the terminal phase. BEEBE & TEE-VAN (1933b) described under *X. rosipes* phase 1 features, under *He. splendens* the terminal phase.

LONGLEY & HILDEBRAND (1941) described under *X. ventralis* different shades, recognizable as my phases 1 and 3. Moreover, they gave under the name *X. martinicensis* – which I, agreeing with RANDALL, consider to be a mis-identification – detailed descriptions of the intermediate and terminal colors of *He. splendens*.

RANDALL (1965, 1968) described phase 1 and 3 as "adult" and "large male" patterns, respectively. Only in some small details do our descriptions deviate. According to RANDALL the area in which the inky side spots are located is yellow, according to the present author grass-green. Both phases 1 and 3 are clearly given in color pictures in RANDALL's "*Caribbean Reef Fishes.*" (The characteristic side spot of the terminal phase has been accidentally removed; fig. 243).

BÖHLKE & CHAPLIN (1968) characterize *He. splendens* by describing terminal phase features; the first adult phase is only indicated by "females have no spot at mid-side."

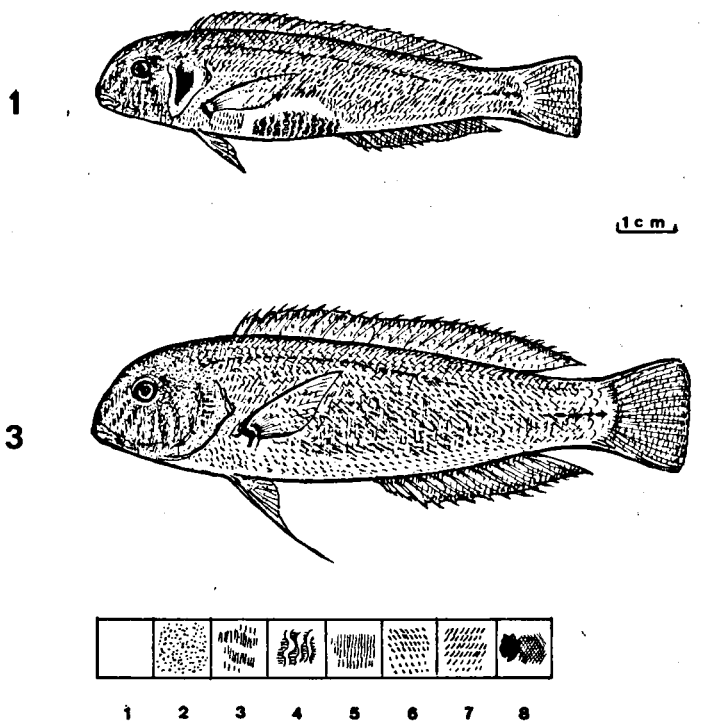


Fig. 8. Color phases in *Hemipteronotus martinicensis.*

1 = white; 2 = yellow; 3 = pink; 4 = red & white;
5 = light blue; 6 = blue gray; 7 = greenish blue; 8 = black & brown
phase 1: first adult color phase
phase 3: terminal color phase

Hemipteronotus martinicensis (Fig. 8)

A first adult phase and a terminal phase with one intermediate phase have been distinguished.

Color phase 1 – *first adult phase* (Fig. 8/1)

The entire body greenish blue; the greenish head becomes light blue under the eye, except for small yellow stripes running from eye towards lips and throat. On the operculum a sharp "V"-shaped white, enclosing a large triangular deep blue area; top of the blue in line with lower edge of eye.

Striking is the area of the belly anterior to the anus; the color is bright orange-red with many vertical, slightly twisting white lines, dorsally running into a large white horizontal patch. (The orange-red is due to the gonads, shining through the thin, transparent skin that alternates with the opaque lines).

Dorsal and anal fin pink; caudal a little darker pink-red; pectorals transparent with light blue base; ventrals slightly elongated.

(ZMA 104.090; 104.094/104.097; 104.099)

Color phase 2 – *intermediate phase*

Colors as described for color phase 1, except for a light gray instead of deep blue wedge behind the eye and a much paler, pink belly.

(ZMA 104.101; 104.102)

Color phase 3 – *terminal phase* (Fig. 8/3)

Body light blue-gray, scales reddish edges. Dorsal part of head yellow; yellow and blue nearly vertical stripes running down from eye to lips and throat (more pronounced than in color phase 1).

Opercles yellow (no white "V," nor deep blue or gray spot).

Belly slightly paler than rest of body. Dorsal pale yellowish-orange, bordered by orange; caudal pale blue-pink; anal pale gray, pink at base and pale orange margin; pectorals transparent, base rather large blue and black spot; ventrals yellow with long protuberances of the first ray.

(ZMA 104.091/104.093; 104.098; 104.100)

HISTORY

In *Xyrichthys lineatus* of CUVIER e.a., as well as in *Novacula lineata* of GÜNTHER and *X. venustus* of POEY, color phase 1 of the present study was described.

The *martinicensis* of CUVIER e.a., GÜNTHER, JORDAN and JORDAN e.a., the *modestus* of POEY and JORDAN e.a. and the *infirmus* of BEAN and JORDAN e.a., all correspond with my terminal phase 3.

JORDAN & EVERMANN separated *infirmus* from *martinicensis* because of a very dark axil of the pectoral in the former. This concerns a characteristic for phase 3. Their *martinicensis* is a description after the original type of CUVIER & VALENCIENNES in the museum at Paris. According to RANDALL (*in litt.*), who saw this type, this also is a specimen in terminal colors.

The descriptions and pictures in RANDALL (1965) are clear examples of the first adult phase and the terminal phase. Here, the only mention of an intermediate is given: "An 85 mm male with small gonads somewhat intermediate in color." Both phases 1 and 3 are given in color in RANDALL's "*Caribbean Reef Fishes*" (1968).

BÖHLKE e.a. (1968) give the essential characteristics of both phase 1 and 3. (Their notations "young" and "adult" respectively, have to be rejected as phase 1 already mainly consists of functional (female) fish; see Chapter X).

SUMMARIZING REMARKS

Surveying the color phases as defined and described above, some preliminary remarks can be made.

1. The elaborate observations of colors in the present study – combined with the data discussed in Chapter VII – did not lead to reconsideration of the systematical classification of the seven Caribbean species.

2. In labrid species color may vary from minimal to extreme during life. Although it is difficult to quantitate alterations of color, it can be concluded that the diversity in grades of color changes, as

found in the seven Caribbean species, by and large represents the variety of this phenomenon in the family of Labridae in general.

TABLE 3

DESIGNATION OF DISTINGUISHED ADULT COLOR PHASES
in *Thalassoma*, *Halichoeres* and *Hemipteronotus* species

(a, b and c refer to transitory variations)

Species	Color phases			contrast between A and C
	first adult phase A	intermediate phase(s) B	terminal phase C	
Hal. poeyi	1	–	–	none
Hem. splendens	1	2	3	moderate
Hem. martinicensis	1	2	3	moderate
Hal. bivittatus	1	2 + 3	4	slight
Hal. maculipinna	1 (a, b, c)	2 + 3	4 (a, b)	great
Thal. bifasciatum	1 (a, b, c)	2 + 3	4	extreme
Hal. garnoti	1	2 + 3 + 4	5	great

Table 3 – summarizing the number of phases distinguished for each species – shows how the species vary in regard to color changes. In *Halichoeres poeyi* only the color pattern of the caudal fin becomes slightly more elaborate during growth; this alteration was considered too small to distinguish a separate terminal phase. In the two *Hemipteronotus* species some areas (sides, belly, operculum) develop really different features, but the overall body colors change only slightly. Only one intermediate phase was distinguished.

On the other hand, in *Thalassoma bifasciatum*, *Halichoeres bivittatus* and *H. maculipinna* two, and in *H. garnoti* even three separate intermediate phases could clearly be distinguished. In *H. bivittatus* the pattern of the first adult phase develops into more pastel, less contrasting hues; no special traits disappear or are newly added. While in *H. maculipinna*, *H. garnoti* and *Th. bifasciatum* a definite change of all features occurs; the final stages are strikingly bright.

3. The number of specimens per color phase is presented in Table 4, expressed as a percentage of the total number caught per species. (*H. poeyi* is omitted, as no subdivision in phases was made.) Again, no trend common to all species can be observed. There are, however, two striking points.

TABLE 4

NUMBER OF SPECIMENS PER ADULT COLOR PHASE
(Curaçao + Puerto Rico)
in *Thalassoma, Halichoeres* and *Hemipteronotus* species

Species	first adult phase	intermediates	terminal phase	*total*
Thal. bifasciatum	1826 (78%)	110 (5%)	387 (17%)	*2323*
Hal. bivittatus	1110 (77%)	230 (16%)	105 (7%)	*1445*
Hal. maculipinna	76 (64%)	20 (17%)	22 (19%)	*118*
Hem. martinicensis	84 (67%)	4 (3%)	38 (30%)	*126*
Hal. garnoti	55 (16%)	206 (62%)	72 (22%)	*333*
Hem. splendens	28 (37%)	5 (7%)	42 (56%)	*75*

a. In four species most specimens were found in the first adult phase; the number of individuals is even at least three to four times that found in the terminal phase. (Also in e.g. *Labrus bimaculatus* (LÖNNBERG e.a.) and *Coris julis* (REINBOTH, ROEDE) fish in the first adult phase colors strongly outnumber those in the terminal color stage.) In *He. splendens*, however, more terminal phase specimens have been collected. In interpreting this finding, one should take into account that the sample of this species might not be representative, because this species may frequent a seagrass covered substrate in addition to the open sand where the specimens were caught.

b. Relatively few specimens in intermediate colors have been found, except for *H. garnoti* of which 60 per cent of the total number caught were color intermediates. This may be explained by its relatively more gradually developing color changes. In literature, intermediates are rarely reported. Morphological color changes proceed slowly, hence, the low representation of intermediates might have other explanations (see Chapter XII).

4. In dimorphic labrid species the colors of the first adult phase are often more dull in contrast to rich and often brilliant colors in the terminal phase. (Yet, in *Th. bifasciatum* the first adult phase may be brightly yellow, small *Bodianus pulchellus* are yellow, and juvenile *H. garnoti* are brightly orange).

Some characteristic features of the patterns of the successive color phases observed in the present study can be found in the description of other labrid species as well. Consequently, other wrasses will also be reviewed.

5. Reddish brown longitudinal bands may be visible in the first adult phase of *Th. bifasciatum, H. bivittatus, H. maculipinna* (and *H. pictus*). Mainly plain red or reddish brown colors are displayed in the first adult phases of *H. garnoti* (and also of *L. bimaculatus, C. julis, G. varius, H. poecilopterus, St. strigiventer, He. novacula* and S. (*C.*) *melops, S. bailloni, S. tinca, S. mediterraneus, S. ocellatus* and *S. melanocercus*).

6. More or mainly turquoise, blue, blue-green or green are the terminal colors of *Th. bifasciatum, H. bivittatus, H. maculipinna, He. splendens* (and also of *L. bimaculatus, C. julis, G. varius, H. poecilopterus, H. radiatus, H. pictus, St. strigiventer, He. novacula* and the above-mentioned six *Symphodus* species). Generally, these optical colors are due to the presence of melanin in combination with iridophores.

7. In some species dark spots occur only in the first adult phase, such as the small black spot at the base of the last dorsal ray in *H. bivittatus* and the blackish area on the opercle in *He. martinicensis* (or the dark blotches along the dorsal base in *L. bimaculatus* and *H. radiatus*).

8. On the other hand, often large, conspicuous black areas characterize the terminal phase. Like the lateral spots in *H. maculipinna* or *He. splendens,* (or *C. julis, H. poecilopterus* and *H. pictus*), the black

tips of the pectorals in *Th. bifasciatum* and *H. garnoti* and the dark spot in the axil of the pectoral fins in *He. martinicensis*.

9. In contrast to longitudinal stripes in the first adult phase, the terminal phase may show dark cross bars as in *H. garnoti* and *Th. bifasciatum* (a yellow-green bar as in *G. varius* or a broad blue cross bar in *Th. pavo* and *H. radiatus*).

10. Another general tendency is a greenish flicker or reddish blaze that may occur on those parts of the body that are mainly whitish. Especially in *H. bivittatus*, but also in the white bellied first adult phase of *Th. bifasciatum*, *H. maculipinna* and in *H. poeyi* such minor deviations have been found.

Similar deviating greenish or reddish hues have also been found in the whitish belly and head of the first adult phase of *Coris julis*. Formerly, in *H. bivittatus* and *C. julis* sub-species have been distinguished on this basis (JORDAN e.a. 1898; GOURRET, 1893). The present author did not consider the slight variations of such importance. She could not find any relation to sex, size, place of collection or time of the year.

From the foregoing it is tentatively concluded that some general tendencies may be present in the patterns of successive color phases of dimorphic labrid species. More comparative research is needed to give a more decisive answer.

VII. MERISTIC DATA AND MORPHOMETRY

In this chapter meristic traits such as fin ray counts and morphometric data such as body proportions are considered. Moreover, the morphology of the shape of the fins will be discussed. Some of these data, essential for identification of the species, were already summarized in the diagnosis in the chapter on taxonomy.

Fin spines and rays

Labridae are characterized by a single, continuous dorsal fin usually with a long spinous portion; the anal fin is similar to the soft dorsal, while the ventral fins are thoracic, each with one spine and five rays. The number of fin spines and soft rays per species is fairly constant and fishes are partly classified by their fin-ray formula. However, for the labrid species studied, some inconsistencies exist between the data given by different authors.

In order to find out which formulae are correct and to investigate possible sex, color and geographical variations, fin-ray counts were made for all seven species studied in a total of 443 specimens. Both dorsal and anal fin-ray counts were designated by the formula: number of spines in Roman numerals, number of soft rays in Arabic numerals. The last ray, even if split to the base, was counted as one.

The results are summarized in Table 5.

TABLE 5

FREQUENCY OF SPINE AND RAY NUMBERS IN THE DORSAL, ANAL, AND PECTORAL FINS

Number of spines in Roman numerals; number of soft rays in Arabic numerals.
N = number of specimens.
In all 443 specimens the pelvic fin had one spine and five rays (I-5).

N	Species and Color phase	dorsal fin			anal fin		pectoral fin		
	Thalassoma	VIII-12	VIII-13	VIII-14	III-10	III-11	I-12	I-13	I-14
	bifasciatum								
65	Curaçao phase 1	—	64	1	1	64	5	60	—
11	Puerto Rico phase 1	—	11	—	—	11	—	11	—
43	Curaçao phase 4	—	43	—	2	41	5	37	1
26	Puerto Rico phase 4	1	25	—	2	24	—	25	1
145	*total*	*1*	*143*	*1*	*5*	*140*	*10*	*133*	*2*
	Halichoeres		IX-11		III-11	III-12	I-10	I-11	I-12
	bivittatus								
77	Curaçao phase 1		77		—	77	1	75	1
18	Puerto Rico phase 1		18		—	18	—	18	—
40	Curaçao phase 4		40		1	39	—	39	1
16	Puerto Rico phase 4		16		—	16	—	16	—
151	*total*		*151*		*1*	*150*	*1*	*148*	*2*
	garnoti								
2	Curaçao phase 0		2		—	2	—	2	—
38	Curaçao phase 1–5		38		1	37	—	37	1
40	*total*		*40*		*1*	*39*	—	*39*	*1*
	maculipinna								
17	Curaçao		17		17	—	—	1	24
16	Puerto Rico		16		16	—	—	—	16
33	*total*		*33*		*33*	—	—	*1*	*40*
	poeyi								
25	Curaçao		25		—	25	1	24	—
4	Puerto Rico		4		—	4	—	4	—
29	*total*		*29*		—	*29*	*1*	*28*	—
	Hemipteronotus			IX-12		III-12	I-10		
	splendens								
20	Curaçao			20		20	20		
	martinicensis								
25	Curaçao			25		25	25		

Occasional deviations from the modal values in fin-ray formulae are known to occur. But no significant differences were found between specimens in their subsequent color phases, nor between fishes of one species whether collected on Curaçao or on Puerto Rico. According to these results the seven species may be characterized by the formulae as listed in Table 6.

TABLE 6

FIN FORMULAE IN *Thalassoma, Halichoeres* AND *Hemipteronotus* SPECIES

Species	dorsal fin	anal fin	pectoral fin	pelvic fin
Thal. bifasciatum	VIII-13	III-11	I-13	I-5
Hal. bivittatus	IX-11	III-12	I-11	I-5
Hal. garnoti	IX-11	III-12	I-11	I-5
Hal. maculipinna	IX-11	III-11	I-12	I-5
Hal. poeyi	IX-11	III-12	I-11	I-5
Hem. splendens	IX-12	III-12	I-10	I-5
Hem. martinicensis	IX-12	III-12	I-10	I-5

Thalassoma bifasciatum is the only Caribbean labrid with eight dorsal spines. *Halichoeres maculipinna* – distinguished from the other *Halichoeres* species because of only one pair of canine teeth on the lower jaw – also deviates in its number of rays in the anal and pectoral fins. Fin formulae are not relevant to separate the other three *Halichoeres* species. *Hemipteronotus* is characterized by its different number of dorsal and pectoral rays.

The anal fin formulae given for the yellow color phase of *Th. bifasciatum* A II-11 (GÜNTHER, 1862) and A II (III)-11 (JORDAN e.a., 1898), as well as the one for the bluehead phase A II-11 (GÜNTHER, JORDAN, e.a. and METZELAAR, 1919), are not in agreement with the present data. FEDDERN (1965) gave a pectoral number of 13 to 15 (14) for *Th. bifasciatum*, but his data are not really different from my results, because he counted all pectoral rays in Arabic numerals. For the anal fin, he found a modal value of A III-11, with only a few counts of III-10, which agrees with the present findings.

In the case of *H. garnoti* I cannot agree either with CUVIER e.a., GÜNTHER, JORDAN e.a. and NICHOLS (1930), who gave an A III-11 formula, or with METZELAAR who

mentioned A II-12. However, the present results do agree with RANDALL & BÖHLKE who reported III-12 for the anal fin of this species. METZELAAR's D IX-10–11 also differs from my results.

For *H. maculipinna* only STARS' (1913) formula D X-10 differs from my results. As discussed above, I consider his *H. penrosei* nevertheless to be a synonym of *H. maculipinna*. The data found for the other species are similar to those given in literature.

MORPHOMETRY

At variance with the usual taxonomic descriptions, in the diagnoses of the species studied (Chapter II) no body proportions have been included as the differences between these characteristics proved to be slight. This is apparent from the following.

Methods

Of a number of specimens next to body length, noted down for all specimens, other dimensions have also been measured. After careful consideration only ten measurements – in general critical for distinguishing between species or sexes – were selected, that are not obviously correlated to each other. It was felt that the inclusion of a larger number of parameters would only add redundant information.

All measurements were taken with a calliper accurate to 0.1 mm. Only freshly killed specimens were used. The measurements are according the standard methods as given by HUBBS & LAGLER (1947: 13–15).

Total length (TL): greatest dimension, measured between the anterior part of the snout to the farthest tip of the caudal fin. – In those fishes in which the profile of the end of the tail was concave, measurement was made to the deepest point of the notch.

Standard length (SL): from the most anterior part of the snout to the caudal base.

Body depth (D): the greatest depth of the body.

Anal depth (Da): body depth, measured just anterior to the anal fin and above the anus.

Depth caudal peduncle (Dc): the least depth of that part.

Head length (H): from the tip of the snout to the most distant point on the opercular membrane.

Snout length (S): from the tip of the snout to the anterior margin of the orbit.

Length of eye (E): greatest distance across the cornea, between the cartilaginous eye-ball.

Interorbital width (Int o): least fleshy width of the interorbital.

Predorsal length (Pre d): from the tip of the snout to the structural base of the first dorsal spine.

Preanal length (Pre a): from the tip of the snout to the structural base of the first anal spine.

Length of caudal (C): from the caudal base to the farthest tip of the fin.

Depth caudal notch (Dcn): from the deepest point of the notch to a point level with the farthest tip of the fin, measured in the midline.

The last two dimensions were only taken in *Th. bifasciatum.*

Often the bellies of the wrasses were protruding, overfilled with bait used for collecting. Maturity of the gonads may also affect the belly line. As these factors could bias the measurement of the body depth in such specimens, depth D was taken after emptying the abdominal cavity. As an added precaution I introduced the depth above the anus Da, a dimension that is hardly influenced by the amount of food in the intestines or by the size of the gonads.

In dead wrasses, emergence of the protractile lips may also cause distorted lengths. In such cases the lips were softly forced back into a resonably normal position.

Especially in the larger specimens of *Th. bifasciatum* where the caudal part of the body becomes uniformly deep dark green after death, it was not always possible to measure the standard length with great accuracy. Accordingly, the total length TL has been used for reference purposes.

Results

For all seven species studied the standard length, the three depth dimensions and the head length have been taken relative to the total length (x); the head and depth have also been expressed in the standard length (x'), while snout and eye have been compared with the head length (x''). Table 7 summarizes the ratios of the means of $\bar{x}$ and $\bar{y}$. The results are given per species for different color phases and for males and females separately.

The standard error of these ratios in percentages may roughly be estimated by $0.067/\sqrt{N}$, N being the number of fishes involved. This estimate is based on the reasonable assumption of a correlation of 0.90 between x and y and a coefficient of variation of 15% for each x and y. Likewise, the standard error of a difference in percentages between two groups of ratios $\bar{x}/\bar{y}$ (with N_1 and N_2) amounts to $0.067\ \sqrt{1/N_1 + 1/N_2}$.

Statistical comparison of the values found for color phase 1 and those for the corresponding terminal color phases is not appropriate, as per dimension, the data given for those two color phases refer to different size phases, thus to different segments of the growth curves.

Allometry of growth and size

Frequently two dimensions of an organism grow in such a way that the ratio between their geometric growth rates remains approximately constant over considerable periods of time. Then the relationship between the two dimensions, X and Y, for that period can be described by the function $Y = bX^{\alpha}$, in which b is a constant and α is the so called constant of allometry (SIMPSON e.a., 1960: 377, 396).

Most frequently α is not unity, which means that the ratio, X/Y, is constantly changing, the two dimensions showing allometric growth. When $\alpha > 1$, the geometric rate of increase is greater for Y than for X and the relation will be described as positive allometry,

TABLE 7

MEAN RATIOS OF BODY MEASUREMENTS ($\bar{x}/\bar{y}$)

Species	Island	sex	N	color phase	mean TL (mm)	TL/SL	TL/D	TL/Da	TL/Dc	TL/H	H/S	H/E	SL/H	SL/D
Thalassoma bifasciatum	Cur.	♀	44	1	65	1.19	5.3	5.9	9.1	3.9	3.7	4.3	3.24	4.42
		♂	37	1	66	1.19	5.3	5.9	—	3.9	3.3	4.3	3.24	4.42
		♂	66	4	95	1.15	5.0	5.6	9.1	3.9	3.2	5.2	3.35	4.35
	P.R.	♀	65	1	61	1.21	5.3	6.2	9.2	3.7	3.4	4.4	3.05	4.41
		♂	65	1	70	1.20	5.2	6.0	9.0	3.6	3.3	4.7	3.03	4.33
		♂	33	4	98	1.17	5.0	5.6	9.3	3.7	3.2	5.5	3.16	4.31
Halichoeres bivittatus	Cur.	♀	81	1	94	1.19	5.0	5.6	8.3	3.9	3.3	5.4	3.24	4.20
		♂	32	1	95	1.18	5.0	5.6	8.3	3.9	3.3	5.5	3.26	4.24
		♂	54	4	137	1.18	4.6	5.0	8.3	3.9	2.9	—	3.26	3.86
	P.R.	♀	46	1	75	1.20	5.0	5.9	9.1	3.6	3.5	4.9	2.98	4.17
		♂	32	1	75	1.20	5.0	5.9	9.1	3.6	3.5	—	2.98	4.17
		♂	11	4	169	1.18	4.4	5.0	7.7	3.7	2.7	6.9	3.14	3.69
Halichoeres garnoti	Cur.	♀	68	1	86	1.19	5.0	5.9	9.1	3.9	3.3	4.8	3.24	4.20
		♀	51	3 + 4	106	1.18	5.0	5.6	9.1	3.9	3.3	5.4	3.26	4.24
		♂	11	3 + 4	121	1.19	4.8	5.6	—	3.9	3.3	—	3.24	4.00
		♂	40	5	147	1.18	4.6	5.3	7.7	4.0	2.8	6.4	3.39	3.86
Halichoeres maculipinna	Cur.	♀	42	1	80	1.22	5.0	5.9	—	3.9	3.3	5.1	3.16	4.10
		♂	7	2 + 3	95	1.19	4.8	5.9	—	3.7	3.0	—	3.11	4.00
		♂	15	4	112	1.20	4.6	5.6	—	3.9	2.9	6.3	3.21	3.79
Halichoeres poeyi	Cur.	♀	33	1	96	1.20	5.0	5.9	9.1	3.9	2.9	5.2	3.21	4.17
		♂	10	1	119	1.19	5.0	5.6	9.1	3.9	2.9	5.7	3.24	4.20
Hemipteronotus splendens	Cur.	♀	26	1	85	1.20	4.4	4.6	9.1	4.0	2.8	4.6	3.33	3.62
		♂	23	3	116	1.22	4.2	4.2	9.1	4.0	2.5	5.4	3.28	3.41
Hemipteronotus martinicensis	Cur.	♀	57	1	87	1.19	5.0	5.0	11.1	4.0	2.8	5.1	3.36	4.20
		♂	20	3	113	1.19	4.8	4.6	10.0	4.0	2.3	5.8	3.36	4.00

while it is said to be negative in the reverse case. When $\alpha = 1$, the two dimensions have the same growth rate and there will be a constant ratio between them, independent of size; the two dimensions grow isometrically.

The data discussed here are obtained from large unselected samples of fish, measured irrespective of age. There is no guarantee that within one species a larger individual is older than a smaller one, since the growth rates for different individuals may differ. But it is reasonable to assume that the relative growth rates of two dimensions is much the same for all individuals of one species, since this is a fairly basic characteristic of a species. Accordingly the data given in table 7 include information on the allometry of size (SIMPSON e.a.: 407).

From Table 7 it results that the total length and the head length maintain a constant ratio of sizes so the relative growth of these dimensions could be interpreted to be isometric in all seven species studied.

The TL/SL ratio as well as TL/D, TL/Da and H/S become slightly smaller with increasing size, which possibly reflects a small positive allometry. However, the differences between the ratios for small and larger specimens are not significant and the coefficients of allometry may be only slightly greater than unity.

A possible small positive allometry has also been found for TL/Dc in four species; the ratios were not affected by size and thus probably isometric, in *Th. bifasciatum*, *H. poeyi* and the two *Hemipteronotus* species.

The H/E ratio showed strong allometry in all seven species.

For the eye the analysis has been continued by calculating more in detail the relation between eye length and total length for all species studied. The results are given in Table 8 and Fig. 9. The Table shows the mean body length ($\bar{x}$) and its standard deviation (s_x) together with the means ($\bar{y}$) and standard deviations of the eye (s_y). The correlation coefficient r and the linear regression coefficient b of the regression of y on x ($y - \bar{y} = b(x - \bar{x})$ are also given.

In *Th. bifasciatum* and *H. bivittatus* the values for *r* and *b* for the regression of the eye on the total length are hardly different for both the females and males of color phase 1. For the larger terminal phase males these values do differ markedly; in the first species the *r* and *b* values are roughly even twice as small. A similar trend is found for *He. splendens*. These results underline the original impression of a strongly negative allometric growth of the eye.

For *H. garnoti* compared with phase 1 (♀♀) a slightly lower correlation coefficient has been found for the intermediates (♀♀) and terminal colors (♂♂).

In *H. maculipinna* and *He. martinicensis* the calculated correlation coefficients were found to be greater in the terminal phase specimens. The same was found for the larger specimens of *H. poeyi*. This does

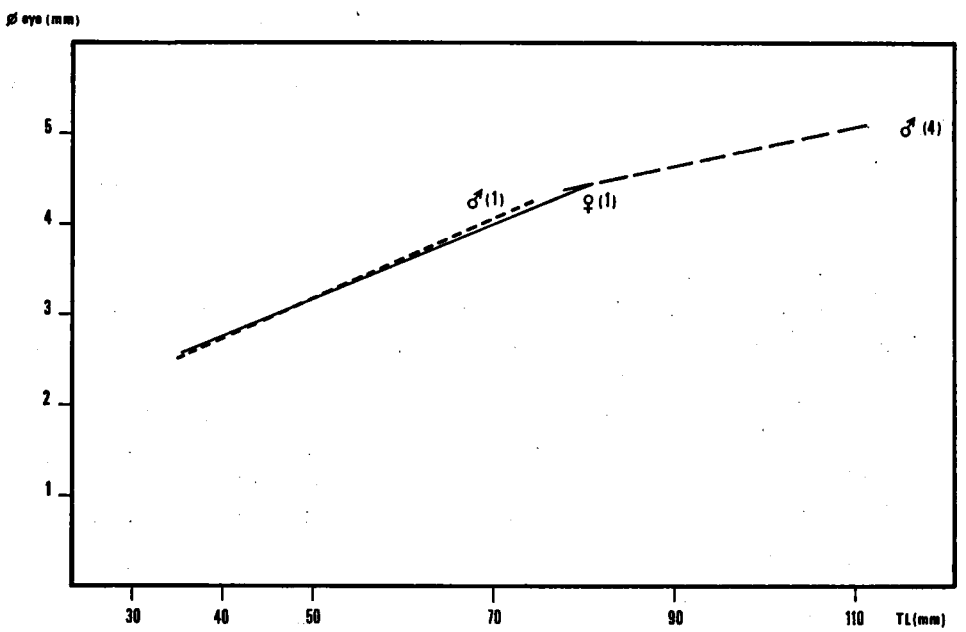


Fig. 9. Regression lines of eye diameter on total length (TL) in *Thalassoma bifasciatum*.

First adult phase females = ♀ (1); first adult phase males = ♂ (1), and terminal phase males = ♂ (4).

TABLE 8

REGRESSION OF LENGTH OF EYE (y) ON TOTAL LENGTH (x)

Species	Island	sex	color-phase	N	$\bar{x}$ (mm)	$\bar{y}$ (mm)	s_x	s_y	r	b
Thalassoma bifasciatum	Cur.	♀	1	44	58.7	3.5	11.3	0.5	0.91	0.041
		♂	1	4	54.8	3.4	9.8	0.4	0.99	0.048
		♂	4	46	94.7	4.7	8.4	0.3	0.54	0.021
Halichoeres bivittatus	Cur.	♀	1	81	93.9	4.5	13.8	0.5	0.80	0.029
		♂	1	11	95.0	4.5	14.3	0.6	0.70	0.028
	P.R.	♀	1	46	74.4	4.2	20.2	1.0	0.96	0.048
		♂	4	11	168.9	6.6	12.4	0.4	0.61	0.018
Halichoeres garnoti	Cur.	♀	1 + 2	68	86.0	4.6	10.9	0.3	0.77	0.023
		♀	3 + 4	36	106.6	5.1	10.0	0.3	0.72	0.020
		♂	5	25	147.8	5.8	11.6	0.4	0.72	0.026
Halichoeres maculipinna	Cur.	♀	1	42	80.5	4.1	11.7	0.9	0.55	0.044
		♂	4	13	113.4	4.7	12.4	0.4	0.68	0.022
Halichoeres poeyi	Cur.	♀	1	31	97.3	4.9	12.9	0.5	0.84	0.031
		♂	1	10	119.2	5.5	22.0	0.6	0.94	0.027
Hemipteronotus splendens	Cur.	♀	1	26	85.6	4.7	11.6	0.6	0.87	0.044
		♂	3	23	116.4	5.4	8.5	0.4	0.52	0.022
Hemipteronotus martinicensis	Cur.	♀	1	57	87.2	4.3	7.0	1.0	0.45	0.020
		♂	3	13	112.9	4.9	9.6	0.4	0.68	0.032

not fully agree with the trend as stated in the ratios of the means (Table 7), but it may be attributable to the rather low numbers of specimens on which the regression calculations had to be based.

For *Th. bifasciatum* the regressions between total length (x) and various other dimensions (y) have been further analyzed for females and males in the yellow phase 1 and for the males of the terminal bluehead colors, all collected on Curaçao. The results are given in Table 9 ($\bar{x}$, s_x; $\bar{y}$, s_y; b and r).

The data in Table 9 provide further support in evidence of the degrees of allometry previously discussed. The correlations with body length are high, though there is a tendency towards a lower r, as well as a smaller value for b in the terminal phase, especially for the depth of the caudal peduncle and the eye. No differences are found between color phase 1 males and females.

TABLE 9

REGRESSION OF BODY DIMENSIONS (y) ON TOTAL LENGTH (x) IN *Thalassoma bifasciatum*

Y			N	$\bar{x}$ (mm)	$\bar{y}$ (mm)	s_x	s_y	r	b
SL	♀	phase 1	233	64.1	53.5	8.5	7.4	0.96	0.842
SL	♂	phase 1	18	63.6	53.2	9.5	7.8	0.99	0.817
SL	♂	phase 4	36	95.0	82.6	9.6	9.5	0.96	0.952
depth	♀	phase 1	227	64.7	12.4	9.0	2.0	0.95	0.208
depth	♂	phase 1	31	66.4	12.5	9.6	1.9	0.97	0.194
depth	♂	phase 4	93	95.0	18.9	9.0	2.0	0.85	0.186
depth a.	♀	phase 1	186	64.2	10.7	9.0	1.7	0.85	0.158
depth a.	♂	phase 1	21	67.4	11.1	10.5	2.0	0.90	0.172
depth a.	♂	phase 4	82	95.9	17.1	8.8	2.1	0.77	0.182
depth c.	♀	phase 1	25	59.6	6.7	10.5	1.5	0.91	0.127
depth c.	♂	phase 1	2	54.8	6.2	7.8	0.7	—	—
depth c.	♂	phase 4	23	94.0	10.7	7.8	1.1	0.64	0.090
pre d.	♀	phase 1	28	61.7	16.8	11.7	3.4	0.97	0.281
pre d.	♂	phase 1	2	54.8	14.8	7.8	2.0	—	—
pre d.	♂	phase 4	18	94.6	24.1	8.6	1.9	0.82	0.181
pre a.	♀	phase 1	28	61.7	31.3	11.8	6.8	0.98	0.566
pre a.	♂	phase 1	2	54.8	26.4	7.8	4.8	—	—
pre a.	♂	phase 4	18	94.6	46.1	8.6	4.2	0.95	0.465
head	♀	phase 1	219	64.6	16.8	8.8	2.4	0.94	0.258
head	♂	phase 1	19	65.8	16.9	10.9	3.1	0.95	0.268
head	♂	phase 4	104	95.6	24.7	8.6	2.2	0.86	0.216
snout	♀	phase 1	39	58.8	4.3	11.0	1.0	0.91	0.082
snout	♂	phase 1	4	54.8	4.3	9.8	1.0	0.98	0.104
snout	♂	phase 4	69	94.8	7.5	8.7	0.9	0.81	0.082
eye	♀	phase 1	44	58.7	3.5	11.3	0.5	0.91	0.041
eye	♂	phase 1	4	54.8	3.4	9.8	0.4	0.99	0.045
eye	♂	phase 4	46	94.7	4.7	8.4	0.3	0.54	0.021
inter o.	♀	phase 1	19	58.2	4.0	10.1	1.0	0.89	0.087
inter o.	♂	phase 1	2	54.8	4.4	7.8	1.1	—	—
inter o.	♂	phase 4	7	93.4	5.6	10.1	0.7	0.86	0.062
caudal	♀	phase 1	123	66.2	10.3	11.4	2.4	0.91	0.192
caudal	♂	phase 1	22	72.7	12.2	12.6	3.0	0.93	0.218
caudal	♂	phase 4	197	94.7	21.8	10.0	4.9	0.85	0.416
c. notch	♀	phase 1	38	75.0	1.4	7.7	0.7	0.79	0.076
c. notch	♂	phase 1	16	78.0	2.1	8.5	1.2	0.82	0.114
c. notch	♂	phase 4	142	94.9	9.3	10.4	4.7	0.85	0.380

The discussed ratios differ little from body proportions given by other authors. Allometric growth in *Th. bifasciatum* is apparently indicated in literature when next to color, differences in ratios were used to separate the yellow and the bluehead phases into two different species. For instance, JORDAN e.a., METZELAAR and NICHOLS mentioned a lower depth ratio in the bluehead stage.

FEDDERN (1965) also found a negative allometry for the eye, and small positive allometry for the snout. In one of his figures one might perceive, though very vaguely, a relative decrease of the head length as related to the standard length. My SL/H data reflect a similar trend; a difference too small to be significant on the 5% significance level.

For the four *Halichoeres* species the ratios given by JORDAN e.a., METZELAAR, NICHOLS, BEEBE e.a. and CERVIGÓN are not really different from my data.

JORDAN e.a. gave rather low depth and head ratios for *He. martinicensis*, while the depth ratios given by RANDALL for both *He. martinicensis* and *He. splendens* and by BEEBE e.a. for *He. splendens* are also smaller as compared to my data.

PARR (1930) contributed to the taxonomic analysis of the various *Xyrichthys* (*Hemipteronotus*) species then distinguished by preparing a table of measurements, including eight different sizes of the head and the depth of the body. (Most probably the data only refer to *He. splendens* and *He. novacula*). His table shows with increasing total length an increase of the depth of the cheek, of the distance of the eye to the snout and of the body depth; the relative snout measurements did not change and the head and eye decreased. This does not disagree with the degrees of allometry found in my data. PARR plotted various relative sizes against the standard length and so found evidence to assume that the old subdivision into *Novaculichthys* and *Xyrichthys* merely represented juvenile and adult groups.

QUIGNARD (1966), studying allometry in 21 European labrid species, is the only investigator who included statistical processing of his results. He concluded that allometry was a general phenomenon in Labridae but, be it positive or negative, of low intensity: also in the European wrasses only the eye showed strong negative allometry.

Sex differences

Per species no differences have been found between the females and males (if present) in color phase 1 in none of the rations and values here discussed. Consequently, external sex determination of one single colorphase is impossible.

The females (phase 1) differ slightly, though not significantly from the males of the respective terminal groups. Rather than a sex difference this phenomenon must be the consequence of the greater mean size of these males. The differences between females and terminal males disappear when the data are standardized for total length. FEDDERN did not find either any sexual dimorphism in morphometric features of *Th. bifasciatum*; nor did QUIGNARD mention any

of such differences between the sexes of European labrids studied.

Geographic differences

Sufficient numbers of *Th. bifasciatum* and *H. bivittatus* were collected in Puerto Rico to make a comparison with those from Curaçao worth-while. The mean head length proved to be relatively slightly smaller in the Puerto Rico specimens, but the differences are too small to be significant.

In *H. bivittatus* the mean ratios H/S and H/E are also slightly different from those of comparable sex and color groups of Curaçao. However, for this species the mean TL of the respective groups was also different and, as discussed, these proportions change slightly with size. The differences found between the two areas must be related to the difference in total length rather than to geographic difference.

No investigations about possible local differences per species were made up to now, but the data given in the literature for scattered collecting places are rather similar. I do not expect real differences up to racial level. The eggs of the species studied are pelagic and the release of the gonadal products happens in the most turbulent superficial layers of the sea. Consequently, the chance of isolation must be small and most probably every species studied belongs to one single breeding community.

QUIGNARD (1966) found for only three of the 21 European labrid species he studied small metric and meristic differences between specimens from the Atlantic and Mediterranean coasts, differences much too small though, to be of racial level either. Two of these three species belong to the genus *Symphodus*, in which nest building and care for the juveniles is displayed by the males. This could promote geographic isolation. On the other hand, QUIGNARD discusses this phenomenon as a homogenizing factor, that should limit differences between populations by its thermoregulating character which favours harmonious development of features that are inclined to vary with temperature.

Specific differences

When comparable color phases (taking specimens of roughly the same mean size) of the various species are compared, no striking differences are found in the ratios. Consequently, morphometric

features are not helpful in differentiating the Caribbean labrid species.

The relations between respective body dimensions among the four *Halichoeres* species are very similar. *Th. bifasciatum* differs from these species only slightly in the TL/D and TL/Da ratios. These as well as the relatively larger eye, expressed by a smaller H/E quotient in phase 1 *Th. bifasciatum* specimens should not be considered as real species differences as they may be due to the smaller size.

The two *Hemipteronotus* species deviate more from the other genera studied. The greater depth of the body results in a lower ratio for both TL/D and TL/Da in *splendens*, and for TL/Da in *martinicensis*. On the other hand the T/Dc ratios of *martinicensis* are slightly higher than in the other two genera. The slightly higher quotient for the TL/H relation may be associated with the "blunter" head of this genus. The more anterior position of the eyes in *Hemipteronotus* is reflected in a lower H/S ratio.

In his comparison of various *Xyrichthys* species PARR (1930) has already remarked that the figures obtained tend to show a discouraging lack of distinction between the forms compared as to their proportional measurements.

Shape of fins

In fishes the fins may provide sexual characteristics. In some groups even copulating organs are formed, for example by the transformation of the anal fin into a gonopodium in the males of *Gambusia*, *Lebistes* and other Poeciliidae, or of the pelvic fins into myxopterygia in the Elasmobranchii. In a greater number of species the fins do not play such an essential part in reproductive behavior, but nevertheless may form a secondary sexual characteristic. In general in such species some of the fins or parts of them are larger or thicker in the males, e.g. the dorsal fin of *Mollienisia* and *Callionymus*, or the thicker pelvic spine in the male of *Tinca tinca*. Well-known is the marked sexual dimorphism of the caudal fin of *Xiphophorus helleri*, the swordtail, where in the male the lower lobe is considerably extended.

For labrid species fin dimorphism has also been mentioned. In *Duymaeria flagellifera*, a Japanese dichromatic wrasse, the first and second dorsal spines are produced into filaments which are longer in [terminal colored] males (OKADA, 1955). In *Coris julis* no differences in fin shape and color exist between first adult color phase males and females. At larger sizes (only males and sex-indeterminates) the first three dorsal spines become elongated; in this proximal portion of the dorsal a bright black spot bordered by red is developed (ROEDE, 1966). In *Bodianus rufus* and *B. puchellus* the dorsal, anal, caudal and pelvic fins become elongated during growth (FEDDERN, 1963).

In this study due attention has been given to the shape of the fins, to check whether differences could be found in relation to color and/or sex, with the following results.

In none of the four *Halichoeres* species were essential differences in the shape of the fins at different sizes or color phases found.

In *Thalassoma*, however, during growth a remarkable change in the shape of the caudal fin of *bifasciatum* occurs, from nearly convex to extremely concave due to increasing exertion of the angles. (See also color descriptions and Fig. 2/1–4 in Chapter VI).

To investigate the relation between caudal shape and color and sex, extra data concerning the tail were collected.

Changes in shape are difficult to tackle and generally shape cannot simply be defined numerically. Accordingly, in a sample of 680 specimens, I noted down an overall impression on the shape of the caudal, using the following scale:

0 = truncate or even slightly convex with central rays the longest (Fig. 2/1);

1 = slightly concave, upper and lower rays hardly longer than median rays (Fig. 2/2);

2 = concave, semi lunar; caudal lobes very slightly protruded;

3 = more lunate (Fig. 2/3);

4 = outer caudal rays much elongated, filamentous;

5 = upper and lower lobes extremely elongated and filamentous (Fig. 2/4).

We tried to express the changes in the caudal shape in numerical terms by single quantitative treatment. The alteration from nearly convex to extremely concave is the result of differential growth of the upper and lower rays as compared with the central rays. To measure the difference in relative size of these rays in a number of about 300 specimens the total length of the caudal (C) and the depth of the caudal notch (Dcn) were noted down.

TABLE 10

MEAN RATIOS OF CAUDAL LENGTH/DEPTH CAUDAL PEDUNCLE (C/Dcn) IN *Thalassoma bifasciatum*

Sex and Color	C/Dcn	s	N
♀ color phase 1	1.29	0.31	17
♂ color phase 1	1.18	0.22	8
♂ color phase 4	2.03	0.22	40

TABLE 11

REGRESSION OF CAUDAL DEPTH Dcn (y) in *Th. bifasciatum*

A – *on caudal fin length* (x)
B – *on total length* (x)

	Sex	Color phase	N	$\bar{x}$ (mm)	$\bar{y}$ (mm)	s_x	s_y	r	b
	♀	phase 1	31	11.9	1.3	2.0	0.7	0.81	0.287
A	♂	phase 1	14	13.3	2.1	2.6	1.3	0.80	0.385
	♂	phase 4	146	22.0	9.4	5.2	4.7	0.95	0.863
	♀	phase 1	38	75.0	1.4	7.7	0.7	0.79	0.076
	♂	phase 1	16	78.0	2.1	8.5	1.2	0.82	0.114
B	?	phase 2 + 3	18	78.6	2.5	4.9	1.5	0.83	0.264
	♂	phase 2 + 3	22	82.6	3.5	5.5	1.9	0.62	0.211
	♂	phase 4	142	94.9	9.3	10.4	4.7	0.85	0.380

a. An essential shape index is given in the ratio of caudal length/depth caudal notch, C/Dcn. The mean ratios are listed in Table 10. No significant differences have been found between the yellow phase males and females, but the larger, bluehead colored males deviate significantly ($p < 0.0005$).

b. The regression of the depth of the notch in the caudal fin Dcn on caudal length C (Table 11a) and on total length TL (Table 11b) have been calculated. Figure 10 illustrates the relation between Dcn and TL. Next to color phase 1 females and phase 1 and 4 males, also intermediate colored males and fish with non-functional gonads are

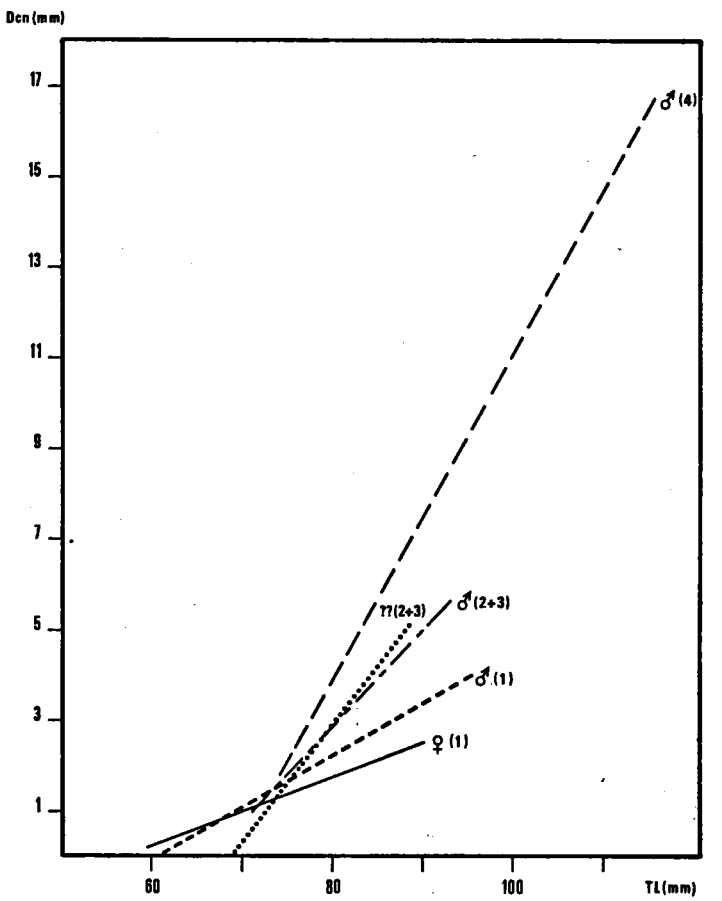


Fig. 10. Regression lines of depth of caudal fin notch (Dcn) on total length (TL) in *Thalassoma bifasciatum.*

First adult phase females = ♀ (1); first adult phase males = ♂ (1); intermediate phases males = ♂ (2 + 3); intermediate phases indistinct sex = ?? (2 + 3), and terminal phase males = ♂ (4).

represented. The lines of the graph are drawn only over the range within two standard deviations of the mean. For comparison also the relation between C and TL is shown for yellow phase 1 males and females and bluehead males (Fig. 11). As shown, the value for *b*, the slope of the regression lines, gradually changes from the phase 1 females to the bluehead males.

c. As the depth of the notch Dcn is an essential parameter for the shape of the caudal fin, I checked whether its increase is parallel to the 0–5 scale of estimated shapes applied (Table 12). Because of the fair correlation between the data of estimated and measured shape, the former were used for further analyses.

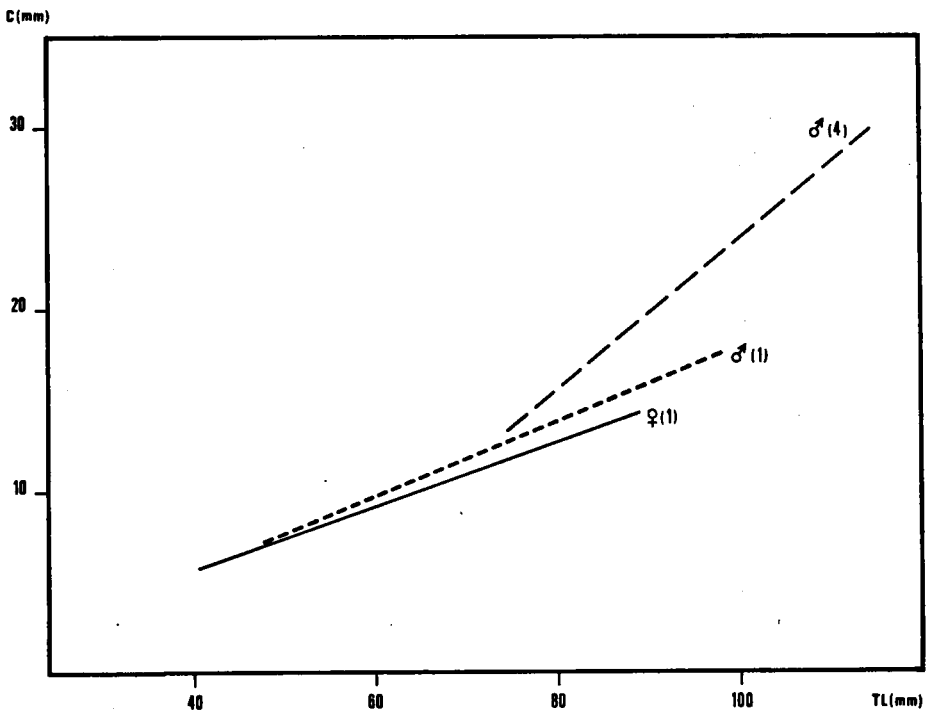


Fig. 11. Regression lines of caudal fin length (C) on total length (TL) in *Thalassoma bifasciatum*.

First adult phase females = ♀ (1); first adult phase males = ♂ (1), and terminal phase males = ♂ (4).

TABLE 12

ESTIMATED SHAPE OF CAUDAL FIN AND MEASURED DEPTH OF CAUDAL NOTCH IN 350 SPECIMENS OF *Thalassoma bifasciatum*

Depth caudal notch (Dcn)	Shape					
	0	*1*	*2*	*3*	*4*	*5*
20–21 mm	—	—	—	—	—	7
18–19 mm	—	—	—	—	3	13
16–17 mm	—	—	—	—	5	21
14–15 mm	—	—	—	1	8	5
12–13 mm	—	—	—	3	14	1
10–11 mm	—	—	—	9	14	—
8– 9 mm	—	—	—	14	7	—
6– 7 mm	—	—	—	30	4	—
4– 5 mm	—	—	10	30	—	—
2– 3 mm	—	2	40	6	—	—
0– 1 mm	49	45	9	—	—	—
Total	*49*	*47*	*59*	*93*	*55*	*47*

TABLE 13

SHAPE AND LENGTH OF CAUDAL FIN (C) IN 350 SPECIMENS OF *Thalassoma bifasciatum*

C (mm)	Shape					
	0	*1*	*2*	*3*	*4*	*5*
32–..	—	—	—	—	2	16
29–31	—	—	—	—	6	18
26–28	—	—	—	3	16	9
23–25	—	—	—	9	15	3
20–22	—	—	—	26	11	1
17–19	—	—	9	34	5	—
14–16	—	3	32	20	—	—
11–13	—	34	18	1	—	—
8–10	49	10	—	—	—	—
Total	*49*	*47*	*59*	*93*	*55*	*47*

TABLE 14

SHAPE OF CAUDAL, AND BODY LENGTH (TL) IN 680 SPECIMENS OF *Thalassoma bifasciatum*

TL (mm)	Shape					
	0	*1*	*2*	*3*	*4*	*5*
110–119	—	—	—	—	6	4
100–109	—	—	—	26	38	12
90– 99	—	2	8	71	30	—
80– 89	—	18	59	72	9	—
70– 79	30	80	35	9	—	—
60– 69	67	22	—	—	—	—
50– 59	52	—	—	—	—	—
40– 49	21	—	—	—	—	—
30– 39	9	—	—	—	—	—
Total	*179*	*122*	*102*	*178*	*83*	*16*

TABLE 15

OBSERVED RANGE OF TOTAL BODY LENGTH (TL) AND CAUDAL SHAPE IN 680 SPECIMENS OF *Thalassoma bifasciatum*

Shape	N	Total length (mm)
0	179	30.5– 79.6
1	122	61.9– 92.5
2	102	70.1– 99.4
3	178	75.9–109.5
4	83	85.0–119.2
5	16	100.7–119.2

d. Correlation tables have been composed for the relation between caudal shape and the caudal length and the body length respectively (Tables 13 and 14). Also the observed range of the total length for each shape group (Table 15) and a correlation table for the caudal shape according to color phase (Table 16) are given. There is in general a strong relation between the color and size of a specimen, but, as can be learned from the tables, the change in the caudal

TABLE 16

CAUDAL SHAPE AND COLOR PHASE IN 680 SPECIMENS OF *Thalassoma bifasciatum*

Color phase	Shape					
	0	*1*	*2*	*3*	*4*	*5*
4	—	7	40	159	82	16
3	—	6	20	11	1	—
2	2	21	17	3	—	—
1	177	88	25	5	—	—
Total	*179*	*122*	*102*	*178*	*83*	*16*

shape is more strictly related to size. In fish larger than 99 cm TL only shapes 3–5 have been found. But in specimens, with fully developed bluehead colors, still of rather small size (7–9 cm) caudal shapes 1 and 2 were found. The tables also show the rather considerable amount of individual variation.

Summarizing it may be concluded that in specimens smaller than 6 cm TL only straight or even convex tail forms have been found. Then the differential growth of the outer lobes slowly starts, accelerating when a size of roughly 9 cm TL is reached. Fin shape is clearly related to body length; a direct relation with color change is less clear.

The change of the caudal shape has been mentioned briefly by NICHOLS, TEE-VAN, LONGLEY e.a., CERVIGÓN and BÖHLKE e.a.; most authors neglected this striking process. Only BREDER (1927) discussed the phenomenon in more detail. In a diagram he indicated that a convex tail occurs in fish up to 40 mm SL; a truncate tail from 43 to 80 mm SL, a lunate tail from 62 to 88 mm SL and a caudal with produced tips from 82 mm SL or larger. This is not essentially different from the present data (Table 14).

A transformation of a truncate into a lunate caudal at larger size has also been described for other *Thalassoma* species, like *Th. pavo* (QUIGNARD, 1966) and several Indo-Australian species, like *Th. janseni* (Blkr.), *Th. hardwicki* (Benn.) and *Th. lunare* (L.) (DE BEAUFORT, 1940), though other species of this genus described by the latter only showed a slightly rounded caudal shape. Other labrid species, e.g. *Gomphosus varius* also develop a lunate tail during somatic growth.

Interesting is BREDER's statement (1926: 226): "The many and various shapes of the tails of fishes are indicative of the speed and type of movement enjoyed by the different forms that use movements of the body for propulsive effect. Fishes with deeply forked or lunate tails are capable of long continued swimming at high velocity, the more lunate the tail the faster being the fish ...."

BREDER compared different species, but the principle may be pertinent to the situation within one species as well. Large bluehead specimens with deeply lunate tail may increase their speed suddenly when defending their territory or chasing females; such propulsive motion is less characteristic for small, straight-tailed specimens (Chapter VIII).

In the genus *Hemipteronotus* fins may also display differential growth.

In various species in the young a prolongation of the first two dorsal spines occurs. I agree with RANDALL (1965) that in *He. splendens* this phenomenon occurs in the smaller specimens of color phase 1. On attaining larger sizes the difference in length diminishes. This feature is clearly related to a certain, small, body length; no relationship to color change has been found.

For instance, a 52 mm TL specimen was the smallest *splendens* caught (ZMA 104.082). It was a young female with very small, developing ovaries. The two first dorsal spines were twice as long as the rest of the spines. In a color phase 1 female of 92 mm TL (ZMA 104.080) with well-developed ovaries, however, the two most anterior spines were only about 2 mm longer than the others. A terminal phase specimen of the same haul of 119 mm TL (ZMA 104.081), a fish with hardly any gonads, had dorsal spines of equal length.

Elongate first dorsal spines also occur in small specimens of *He. novacula* (L.) (RANDALL, 1965) and *Novaculichthys bifer* (L. & B.) (DE BEAUFORT, 1940).

In small *He. martinicensis*, neither RANDALL, who even examined a specimen of only 30 mm SL, nor the present author found elongate first dorsal spines.

Most striking is the extra increase of the length of the first ventral ray in the larger specimens of both species studied. In *He. splendens* the tip of the filament may even extend posteriorly to the origin of the anus up to the base of the 4th anal ray; in *He. martinicensis* the less extremely elongated ray may extend slightly beyond the anus (Fig. 7, 8). In both species phase 1 specimens may already have

slightly elongate pelvic fins but the actual differential growth starts around a body length of about 9 cm in *He. splendens*, and of about 8 cm in *He. martinicensis*, i.e. where intermediate colors also start to develop. Since the filamentous protuberances of the ventrals may be damaged easily, measuring lengths of the pelvic fin may give incorrect information and no such data have been included in this study.

For detailed information I refer to RANDALL's monograph (1965) on *Hemipteronotus*. His figure 2, representing the relationship of pelvic length to standard length shows how after a certain SL the dots become gathered around a much more steep line for both *He. splendens* and *He. martinicensis*. The first author who actually measured the relative length of ventral fins was PARR (1930). Though finding discrepancies in the data, he expected correctly that a gradual increase in ventral lengths would prove to be a common feature in development.

As in *He. martinicensis* males were only found among the large, terminal phase, in this species the longer pelvic fin length seems to run parallel with sex. RANDALL considers the produced ventrals in *He. splendens* also, as sexual dimorphism. In the present study, however, of the 28 phase 1 specimens of *splendens* dissected one proved to be a real functional male (though it slightly deviated in color; see Fig. 7, phase 1a; see Chapter X). (Sexing of small samples of wrasses of small size is easily misleading; a minority of functional males may elude observation).

Until the reverse is proved, the present author is inclined to regard fin length differences not as a sexual dimorphism, but only as a characteristic of a certain size. She considers here the results in *C. julis* and *Th. bifasciatum*, where elongation of fin species or rays is correlated strongly with body size only, and consequently does not occur in a large part of the males (the small, first adult phase ones). In those labrid species, where sex and color phase are somehow related (Chapter X), elongate fins and male sex may run parallel accidentally. Injections with sex hormones had little or no effect on the length of the fins (Chapter XIII). Further investigations may definitely show whether elongation of fins depends more on size than on masculinisation.

In this respect LETACONNOUX's study (1949) of *Callionymus lyra* is worth mentioning. In this species the anterior of the two dorsal fins is much elongated in males, but this feature diminishes with age. LETACONNOUX concluded that this characteristic was not actually controlled by sex hormones, but formed a "neutral"sexual feature. Experiments with *Lebistes* (e.g. GALLIEN, 1948) showed also only imperfect masculinisation of the anal fin after treatment of females with androgenic hormones.

No more, does there seem to be any relation between the grade of color change during life and the occurrence of fin length differences. Differential growth of some parts of some fins has been found in species with a striking change of color, such as *Th. bifasciatum* (tail), *Coris julis* (dorsal) and *Bodianus pulchellus* (dorsal, anal, caudal and pelvic); yet, it does not take place in fish with radical changes like *H. maculipinna* or *H. garnoti*. On the other hand, the phenomenon occurs also in species with less striking color changes, such as *Th. pavo* (tail), *He. splendens* and *He. martinicensis* (pelvics) or *Bodianus rufus* (dorsal, anal, caudal and pelvic fins). While in other fish without striking color alterations, no elongate fin parts are found, e.g. *H. poeyi*.

Conclusions

1. Fin formulae are given in Table 6.

2. The differences in various relative body dimensions between the species are too small to be used for classification; only the genus *Hemipteronotus* has some slightly deviating proportions.

3. Some slightly positive allometry is found, next to isometric relations; only the eye displays significantly negative allometry.

4. Females and males of homologous color phases (in most cases the first adult phase is concerned) do not show morphometric differences. Allometry accounts for some slight differences found between females of the first adult phase and males of the large terminal phase.

5. Per species no differences have been found between specimens of Curaçao and Puerto Rico.

6. Differential growth of some of the fins is found in three species. In *He. splendens* in very small fish the first two dorsal spines are elongated. In both *Hemipteronotus* species the first ventral ray of the pelvic fin is very long in large specimens. In *Th. bifasciatum* the shape of the caudal fin starts to change considerably at about 9 cm Tl; in large fish the fin is deeply forked. – These features are clearly related to body length; less strictly to color change.

VIII. BEHAVIOR

In view of the impact of behavior on sampling and on the interpretation of the final results, detailed life observations on wrasses in their natural environment as well as in laboratory tanks were made throughout this study, although no attempts have been made to analyze the behavior patterns quantitatively. The essential points of the behavior are reported here.

The gregarious wrasses form loose aggregations. *Hemipteronotus martinicensis* lives separated from other labrid species, but the remaining six species – if present – often frequent the same areas forming heterospecific groups.

Locomotion and Orientation

Watching a group of wrasses is like enjoying the performance of a graceful ballet with quick, delightful movements in a perfect precision.

Many coral fishes move around in state. The kingly Angelfish and the Butterflies (Chaetodontidae) appear to sail along; the Triggerfishes (Balistidae) stride through the water, while the Trunkfishes (Ostraciidae) move like an unwieldy battleship. The labrid fish, however, swim in a playful, mobile way. Though the body is usually kept noticeably still, they nimbly dive down, slip upwards, side-

wards and backwards with repeated, sudden spins and turn around with a remarkable accuracy for such rapid shifts.

Characteristic is the pectoral propulsion. In contrast to many other fishes the wrasses are driven forwards by simple synchronous flapping of the pectoral fins. (This exclusive form of localised ostraciiform motion is distinguished by BREDER (1926) as "labriform." Ostraciiform locomotion consists of hardly any curve-forming at all). They may cease the operation of one fin while the other continues as before. The other fins are depressed most of the time. Quick unfolding and undulating of the dorsal and anal fins is executed when manoeuvring. The caudal fin is only occasionally unfolded for steering and stabilisation; turned to one side, it may act as a rudder. According to NEU (1935) in Labridae the center of gravity falls within the air bladder so the fish are in a stable equilibrium; no fins have to be used for keeping a horizontal position. This explains why most fins can be depressed most of the time, and partly accounts for the ease with which labrids swim on their sides at times.

The wrasses may suddenly accelerate their speed and flash away two to four times more rapidly than in the normal tempo. Some fast twistings of the caudal fin or of the caudal part of the body accentuate the impelling effect of the pectoral fin at the start of this scampering away that mostly lasts only a few seconds.

A very special way of swimming is displayed by cleaning labrid specimens. When following other fish trying to start picking away ectoparasites, there are characteristic oscillations of the posterior part of the body.

Thalassoma bifasciatum, *Halichoeres bivittatus* and *H. maculipinna* are the most agile moving fish. Often small, first adult phase *bifasciatum* specimens – exhibiting the most yellow variation of phase 1 – and small *bivittatus* and *maculipinna* specimens were seen in the uppermost water layers, darting to and fro in the surf with swift turns. Larger specimens in phase 1 to 4 colors were more often swimming close to the bottom, picking at sand, corals and rocks.

Halichoeres garnoti never was as frisky. The small, more slender specimens are clearly more mobile than the larger individuals. The

specimens of the other, less abundant species were seldom noticed in frolicsome play, defying the surf. *H. poeyi* is in general a more quiet fish, with less striking movements. More compressed *Hemipteronotus splendens* is by nature less supple; it swims with more stately movements and fewer turns.

While these six species swim in a horizontal position most of the time, the last species studied, *Hemipteronotus martinicensis*, was observed mostly standing in nearly perpendicular position, head upward, some one to two meters above the sandy area they inhabited. However, the head could be pointed down. Only a minority of the colony was slowly swimming around.

The rapid labrids react very quickly to disturbances. When they are just bothered, they will dash away one or two meters. When scared, they will slip in nearby cracks and in real danger burrow themselves in the sand. In plain tanks with no sand or stones for hiding, the wrasses were obviously more nervous.

The pattern was slightly different in *Hemipteronotus martinicensis*. These are more easily disturbed; often they skittishly disappear into the sand with a kind of anguilliform shudder. In contrast to the explicit downward flight reaction of the other fishes, this species often was dashing upwards and prone to jump out of the hoopnet during collecting.

Labrids were often observed resting, the belly flat on the bottom and the pectoral fins spread at a straight angle to keep their balance. Often, the caudal fin is turned sidewards. They could also be lying on their side, fins folded against the body. These positions can be held for hours. When more vivacious wrasses disturb a resting fish, the latter will often slip to a place at short distance and continue its reposing. This behavior was noticed mostly in larger, terminal phase specimens such as bluehead *bifasciatum*, pastel colored *bivittatus* and yellow-head *garnoti* specimens. No strict separation can be made, though, as – for instance during captivity – even the smallest individuals could be resting as described.

Resting seems to be a common habit among labrids. It has also been described for *Coris julis* (especially in the larger, strikingly colored fish, MACHTELD ROEDE, 1966) and in three *Crenilabrus* species (NEU, 1935).

The manoeuvring capabilities of labrids are great. Sudden swift turns in any direction are even displayed in areas where surf breaks on emerging corals and rocks and the water is in constant motion. This is often observed in small, yellow *bifasciatum* specimens. Also small *bivittatus* and *maculipinna* are well-adapted for such playing around.

The wrasses further display their utmost manoeuvring abilities when agilely swimming in and out of small cracks and crevices among sharp rocks and moving around between branching corals and sea urchin spines.

Some labrid species frequent areas of algae and seagrasses. In this tangle of plants it also must be of advantage to be able to move around with precision. This seems to hold for Caribbean species as *H. poeyi, He. splendens* and *Doronatus megalops*.

The rapidity of the movements and the remarkable precision suggest the presence of a well adapted, good vision. According to live observation by the present author the Mediterranean labrid *Coris julis* moves in a way comparable to that of the nimble Caribbean wrasses. VERRIER (1933) found that *julis* posesses the most complex fovea to be found among fishes. The retina contains numerous cones while in the perifoveal region a group of rods alternates with a voluminous cone. The complicated construction approaches the situation found in higher vertebrates. Further, in contrast to most fishes, in labrids the eyes move independently of each other (HERTER, 1953).

MAES (1930; in HERTER) carried out discriminance-learning experiments with the wrasses *Crenilabrus pavo* and *Coris julis*. When offered a series of openings of the same shape from which to escape, the larger openings were more often used; among passages of the same surface area the vertical shaped openings were preferred. Experiments, in which normal and blindfolded wrasses had to choose between passages of different shape, some of which had been blocked with glass, gave further evidence for the optical basis of the orientation.

Phototropical reactions are in many fishes an important factor in their spatial orientation. For some labrid species it has been proved that they react very strongly to light: to variations of the light intensity (VERRIER & ESCHER-DESRIVIÈRES, 1937; *Coris julis*) and to direction and duration of the exposure (VAN HOLST, 1935; *Crenilabrus rostratus*).

Sound may be another factor contributing to the accurate spatial orientation. However, labrids have been classified with the non-ostariophysic fish that in general are less sensitive to sound stimulation (HERTER). Studies on the lateral line in labrids are unknown to the present author.

Though the wrasses form loose aggregations, they are influenced by the doings of other wrasses around them, e.g. in fright and in being attracted to food. When at the laboratory feeding was started in one aquarium the other fish, even in tanks at some meters distance, became restless, dashing up and down along the glasswall nearest to the eating fish. When for collecting in the sea the use of glass jars was tried, it was seen to happen again and again that the fish started to pick at the bait through the glass wall. When one or two had managed to come inside and started eating, this was a stimulus for the outsiders to renew their efforts to snap at the unattainable bait.

WRASSES AT NIGHT

Sleeping of fishes has been known for a long time. OPPIANUS (II 661 ff) wrote: *Scarus* alone their faded eyelids close, in grateful intervals of soft repos. However, already ARISTOTLE and PLINY wrote how nearly all fish sleep at night: though their eyelids are not closed. Nowadays we know that a fish has no eyelids to close and that especially during the night many fish become more active. However, it may well be that most species of fish at some time during 24 hours do have a period of lowered activity. Some fish are observed sleeping suspended in the water. Schools of fish often spread at night; often schools have been seen asleep passively floating up and down, back and foreward with the motions of the water. Some fish are described to rest on their belly or on their sides on the bottom (STARCK & DAVIS, 1966).

Parrot fishes (Scaridae), close relatives of wrasses, rest at night in protected areas or places on the bottom. In some sparid species an ovoid envelope of large and conspicuous mucous folds that covers the whole fish is formed at the beginning of every night (WINN, 1955). It is thought to reduce nightly predation of moray eels (WINN & BARDACH, 1959).

Labrid fish develop an extreme way of defence for their periods of lowered activity. They completely disappear. At the end of the afternoon the numbers of wrasses visible imperceptibly decrease in the sea as well as in the aquarium. About 45 to 30 minutes before sunset no wrasses will be found. They have slipped into crevices and holes in the rocks and corals or have burrowed themselves into the sand. "Burrowing is generally effected by an active swimming with the nose pointed into the sand. This is continued until a sufficient length is covered to allow the various muscular contractions to obtain a grip on the sand, after which progress is more rapid, the tail portion then frequently trailing into the burrow passively" (BREDER, 1926: 219).

In the laboratory their act of concealment could be noticed frequently. That is, an initial vertical dive down followed by a sharp turn, bringing the fish in a horizontal position as soon as the anterior part of the body had disappeared into the sand. Close observation reveals how the fish blows the sand away during the dive down so that a small crater is formed just before disappearing in the now loosened substratum. The whole act may last less than 0.1 second. Slight undulating of the surface of the sand tells that the fish may move on horizontally for some distance from the point of entrance.

As in the aquarium the wrasses frequently subsided close to the glass wall, it was observed that they may nestle themselves a few

centimeters deep. But mostly they are covered by only a thin layer of sand. Usually they turn on one side. A just visible rising and falling of a small area of the sand surface may indicate the position of the upper gill.

It is surprising to see how these fast fishes, so difficult to catch during daytime, are in a complete state of torpor at night. It is possible to remove the sand and observe the breathing of the lethargic, sleeping fish. The gill movement occurs at a rate of about a dozen times per minute which is considerably lower than during the day. It is even possible to stroke the fish gently with a glass rod or pencil. When actually bothered, the inert fish will awake and indolently move away. Only when it is wide awake it may burrow itself completely again.

All seven species were observed sleeping in the laboratory. No wrasses have ever been seen during my swimming trips early in the morning or at the end of the day.

Published information about nightly field observations is limited but according to night diving ichthyologists no active wrasses were found during the night (HOBSON, 1965; STARCK & DAVIS, 1966).

Collecting by rotenone in a rocky area at night resulted in a number of *Th. bifasciatum* specimens emerging from the crevices (STARCK e.a.) FEDDERN (1965) reported how individuals of this species, inhabiting a limestone ledge emerged from these rocks in the morning preferring hiding there to migrating to the nearest sandy area for their night's rest. It seems to depend on the type of area available, whether the fish hide in small holes or dive into the sand. In the aquarium both were observed without distinct preference.

Disappearing under the sand to sleep at sundown has further been reported for e.g. the Caribbean *Halichoeres radiatus* (MOWBRAY, 1931), the Californian wrasse *Oxyjulis californica* (HERALD, 1961) and the Mediterranean *Coris julis* (ROEDE, 1966). Retiring to rock crevices was observed for the medium to large sized specimens of *Bodianus rufus*, the hogfish *Lachnolaimus maximus* (STARCK e.a.) and for the Californian *B. diplotaenia* and *Thalassoma lucasanum* (HOBSON, 1965). The hiding and resting at night might well be a characteristic shared by all members of the family.

States of suspended animation are not restricted to the Labridae. For instance, RANDALL (1961) described similar characteristics for the Pacific surgeon fish *Acanthurus triostegus sandvicensis*.

The existence of an inner clock system for hiding every night is plausible. On numerous nights it was noticed that when lamps were burning in the laboratory around the time of sunset, the wrasses

nevertheless vanished. Once the state of torpor is started, light stimulus has no effect on the fish any more before it is daytime. As has already been remarked, fish that were awakened during the night stayed very inert though lamps were on.

Yet, the stimulus to emerge is not merely the passing by of a definite number of hours. In the tanks where the light usually was less intense than in the open sea during daytime, often wrasses stayed hidden longer. This may also happen in their natural environment. The number of observable wrasses seems to have a correlation with the intensity of sunlight and the clearness of the water. On cloudy days only very few labrids were found. After the stormy conditions caused by the passage of hurricane Flora the coastal waters were very turbid and no wrasses were seen around for more than a week until the light could shine unhampered through the water again. A similar situation occurred daily near the entrance to the muddy Piscadera inner bay at Curaçao: The first hours of low tide no wrasses were found in the cloudy waters where for the rest of the day labrid fish could be observed frequently.

About noon when a bright sun was shining nearly perpendicularly into the sea, the abundance seemed to be slightly lower also. Light must be an important factor in the hiding rhythm. It is relevant to refer here to the above-mentioned reports stating that wrasses are very sensitive to light intensity.

Consequently, the observable labrid fishes may not represent the whole population of that area. For instance, *He. martinicensis* has only been collected from one spot on Curaçao. No specimens were met with at some distance from the colony and the possibility of temporary migration must be low. Nevertheless, even when collecting was done every two, three days, at each visit their habitat was occupied by about the same amount of visible fish. By collecting on different times of the day and on numerous days we tried to obviate this biasing phenomenon.

Food and feeding habits

In general Labridae are benthophagic carnivores. Gohar & Latif (1961a, b; 1963) regarded the labrid fishes as molluscivorous; others considered the wrasses as

crustacean feeders. Analyses of labrid intestines have been given by OLIVER & MASSUTI (1952) [who found in *Xyrichthys novacula* Foraminifera, Bryozoa, echinoids, molluscs, crustaceans as well as Coelenterata and fishes], by RANDALL & RANDALL (1960), and by RANDALL (1967). QUIGNARD (1966) reported that European labrids feed on animals with hard skin, carapax as well as calcareous shells.

Labrids have been classified among the 15% of teleost fish that do not possess a morphologically differentiated stomach (JACOBSHAGEN, 1937); the intestinal bulb and the intestines as a whole carry out this function; pyloric caeca are absent (AL-HUSSAINI, 1947). The length of the alimentary tract (the distance between the hind-end of the pharynx to the anus) is short. It is not much more or less than the standard length of the fishes. Especially the anterior part of the intestines is very elastic and can be extremely dilated. Enterokinase is secreted by the anterior part of the intestines; trypsine and carboxypeptidase by the pancreas and the intestinal mucosa as well; also lipase and amylase have been detected. Enzymes affecting the breakdown of cellulose and lichenin seem to be absent while peptic digestion is missing (GOHAR & LATIF, 1961; 1963).

In Chapter V the proverbial voracity of wrasses has already been mentioned. Such a greedy character is demonstrated by the eagerness with which they use to react to the sea urchin bait. The species studied were frequently seen picking food from sand, corals and rocks by means of the strong canine-like front teeth. Moreover, some specimens were seen removing ectoparasites from other fishes.

Detailed information on cleaning behavior has been given by DOTY & MORRISON (1954), EIBL-EIBESFELDT (1955) and RANDALL (1955, 1958, 1962). Cleaning fishes – often displaying specific, twisting movements of their body – are picking at the heads, bodies and fins of larger fishes; they even may slip inside the buccal and gill cavities. The larger fish do not merely accept the cleansing but invite it by taking special positions; a temporary changing of color of the host has been noticed.

Some labrid species are very specialized in this feeding on ectoparasites, as the genus *Labroides*, tiny, very elongate fishes with a slightly different mouth. Cleaning fishes are non-specific in the fishes which they serve. Among the hosts are e.g. Acanthuridae, Pomacentridae, Scaridae, other Labridae, Mullidae and also Carangidae and Serranidae which habitually prey upon small reef fishes.

It may be interesting to touch lightly here on the bad reputation of the wrasses in ancient times. In classical publications labrid fish appear as notorious, disreputable creatures. The dangerous, poisonous bite of *Coris julis* was a widespread tale; the wicked girelle was thought to render other fish of no use for consumption by biting it. D'ARCY THOMPSON (1947) postulates that a false etymology of ἰουλίς from ἰός, poison, has been dissembling. Actually, in dead labrid fish the protractile lips are often withdrawn in which case the uncovered strong teeth give a frightening expression, but nothing has been reported recently about damage inflicted on other fish. The present author inclines to recognize in the old descriptions misinterpreted observations of cleaning behavior. It may even be possible that cases of mimicry have been observed (see below) though labrids imitating species have not yet been described for the Mediterranean area.

Their habitually wagging and hiding behind the back of other fishes contributed to their bad reputation. (Moreover, the sexual life of the wrasses was misunderstood; they were considered to be homosexuals; Chapter X.) By ARISTOTLE, as well as by

EPICHARMUS, DIOCLES and NUMENIUS (cf. ARTEDI 1738, 1792) one finds epithets like ἁλφηστής, κόσσυφος, κίρις, κίχλη, and φυκίς, coarse four-letter words specifying the suspected character of the wrasses. POLLUX improved this with synonyms as καταπύγων, θηλυδρίας, γυναικίας, ἀνδρόγυνος and θῆλυς τὴν ψυχήν (weak, lustful, unmanly, effeminate). According to the anthropomorphic concepts of those days comparisons were made between labrid fish and contemporaries of the author. ARISTOTLE condemned the picking behind the head of other fish and named some poets displaying similar types of underhand acting. ATHENAEUS also regarded the hiding habit as a symbol of weakness; as severe offense he called some poets by the name "labrid."

Again it is probable that the first observations on cleaning behavior have been given in these classical reports. Instead of cowardly looking for shelter, the wrasses may have been seen busy with picking away ectoparasites.

Cleaning wrasses do not distinguish between humans or fish. In this connection it is curious to find in RADCLIFFE (1921) a poem by LEONIDAS OF TARENTUM (a younger contemporary of the writer THEOCRITUS), describing how a certain Parmis found his death:

Parmis had lured / A *Julis* from its rocky haunts, secured / Between his teeth the slippery Pert, when, Io! / It jerked into the gullet of its foe, / Who fell besides his lines and hooks and rod, / And the choked fisher sought his last abode. / His dust lies here. Stranger, this humble grave / An angler to a brother angler gave.

Historically exact or not, after the above described habit of wrasses to slip into mouths, this story sounds not overly-impossible.

During the present study some information on the diet was obtained as for examination of the gonads the posterior part of the intestines had to be removed. In investigating the gut contents more in detail the kind help of Mrs. Dr. GERMAINE L. WARMKE and Prof. Dr. JAN STOCK was greatly appreciated.

An essential advantage of the employed method of killing and transport was that by putting the fish on ice cubes the activity of the digestive enzymes after the quick death was considerably hampered. The disadvantage of collecting with bait is that the intestines were filled up with sea urchin meat.

Empty stomachs and no interest in bait have been reported for fishes during their spawning period (RANDALL & BROCK, 1960). As among the wrasses collected specimens with very mature gonads as well as with small, still developing gonads have been found, the risk of involuntary selection on gonad activity by the method used for collecting can be considered of no important disturbing influence. Incidentally, an individual with an empty "stomach" has been found but there was no relation either to size, color phase or gonad activity.

According to QUIGNARD (1966) juvenile European labrids up to a body length of 2 cm, feed on copepods, cladocera and nauplii. The presence of juvenile specimens (< 3 cm) of *Th. bifasciatum* and *H. bivittatus* among sea urchin spines in the vicinity of clouds of copepods does not contradict his statement. The intestines of the smallest specimens analyzed, a *bifasciatum* of 28 mm SL, contained mainly copepods, though also parts of a small ophiuroid were found. A 35 mm SL *bivittatus* contained for 90% copepods of 0.6–1.0 mm and some small pieces of lamellibranchiates.

Thalassoma bifasciatum

According to BEEBE & TEE-VAN (1928) the yellow colored fish devour worms and crustaceans, the bluehead colored specimens polychaete worms. LONGLEY & HILDEBRAND (1941) reported that small crustaceans provide the greater part of the food. LONGLEY was one of the first who suggested that yellow specimens were relieving other fishes of ectoparasites though he could not find such creatures in their stomachs. "These young parasite-pickers ... may be seen in action daily at the same place, and continue this practice until the change to adult coloration occurs."

Cleaning behavior of the yellow phase specimens also has been observed by EIBL-EIBESFELDT (1955), RANDALL & RANDALL (1960) and FEDDERN (1965) as well as by the present author.

With RANDALL and FEDDERN I consider the cleaning service as occasional; the major portion of the food is obtained by picking at rocks, algae and sand.

The cleaning specimens mostly display the transitory stage 1b of the first adult phase, which is characterized by a clearly visible brown lateral band, bordered by a bright yellow back. A longitudinal, often yellow or brown colored stripe has been reported for most other cleaning species. It probably has a functional meaning.

Even cases of mimicry have been described. Thus, the blenny *Hemiemblemaria simulus* is remarkably similar to color phase 1b *Th. bifasciatum*. (Further, the blenny *Aspidontus taeniatus* is similar to the cleaning labrid *Labroides dimidiatus*.) (RANDALL e.a.). Not only do general shape and colors agree but these blennies even move and act in labrids ways. Instead of cleaning, though, the blenny fish feeds by tearing off pieces of the fins of the host fishes.

No cleaning by large, bluehead colored specimens of *Th. bifasciatum* has ever been observed.

RANDALL & RANDALL (1960) found in 32 specimens of 29 to 63 mm SL that most gut material consisted of free-living pelagic crustaceans, especially copepods. RANDALL (1967) summarized gut contents of 60 specimens of 36 to 105 mm SL and 12 bluehead specimens from 85 to 105 mm in SL. The terminal phase apparently had consumed relatively more crabs, fishes, polychaetes and pycnogonids, and even four times more ophiuroids, but less shrimps and isopods while no copepods or gastropods were found.

The present author found in terms of percentage volume in the gut contents of 8 first adult phase specimens of 45 to 55 mm SL many fish scales, about 30% harpac-

ticids, a complete and a posterior part of a Mysidacea, 40% other small crustacean remains, pieces of polychaetes and an isopod. The gut material of 3 phase 1 specimens of 64 to 67 mm SL consisted of pycnogonid legs, amphipod legs, a nematode, antennae of amphipods, pieces of *Aplysia* and a harpacticoid copepod.

Halichoeres bivittatus

LINTON (1907) found in five specimens shells and byssus of mussel, annelid, and sea urchin spines. LONGLEY e.a. (1941) concluded from investigations of only a few gut contents that the fish "seems to feed chiefly on fish." The present author, however, observed *bivittatus* in general picking food from sand, rocks and corals. Cleaning behavior was occasionally noticed for small, first adult phase fish – then, like other cleaning creatures, characterized by a lateral stripe, bordered by a yellow lining.

RANDALL (1967) found especially crabs (22%), echinoids (18%), gastropods (12%) and ophiuroids (7%) in the guts of 46 specimens from 67 to 153 mm SL. It was noticed that this species tends to select the more brightly colored gastropods.

My own investigations showed that in two specimens of 61 and 70 mm SL the guts contained legs of *Petrolisthes*, parts of amphipods, an isopod, seven harpacticids and a cyclopoid copepod; no molluscs were found. Two specimens of 74 and 78 mm SL contained chiefly polychaetes, while in six specimens of 69 to 77 mm SL 70% small mollucss of no more than about 1 mm diameter, pieces of a small ophiuroid, and some crustacean legs were found.

In five first adult phase females of 83 to 91 mm SL the material consisted of a juvenile eel (*Gymnothorax*) of 45 mm, 5% molluscs e.g. thrice a *Cerithium*, the rostrum of a shrimp, twice a Cumacea, 1 amphipod, Anisopoda, remains of Brachiura and 10% Sabellidae.

In 10 terminal phase specimens of 105 tot 149 mm SL the guts contained a variety of 30% Crustacea, 25% pelecypods, 10% gastropods, 10% nematods, pieces of echinoids (also in a specimen not collected with sea urchin bait), a still living foraminifer, very small otoliths and a very small skull of a fish.

Halichoeres garnoti

According to BEEBE & TEE-VAN (1928) the food is varied in nature and includes small crustaceans, sea urchin spines and molluscs with their shells. RANDALL (1967) found that 14 specimens of 64 to 159 mm SL had mainly swallowed crabs (21%), ophiuroids (16%) and gastropods (14%); four specimens had empty stomachs.

The present author did not analyze gut contents of this species.

Halichoeres maculipinna

RANDALL found in five small specimens of 45 to 50 mm SL up to 50% copepods, and in 19 specimens ranging from 71 to 110 mm SL, a preference for polychaetes (more than 47%). One 79-mm fish contained only a small octopus.

The present author found in two mature first adult phase females of 90 and 91 mm SL, 99% small crabs and one gastropod.

Halichoeres poeyi

RANDALL found that of 34 specimens of 50 to 140 mm SL, three had empty stomachs. In the remaining 31 crabs (25%), gastropods (21%) and ophiuroids (10%) were found, among fish remains (5%) and sipunculids (5%). Moreover about 7% echinoids were found among which remains of adult *Diadema*. He suggests that probably the fish (and also *H. bivittatus*) fed upon the *Diadema* after the latter were made available by a larger predator.

Hemipteronotus splendens

According to RANDALL this species feeds primarily on zooplankton. He examined 14 specimens of 57 to 108 mm SL of which two proved to be empty. The remaining fish contained about 61% copepods; even the largest fish, 108 mm SL, had eaten copepods. Further, a.o. amphipods (13%) and shrimp larvae (11%) were found.

Hemipteronotus martinicensis

Of this species no data on its diet are yet available. It was not observed in the close vicinity of any other fish and it is doubtful whether it ever feeds on ectoparasites of host fishes. *Hemipteronotus* species have not yet been reported as cleaning fish; their more blunt body shape may be less adapted to it.

Roughly speaking it can be said that the Caribbean wrasses are not over-particular in the choice of their food; according to size the diet changes from copepods to mainly crustaceans and in the larger specimens molluscs as well. Notwithstanding the powerful pharyngeal plates, well-adapted for the grinding of calcareous material, great parts of the food are only crushed into coarse fragments or swallowed whole. Some interspecific differences in diet seem to exist. Food competition must be slight as wrasses mostly occur in large, heterospecific groups.

REPRODUCTIVE BEHAVIOR

The number of studies on piscine reproductive behavior in general is quite extensive (BREDER reviewed more than 3000 papers

on this subject). Many of these cover reproduction of viviparous poeciliid fishes which display characteristic morphology and behavior during the breeding periods. Often, it is possible to evaluate the sexual stage of the gonads by analyzing behavior patterns. POLDER, for instance (1971) combined histological investigations of the cichlid *Aequidens portalegrens* with analysis of distinguishable changes of behavior which enabled him to estimate externally the moment of ovulation.

In the present study it was likewise tried to combine information in order to understand better the relationship between color, size, and sexual function in wrasses. Labrids, however, are, also in this respect, slippery to handle. There are no morphological characteristics to distinguish between the sexes of the same color phase, or between mature and immature fish as no special nuptial colors are developed. Moreover, their actual mating may happen in such a short interval of time that the process easily escapes observation. As a consequence, publications on the spawning of labrids are scarce.

It is worthwhile to mention here RANDALL & RANDALL's (1963) comparative descriptions of mating behavior in Caribbean scarid and labrid species. (In Scaridae the quite different, bright colors of the larger specimens caused also description of an excess of species, BROCK e.a., 1954; WINN e.a., 1957, 1960; RANDALL, 1963).

Thalassoma bifasciatum

Randall e.a. (1963: 55) observed two patterns of reproduction:

Aggregate spawning, involving a number of females and males of about only 50 to 60 mm in total length, and of the same yellow color. "Within the aggregation ... smaller groups of about 5 to 10 or more fish began to swim more rapidly in one direction and then another. ... there was a sudden upward ... movement which resulted in the fish being a maximum of about 2 feet above the rest of the group."

Pair-spawning, in which the sexes are of different hues. "After a very short chase the female fish [yellow] darted upward with the male bluehead and they spawned."

This second type of mating was only observed on few occasions; RANDALL e.a. concluded that a high percentage of the reproduction of *Th. bifasciatum* is carried out by mass mating of monophase fish (thus paralleling the mode of reproduction in the scarid *Sparisoma rubripinne*).

Aggregate spawning runs were described by HOBSON (1965) for *Th. lucasanum* of Californian waters. FEDDERN (1965) observed four or five temporary spawning groups of yellow phase *bifasciatum*, each of about 10 to 15 specimens. Only after a few minutes, wherein three spawning runs occurred, the group broke up and the specimens resumed normal aggregate behavior. He did not notice the individual pair-type of spawning.

Both spawning patterns have been observed by the present author though the actual release of sperm and ova was difficult to notice.

First adult phase fishes usually swim more aggregatedly than large bluehead colored specimens and are more playful. Sometimes, however, extra-active yellow specimens were seen to be gathering much more closely.

March 6th 1963 (4 days before full moon), at the end of the morning at the reefs of San Laurel, P. R., extremely active groups of yellow fish were observed. They concentrated around emerging rocks at the most outward part of the reef, staying close together, turning, dashing around and strictly following each other, up and down with the rather turbulent water. Their yellow was of a brilliant hue (phase 1a). The greatest number, 74 out of 84 collected, proved to be very mature males; many already lost sperm on slight pressure. Of the 10 females examined, 2 had still developing gonads; 8 contained spent ovaries, occupying only $\frac{1}{8}$ to $\frac{1}{4}$ of the abdominal cavity; some already ovulated eggs were still present.

This was an extraordinary situation, as mostly in the first adult phase the number of females strongly outnumbered that of the males. For instance, on March 13th on the same San Laurel reef, the sex ratio was 4 males to 16 females, agreeing with what is usually found (Table 24). However, on March 18th (last quarter of the lunar month), I noticed another busy and active close gathering at the same place. The sex ratio of the individuals collected then proved to be 36 males to 7 females. Again, all 36 males were very mature. Of the 7 females 3 had large, very mature ovaries; 1 had already released many eggs, while the other 3 had small, still developing ovaries.

RANDALL e.a. reported for the scarid *Sparisoma rubripinne* also a preponderance of males in the large spawning aggregations, suggesting that one fish, perhaps a female, is the lead fish of the small spawning groups and the rest are males.

Individual spawning behavior was noticed several times.

For instance, on April 23th 1963 (new moon) in the Boca San Michiel, Curaçao, a bluehead was pursuing a yellow specimen; they dashed around rapidly, the bluehead just a few centimeters above and behind the leading yellow fish. Most of the

synchronised swift turns and moves happened not far away from the bottom but now and then they wheeled upwards amidst the aggregation of the rest of the wrasses. A few times the yellow fish dashed away into interstices of nearby coral and rocks, leaving the bluehead confused behind; then the chasing was continued again for several minutes. The final dashing upwards to the surface happened so suddenly that it nearly escaped my attention. Immediately thereafter the two had apparently lost interest in each other; the yellow fish turned back amidst the other wrasses, the bluehead dived rapidly down to the bottom and after a swift turn rubbed its side over the sand, then started picking at the sand. Pursuing and side rubbing was observed also on other occasions, e.g. the next day, April 24th. Most fish collected then proved to contain (rather) mature gonads.

Excited blueheads are rather aggressive. Again and again they will try to court a yellow fish; when it does not respond in the appropriate way the bluehead immediately tries another one. The chasing does not always end in a climax at the surface.

In the laboratory no complete mating has been observed. Only a few times rapid dashing up and down along the glass wall was seen, more frequently in the larger tanks. Once a first adult phase fish was seen chasing others, being rather aggressive towards the glass wall, perhaps because there its image was vaguely reflected. This specimen, though, had received a large dose of testosterone so this can not be considered a normal situation.

DORIS ZUMPE (1963) observed in four yellow phase specimens in captivity, how one of them changed towards the bluehead colors; then mated with the three yellow individuals. First, the bluehead started aggressively fighting with its reflected image; after some courting and chasing a short spawning run to the surface followed. She also reports rubbing against stones during intervals of the courting and after the mating. The female then swims with strongly downward bent back.

Halichoeres

RANDALL & RANDALL did not notice dual patterns of spawning for *H. bivittatus*, *H. garnoti*, *H. maculipinna* nor for *H. radiatus*; only spawning by individual pairs was observed.

Though I did not see the actual release of gonadal products, the chasing behavior observed agrees with the type of individual mating. Large, more richly colored *bivittatus* and *garnoti* specimens were following smaller, plain specimens of their own species for some minutes. Only once was a similar behavior between two *maculipinna* specimens noticed.

Several times groups of small first adult phase *bivittatus* as well as *maculipinna* were very actively dashing around each other, making swift, fast turns. Though this

might well have been just playful behavior, these activities had much in common with the behavior during mass mating in *Th. bifasciatum*.

Hemipteronotus

On April 24th, 1963, the same day on which pursuits were observed in *Th. bifasciatum* and in *H. bivittatus*, I noticed a group of six specimens of *He. splendens* in the Boca San Michiel. This was exceptional as usually only one or two specimens of this species were present among the other wrasses on the reefs. These six specimens were staying close together and followed each other's moves strictly. On April 27th (four days after new moon) two *splendens* specimens – of about the same rather small size and apparently in color phase 1 – were turning and twisting around each other in fluent turns for some minutes. Several times, instead of dashing to the left, right or downwards, they darted one or two meters upwards but clouds of sperm and ova could not be noticed. After swimming to lower areas they started the same pattern of behavior all over again. These activities might well have been part of a spawning scene.

For *He. martinicensis* only once on November 7th, 1963 (one day before last quarter) some chasing of individual specimens in color phase 1 (which in this species proved to be all females) by a terminal color phase specimen was observed.

Summarizing: In all seven species indications of reproduction by individual pair spawning were seen. Moreover in *Th. bifasciatum* group mating was noticed; rather similar group activity was observed for *H. bivittatus* and *H. maculipinna*.

These observations are too scanty to be of real use in determining eventual spawning periods. Yet, they indicate (for *Th. bifasciatum*) that indeed small first adult phase males not only take part in reproduction, but even may outdo the large, terminal phase males in this respect.

Isolating mechanisms

Interbreeding of labrid species under artificial conditions proved to be successful. LIST (1887) reared hybrids out of four *Crenilabrus* species; they died during the larval stage. Likewise, HAGSTRÖM & WENNERBERG (1964) found almost no barriers to cross fertilization in their hybridization experiments with Labridae. Most of the crosses could be reared up to free-swimming larvae. Yet, in nature, interbreeding of sympatric labrids species may hardly occur. I did not find any hybrids among the great numbers of wrasses collected.

Several authors, e.g. BLAIR (1951) indicated that interbreeding under natural conditions is prevented by a complex of isolating mechanisms. These involve the following:

= Habitat preference. – However, as previously noted, the ecological separation of the species studied is to be neglected. In many of the collecting stations several species were often caught in the same haul.

= Different breeding season. – However, the tropical Caribbean wrasses were maturing the whole year round. On the same day mature individuals of different species were regularly found.

= Courtship patterns. – Though the mass mating as observed for *Th. bifasciatum* has not been noticed in the other species, all seven displayed pair spawning.

= Mating preference. – No heterospecific courtship has been observed. Though large males were seen chasing specimens of their own as well as of other species during territorial defence, the prolonged courting chase was only homospecific.

In the heterospecific aggregations of wrasses, the males must be able to recognize the females of their own species, whether by color or by other signs, e.g. the willing female's special response to the courting male's aggressive chasing. In captivity the wrasses hardly displayed any sexual behavior, so no experiments to evaluate threshold differences for various sexual responses could be made.

Most probably the short time of homospecific segregation caused by the dashing up to the surface for the release of the gonadal products ensures sufficient isolation to prevent interbreeding. If hybrids occur, death in the larval stage in the Caribbean wrasses might prove to be an additional, post-copulation, barrier to hybridization.

Nest building and parental care

For several labrid species nest building as well as parental care has been reported. *Symphodus cinereus* (Bonn.) nests were described by GERBE (1864), MOREAU (1881) and GUIGNARD (1962), and *S.* (*Crenilabrus*) *melops* (L.) nests by GERBE and LE DANOIS (1913). Females and males work together in constructing the nest of algae. *Labrus berggylta* (Asc.) makes its nests of seaweed and tufts of coralline wedged into crevices of rocks between the tide-levels (MATTHEWS, 1887; LE DANOIS, 1949). Also nests have been found of *S. pavo* (Brünn.), *S. mediterraneus* (L.) and *L. mixtus* (L.) (MOREAU, 1881; QUIGNARD, 1967; HEFFORD, 1910, respectively). Lo BIANCO (1888) reported that males of *L. festivus* Risso and *L. turdus* Bloch guarded the eggs that were fixed on *Posidonia* leaves.

SOLJAN (1930a, b; 1931) wrote some detailed articles on this subject. Of interest in relation to the present studies is his description of the colors and sizes as well as of the behavior of the females and males. In *Symphodus ocellatus* Forskål large males with bright colors construct nests of *Cladophora*, then try to chase one of the plain brownish females that swim around in small groups, into the nest. After fertilizing the eggs, the male covers the fry with fresh filaments of *Cladophora* and starts another courtship. The algae continue to live and thus ensure the presence of sufficient oxygen; moreover, the male provides for ventilation by rapid pectoral flappings. The male stays in and nearby the nest and aggressively defends the eggs and larvae against cannibalistic females and other fishes. A similar type of care is displayed by the large, bright males of *Symphodus* (*Crenilabrus*) *quinquemaculatus*. These fish build semi-lunar nests of dark pieces of *Cystosira*. The male pushes the eggs horizontally into the concave wall of the nest, then covers them by fresh pieces of the algae. Here usually only two females swim in the neighboorhood of the nest.

Remarkable is the behavior of the other type of males. These are of smaller size and of the same color pattern as the females; the testes may be functional, but they never build nests, nor take any care of the offspring, nor invite females. However, on the culminating point of the courtship, these small males dash forward and the actual fertilizing is often done by these "outsider der Befruchtung" (see also FIEDLER, 1964).

Parental care, however, is not a general characteristic among labrids. VALENCIENNES (1839), LIST (1887) and GOURRET (1893) denied such behavior. The pelagic eggs of numerous species often containing an oildrop, are released in the open sea without further attention from the parents, in contrast to the adherent ova of the *Labrus* and *Symphodus* (*Crenilabrus*) species that protect their fry.

In the seven Caribbean species neither nest building nor care for the offspring have been noticed. *Thalassoma bifasciatum*, as well as *Halichoeres bivittatus*, *H. garnoti* and *H. maculipinna* have been seen to spawn. Right after the release of the pelagic eggs, loose near the watersurface, the parents left. In the flat, bare sand area where *Hemipteronotus martinicensis* was found, nest building has not been observed either. Though *H. poeyi* and *He. splendens* both frequent areas covered with seaweed and turtlegrass as well, it is assumed that also in these species no nest building occurs.

TERRITORIAL DEFENCE

The more solitary, less playful large individuals in terminal colors regularly stayed close to the bottom; here, a kind of territorial defence could be displayed. I noticed this frequently for *Th. bifasciatum* and *H. bivittatus* specimens, less often for *H. maculipinna* and *H. garnoti*. The fish is swimming around slowly within a radius of no more than 10 to 25 centimeter. No special characteristic distinguishing the territory from the rest of the environment could be detected. As soon as another wrasse of the same or another species comes closer than about 30 cm, the "owner" of the area aggressively starts to chase the intruder away. The unwanted visitor may be pursued over several meters distance; then, the defender returns to its spot.

Unfolding of the anterior part of the dorsal fin is very characteristic. The fin can be held upward as a signal standard or some quick

un- and refoldings may occur. (Otherwise in locomotion the dorsal fin is hauled down flat against the body). The unfolding of the brightly colored part of the fin suggests that it may serve as a warning signal.

In this respect it may be pertinent to repeat briefly the conspicuous features developed in the terminal phases (see Chapter VI). Often, the head becomes a prominent portion of the body such as in the bluehead *Th. bifasciatum* and the yellowhead *H. garnoti* phase; striking red and pink bands become apparent on the head in *H. bivittatus* and *H. maculipinna*. The sides may show dark cross bars (*Th. bifasciatum, H. garnoti*) or marked side spots (*H. maculipinna, He. splendens*). In various labrid species anteriorly in the dorsal fin striking colors developed; the first dorsal spines may then be enlarged. *Th. bifasciatum* shows such a marked dark area in the dorsal. In *H. garnoti* the dorsal gets numerous bright blue spots. In *H. maculipinna* the black spots at the end of the spinuous part of the dorsal grow considerably larger.

Yet, this territorial defence is not strongly developed. I regularly noticed how as soon as bait had been placed nearby, the defending fish left its private area and mingled with the other feeding wrasses, no longer showing any aggression. Moreover, the same territory was not occupied for a prolonged period; on return visits; it was never exactly the same spot that was found to be defended.

The behavior as described here does not include *He. martinicensis*. This was the only species in which all specimens – of all sizes and of colorphases 1 to 3 – showed a strong relationship to a special area, in which each fish seemed to have its own location. Among the specimens of this species I did not see aggressive chasing.

Comments

The following aspects of behavior are relevant to the present study.

The hiding mechanism of labrids may certainly influence sampling. It may partly explain the relatively low numbers of fish in intermediate colors that could be collected (see Table 4, Chapter VI and XII). Attention to the method of collecting is recommended when samples of wrasses are wanted for sex determination.

Removal of ectoparasites from host fishes is generally performed by smaller specimens in first adult phase colors, often characterized by longitudinal bands. Their color patterns may have a biological meaning. Combined with specific, twisting movements of the body, they are recognized as welcome guests by many other fish.

Food competition must be slight; often, the wrasses form large, heterospecific groups. Yet, sufficiently well-developed isolation mechanisms to prevent interbreeding seem to be extant. Color patterns may be relevant in recognizing the desired sex partner(s); dashing up to the surface to release the gonadal products may be another factor.

The conspicuousness that characterizes the terminal phases – bright colors, often striking dark side spots or cross bars, sometimes elongate fins – may have a biological meaning both in the act of pair spawning (with a smaller female in first adult colors) and in moments of territorial defence. In nest building and nest defending labrids (always the large, bright male) colors certainly may have a signal effect. (The eye of the labrid is rather complex and well-developed; experimental studies by others indicated that they react to certain colors and shapes).

The situation in the labrids deviates in an essential aspect from the report by LORENZ (1965). He stated that coral fishes display bright colors when young, when they live solitarily and are aggressive territory defenders. The signal colors and aggressive behavior was to ensure economical distribution of the food available. When sexual maturity is attained, they lose the warning colors and aggressive attitude to make mating procedures possible. Whereas in wrasses – typical coral fishes – the small specimens are less colorful and more apt to shoal, while the large, more solitary ones have bright colors and may show territorial defence. The absence of signal colors may be advantageous for mass mating of first adult phase specimens.

In a number of species a considerable amount of functional males is present among the first adult color phase (Chapter X); the activity

of their testes is generally greater than that of the terminal phase males (Chapter XI). Yet, until now, only in *Th. bifasciatum* actual spawning of first adult phase males has been observed. It is striking that these smaller males indulge in a different sexual act, namely group spawning.

Since the present study unsettles the alleged relation between color and sex (it was generally assumed that the first adult phase were females, the terminal phase males) it is worth considering the impact of color on sexual behavior. The present author agrees with RANDALL & RANDALL (1963: 50); they observed also in the parrot fish *Sparisoma rubripinne* two types of spawning patterns, namely group spawning of males and females of similar colors, and spawning in pairs in which the sexes are of different hues. They postulated:

"It has been presumed that the brighter color of male parrot fish is associated with sexual maturity. The observation of *like-colored* male and female individuals of *rubripinne* necessitates a modification of this concept. The attainment of the "*axillare*" [the terminal colors] color phase by the male is not associated with maturity but with the adoption of a new pattern of spawning behavior .... It is expected that many other sexually dichromatic scarid and labrid fishes will be shown to have similar dual patterns of reproductive behavior."

In spite of hours of observation, the present author cannot add any supplemental facts to this charming question.

Those species in which two types of propagation are performed are the most abundant and widely spread (Chapter IV). We may speculate whether mass mating of individuals of similar colors and shape is selectively more advantageous compared to mating of two individuals of differently colored patterns.

IX. REPRODUCTIVE ORGANS

All 4474 labrids were dissected to establish the sex and estimate the stage of development and maturity of the reproductive organs. Since no distinctive secondary sex characteristics could be found, sex determination was only possible by examination of the gonads. Only in extremely mature fish was sex evident from the release of sexual products upon light abdominal pressure. Gonads of 360 specimens were examined histologically.

METHODS

All observations were made on freshly caught material, examined on the beach or after a minimum of delay required for transportation to the laboratory. During this transport the fish were kept on ice cubes. A small part of the material had to be stored at minus 20°C for periods varying from a few hours to three days. After thawing classification according the defined criteria (see below) was possible, though the quality of the gonads was less optimal than in fresh specimens. Consequently no such specimens were used for weighing or measuring the gonads.

The day of collection, color, metric and meristic data were noted down. Then, the belly was dissected, using small scissors, by making an incision along the midventral line, starting in the anal opening. The intestines were laid aside and when necessary the most posterior part was cut away in order to expose the gonads.

For every specimen were noted: sex, stage of gonadal activity, and estimated size of the gonads. Moreover, in part of the material we measured: length and greatest width of the gonads, and weight of the gonads.

This chapter outlines how these parameters have been determined; conclusions resulting from these data will be discussed in Chapters X, XI and XII.

Sex

By and large bisexual reproduction is the rule in fishes. However, there is a large variety of patterns along which the development of separate females and males is achieved, more in particular among the less primitive group of the Teleostei. In the Serranidae and the Sparidae (closely related to the Labridae), specimens with ovariotestes co-occur with actual females and males. In the ovariotestes distinct ovarian and testicular zones can be macroscopically recognized (REINBOTH, 1962a). Labridae, however, in general show complete separation of the sexes. Macroscopically, none of the 4474 specimens dissected showed two distinctly different zones in the sexual glands.

In labrids, as in fishes in general, the rather symmetrical gonads are internal and consist of a pair of elongate lobes, joined posteriorly, before opening to the exterior, into a common trunk; they are suspended by lengthwise mesenteries in the posterodorsal section of the abdominal cavity and are situated close together just below the air bladder. In the great majority ovaries and testes can be easily recognized by the naked eye. Accordingly, the following three groups were distinguished:

Females (♀♀) – ovaries rounded, loose and more or less granular.

Males (♂♂) – testes pointed, compact, smooth, opaque and often milky.

Miscellaneous (??) – non-functional gonads.

The miscellaneous group includes:

Fish without gonads.

Fish with no clearly differentiated gonads.

These are very young, or degenerating gonads. Though immature gonads differ from the latter because of their more firm character, histological investigation offered useful supplement.

Intersexes.

In some non-functional gonads histological examination revealed intersexual characteristics, consisting of small islands of ovarian tissue scattered among a testicular matrix.

Stages of gonadal activity

Eight distinct stages of maturity were distinguished according to the external appearance of the gonads and the proportions, relative to the size of the abdominal cavity. HEINCKE (1898) was the first to describe maturity stages in fish. KISELJOWITSCH (quoted by SUWOROW, 1959) distinguished five stages. Essentially the latter classification is followed in the present paper, with one regressive stage added.

Stage 0. *No gonads found*

Stage I. *Immature*

Gonads very thin, narrow threads, nestled against the swimbladder. On gross inspection sex determination is impossible.

Stage II. *Immature, but more developed*

Gonads narrow bands, but sex determination may be possible.

Stage III. *Developing*

Gonads relatively well-developed. Ovaries occupying approximately $\frac{1}{3}$ of abdominal cavity; testes more or less $\frac{1}{4}$. Ovaries compact and firm, surface smooth.

Stage IIIa. (Only distinguished in females)

More advanced than stage III; ovaries occupying $\frac{1}{3}$ to $\frac{2}{3}$ of abdominal cavity; compact, surface granular.

Stage IV. *Nearly mature*

Ovaries turgid and occupying $\frac{2}{3}$ of abdominal cavity, testes $\frac{1}{2}$. Eggs nearly ripe; surface of ovary partly granular, partly foamy but shape still intact and compact; testes milky.

Stage V. *Mature*

Ovaries and testes large, occupying all available space in body cavity. Ovary all over foamy; testes milky white. On light pressure, eggs and sperm are easily released, consequently the gonads may be less turgid than in stage IV.

Stage VI. *Spent*

Ovaries and testes emptied, flaccid, no longer filling the whole abdominal cavity. Their center may still have the characteristics of stage V, but the sides are loose and, especially in testes, rather transparent.

Stage VII. *Regressing*

Gonads small, shapeless and flabby; not even much different from stages I and II, only less compact.

Estimated size of gonads

Approximate estimations of the absolute volume of the gonads have been made in all 4474 dissected wrasses according to a nine digit scale, ranging from category *1* (very thin, flat gonads of no more than about 1.5 mm width) to *9* (large, bulging gonads of more than about 15 mm length). Size is a complex item, as the volume of the gonad lobes is determined by the gonadal activity stage as well as by the dimensions of the abdominal cavity, i.e. by the total length of the body. Moreover, during the process of maturation there are changes in shape. In the first developmental stages there is mainly an increase in width, while in more advanced stages of ripeness the length of the gonad lobes increases as well.

TABLE 17

MEANS OF LENGTH *l* AND GREATEST WIDTH *w* OF THE GONADS
grouped according to a nine digit size estimation scale in a number N of specimens of three Caribbean labrid species

Scale of gonad size	Mean measurements (in mm)																	
	ovaries									testes								
	Th. bifasciatum			*H. bivittatus*			*H. garnoti*			*Th. bifasciatum*			*H. bivittatus*			*H. garnoti*		
	N	*l*	*w*	N	*l*	*w*	N	*l*	*w*	N	*l*	*w*	N	*l*	*w*	N	*l*	*w*
1	4	5.0	1.0	3	5.9	1.1	2	6.9	0.7	11	8.9	1.2	4	9.8	1.3	9	10.4	1.2
2	6	5.3	1.8	5	6.3	1.7	3	7.5	1.6	9	9.2	2.4	5	12.6	2.1	4	15.5	1.9
3	7	6.1	2.2	6	7.4	2.3	6	6.8	2.2	15	11.3	2.9	13	16.8	3.4	10	16.4	3.3
4	31	7.2	2.8	15	8.7	2.9	10	8.6	3.5	19	12.7	3.8	24	16.3	4.2	14	17.7	4.0
5	69	9.1	3.7	44	10.3	4.2	27	11.3	4.6	17	11.8	4.7	18	13.1	5.3	—	—	—
6	14	11.6	5.4	43	12.4	5.0	24	12.6	5.5	7	12.3	4.8	18	12.8	6.1	—	—	—
7	9	12.3	5.6	43	14.9	6.1	29	14.8	6.2	14	16.3	6.3	15	15.1	6.3	—	—	—
8	5	12.7	5.8	12	15.7	7.5	3	14.1	6.7	9	13.3	6.7	4	15.5	7.2	—	—	—
9	4	13.6	5.6	8	17.5	6.1	—	—	—	14	15.9	6.9	3	16.4	7.0	—	—	—
Total	*149*			*179*			*104*			*116*			*104*			*27*		

TABLE 18

STAGES OF ACTIVITY AND ESTIMATIONS OF SIZE OF THE GONADS IN *Thalassoma bifasciatum*

18a – Gonads from females in color phase 1
18b – Gonads from males in color phase 1
18c – Gonads from males in color phase 4

18a	OVARIES							
Size \ Activity	II	III	IIIa	IV	V	VI	VII	*Total number*
1	2	—	—	—	—	—	6	*8*
2	2	1	—	—	—	—	17	*20*
3	10	5	3	—	—	8	48	*74*
4	11	53	32	5	5	41	56	*203*
5	1	132	107	20	14	116	36	*426*
6	—	37	38	12	12	61	5	*165*
7	—	14	50	19	15	29	—	*127*
8	—	—	3	18	41	16	—	*78*
9	—	—	1	15	79	53	—	*148*
Total number	*26*	*242*	*234*	*89*	*166*	*324*	*168*	*1249*

18b	TESTES						
Size \ Activity	II	III	IV	V	VI	VII	*Total number*
1	3	4	—	—	—	—	*7*
2	—	2	—	1	1	—	*4*
3	—	9	—	1	4	1	*15*
4	—	3	4	—	12	1	*20*
5	—	2	22	3	26	—	*53*
6	—	—	28	1	10	—	*39*
7	—	—	50	4	16	—	*70*
8	—	—	46	3	21	1	*71*
9	—	—	46	35	13	—	*94*
Total number	*3*	*20*	*196*	*48*	*103*	*3*	*373*

18c	TESTES						
Size \ Activity	II	III	IV	V	VI	VII	*Total number*
1	70	2	—	—	—	4	*76*
2	42	13	—	3	—	4	*62*
3	7	61	—	3	1	—	*72*
4	1	43	3	—	2	—	*49*
5	—	—	8	2	—	—	*10*
6	—	—	2	—	—	—	*2*
7	—	—	1	1	—	—	*2*
8	—	—	—	—	—	—	—
9	—	—	—	2	1	—	*3*
Total number	*120*	*119*	*14*	*11*	*4*	*8*	*276*

Measured length and width of gonads

In 18 per cent of the specimens (521 ♀♀ and 287 ♂♂) the length and greatest width of the gonad lobes have been measured with an accuracy up to 0.1 mm. Measuring both lobes of the paired organ of 100 randomly chosen specimens showed that in one single fish the two lobes are of about the same size, thus of the remaining 708 specimens only one, the left, lobe has been measured.

In those 18 per cent of the specimens a comparison of the estimated and measured data was possible. Per estimated size category a rather great variability was observed for both accurate parameters. This may be explained by the fact that in the *1–9* estimations an impression is given of the volume as a whole, while length and width alone are less representative for the three dimensional size of the gonad.

For *Thalassoma bifasciatum*, *Halichoeres bivittatus* and *H. garnoti* the mean length and width per estimated size of the gonad is given in Table 17. These data illustrate that with increase in category number, the means of measured length and width gradually increase. After reaching scale 4 the gonads become relatively more slender. Substitution of accurately measured variables by the nine digit estimation scale is justified by the fair correlation between the data for estimated and measured parameters.

A comparison of the estimated size of the gonads (*1–9*) with the estimated stage of gonadal activity (II–VII) is presented in Table 18. Their relation is not linear due to considerable variation in volume corresponding to the degree of maturity of the specimen. The largest size is attained in stage V (mature), while stage VI (spent) and VII (regressing) are smaller again. Moreover, Table 18 shows the diversity in absolute size found for gonads in identical stages of activity, depending on the differences in body lengths.

The above information justifies using the estimated stage of activity rather than the size of the gonads as a parameter in the discussion of the relationship between color, size, sex, and sexual activity (Chapter XI).

Weight of gonads

The gonads of a number of specimens were weighed with an accuracy up to ± 0.1 mg. The weight includes both lobes of the reproductive organ. If the gonads were moistened – this often happened when during dissection the intestines, full of sea urchin bait had to be removed – they were dried carefully with some "kleenex" tissue. Extremely mature gonads were difficult to weigh accurately because even with the most careful removing and handling, some loss of ripe eggs or sperm occurred.

The weights do not include adipose tissue. Especially in large males small opaque yellowish bands of fat adhere to the testes sometimes. This accessory tissue was cut away before weighing.

In some fishes the adipose tissue formed large fringe-like structures. In a 14.4 cm TL terminal color phase *H. garnoti* male the fat lobes measured 168 × 15, 134 × 15, 171 × 12 and 110 × 11 mm, with a total weight of 75 mg, while the testes lobes (Plate V-c) were 136 × 37 and 144 × 41 mm and weighed 128 mg. A terminal phase *H. maculipinna* male of 10.3 cm TL had its testes of 21 mg muffled by 18 mg fat. A similar phenomenon was found in bluehead phase *Th. bifasciatum*, such as four males of 10.2, 10.3, 10.6 and 10.6 cm TL (Plate V-e). Microscopically the adipose tissue showed soft pink meshes without any interstitial tissue, typical of fat tissue.

Histology

The main goal of our histological investigations was to verify to which extent the macroscopical classification of developmental stages suggested above, corresponds to histological recognizable phases of maturity. Also, determination of sex and function in the small threads of gonadal tissue found in a minor portion of the specimens requires histological examination. In conclusion, microscopical investigation is also indispensable for the identification of intersexual stages in Labridae.

The complete gonads were removed and preserved in Bouin's solution. The paraffin sections, thickness 5–7 μ, were stained with Harris' hematoxylin and eosin. Thanks are due to Dr. R. Eibergen and his staff of the Laboratorium voor Volksgezondheid, Curaçao, where sectioning and staining was performed.

Histological slides were made of a total of 360 labrids as follows: *Thalassoma bifasciatum* – 120 specimens; *Halichoeres bivittatus* – 118 specimens; *H. garnoti* – 37 specimens; *H. maculipinna* – 25 specimens; *H. poeyi* – 17 specimens; *Hemipteronotus splendens* – 19 specimens and *He. martinicensis* – 24 specimens.

Usually cross sections were made of the embedded gonads; a number of them, however, were sectioned in longitudinal direction. Of each gonad slides were made from different, randomly selected areas to cover possible topographical variability of sexualization within one gonad.

The material includes a number of specimens stored at minus 20°C. These were not used for description of cytological details.

In general, the process of the development of the gametes proved not to differ from that in other teleosts (e.g. STENGER, 1959). In regard to ovulation and atretic follicles, however, features were observed which deviate from those described in most other publications, but which agree with those in POLDER's reports (1964, 1971). In the seven Caribbean labrid species no limited spawning season occurs. But the cyclic changes in the microanatomy of the gonads proved to conform to descriptions of seasonal fluctuations in teleosts of temperate regions (e.g. MARIAN JAMES, 1946a; POLDER, 1961; NANCY HENDERSON, 1962, 1963a).

Ovary

Morphology

Each lobe of the paired ovary is covered by peritoneum, some smooth muscle fibers, connective tissue and internal epithelium. The ovary wall projects as septa into the center of the ovary. These septa support the ovigerous lamellae which almost completely fill the ovarian cavity; between the lamellae only small spaces are left (Plate II). In these ovarian lamellae different growth and maturation stages of development of the female germ cells, from oogonia via oocytes towards maturing and ripe eggs, may be present.

A distinction can be made between ovaries which for the first time are involved in the maturation process (virgin ovaries), as opposed to others that have already undergone it at least once before, recognizable by the remnants of former maturation cycles. (The same is true for sperm formation, see below).

Development of oocytes (Plate I)

The smallest premeiotic oocytes are triangles of deeply purple-blue stained, fine cytoplasma with a diameter not exceeding ten mikrons (Plate III-b). When they are somewhat larger, their form is still angular and they remain strongly basophilic; their main content is the large nucleus, in which a darkly stained nucleolus and a fine network of distinct chromatin threads are to be seen (Plate I-a, b, d). When reaching a diameter of about 30 mikrons, oocytes become less basophilic; they are

still yolkless and become surrounded by small, isolated connective tissue nuclei, the number of which will increase progressively during further development. In the egg nucleus next to the original nucleolus several other chromocenters are formed (Plate I-b). (For details on the histomorphological and cytochemical changes in the nucelus of teleost oocytes, see RASTOGI, 1968).

Then, in more advanced stages of oogenesis, maturation is characterized by a marked increase in total size, while the ratio of nuclear volume to oocyte volume progressively decreases (cf SADOV, 1957). First, the oocytes become slightly acidophilic and are enclosed by a one-layered membrane, presenting itself as a string of closely packed, small nucleoli; the oocyte nucleus now contains many peripheral nucleoli. Next, small vacuoles appear in the cytoplasma and the follicular cells surrounding the egg become more dense, forming separate, thin layers (Plate I-e). In medium sized ova (40 to about 100 μ) primary yolk formation starts, as well as the development of the oolemma, the membrane surrounding the ovum (zona pellucida) (Plate I-b, d).

When passing into the nearly mature stage, eggs are filled with a large amount of yolk globules, occupying most of the cytoplasma area. Only a relatively small central nucleus is visible, that is less, or even no longer, multinucleate (Plate I-b).

Subsequently, in the near-mature egg (300–400 μ), the thick oolemma is clearly visible; smaller yolk globules are fused into larger ones and the amount of yolk is so much increased that it now occupies all the cytoplasma; it gives the egg (at gross examination) still a rather opaque aspect. The nuclear membrane often has disappeared and the ooplasma and nucleoplasma meet freely (Plate I-b).

Ovulation comes at the end of this developmental stage. The protecting cover ruptures and the egg, that is now entirely free, takes up liquid. Consequently, there is a further marked increase of its diameter (up to about 1,5–2 times that of the egg just previous to ovulation) and the opaque aspect changes into a transparent one. Due to the greater liquidity, ovulated eggs are much more strongly distorted by the manipulations of fixation and staining techniques than the surrounding tissues (Plate I-f, g). Eggs just on the point of ovulation histologically show a slight curdling of the cytoplasma and a loosening oolemma (Plate I-g). Eggs, in which liquid uptake had been completed show very curdled cytoplasma, and an extremely folded and shrunken wall; often, the oolemma is torn loose from the egg (Plate I-f). Consequently data on diameters of these eggs are not reliable. Fresh, not fixated ovulated eggs, are about 0,6–0,7 mm in diameter (exact data on diameters of fresh eggs of different stages of ripeness of *Th. bifasciatum* can be found in FEDDERN, 1965).

When the ovulated egg has left the follicle, the ruptured follicular wall remains as a so called "calyx." These calyces contract and decrease in size, passing stages α, β, γ, until hardly any "scars" are left (Plate I-d, e). (Calyces, formed subsequently to ovulation, have often been named "(post-ovulation) corpora lutea").

For all vertebrates it has been described how oocytes of some follicles undergo resorption. This degeneration or atresia may occur at any stage of the development. (Repeatedly, such atretic follicles in fishes have been indicated as "(pre-ovulation) corpora lutea.") Below, it will be discussed how in labrid ovaries atretic follicles have been found only incidentally.

Atresia refers to a very local situation as the follicle in involution is surrounded by normal tissue, in contrast to overall resorption of the gonad that will be described for a minority of the labrid gonads (stage VII, Plates I-c, IV).

Histologically discernible stages (Plates II, III, IV)

I. Very young, just differentiated ovary

As said before, sex determination of the small threads of gonadal tissue can only be done by microscopical examination. Thus examined, a number of stage I gonads actually proved to be very young, virgin ovaries. This is evident because of the occurrence of numerous nests, containing germ cells, conglomerates of oogonia and small, primary oocytes of identical size, next to much collagen, muscle tissue and capillaries (Plate I-a).

II. Young ovary

Though connective tissue still occupies a considerable portion of the immature ovary, the main part now is filled by the clearly metamere, long finger-like protrusions of lamellae. The parenchymous stroma contains many oocytes in primary and secondary growth phases. Incidentally, oocytes are present in which small vacuoles appear in the peripheral cytoplasma (Plate II-a).

III. Developing ovary

The growth of the ovary, that now fills about $\frac{1}{3}$ of the abdominal cavity is caused by the increase in size of the developing eggs. In most of the oocytes yolk formation has just started; in some larger eggs already numerous yolk globules have appeared. Among the growing eggs rows of very small, still deeply basophilic primary oocytes are present, the recruitment stock, that most probably will grow further in a subsequent maturing cycle. In the virgin ovary, the whole structure of the ovary is firm and dense. In the recovering ovary the whole appearance is more loose; in the ovigerous lamellae show open places, sites of former, already spent ova; the free space is filling up with newly developing eggs (Plate II-b, c).

III-a. More developing ovary

Ovaries in this stage, with no longer a smooth external surface, are for the greater part filled with eggs in more advanced stages of oogenesis. That is, opaque eggs full of yolk (Plate I-b).

IV. Maturing ovary

Ovaries with the appearance of a bunch of grapes and occupying about ¾ of the abdominal cavity, are for the greater part filled with large eggs. These are visible with the naked eye and characterized by a marked increase in the amount of yolk. In most eggs the nuclear membrane has already disappeared. These ovaries are clearly destined to be spawned soon. A minority of eggs has already reached the point of ovulation and show ruptured follicular walls and first curdling of the cytoplasma. Scattered among the ripening eggs small, basophilic oocytes are present as well as eggs in just the first maturing stages (Plates II-d, III-a).

V. Mature ovary

The foamy looking, very swollen ovaries which fill all available space of the abdominal cavity are strongly affected by the deteriorating effects of the histological technique. There are many holes, apparently openings where ovulated eggs got lost during manipulation of the ovary. The greater part of the section is occupied by extremely shrunken, curdled ovulated eggs; often, the contents of the ova are completely separated from the covering oolemma. The small spaces left between the ripe and ovulated eggs are occupied by basophilic recruitment stock. Also ova in the near-ovulation stage might be present (Plate III).

VI. Spent ovary

This stage covers partially spent ovaries and those of which all mature eggs have been shed. The first are no longer compact but still of average size. The histological picture shows mainly damaged egg lamellae with many holes and remnants of the folliculae from which ova have been discharged. Both nearly mature and shrunken, not yet discharged ovulated eggs are present. As this has been found very often, it may be assumed that mature eggs are not released at once but in subsequent spawning acts. Completely spent ovaries are much more shrunken and have more undulated walls. Between the numerous loose, frayed open spaces many calyces are present, next to small primary oocytes at the periphery of the distorted lamellae (Plate III-b).

VII. Ovary in regression

Macroscopically these gonads show as slack, small threads without turgor (virgin stages I and II are also small, but compact and firm). Histological inspection shows mostly a complete state of regression with total phagocytose, not only of the larger ova but of the small, basophilic oocytes as well. In early stages of regression only the larger, yolk containing eggs are in resorption, while the smaller oocytes still have a rather normal aspect (Plate IV-d). More than in the other stages the space between the eggs is occupied by connective tissue; the whole gonad is strongly provided with capillary bloodvessels. The follicular epithelium may be high, penetrating deeply into the ovum; the nuclei of the epithelium may be distinctly visible in the cytoplasma of the egg.

Necrotic ovaries are often surrounded by fat tissue. Frequently the shrunken, undulated ovary wall with large, wide folds, indicates that the size of the gonad has been larger in a former stage (Plate IV).

Disintegration and overall resorption of the gonad cannot be explained as caused by the end of the spawning season as tropical wrasses proved to be ready to spawn the whole year through. Individuals with gonads in reduction often were caught together with specimens with functional, mature gonads. Reductions of the gonad were found to coincide more or less with changes of color pattern and a certain body length. This will be discussed in Chapter XII.

TABLE 19

FREQUENCY OF FIVE CATEGORIES OF EGG DEVELOPMENT PER MACROSCOPICALLY DISTINGUISHED GONADAL ACTIVITY STAGE

based on percentage-estimation in histological slides of 118 ovaries of seven Caribbean labrid species

a = early oocytes; *b* = less acidophilic oocytes; *c* = maturing ova with yolk formation; *d* = mature ova; *e* = ovulated ova
calyces: + = present; ++ = 2–4 present; +++ = > 4 present

Activity stage of ovary	Developmental stages of the ova					calyces	N of ovaries
	% *a*	% *b*	% *c*	% *d*	% *e*		
I very young	40	20	—	—	—		4
II immature	45	55	—	—	—		9
III developing	8	9	73	9	1		23
IIIa more developing	7	9	53	27	4		19
IV nearly mature	6	7	31	46	10	+	21
V mature	5	9	9	12	65	+++	26
VI spent	5	11	23	7	54	++	16

Table 19 compares the microanatomy of 118 ovaries with the classification by naked eye inspection of the dissected specimens into stage I to VI. The histological aspects have been quantified by estimating the percentages per section, occupied by the following developmental stages of oogenesis:

a – small, deeply basophilic primary oocytes up to 25 μ

b – larger, still yolkless and basophilic oocytes

c – medium sized ova full of yolk

d – eggs just before ovulation with first signs of loosening oolemma and curdling of the cytoplasma

e – ovulated eggs in which fluid uptake has been completed.

In Table 19 the presence of observable calyces is indicated as well.

After inspection of slides of 131 ovaries and of the data as summarized in Table 19 it may be remarked that:
1) The histological data correspond with the macroscopical classification into eight stages of gonadal activity. This justifies the use of these stages in the discussion in Chapter XI and XII.
2) No essential differences in general microanatomy exist for the seven species.
3) Non-virgin ovaries contain a mixture of eggs in the most diverse stages of development. – This is an indication of the continuous spawning periods of the Caribbean labrids; in fishes with a short, limited spawning season all maturing eggs will be of about the same size (HICKLING & RUTENBERG, 1936).
4) The final processes of ovulation and subsequent swelling of the eggs takes place in many ova simultaneously.
5) Calyces are only clearly observable in just spent ovaries. – In ovaries in which already a new maturing cycle has been started hardly any calyces are recognizable. Apparently in labrids such remaining parts are completely absorbed during reorganisation and rebuilding of the ovary after spawning.
6) Atretic ova have only incidentally been met with.

This last point is in contrast to what has been mentioned for other species of fish in which atresia was reported as of common occurrence (e.g. HISAW & HISAW, 1959). Atresia has been explained as a mechanism to give room to increasing maturing eggs. In labrids – with continuous, successive spawning cycles – only part of the small oocytes seem to continue maturing while the rest stops growing, forming recruitment stock for a following maturation cycle. This might explain that local involution of eggs only happens incidentally.

"Corpus-luteum"-like structures have been described e.g. by SAMUEL (1943) and MATTHEWS (1938). BRETSCHNEIDER & DUYVENÉ DE WIT (1941, 1947) advanced the hypothesis that "pre-ovulation corpora lutea" become sites of hormonal production. This idea has long prevailed in articles and textbooks (BROWN, 1957). Yet, some authors have cast doubt upon such endocrine function (PICKFORD & ATZ, 1957; HISAW & HISAW, 1959). POLDER (1964) presented conclusive evidence for the fact that the high percentage of atretic follicles found in the ovaries of the bitterlings studied by BRETSCHNEIDER c.s. most probably were caused by an unnatural stress

situation during the experiments. They kept their females removed from both mussels and sex partners, circumstances ideal for inhibiting spawning, resulting in overall resorption of not ovulated eggs.

Our own observations on wrasses agree with POLDER's thesis. All labrids used for the present study were freshly collected in the sea. Consequently the ovaries under discussion were obtained from females that had been under normal, natural circumstances until the moment of fixation of the gonads, without any induced drags on the occurrence of ovulation at the end of the maturation period.

Some investigators also reported only a low incidence of atretic eggs (NANCY HENDERSON, 1963b). The present author would like to suggest that in some other publications, the term atresia was used incorrectly to describe shrunken, curdled phenomenons of not regressive, but already ovulated so relatively more humid eggs (STENGER, 1959, in his description of spent ovaries of *Mugil cephalus*).

Testis

Morphology

The two lobes of the paired testis, each at the outside covered by the tunica propria, are composed of many elongated and complicatedly subdivided lobules (Plate V-b, VI-a). The lumina of the lobules are continuous with the lumen of the spermatic duct (Plate V-d). In the walls of the testis follicles different stadia of spermatozoa development occur, spermatogonia, primary and secondary spermatocysts, and the final stages, maturing and mature spermatozoa, as typical for fishes without a limited spawning season. All testes proved to be less affected by fixation than the ovaries. The interstitium contained no cells which resembled Leydig cells.

Histologically discernable stages (Plates V, VI), (IX)

I. Very young testis

Part of the small gonadal threads can be identified histologically as young testicular tissue. Once the inception of sexualization into the male direction starts, the whole process of further differentiation seems to develop rapidly. Though the size of the gonad is still very small, histological investigation reveals cysts of young spermatogonia, as well as more advanced stages of sperma development (Plate IX-d).

II. Immature testis

Though the gonads are not yet large, the inside shows many cysts undergoing spermatogenesis. Many places, however, are still in the spermatogonia phase (Plate IX-b).

III. Developing testis

Histologically many lobules can be distinguished clearly. They are full of cysts in various stages of meiosis and spermatogenesis. Some lumina already contain small

clusters of mature sperm. As in the ovaries, some testes appear to have been ripening for the first time (Plate IX-f). But the majority evidently are recovering testes, that have already gone through previous maturation cycles, recognizable by remnants of sperm in the ducts (Plate V-c).

IV. Maturing testis

Though at the periphery young, more immature stages are present, the major portion of the testis is full of maturing and mature sperm. Most lumina are tightly packed with mature sperm, which begins to fill the efferent ducts (Plate V-f).

V. Mature testis

In the ovary the moment of ovulation, with consequent swelling of the egg due to fluid-uptake, is more marked and can be more strictly defined. In the testis the transit of stage IV towards V occurs more gradually, and hence the classification is more arbitrary. A useful characteristic of stage V is the externally obvious functional maturity: the slightest manipulation of the fish causes release of sperm. In sections all lumina are full of large masses of sperm; the primary and secondary efferent ducts are filled with mature sperm. Even in this stage cysts of spermatocysts and spermatids are also present in the peripheral regions of the lobules (Plate V-a, d).

VI. Spent testis

After the sperm has been discharged the testis reduces in size. The release of sperm causes distorted tubules. However, the decrease and internal disorganization is never as severe as in the just spent ovary. Almost all spent testes proved still to contain sperm in the ducts (Plate V-b).

VII. Testis in reduction

In degenerating ovaries the whole gonad is subjected to regression. Testes, however, may show more topical areas of reduction. When most of the gonadal lobe is in regression, the gonad is in general small and can already macroscopically be classified as stage VII. Yet, spermiogenesis may still occur in some places and consequently the ducts may contain small quantities of sperm (VI-b, e).

Necrotic islets in testes of large males

In testes of males of intermediate and large sizes certain islets were frequently observed. They consist of a type of indefinite, necrotic tissue, showing a yellowish or pink color in H.E. stained sections. They have a homogeneous appearance, without any clear organisation and are often surrounded by fat and vacuoles and sometimes by leucocytes. They occur scattered through the gonad, and are frequently situated along the trabeculae that – curiously enough – are present in many testes of large males. Definite histological identification was impossible. They have been

encountered in all species; especially in *H. garnoti* and *H. maculipinna* was their presence obvious. Yet, these islets do not occur in all larger males; sometimes there are only a few of such isolated areas, sometimes they are scattered throughout the whole testis. In a very few cases these strange areas have been found in males still having characteristics of the first adult phase.

Such as a *Th. bifasciatum* specimen, with first signs of bluish hues on the head, of 7.8 cm TL. The small gonads proved to be young, developing testes with numerous scattered yellowish islets. In most color phase 1 and 2 males, however, the islets were absent.

They may be remains of ovary tissue, or areas of secretory activity, though the typical islets certainly do not occur in all terminal phase fish. Settling the character of these spots requires more specific histological and histochemical work (Plate VI-a, c, d).

TABLE 20

FREQUENCY OF FOUR CATEGORIES OF SPERM DEVELOPMENT PER MACROSCOPICALLY DISTINGUISHED GONADAL ACTIVITY STAGE

based on percentage-estimation in histological slides of 80 testes of seven Caribbean labrid species

a = spermatogonia; *b* = young cysts of spermaticids; *c* = mature sperm in the cysts; *d* = mature sperm present in the primary and secondary ducts

Activity stage of testis	Developmental stages of the sperm				N of testes
	% *a*	% *b*	% *c*	% *d*	
I very young	55	30	5	—	3
II immature + recovering	30	30	36	4	19
III developing + recovering	19	22	37	22	20
IV near-mature	15	17	35	33	14
V mature	19	20	23	38	15
VI spent	25	27	38	10	9

Table 20 compares the microanatomy of 80 testes with the classification by naked eye inspection of the specimens dissected. The histological aspects have been quantified by estimation of the percentages per section, occupied by the following developmental stages of the sperm:

a – spermatogonia
b – young cysts of spermaticids
c – mature sperm in the cysts
d – mature sperm present in the primary and secondary ducts.

In the testis the differences between the activity stages are less distinct than in the ovary. Young testes may already contain mature sperm, whereas final maturing and ovulation of eggs takes place simultaneously i.e. just before spawning. By and large correlation of eye inspection and histological examination seems to justify substituting the former method for the latter one.

Intersexes

Microscopical examination revealed that a small portion of the small gonads classified as stage I, II or VII actually were intersexes (Plates VII, VIII, IX). Intersexual gonads may be in various stages of transition: from mainly ovarian tissue in overall regression with scattered spermatogenous centers to cases in which the gonad is mainly testis with here and there ovarian remains. In some cases a few, isolated primary or secondary oocytes in reduction occurred amid maturing sperm; in other instances there were clusters of degenerating oocytes, among which ova that apparently had reached advanced stages of maturation before regression took place. Series of sections show that developing spermiogenesis among regressive ovarian tissue or ovarian remains among testicular tissue occur throughout the whole intersexual gonad. To the naked eye the, mostly small and loose, intersexual gonad sometimes resembled an ovary, sometimes gave the impression of a testis, but mostly was of indefinite sex externally. The walls of the gonad and of the efferent ducts often were rather thick, a feature that fits in with the morphology of the ovary. These characteristics of the intersexual gonads are an indication that a transition from ovary into testis may occur in labrids. Functional intersexual gonads, in which both the female and the male part are normal and active, have not been found.

Plate VII gives an impression of intersexual gonads that are still mainly ovarian. The ovarian tissues are rapidly regressing; all oocytes are in clearly reductive stages. In the gonads pictured in Plate VII-c (a yellow phase *bifasciatum*, 8.3 cm TL) there are first stages of spermiogenesis here and there; in Plate VII-a (an intermediate phase 3 *bivittatus*, 11.8 cm TL) spermiogenesis is developing everywhere. In transitional gonads areas with vacuoles and fat often occur, characteristic of resorption. Remarkable are the numerous, large vacuoles present in the intersexual gonad represented in Plate VII-b (an intermediate phase 2 *bifasciatum*, 8.6 cm TL).

Plate VIII shows sections of intersexes in which sperm production is in a more advanced stage. In the gonads of a first adult phase *bivittatus*, 11.2 cm TL in the loose tissue full of primordial cells, here and there greatly reduced oocytes are present; spermatogonia, primary and secondary spermatocytes occur everywhere (Plate VIII-b, c). Severall small, loose gonad threads proved to contain well-developed testis tissue (Plate VIII-e, f); next to decaying oocytes intricately folded structures occur, resembling oolemma's (Plate VIII-d, f). The slides indicate that eggs that were (nearly) mature on the moment of onset of sex reversal, may develop into the yellowish or pink islets that often characterize testes of large sized fish.

Plate IX shows sections of small, but well-developed testes in which here and there some clearly recognizable, barely resorbed large eggs are present, next to some scattered oocytes in regression. For instance, a *H. maculipinna* specimen of 14.3 cm TL, in terminal phase colors, had small, but rather firm testes (estimated size 2). Histological investigation revealed an actual testis, full of tissue in young and maturing stages; scattered here and there were yellowish islets (reduced eggs?); at some places clear remnants of eggs and oolemma's occurred (Plate IX-a). Plate IX-c, d, e (a first adult phase *bivittatus*, 6.1 cm TL) shows how sometimes parts of an otherwise normally developed testis are loose and disordered; here, most ovarian remains were found.

A deviating case of an intersexual gonad was found in a terminal phase *He. martinicensis*, 10.6 cm TL, as here the testicular and the ovarian part were separated; in spite of a series of sections it could not be checked whether somewhere these two parts united (Plate VIII-a).

At which sizes and in which color phases the various types of gonads occur will be discussed in Chapters X and XII.

X. RELATION BETWEEN COLOR, SIZE, AND SEX

The prominent aspect of color in live labrid fish has caused numerous attempts to use this landmark in taxonomy and for correlations with sex, size, and behavior. The available information on these correlations is, however, confusing, often controversial, and rarely complete. This has been the main stimulus to the present study, especially as information on Caribbean wrasses is particularly scanty.

In a previous chapter the subsequent color phases per species have been analyzed. In this chapter the range of the body length in which those color phases occur will be discussed. In addition, attention will be given to the sex of the various color and size forms.

HISTORY

Initially the two distinct color phases of dichromatic labrids were considered to be separate species. When taxonomy was settled, it became apparent that the individuals with bright, more polychrome colors, were always large fishes, as exemplified in *Crenilabrus ocellatus* (SOLJAN, 1930a, b), *Labrus bimaculatus* (LÖNNBERG e.a., 1937), *Gomphosus varius* (STRASBURG e.a., 1957), *Stethojulis strigiventer* (RANDALL, 1955a) and *Halichoeres poecilopterus* (OKADA, 1962).

Detailed studies of the relation between color and size were done in *Coris julis*. In this species reddish brown fish occur up to about 15 cm TL, while turquoise terminal

colors may be displayed by specimens of about 11 cm TL and more. Consequently, there is just a small range of some four centimeters in which both appearances can be found (BACCI e.a., 1957, 1958; REINBOTH, 1957; ROEDE, 1966).

For a long time dichromatism in labrids was regarded as a sexual dimorphism. The smaller, more plain colored specimens were considered to be females and immature males, while the larger gaudy colored fish were looked upon as functional males.

SOLJAN (1930a, b) described already a situation that contradicted the alleged relation between color, size, and sex.

During field observations of the Mediterranean wrasse *Symphodus* (*Crenilabrus*) *ocellatus* SOLJAN noted the occurrence of two types of males. Some males were indeed large, brightly colored fish of 92 cm body length or more. The other type, however, was smaller, not exceeding a length of 82 cm and yellowish brown; they looked similar to the females. These two types of males exhibit essentially different behavior. The large males build nests, court females, and take care of the fry. The small males – denoted by SOLJAN as "Outsider der Befruchtung" – often fertilize part of the eggs as they rush forward on the moment the eggs are released. A similar situation occurs in *Crenilabrus quinquemaculatus* (SOLJAN, 1931).

A few years later the existence of two types of males was reported for *Labrus bimaculatus*. Obtaining correct information on the actual color, size, and sex relation in *Coris julis* took more time. Of many other labrid species the dimorphic nature is just being disclosed; this focuses attention on morphological differences between successive color stages and the possible existence of a "lady with two lovers" situation has not yet been looked into.

Labrus bimaculatus

As early as 1800 RETZIUS united both color forms of the Striped Wrasse into one species, suggesting that the mainly red, smaller specimens were all females and the large blue fish males. This was confirmed by Fabricius (1809) and FRIES (1835). Then, NILSSON (1835) remarked: "Young males are supposed to resemble the females in colour"; LILLJEBORG (1891) made a similar restriction (cf. LÖNNBERG e.a., 1937). To solve the problem of these discrepancies LÖNNBERG & GUSTAFSON examined specimens of different color and size. Among 80 small, red fish six specimens with male gonads were found: three had functional testes containing living spermatozoa, the other three gonads were still developing. Nine larger specimens showed intermediate colors as, notwithstanding blue-striped features, the dorsal spots from the red phase still persisted. From these, six proved to be real females. Of 36 large and blue-striped fish 35 were males. LÖNNBERG e.a. conclude that most female specimens

become ripe while retaining the red color pattern. At least part of the males becomes ripe while in the red phase; however, their chief reproductive function takes place in the blue-striped phase.

Coris julis

In 1868 STEINDACHNER – uniting the subsequent color forms of the "girelle" into one single species – stated that the reddish brown fish were female, the turquoise male. His revision of systematics was not accepted; attention remained focussed on morphological differences like color and shape of the dorsal fin, leaving essential characteristics such as body length and sex out of discussion. FACCIOLA (1916) and FOWLER (1936) support STEINDACHNER's concept of sexual dichromatism. LO BIANCO (1909), however, described both sexes for both "species". Also ROSA DE STEFANI (1955) – who still considers the different color forms as separate species – found among ten small, reddish brown fish two males, and one female among eight large, turquoise specimens.

New, revealing information on the actual sex relations of the "girelle" was given by BACCI & RAZZAUTI (1957, 1958). Of a total of 118 specimens in which the gonads were examined, the red-brown group – mean length 9.3 cm – existed mainly of females but about 16 per cent proved to be males. Of individuals with intermediate features, mean length 12.8 cm, a percentage of 66.6 were males. The turquoise fish, mean length 14.8 cm, were all males. They conclude: "Thus the livery appears to be partly independent of sex-conditions."

REINBOTH (1957) found among 133 specimens, 86 individuals in the plain red-brown colors: 64 females and 22 males, while 33 males were found with turquoise colors. RENATA VANDINI (1965) detected in the red-brown group next to 254 females a minority of 54 males. MACHTELD ROEDE (1966) found among 263 first adult phase specimens 164 females and 79 males, next to 20 specimens with gonads too small to be sexed; of 22 large, turquoise terminal phase fish 13 were functional males.

Summarizing, in *C. julis* female sex is restricted to small size and first adult colors, but there is no clear relation between male sex and color/size.

The fact that distinction of the sexes on the basis of color and size is only partly useful, also holds for *Halichoeres poecilopterus*. KINOSHITA (1935) already mentioned the occurrence of testes in a specimen "in which the secondary sexual characters [i.e. terminal colors] were not yet developed." OKADA (1962, 1965) found a not negligible minority of males among the size and color group in which the females occurred.

In his discussion on "sexual dimorphism" in *Stethojulis strigiventer* RANDALL (1955) mentions that all 18 large, gorgeously colored fish were males. On the other hand, also 12 males, with well-developed testes, were found among a sample of the smaller, brown form, further comprising 30 females. He concluded: "Maturity in the male seems to be reached before the *renardi* form [terminal phase] is assumed."

REINBOTH (1962a), the first to distinguish clearly two types of males in *Coris julis*, discusses a similar situation for *Thalassoma pavo*. A number of 15 large males were found with a marked blue cross bar. Moreover, among 103 smaller specimens, characterized by five small green-bluish cross stripes, also 20 males were found. The other fish in the latter sample were females.

However, not in all labrid species do two types of males seem to occur.

STRASBURG & HIAT (1957) found among 54 smaller, somberly colored specimens of *Gomphosus varius* 39 females, next to 15 immatures. Among ten larger and rich blue-green colored fish eight males were found; one was decomposed internally, one immature. This finding does agree with the former concept of dichromatism as a sexual dimorphism.

SORDI (1962) investigated some hundreds of individuals of *Labrus merula* and *L. turdus* (*viridis*) – examples of labrid species in which no extreme changes of colors occur during a lifespan. He has demonstrated that (p. 85): "All individuals of the two species are female up to a length of 270 mm. One half of the individuals is male in the higher size classes of *L. merula*. The whole of individuals seem, however, to pass to the male phase in the highest size classes of the species *L. turdus*."

In the majority of the publications on Caribbean labrid species, the process of morphological color change is not or only vaguely mentioned and consequently too little has been written on the relation between color pattern and body length. Whilst for some European dichromatic labrid species often violent discussions dwelt upon color and sex, in the descriptions of Caribbean wrasses sex was mostly omitted.

Bodianus

FEDDERN (1963: 233) included in his discussion of color and growth of two *Bodianus* species for *B. pulchellus* no data on sex; for *B. rufus* he remarked: "Both sexes apparently have identical color patterns at comparable sizes."

Thalassoma bifasciatum

In Chapters II and VI the authors have been mentioned who identified the yellow and the bluehead phases as separate species, *nitidum* and *bifasciatum* respectively; they omitted the essential difference that on the average the former specimens are smaller than the latter ones. First, the color and size relation was discerned; then, the existence of two types of males reported.

LONGLEY (1914, 1915), who united both color forms into one single species denominated the yellow fish as "immatures," the bluehead fish as "matures." BREDER (1927) is the first who clearly mentions sizes in relation to color: an unbroken banded phase up to 40 mm SL, a broken banded phase from 43 to 80 mm SL, a lighter broken banded phase up to 85 mm SL and adult coloration from 84 to 108 mm SL color phases [1b, 1c, 1c + 2 and 4, respectively]. (His data are actually not different from the results of the present study; only BREDER's range for bluehead colored fish is smaller).

The first to mention sex were BEEBE & TEE-VAN (1928, 1933b), considering the yellow fish as representing females and young, the blueheads adult males. Body sizes were not discussed. TEE-VAN (1932) found that any fish, showing a trace of bluehead colors, was male. He concluded that smaller males may occur in the same general color and pattern as the females and at a little over three inches in SL gradually assume the more striking coloration.

LONGLEY e.a. (1941) emphasized the occurrence of males among the yellow phase (85 females to 30 males); 50 females ranged from 64 to 117 mm, 19 males from 84 to 114 mm in length. Thirty specimens with *bifasciatum* colors, eight of which were 114 tot 146 mm long, proved to be all males. LOUISE STOLL (1955: 125) concluded: "the males are sexually mature some time before they develop their strikingly different secondary sex characters."

RANDALL & RANDALL (1963) correctly denoted the yellow form as mature females, mature male or immature, the bluehead phase as male. FEDDERN (1965) mentions that both sexes exhibit the yellow colors, but that the blueheads are exclusively male. For the yellow phase he gave a maximum length of about 80 mm, while the largest bluehead he collected was 85.5 mm SL. RANDALL (1968) described the yellow one as a smaller phase, the bluehead as the largest. BÖHLKE & CHAPLIN (1968) also mention how not only the bluehead fish are males, but numerous yellow ones as well.

CERVIGÓN (1966) sticks to the obsolete opinion that the yellow fish are only females and immature males, while adult males have the bluehead colors.

Halichoeres

For *Halichoeres* species the information about the relation between color, size, and sex is more limited.

For *H. bivittatus* JORDAN & EVERMANN (1898) mention some changes in coloration due to age. MOWBRAY (1931) on the other hand, wrote that *bivittatus* is constant in pattern. This was illustrated by a picture of a series of twelve specimens, ranging from 12 to 102 mm. As most of the Slippery Dicks up to 100 mm TL display phase 1 colors, in such a series indeed no color changes can be traced. BEEBE & TEE-VAN (1933b) gave some indications of the attainment of terminal colors in larger Slippery Dicks, which they, incorrectly, referred to as "adults." Only in RANDALL & BÖHLKE (1965) and RANDALL (1968) is the connection of color with size mentioned, though no exact ranges are given. They refer to the terminal phase as "adult males," but whether or not males occur as well at smaller sizes is not discussed. BÖHLKE & CHAPLIN (1968) do not give any indication about sex, only refer to the terminal phase as "adults."

In LONGLEY & HILDEBRAND (1941) some indications are given of color changes in *H. garnoti* during growth. RANDALL & RANDALL (1963) are the only authors who clearly connect color pattern and size. They, and BÖHLKE e.a. remark that the vertical bar develops in the adult male. [Such a pattern, however, is displayed by some large females as well]. RANDALL e.a. also indicate the large, terminal phase of *H. maculipinna* as "adult males"; BÖHLKE e.a. as "mature males."

Hemipteronotus

Concerning the sex and size relations in this genus not much data are available.

For *Hemipteronotus splendens*, LONGLEY (1941: 202) remarked: "Sexual dimorphism in color and structure makes its appearance in specimens of larger size." He described terminal colors as "male" colors, but did not elaborate size and sex differences. RANDALL (1965, 1968) and BÖHLKE e.a. (1968) also described terminal colors as the pattern of adult males. RANDALL is the only author who, for *He. martinicensis*, described both phase 1 and 3 colors, correctly referring these to females and males respectively. His largest female was 4.5 inches, his largest male nearly 6 inches long. BÖHLKE e.a. consider phase 1 of *martinicensis* as young, phase 3 as adult. This disagrees with the results from the present study – see below.

Recent fish guides and monographs seldom give correct information on sex ratios per color form. OKADA (1955), CERVIGÓN (1966) and QUIGNARD (1966) simply indicate first adult and terminal colors as "female" and "male" colors, respectively. For labrids with hardly any color changes during life, the relation of sex and size is not mentioned. RANDALL (1965, 1968) and RANDALL & BÖHLKE (1965) give only incidental information on sex of small specimens in first adult colors. Terminal colored fish are denoted as "large adult males"; as will be discussed below, this does not apply to all labrid species. BÖHLKE & CHAPLIN (1968) used incorrectly the term "adult" for terminal colored specimens only, passing over the many mature fish in first adult colors.

The reports reviewed illustrate how in labrid species with their wide color diversity, sex is another elusive item. Table 21 summarizes the publications which are most pertinent to our own observations.

The literature cited suggest:

In species without, or with hardly any color changes:

- in some species small specimens are females, large ones males (SORDI);
- for most species no sex analysis has been carried out.

In species with different color patterns during a lifespan:

- successive color forms often have simply been labeled as "female" and "male," respectively;
- in some species such naming proved to be correct (STRASBURG e.a.);
- in other species male sex is not correlated with color (LÖNNBERG; REINBOTH);
- for one species relation of color with sex proved to be absent (FEDDERN).

TABLE 21

DIMORPHIC LABRID SPECIES IN THE LITERATURE

Species	Authors	First adult colors: main color	N	range body-length (mm)		sex	Terminal colors: main color	N	range body-length (mm)		sex	Existence of sex reversal
Crenilabrus ocellatus	SOLJAN 1930	yellow-brown	21	54– 82		♀♀ and ♂♂ (48%)	orange and olive-blue	6	92–101		♂♂	– ?
Labrus bimaculatus	LÖNNBERG e.a. 1937	plain red	80	110–310		♀♀ and ♂♂ (7,5%)	rich blue	44	225–345		♂♂	+
Thalassoma bifasciatum	LONGLEY e.a. 1941	yellow	50 19	64–117 84–114		♀♀ ♂♂	blue and green	8	114–146		♂♂	?
Stethojulis strigiventer	RANDALL 1955	plain brown	47	33– 68	SL	♀♀ and ♂♂ (33%)	rich blue	23	72– 81	SL	♂♂	?
Gomphosus varius	STRASBURG e.a. 1957	brown-black	54	38–134	SL	♀♀ and immatures	blue-green	10	104–166	SL	♂♂	?
Coris julis	BACCI e.a. 1957, 1958	reddish-brown	455	50–150	TL	♀♀ and ♂♂ (16%)	turquoise-blue	271	110–190	SL	♂♂	+
	REINBOTH 1957		86	80–159	TL	♀♀ and ♂♂ (30%)		33	120–179	SL	♂♂	+
	ROEDE 1966		263	60–120	SL	♀♀ and ♂♂ (33%)		22	102–124	SL	♂♂	?
Thalassoma pavo	REINBOTH 1962	5 small blue vertical lines	103	94–164		♀♀ and ♂♂ (25%)	1 blue vertical bar	15	135–174		♂♂	+ ?
Halichoeres poecilopterus	OKADA 1962, 1965	reddish-brown	?	?		♀♀ and ♂♂ (14%)	blue-green	?	?		♂♂	+

Present Investigations

Of 4474 specimens the following data were noted:

Day of collecting. – This was essential to ascertain seasonal differences in gonadal activity and a possible relation with the lunar month.

Body length. – Total length (TL) was used as an indication of size, as it proved to be difficult to measure the standard length accurately, especially in the terminal phase individuals of *Thalassoma bifasciatum.*

Color. – The specimens were classified according to the color phases defined in Chapter VI.

Sex. – In Chapter IX the criteria for the classification into females, males, or sex indeterminates with small non-functional gonads are given. There also the criteria for the *stages of gonadal activity* have been formulated.

The results of the present investigations are summarized in Tables 22–26. Moreover, these data are illustrated in histograms, Fig. 12–20. Here the frequency distribution of total length is given per species, separately for the successive color phases, for females and males (gonadal stages II–VI) and the miscellaneous group (gonadal stages 0, I, II and VII). For *Thalassoma bifasciatum* and *Halichoeres bivittatus* separate histograms have been made of the material collected in Curaçao (Fig. 12, 14) and in Puerto Rico (Fig. 13, 15). For *H. maculipinna* (Fig. 17) and *H. poeyi* (Fig. 18) the small numbers of specimens found in Puerto Rico have been added to the histograms of the Curaçao specimens.

A survey of the total material is presented in Table 22, which indicates that:

– Significant differences in the total numbers of specimens per species are found, as has already been discussed in Chapter IV. In view of the method of collecting and the places of collection, the numbers are considered as reflecting the relative frequency of the species.

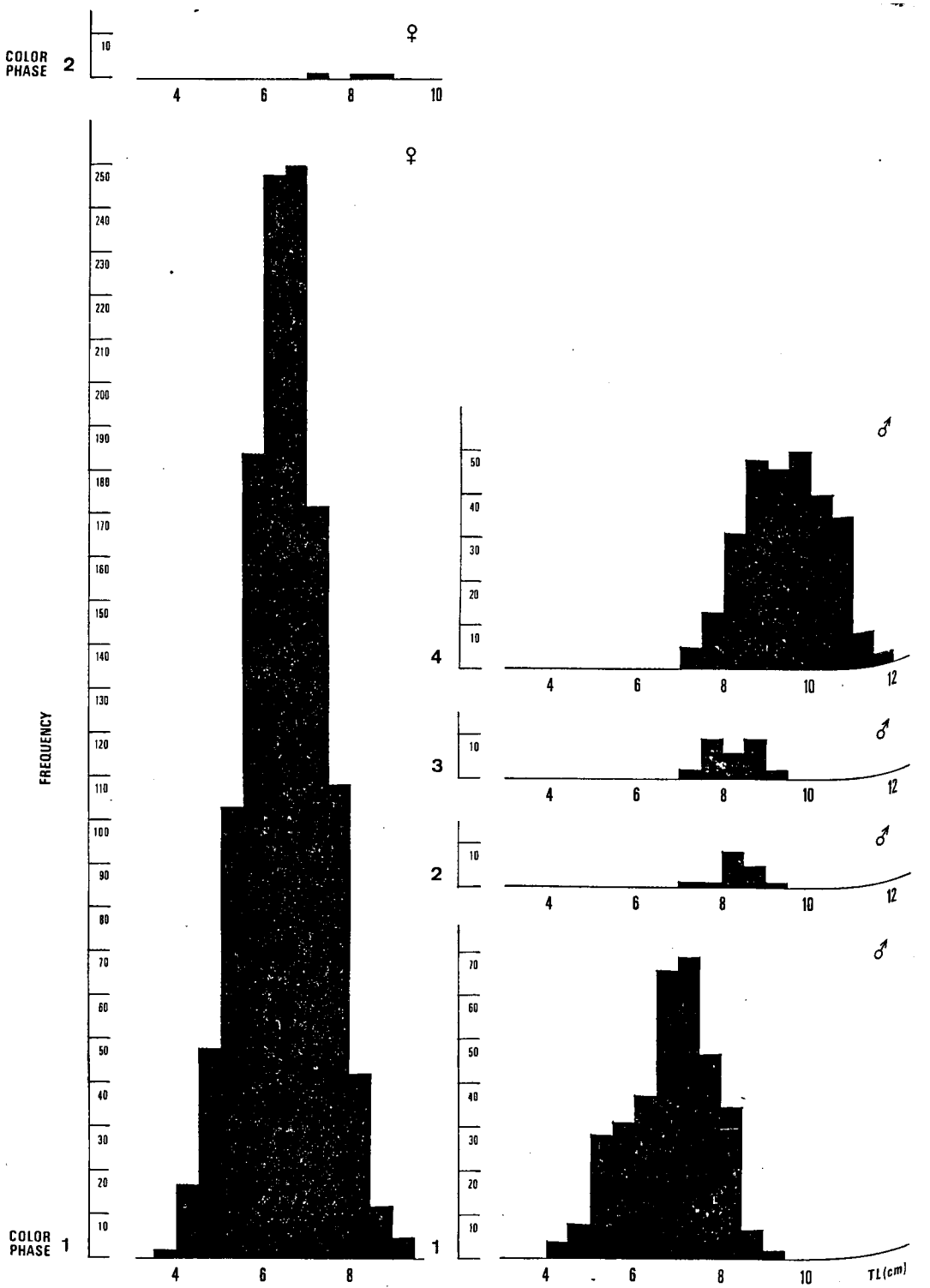


Fig. 12a. Histograms of frequency distributions, per color phase, of males and females, in *Thalassoma bifasciatum*, collected in Curaçao.

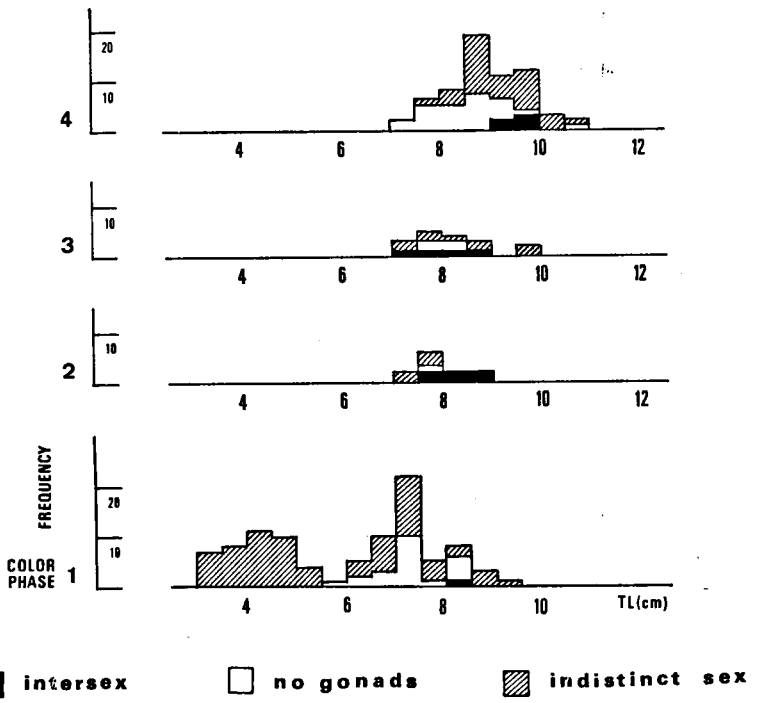


Fig. 12b. Histograms of frequency distributions, per color phase, of fish with nonfunctional gonads, in *Thalassoma bifasciatum*, collected in Curaçao.

– No equal numbers of females and males are found; neither, when the totals are compared, nor, when sex ratios per color phase are studied.
– Next to females and males, a not negligible number of fish without gonads or without clearly differentiated gonads were present in the samples.
– The numbers of specimens per color phase are not equal; the first adult phase strongly outnumbers the large terminal phase, while only few specimens in intermediate colors were found (see also Tables 3 and 4, Chapter VI).

The latter three points will be discussed in detail below.

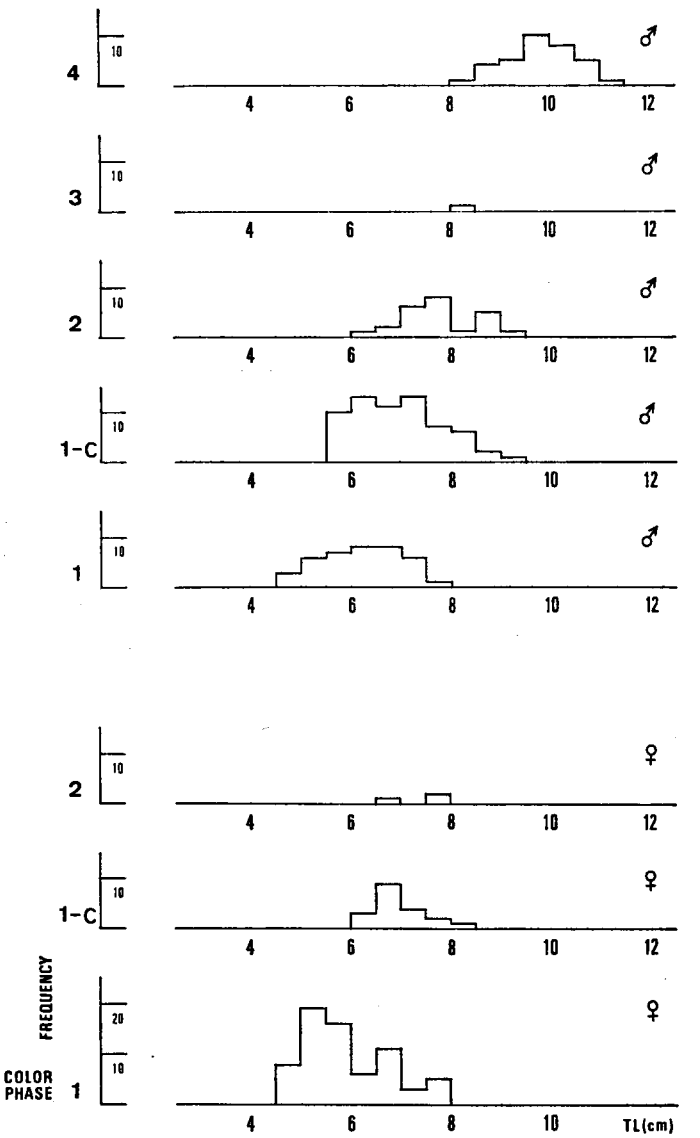


Fig. 13a. Histograms of frequency distributions, per color phase, of males and females, in *Thalassoma bifasciatum*, collected in Puerto Rico.

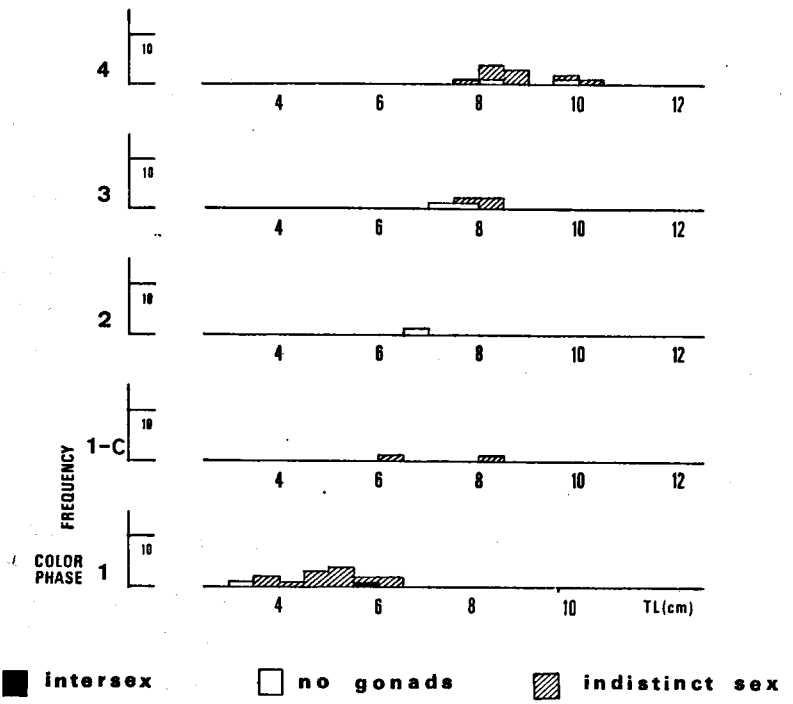


Fig. 13b. Histograms of frequency distributions, per color phase, of fish with nonfunctional gonads, in *Thalassoma bifasciatum*, collected in Puerto Rico.

Color and Size

The close relation between the size of the fish and the colors of the body is obvious. During observations in the sea it was already noted that the more gaudily colored specimens were of larger size. Accurate information on this phenomenon is given in Tables 23 and 25 where the observed ranges and mean total length per color phase are listed. The same can been seen in the histograms.

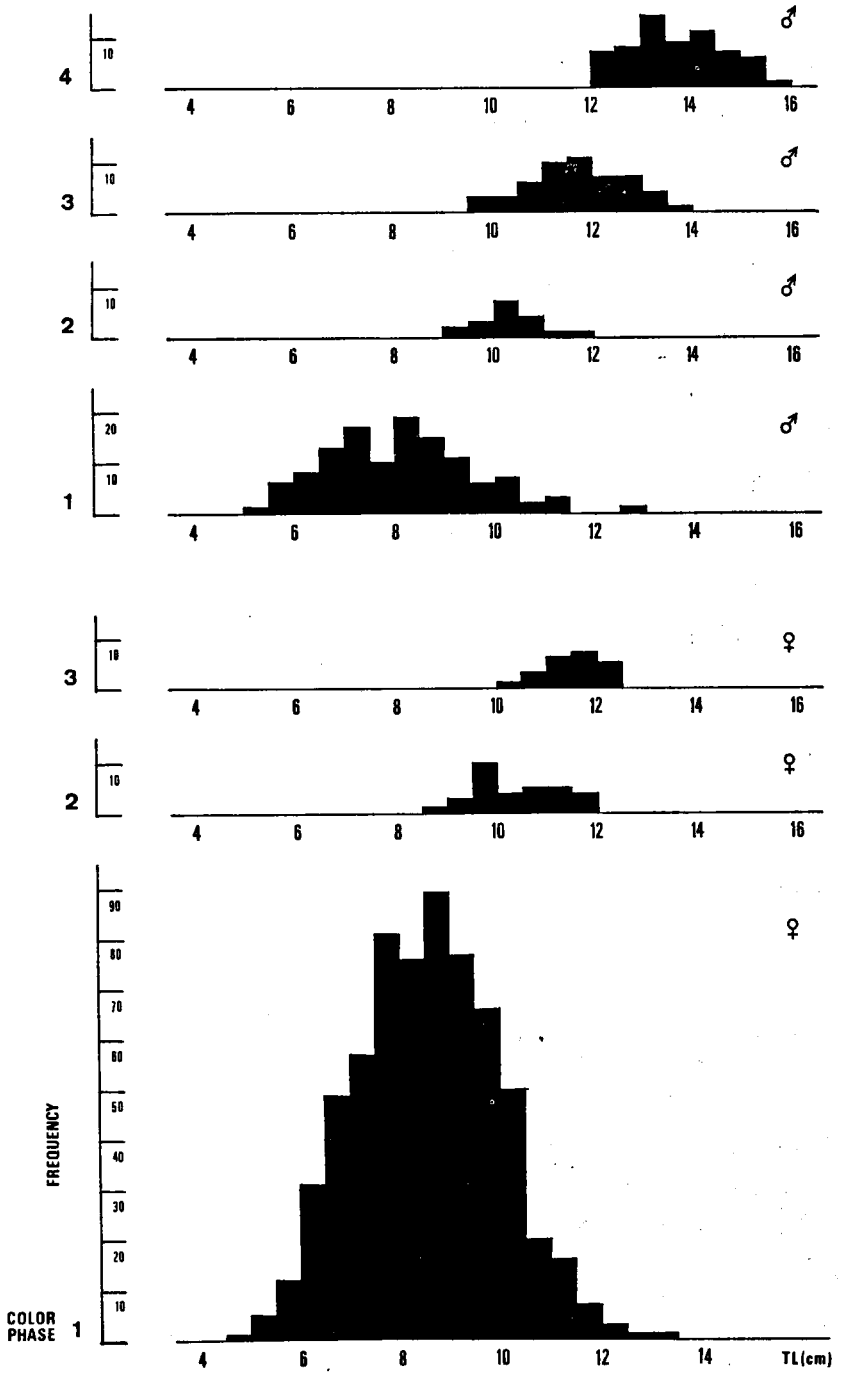


Fig. 14a. Histograms or frequency distributions, per color phase, of males and females, in *Halichoeres bivittatus*, collected in Curaçao.

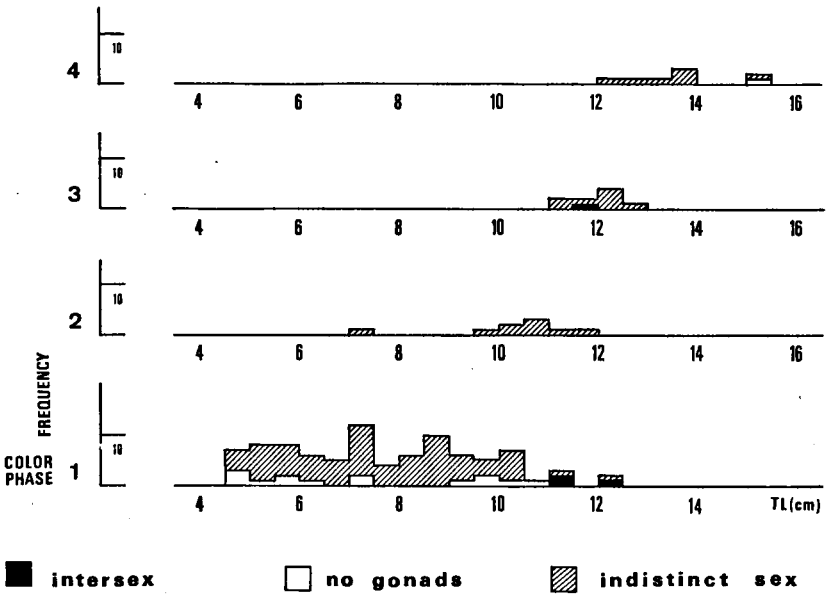


Fig. 14b. Histograms of frequency distributions, per color phase, of fish with nonfunctional gonads, in *Halichoeres bivittatus*, collected in Curaçao.

From the Tables and Fig. 12–20 the following can be inferred:
1. When a certain body length is reached, the number of individuals with first adult colors decreases abruptly and no such colors are found in specimens of only a few centimeters larger.
2. Fish in bright terminal colors only occur after a certain body length is reached. The mean TL fish in the terminal phase is significantly higher than in the first adult phase.
3. The overlap between fish with the first adult colors and those with the final colors is only a few centimeters of body length.
4. Fish with intermediate colors are found in this overlap area.

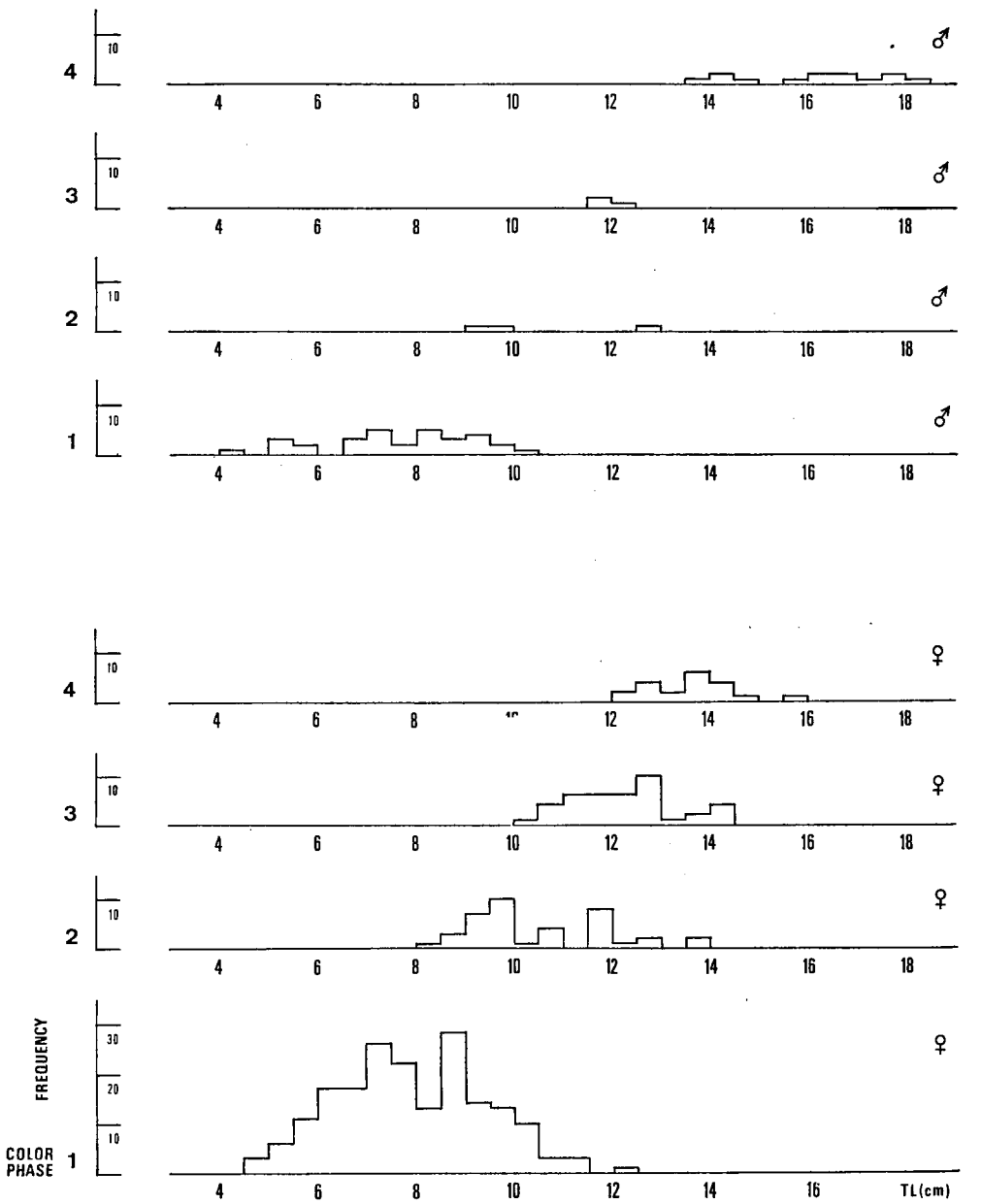


Fig. 15a. Histograms of frequency distributions, per color phase, of males and females, in *Halichoeres bivittatus*, collected in Puerto Rico.

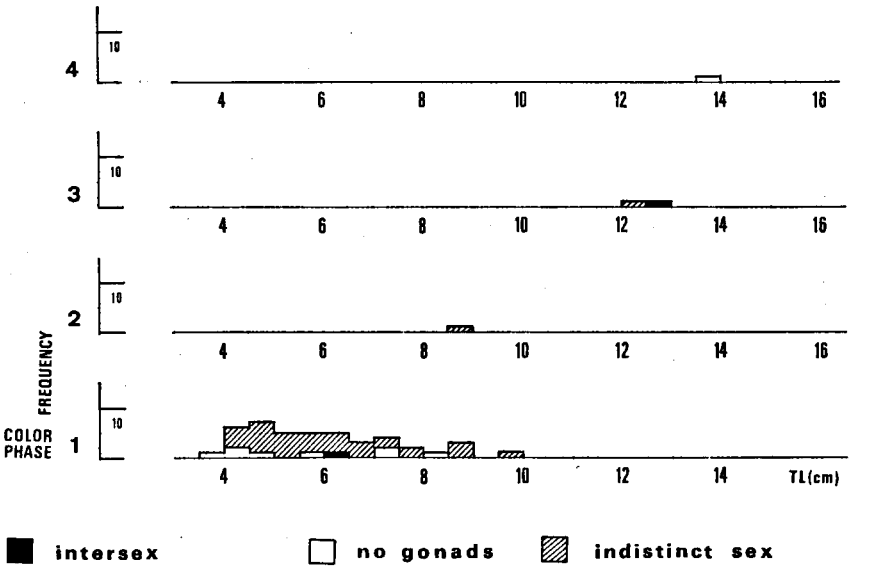


Fig. 15b. Histograms of frequency distributions, per color phase, of fish with nonfunctional gonads, in *Halichoeres bivittatus*, collected in Puerto Rico.

Color and Sex

One of the main questions of this study was to establish the distribution of males and females over the successive size and color groups.

Sex ratio per species

In Table 24 the total numbers of females and males found for every species are given. The total number of females proved to be significantly higher, twice to four times as many females as males being found, in six of the seven species. Only for *He. splendens* – of which a rather small sample was investigated – the same amount was obtained for both sexes.

As collecting was done in places where the wrasses live or which they frequent, i.e. in rocky and coral-sand areas, the samples fairly well represent the natural populations. A restriction has to be made for *H. poeyi* and *He. splendens*, because these two species may also be found in sea grass-covered habitats.

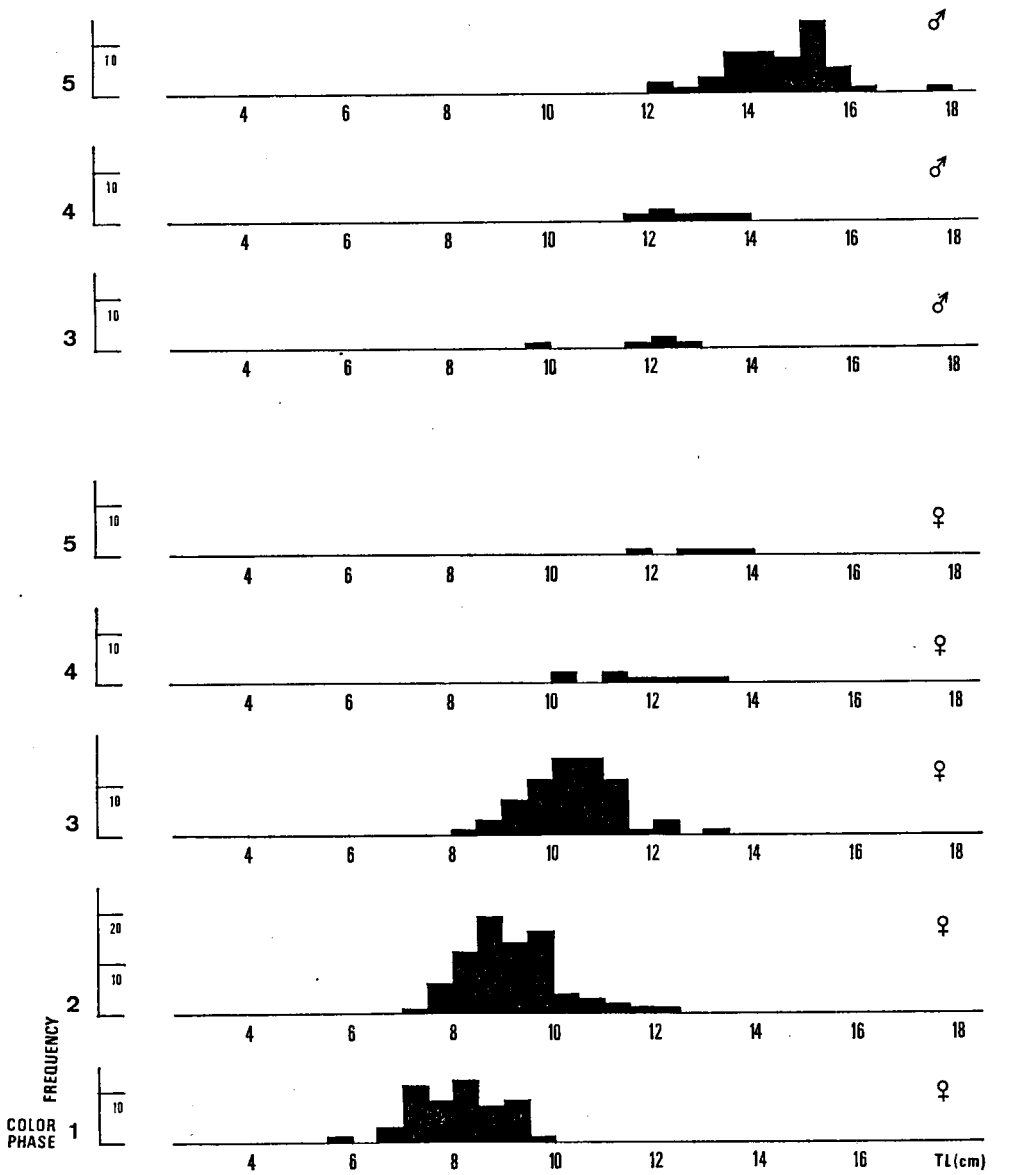


Fig. 16a. Histograms of frequency distributions, per color phase, of males and females, in *Halichoeres garnoti*, collected in Curaçao.

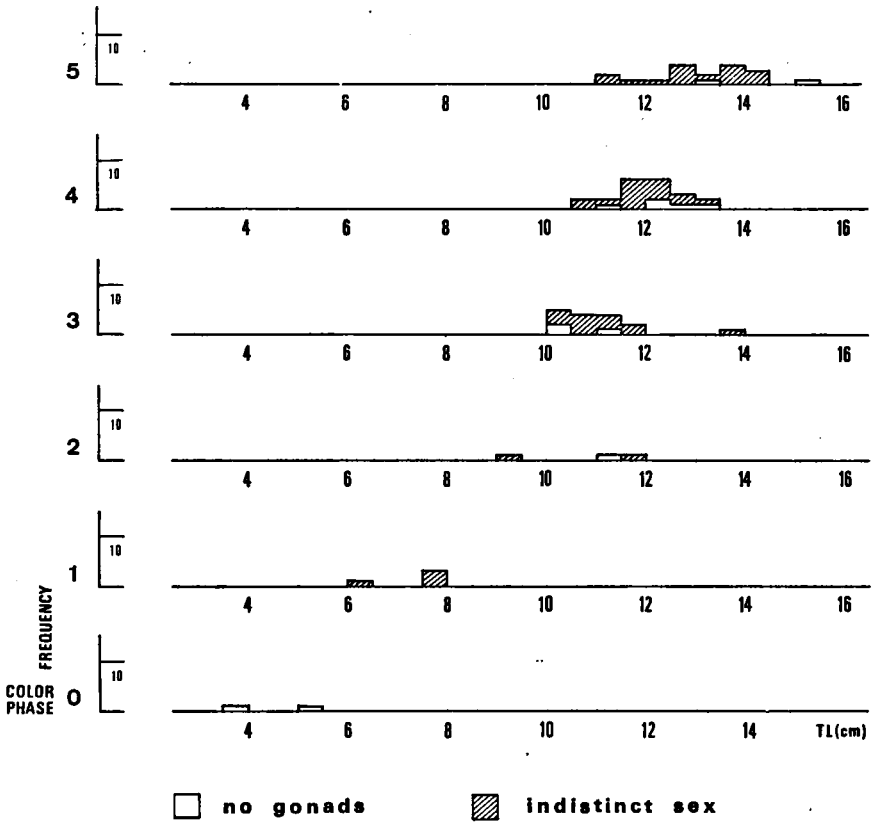


Fig. 16b. Histograms of frequency distributions, per color phase, of fish with nonfunctional gonads, in *Halichoeres garnoti*, collected in Curaçao.

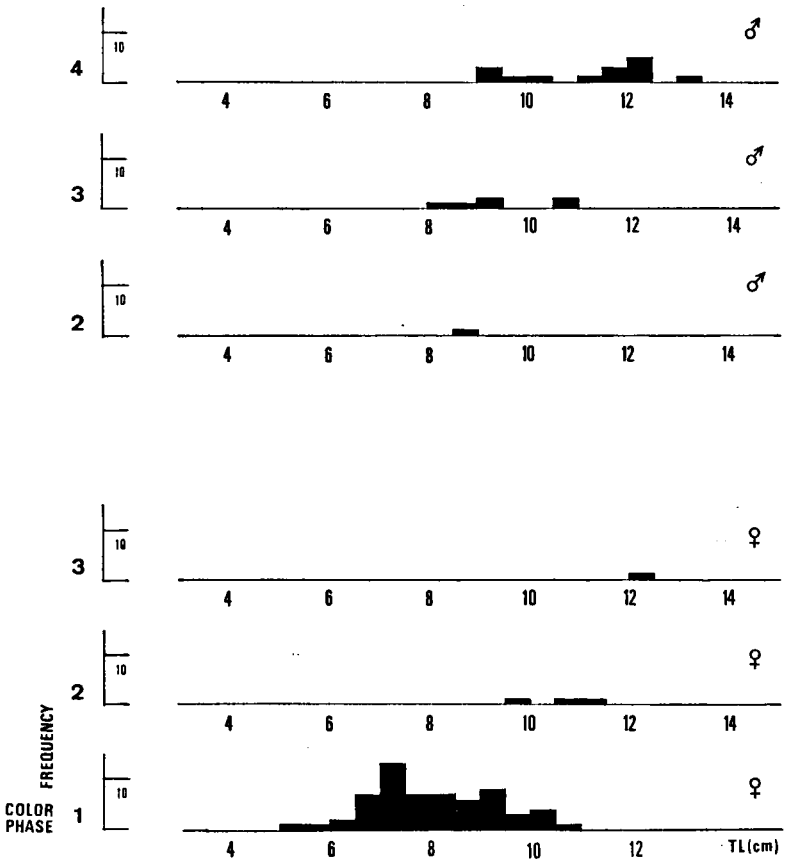


Fig. 17a. Histograms of frequency distributions, per color phase, of males and females, in *Halichoeres maculipinna*, collected in Curaçao and Puerto Rico.

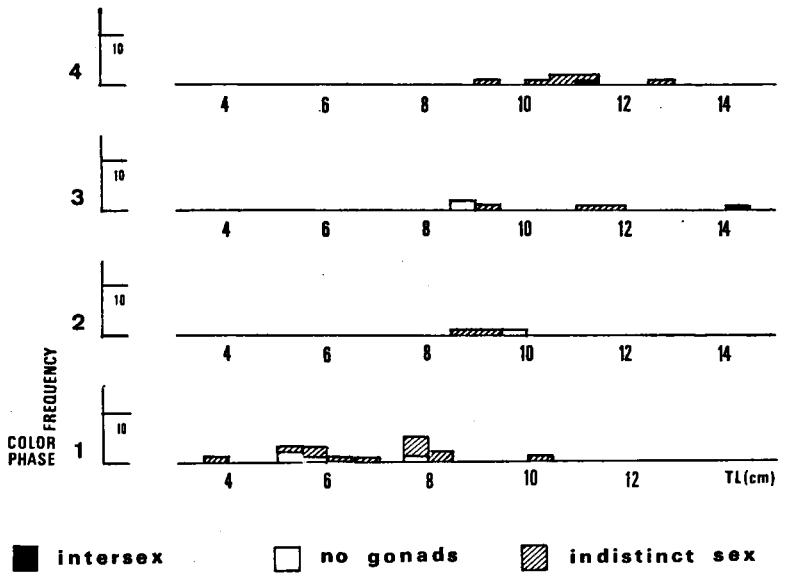


Fig. 17b. Histograms of frequency distributions, per color phase, of fish with non-functional gonads, in *Halichoeres maculipinna*, collected in Curaçao and Puerto Rico.

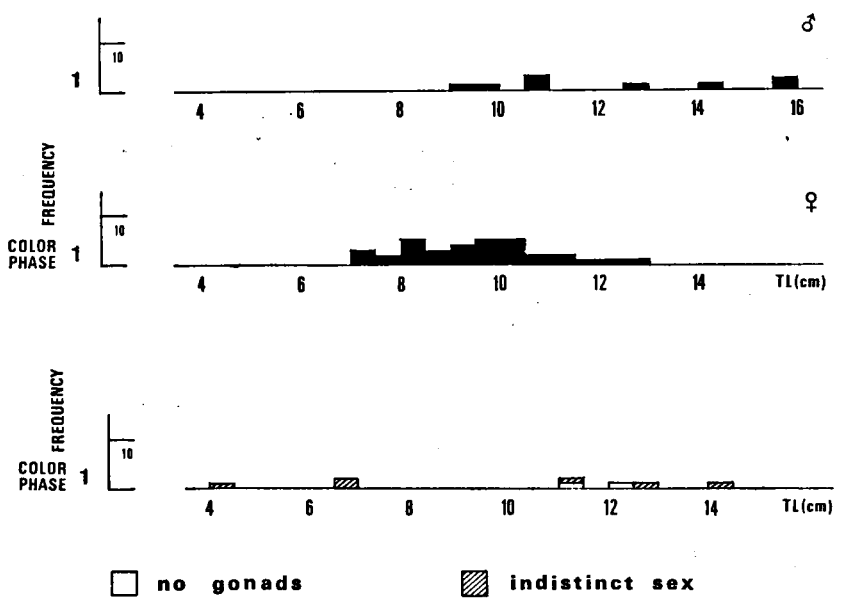


Fig. 18. Histograms of frequency distributions, per color phase, per sex group, in *Halichoeres poeyi*, collected in Curaçao and Puerto Rico.

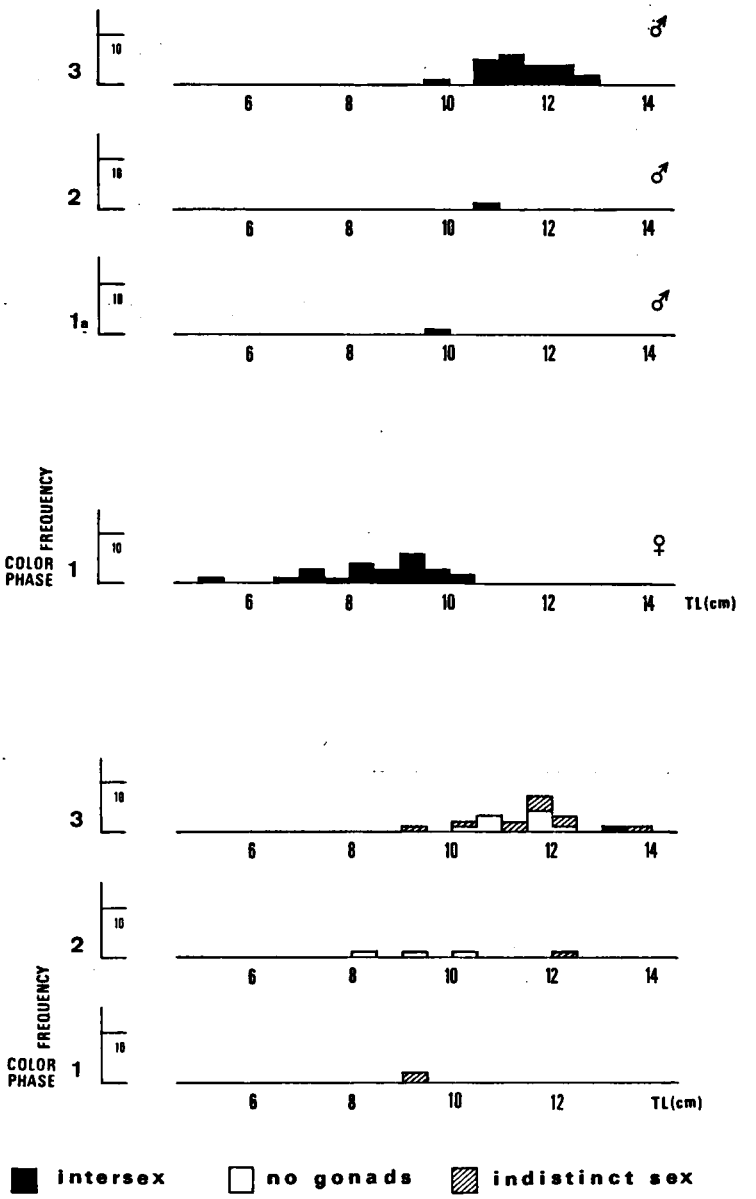


Fig. 19. Histograms of frequency distributions, per color phase, per sex group, in *Hemipteronotus splendens*, collected in Curaçao.

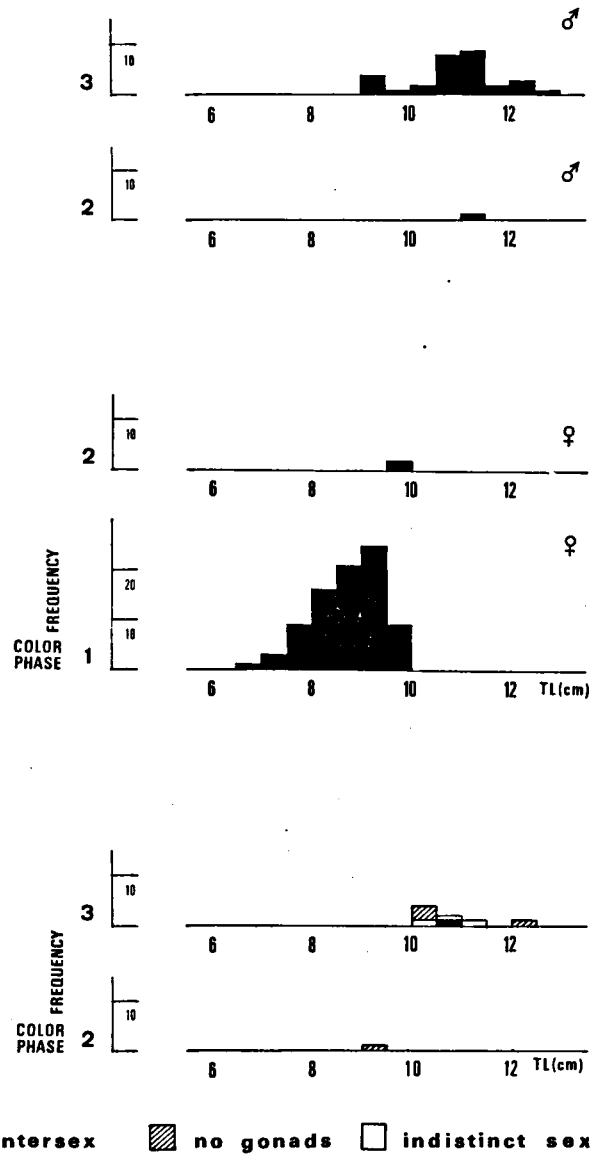


Fig. 20. Histograms of frequency distributions, per color phase, per sex group, in *Hemipteronotus martinicensis*, collected in Curaçao.

TABLE 22

NUMBERS OF SPECIMENS PER COLOR PHASE AND SEX GROUP

a = no gonads; b = indistinct sex; c = intersex

Species	Color phase	Non functional gonads a	b	c	*sub total*	Females	Males	*Grand total*
CURAÇAO								
Thalassoma bifasciatum	1	22	72	1	*95*	1191	334	*1620*
	2	1	5	6	*12*	3	16	*31*
	3	4	9	4	*17*	0	28	*45*
	4	25	33	5	*63*	0	279	*342*
	totals	*52*	*119*	*16*	*187*	*1194*	*657*	*2038*
Halichoeres bivittatus	1	14	72	3	*89*	642	119	*850*
	2	0	9	0	*9*	32	18	*59*
	3	0	8	1	*9*	22	52	*83*
	4	1	7	0	*8*	0	63	*71*
	totals	*15*	*96*	*4*	*115*	*696*	*252*	*1063*
Halichoeres garnoti	0	2	0	0	*2*	0	0	*2*
	1	0	4	0	*4*	51	0	*55*
	2	1	2	0	*3*	79	0	*82*
	3	3	13	0	*16*	68	5	*89*
	4	5	16	0	*21*	8	6	*35*
	5	2	16	0	*18*	4	50	*72*
	totals	*13*	*51*	*0*	*64*	*210*	*61*	*335*
Halichoeres maculipinna	1	2	9	0	*11*	50	0	*61*
	2	1	2	0	*3*	1	1	*5*
	3	2	3	0	*5*	0	6	*11*
	4	0	6	1	*7*	0	15	*22*
	totals	*5*	*20*	*1*	*26*	*51*	*22*	*99*
Halichoeres poeyi	1	2	6	0	*8*	33	8	*49*
Hemipteronotus splendens	1	0	2	0	*2*	25	(1)	*28*
	2	2	2	0	*4*	0	1	*5*
	3	9	10	1	*20*	0	22	*42*
	totals	*11*	*14*	*1*	*26*	*25*	*24*	*75*
Hemipteronotus martinicensis	1	0	0	0	*0*	84	0	*84*
	2	0	1	0	*1*	2	1	*4*
	3	3	4	1	*8*	0	30	*38*
	totals	*3*	*5*	*1*	*9*	*86*	*31*	*126*

Species	Color phase	Non functional gonads a	b	c	*sub total*	Females	Males	*Grand total*
PUERTO RICO								
Thalassoma bifasciatum	1	1	13	1	*15*	68	39	*122*
	1-c	0	2	0	*2*	19	63	*84*
	2	1	0	0	*1*	3	24	*28*
	3	2	3	0	*5*	0	*1*	*6*
	4	2	9	0	*11*	0	34	*45*
	totals	*6*	*27*	*1*	*34*	*90*	*161*	*285*
Halichoeres bivittatus	1	8	33	1	*42*	187	31	*260*
	2	0	1	0	*1*	39	3	*43*
	3	0	1	1	*2*	40	3	*45*
	4	1	0	0	*1*	20	13	*34*
	totals	*9*	*35*	*2*	*46*	*286*	*50*	*382*
Halichoeres maculipinna	1	2	3	0	*5*	10	0	*15*
	2	0	0	0	*0*	2	0	*2*
	3	0	0	1	*1*	1	0	*2*
	4	0	0	0	*0*	0	0	*0*
	totals	*2*	*3*	*1*	*6*	*13*	*0*	*19*
Halichoeres poeyi	1	0	0	0	*0*	2	1	*3*

In *Th. bifasciatum* the total number of females (1284) is considerably higher than that of the total of males (818). In Puerto Rico, however, only 90 females against 161 males were collected. No doubt the numbers found in Curaçao (657/1194) give a more accurate expression of the male/female ratio of the total population; the Curaçao numbers have been obtained on numerous collecting trips during 15 months, while in Puerto Rico only 12 collecting trips in two months were made. Twice, the specimens collected near La Parguera, P.R., proved to be almost exclusively very mature males. Most probably those samples were drawn from a temporary concentration of males, due to sexual activity (cf. Chapter VIII).

In ancient times sex of labrids already caused confusion. Wrasses were in disrepute then because of their habit of gliding behind the back of other fish which was interpreted as weakness or even cowardice, but which most probably was part of cleaning behavior. For the "girelles" OVID (Halieuticon, v 108) and PLINY (xxxii, 146) mention fraud at the act of pairing and a propagation "ex se" (by itself). In agreement with recent data is PLINY's remark (lib. IX, cap. xvl; lib. XXXII, cap. ult) that there are more females than males and sometimes even no males at all, as all captured fish were full of eggs ("omnis enim ovis gravidae capiuntur").

Sex ratio

As to the origin of the phenomenon of diversity in sex ratio among the adult labrid individuals we can only speculate. The theory outlined by FISHER (1930) about the selective advantages of an 1:1 sex ratio within a population was put on analytic base by BODMER & EDWARDS (1960). KALMUS & SMITH (1960) further discussed the selective forces towards equal numbers of males and females for selection among populations. Though EDWARDS (1960) remarked: "In polygamous species, in which a single male ... fertilizes a large number of females, there is no longer any reason for it to be advantageous if the chance of encounter of a male and a female is at a maximum ...," he concluded "nevertheless, the sex ratio in such species to be about one half."

Yet, next to the present results in labrid fishes, sex ratios deviate from unity also in a variety of other teleosts (FULTON, 1891). Thus, in fish for a maximum of genetic contribution to the future generation no equal portion of males and females is required, in deviation of FISHER's law.

SCUDO (1967, 1969) analyzed the adaptive values of sex ratio, exemplified by a number of mathematical models. He argues that only when a certain degree of anisogamy has been reached (i.e. sexually differentiated gametes) the special 1:1 ratio becomes selectively advantageous. In case of isogamy to selective force arises towards equal numbers of both sexes. SCUDO's thesis may be more apt for discussing the labrid situation. (In fish, morphologically different sex chromosomes do not occur). In those species in which males already occur at small size, the longevity of the male – enabling him to spawn more often than the females, restricted to the first adult phase – may compensate for the lower number of actual males present in the population.

SCUDO exemplified with a number of models that the change from bi- to unisexuality alone causes a drastic "loss in performance." To result in a higher overall adaptation, it must be accompanied by a marked increase in the efficiency of some other, common environmental resources between the adults of the two sexes. In the labrids, the change from pair to mass spawning may be such a factor. It should be interesting to try to obtain more information to check whether in the less abundant labrid species, in which propagation seems to be still of a strict protogynous type, indeed only pair spawning occurs. The present author, alas, could not get a decisive answer to this question.

TABLE 23

OBSERVED RANGE AND MEAN TOTAL LENGTH (TL) PER COLOR PHASE, complimented by percentages of the three main sex groups for Curaçao specimens

Species	Color phase	observed range of total length (cm)	mean TL (cm)	% ♀♀	% ♂♂	% ??	N
Thalassoma bifasciatum	1	3.5– 9.5	6.5	73	21	6	1620
	2	7.0– 9.5	7.9	10	51	39	31
	3	7.0–10.0	8.2	0	62	38	45
	4	7.0–12.0	9.3	0	82	19	342
Halichoeres bivittatus	1	4.5–13.5	8.3	76	14	10	850
	2	7.0–12.0	10.3	54	31	15	59
	3	9.5–14.0	11.7	26	63	11	83
	4	12.0–16.0	13.7	0	89	11	71
Halichoeres garnoti	1	5.5–10.0	7.9	93	0	7	55
	2	7.0–12.5	8.9	96	0	4	82
	3	8.0–14.0	10.6	76	6	18	89
	4	10.0–14.0	11.0	23	17	60	35
	5	11.0–18.0	14.1	6	69	25	72
Halichoeres maculipinna	1	3.5–11.0	7.8	82	0	18	61
	2	8.5–11.5	9.1	20	20	60	5
	3	8.5–12.5	9.7	0	55	45	11
	4	9.0–13.5	11.1	0	68	32	22
Halichoeres poeyi	1	4.0–16.0	10.0	33	16	16	49
Hemipteronotus splendens	1	5.0–10.5	8.6	89	4	7	28
	2	8.0–12.5	10.2	0	20	80	5
	3	9.0–14.0	11.4	0	52	48	42
Hemipteronotus martinicensis	1	6.5–10.0	8.7	100	0	0	84
	2	9.0–11.5	10.0	50	25	25	4
	3	9.0–13.0	11.1	0	79	21	38

TABLE 24

TOTAL NUMBERS OF FEMALES AND MALES FOUND

C = Curaçao; PR = Puerto Rico

Species	Females (C + PR)	Males (C + PR)	♂/♀
Thal. bifasciatum	1284 (1194 + 90)	818 (657 + 161)	0.64
Hal. bivittatus	982 (696 + 286)	302 (252 + 50)	0.31
Hal. maculipinna	64 (51 + 13)	24 (24 + —)	0.38
Hal. poeyi	35 (33 + 2)	9 (8 + 1)	0.26
Hal. garnoti	210	61	0.29
Hem. martinicensis	86	31	0.36
Hem. splendens	25	24	0.96

TABLE 25a

MEAN TOTAL LENGTH PER SPECIES, COLOR PHASE AND SEX

Species	Color phase	sex	Curaçao N	mean TL (mm)	s	Color phase	sex	Puerto Rico N	mean TL (mm)	s
Thalassoma bifasciatum	1	??	95	59.4	—	1	??	17	51.3	—
	1	♀♀	1191	64.5	9.32	1	♀♀	87	60.7	9.15
	1	♂♂	334	68.1	9.98	1	♂♂	102	66.0	9.14
	2	♀♀	3	76.0	—	2	♀♀	3	73.3	—
	2 + 3	??	29	79.6	—	2 + 3	??	6	75.7	—
	2 + 3	♂♂	44	81.6	7.67	2 + 3	♂♂	25	77.7	7.45
	4	??	63	88.7	—	4	??	11	86.5	—
	4	♂♂	279	94.1	9.61	4	♂♂	34	97.9	6.79
Halichoeres bivittatus	1	??	89	76.1	—	1	??	42	61.1	—
	1	♂♂	119	81.1	14.58	1	♂♂	31	75.5	15.72
	1	♀♀	642	84.6	14.13	1	♀♀	187	77.2	16.11
	2 + 3	♀♀	54	108.2	9.42	2 + 3	♀♀	79	113.1	14.72
	2 + 3	??	18	110.9	—	2 + 3	??	3	110.3	—
	2 + 3	♂♂	70	112.7	10.79	2 + 3	♂♂	6	110.3	—
						4	♀♀	20	135.8	8.43
	4	♂♂	63	136.5	8.90	4	♂♂	13	161.5	—
	4	??	8	137.2	—	4	??	1	135.0	—
Halichoeres garnoti	1 + 2	♀♀	130	86.9	10.30					
	1 + 2	??	7	88.1	—					
	3 + 4	♀♀	76	105.1	10.31					
	3 + 4	??	36	115.4	—					
	3 + 4	♂♂	11	121.4	9.54					
	5	♀♀	4	127.4	—					
	5	??	18	132.4	—					
	5	♂♂	50	145.0	11.28					

TABLE 25b

MEAN TOTAL LENGTH PER SPECIES, COLOR PHASE AND SEX

Species	Curaçao: Color phase	sex	N	mean TL (mm)	s	Puerto Rico: Color phase	sex	N	mean TL (mm)	s
Halichoeres maculipinna	1	??	11	71.0	—	1	??	5	57.6	—
	1	♀♀	50	78.7	12.12	1	♀♀	10	89.9	9.17
	2 + 3	♂♂	7	94.6	—					
	2 + 3	??	8	95.5	—	3	??	1	143.0	—
	2	♀♀	1	98.0	—	2 + 3	♀♀	3	113.0	—
	4	??	7	108.9	—					
	4	♂♂	15	112.3	12.96					
Halichoeres poeyi	1	♀♀	33	95.5	13.48	1	♀♀	2	83.5	—
	1	??	8	99.0	—					
	1	♂♂	8	118.7	21.96	1	♂♂	1	158.0	—
Hemipteronotus splendens	1	♀♀	25	85.2	11.60					
	1	??	2	93.0	—					
	1	♂♂	1	99.9	—					
	2	??	4	101.0	—					
	2	♂♂	1	108.9	—					
	3	??	20	112.2	—					
	3	♂♂	22	115.9	8.46					
Hemipteronotus martinicensis	1	♀♀	84	86.8	6.86					
	2	??	1	93.3	—					
	2	♀♀	2	98.1	—					
	2	♂♂	1	112.0	—					
	3	??	8	107.4	—					
	3	♂♂	30	109.1	9.41					

Sex and color phase

In Table 23 the percentages of the three main sex groups (♀♀, ♂♂ and ??) are given per color phase, while in Table 25 the exact number of specimens found is listed, together with the mean total length.

In six of the seven species different color phases could be distinguished. Only in *Halichoeres poeyi* did all specimens show colors of a

same pattern, so that this species must be left out of the following discussion.

For the other six species the numbers in Tables 23 and 25 obviously demonstrate not only a decrease in the total number in each successive color phase, but also a change in the sex ratio. While in the first adult phases the females are in the majority, in the gaudily colored terminal phases mainly or exclusively males have been found. Per species, however, this phenomenon is different. No simple, general rule can be formulated concerning the relation between color and sex, as will be discussed now.

Females

The histograms, Fig. 12–20, and Tables 22, 23 and 25 clearly show that there is a distinct relation between the occurrence of female sex and first adult phase colors. This relation is very obvious in *Thalassoma bifasciatum*, *Halichoeres maculipinna* and the two *Hemipteronotus* species.

In *Th. bifasciatum* 1278 of the total of 1284 females collected on Curaçao and Puerto Rico had the mainly yellow phase 1 colors. Only six females – three on Curaçao, three on Puerto Rico – were found with yellow intermediate colors, described as phase 2. No females were found in the bluehead phases 3 and 4.

In *H. maculipinna* a similar tendency is found. Of the grand total of 64 females, a number of 60 were displaying the predominantly whitish body with one dark longitudinal band described as first adult phase. In Curaçao only one female in the slightly deviating first intermediate phase, phase 2 colors was found; in Puerto Rico of the 13 females collected two were in phase 2 while one female had the more greenish appearance with the first signs of a dark area at the sides of the second intermediate phase. Among the terminal phase 4, however, no females have been found.

In *He. splendens* all 25 females showed the brownish-green colors of the first adult phase. Neither among the five specimens in the

intermediate phase colors, nor among the 42 specimens with the green body pattern of the terminal phase, were females found.

In *He. martinicensis* of the total of 86 females found, 84 displayed the greenish-blue colors with the strikingly bright orange-white belly of the first adult phase. Only two females were classified as having intermediate colors, mainly because of the pale belly (due to less brightly orange gonads, cf. Chapter VI). No females were found in the blue-gray terminal phase.

So, in the four species discussed above, only few females were found in the intermediate phases and no females among the large, terminal phases.

In *H. poeyi* no marked change of colors occurs. Yet, here also the female specimens were found among the individuals with smaller body length.

In *H. bivittatus* and *H. garnoti* the majority of females was also found among the first adult phase 1 specimens. But in contrast to the other species, a not negligible number of females was found to show the intermediate colors, females even being found among the terminal colored, large specimens.

In *H. bivittatus* 829 females proved to have the typical phase 1 colors described for this species, with two longitudinal stripes over a mainly whitish body; 71 females were found with phase 2 colors which slightly deviate from phase 1 and 62 females with the more different, already rather pastel colored appearance of the second intermediate phase. On Curaçao none of the 696 females displayed terminal phase colors. But on Puerto Rico among the 289 females, 20 were obviously of large size and in the terminal phase, this being 59% of all the terminal phase specimens of this species collected in that area.

In *H. garnoti* most females were found among the smaller specimens with the rather drab yellowish olive sides and maroon violet on head and back, characteristic for phases 1 and 2, 51 and 79 specimens respectively. A number of 68 females were larger and showed a vague vertical band at the sides, described as phase 3. A number of eight females had features of the last intermediate phase, with already bright yellow on the head; four females had the most

gaudy terminal phase 5 appearance, though they formed only a small minority of the total of 72 specimens found in this phase.

Males

The relation between male sex and color is in general the reverse of that found for the females. In five species the occurrence of males is strongly correlated with larger sizes and the attainment of terminal colors. Two species, however, strongly differ in this respect.

No males were found among the smaller specimens in first adult colors in *H. garnoti*, *H. maculipinna* and *He. martinicensis*, while in *He. splendens* only one male was found in this phase. In *H. poeyi* (no phases in color) also not a single male was found among the smaller specimens.

While in *H. garnoti* no males were found in phase 1 nor in phase 2, only five males with the intermediate phase 3 and six with the intermediate phase 4 colors were found. However, 50 males were found among the large brightly colored terminal phase individuals.

In *H. maculipinna* the majority of the males (15 out of 20) were also large and in the bright terminal colors with a large inky spot on the sides. Six males were found with still the intermediate colors of phase 3. Only one male was classified into the first intermediate phase, phase 2, as there was not yet any sign of a side spot even though the body was already greenish and the body length greater than some of the phase 3 specimens.

In *He. splendens* a quite similar situation was found. Of the total of 24 males found, 22 displayed the terminal green body colors with an inky side spot. Next to one male in intermediate colors (ZMA 104.088), one male was found with first adult phase 1 features (ZMA 104.077). This male (histological examination of the gonads confirmed their sex; the testes were small and not active, though) was of significantly larger body size than most females found in this phase group. It is remarkable that this one male specimen deviates from the characteristic phase 1 colors by having two small, inky spots at

uncommon places: at the base of the dorsal and anal fin (described as phase 1a; Chapter VI, Fig. 7).

In *He. martinicensis* of the 31 males found, 30 displayed the pale blue-gray terminal phase colors. Only one male (ZMA 104.101) still had a light gray wedge behind the eye – a remnant of the deep blue wedge of phase 1 – and was consequently classified into the intermediate phase.

In *Th. bifasciatum* and *H. bivittatus* a considerable number of males has been found among the smaller specimens in the first adult phase also, this in contrast to the five species discussed above.

For *Th. bifasciatum* 657 males were found in Curaçao and in Puerto Rico 161. Of this grand total of 818 males, 313 displayed the bluehead terminal phase colors and 29 the advanced colors of the second intermediate phase. Among the total of 59 specimens with the yellowish first intermediate phase colors a majority of 40 males was found. And among the 1826 specimens in the yellow phase 1 a notable number of 436 males was found, which is more than 50% of all males collected of this species. In Curaçao, these yellow males formed 21% and in Puerto Rico – where, as said, collecting was done amidst temporary concentration of this sex – even 50% of this small, first adult phase.

For *H. bivittatus* in Curaçao 252 and in Puerto Rico 50 males have been found. Of these 302 males, 76 were large and in terminal colors. Of the total of 128 specimens in intermediate phase 3, 55 males were found, while of the total of 102 specimens in intermediate phase 2 colors, 21 were males. Remarkable is the number of 150 males found among the total of 1110 specimens with the two pronounced longitudinal bands of phase 1; this is 14% in Curaçao and 12% in Puerto Rico of this phase.

Miscellaneous

In Curaçao macroscopical sex differentiation was not possible in about 12% of the specimens (433 out of the 3785). A similar percentage was found in the Puerto Rican material (86 out of 689, i.e. 13%) (Table 22).

The individuals in which sex differentiation on gross inspection is impossible can be divided into two essentially different groups:
- with gonads in a very early stage of development (stage 0, I);
- with gonads in reduction (stage VII).

These phenomena – of paramount importance for our study of sex reversal in labrids – will be analyzed further in Chapter XII.

Conclusions

The results concerning the relation between sex, color, and size are summarized in Table 26. – So far, the observations referred to under *4* and *5* have not been reported elsewhere in the literature.

1. In *H. maculipinna*, *He. splendens* and *He. martinicensis* color and size run parallel with sex. Females occur in the smaller first adult phases, males in the larger intermediate phases and especially in the large terminal phases. These facts do not disagree with the common opinion that sexual dimorphism in labrids is characterized by dichromatism.

2. In *H. poeyi* – in which no striking changes of color occur during growth – females are also on the average smaller than males.

3. In *Th. bifasciatum* – as in the previous species – females are restricted to the small first adult phase. Males, however, occur in all size and color groups: Here a relation between male sex and size-and-color is absent.

4. In *H. garnoti* the occurrence of males is limited to the larger phases. Females, however, are found in various size and color groups. Though most females occur at small sizes, a minority is found among the larger intermediates and even among the large terminal colored specimens: Here a relation between female sex and size-and-color is not obvious.

5. *H. bivittatus* occupies a special position, since many males already occur among the smaller phase 1, and a few females have still been observed in the larger intermediate phase 3. In the Puerto

TABLE 26

SCHEMATICAL SURVEY OF THE RELATIONS BETWEEN COLOR, SIZE, AND SEX IN CARIBBEAN *Thalassoma*, *Halichoeres* AND *Hemipteronotus* SPECIES

Large body length & Terminal colors	No ♀♀ in: *bifasciatum* *bivittatus* (Cur.) *maculipinna* *poeyi* *splendens* *martinicensis* a low % of ♀♀ in: *bivittatus* (P.R.) *garnoti*	a minority has non-functional gonads	A MAJORITY OF ♂♂ in all species
Fairly large body length & Intermediate colors	No or very few ♀♀ in: *bifasciatum* *maculipinna* *poeyi* *splendens* *martinicensis* a not negligible % of ♀♀ in: *bivittatus* *garnoti*	A CONSIDERABLE PART HAS NON-FUNCTIONAL GONADS (ovaries in reduction) (intersexes) (young testes)	a considerable part of ♂♂
Small body length & First adult colors	A GREAT MAJORITY OF ♀♀ in all species	a low % of non-functional gonads	a not negligible % of ♂♂ in: *bifasciatum* *bivittatus* (hardly) no ♂♂ in: *garnoti* *maculipinna* *poeyi* *splendens* *martinicensis*

Rican material, females are even found among the large terminal color phase. In this species there is no clear relation between sex and size-and-color for both males and females.

It may be worth mentioning that in *H. bivittatus* and *H. garnoti* – with various color-and-size types of females – color changes are more gradual, in contrast to dichromatic species in which only two types of extremely different males occur.

Absence of a clear relation between sex and color-and-size as observed in *H. bivittatus* was briefly mentioned by FEDDERN (1963) in regard to *Bodianus rufus*, but details on the size of his sample and methods of sexing were not given. The situation in *Th. bifasciatum* is similar to two-types-of-males occurence as reported for *Th. pavo, Labrus bimaculatus, Crenilabrus occellatus, Stethojulis strigiventer, Coris julis* and *Halichoeres poecilipterus*.

In Labridae sex proves to be a rather unpredictable phenomenon. In the literature first adult phases are called "females" or "females and immatures." The present author rejects such notations as incorrect. Immatures only prevail at the smallest sizes of the first adult phase, while the number of functional males (in various species) contradicts a "female" notation.

It may be erroneous as well to use the generalisation "male phase" to indicate the terminal phase, since in a few species females occur. Moreover, the testes of large, terminal phase males are often less active compared to those in first adult phase males (cf. Chapter XII).

Attempts to formulate rules on the relation between color and sex in labrids often have been erroneous on account of too small a number of individuals examined. Only investigations of sufficiently large, unselected samples can give correct information on the true sex ratios per color phase.

XI. GONADAL ACTIVITY

Gonadal activity in relation to color and size

It was thought essential to use the activity stages of the gonads as a parameter in our correlative study on color, size, and sex.

Gonadal activity per color phase

Of all 4476 wrasses the gonadal activity was registered according to the classification into eight different stages of maturity, as defined in Chapter IX. The percentage has been calculated of the fishes that on dissection proved to contain nearly mature, mature, or just spent gonads. Labrids with gonads in these three stages, stage IV, V, and VI respectively – will be referred to as fish with "active gonads." The percentages of fish with active gonads are listed in Table 27.

Females – Table 27 shows that in *Halichoeres maculipinna*, *H. poeyi*, *Hemipteronotus splendens* and *He. martinicensis* – where female sex is strongly correlated with small body length and first adult colors – roughly $\frac{1}{4}$ to $\frac{1}{3}$ of all females proved to be in the most active sexual period.

In *Thalassoma bifasciatum* – in which species females also only occur in the first adult phase – of the 1191 females even almost half were classified as being in stage IV, V, or VI.

As discussed in the previous chapter, *H. bivittatus* and *H. garnoti*

stand out, because in these two species females have also been found at larger sizes, when intermediate colors or even the final terminal colors are developed.

Table 27 shows that in *bivittatus* roughly 30–50% of the females with intermediate colors proved to have very active gonads. On Curaçao no large females have been found, but of the 20 large terminal phase females collected on Puerto Rico 35% appeared to be sexually active. Histological investigations of these large mature females showed the normal picture of such ovaries. Thus, in *H. bivittatus* females may continue to grow and pass through the processes of color change without reduction in function of the ovaries.

In *H. garnoti* of the 130 females found in color phase 1 and 2 only 19% had active gonads. So in this species, exceptionally, there are not yet many functional fishes among the smaller specimens, though these were already present in the aggregations among which collection took place. The females in the intermediate phases 3 and 4 and also the four large females in the terminal colors were for a considerable part mature. As in *bivittatus*, the ovaries of these larger females histologically showed a normal and certainly not degenerating picture.

For instance, a female Slippery Dick of 12.2 cm TL – in the advanced second intermediate color phase, almost of the final terminal pattern – contained large ovaries that filled all the space available in the abdominal cavity. The external appearance of the gonads was that of the nearly mature stage IV. Cross section revealed about 15% early oocytes and about 40% maturing eggs full of yolk; about 20% was filled by nearly ripe eggs on the point of ovulating, while 15% showed the wrinkled appearance, characteristic of already ovulated eggs. Between the maturing eggs calyces in stage γ were found, relics of earlier spawnings. A very mature ovary (stage V) was present in a *H. bivittatus* of 11.2 cm TL, in intermediate phase 3 colors (dissected and fixated immediately after being caught) (Plate III-d).

An intermediate phase 4 specimen of *H. garnoti*, 12.0 cm TL, had large maturing ovaries (stage IV), containing numerous eggs full of yolk next to smaller oocytes and calyces. A terminal phase 5 *garnoti*, 13.0 cm TL, had large, mature ovaries (stage V) (Plate III-c).

Males – As to the males, the situation is even more interesting. In *H. garnoti*, *H. maculipinna* and *He. martinicensis* – where no males were found among the small first adult phase – and in *H. poeyi* – where males also only occur at larger sizes – merely a minority of the large males possessed active gonads. The same holds good with

TABLE 27

GONADAL ACTIVITY PER COLOR PHASE AND SEX

Species	Island	FEMALES color	FEMALES specimens with active gonads (%)	FEMALES total number	MALES color	MALES specimens with active gonads (%)	MALES total number
Thalassoma bifasciatum	Cur.	1	47.1	1191	1	92.2	334
		2	33.3	3	2 + 3	26.7	44
		3 + 4	—	0	4	6.9	279
	P.R.	1	36.4	87	1	98.1	103
		2	33.3	3	2 + 3	96.0	25
		4	—	0	4	29.4	34
Halichoeres bivittatus	Cur.	1	43.1	642	1	16.4	119
		2 + 3	55.6	54	2 + 3	8.6	70
		4	—	0	4	15.9	63
	P.R.	1	29.4	187	1	53.1	31
		2 + 3	29.1	79	2 + 3	33.3	6
		4	35.0	20	4	23.1	13
Halichoeres garnoti	Cur.	1 + 2	19.1	130	1 + 2	—	0
		3 + 4	26.9	76	3 + 4	9.0	11
		5	25.0	4	5	10.0	50
Halichoeres maculipinna	Cur.	1	16.0	50	1	—	0
		2 + 3	0	1	2 + 3	0	7
		4	—	0	4	37.3	15
	P.R.	1	40.0	10	—	—	—
Halichoeres poeyi	Cur.	1	24.2	33	1	10.0	10
Hemipteronotus splendens	Cur.	1	30.8	25	1	0	1
		2	—	0	2	0	1
		3	—	0	3	13.6	22
Hemipteronotus martinicensis	Cur.	1	22.6	84	1	—	0
		2	0	2	2	100.0	1
		3	0	0	3	15.4	30

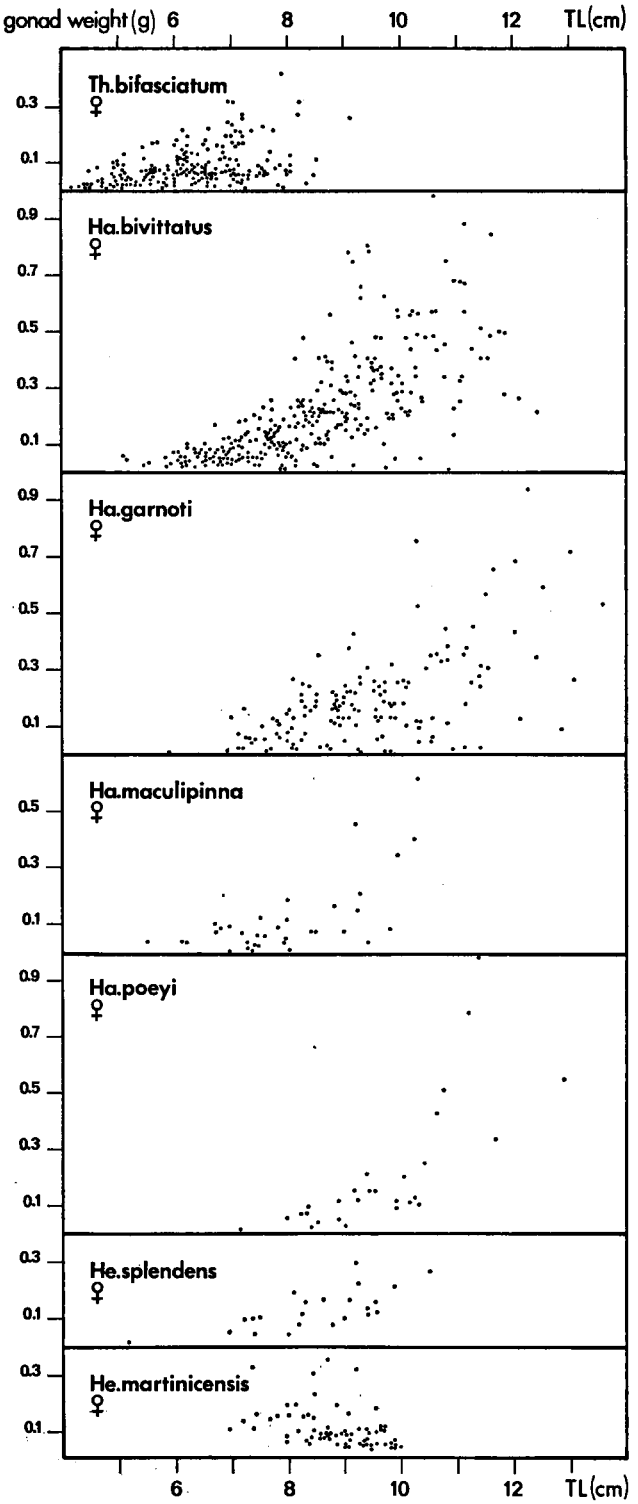


Fig. 21a. The relationship between ovary weight (g) and total length (TL) in seven Caribbean labrid species.

regard to *He. splendens*; the testes of the only first adult phase male (with the deviating phase 1a colors) were small and not active.

Of *Th. bifasciatum* and *H. bivittatus* a large number of males was collected. In *bivittatus* both in phase 1 and in terminal phase 4 a

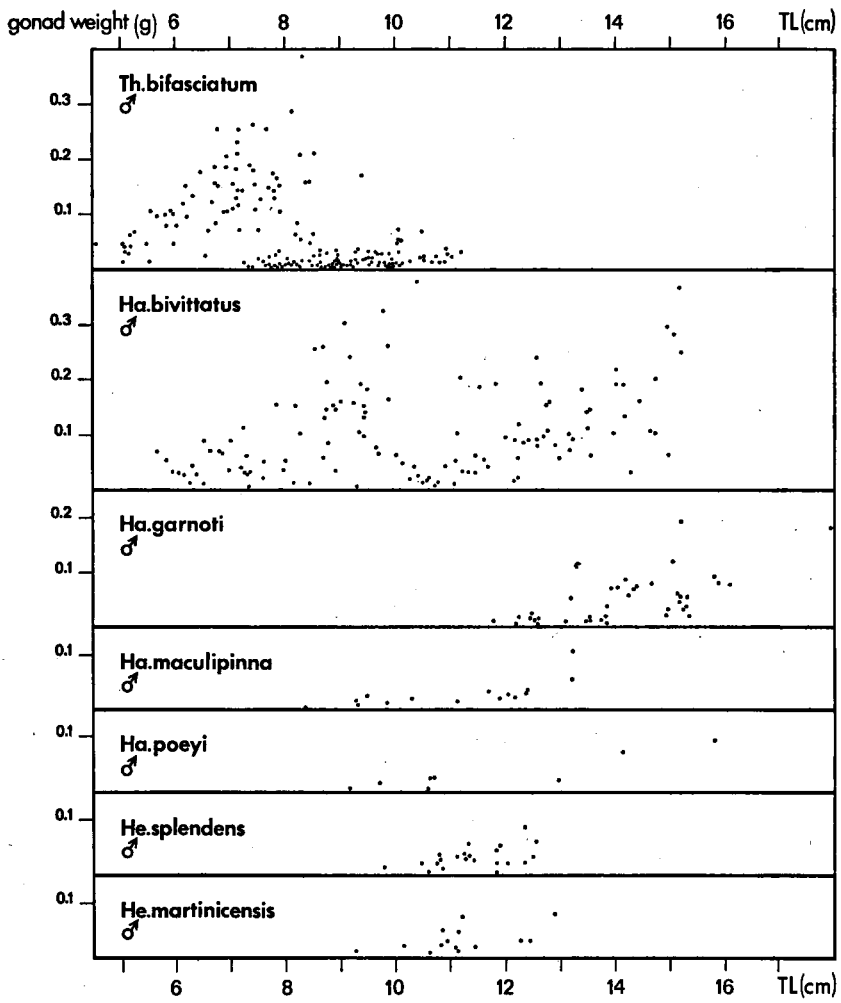


Fig. 21b. The relationship between testis weight (g) and total length (TL) in seven Caribbean labrid species.

minority of about 20 per cent had very functional testes. A considerably lower percentage was found among the intermediate color phase specimens collected in Curaçao. In Puerto Rico, however, of all males – in all phases – more than half was mature.

In *Th. bifasciatum* the great majority of the males found in the yellow first adult phase contained very mature testes. In Puerto Rico where temporary concentrations of males were met (Chapter VIII) – even among intermediate colored fish almost exclusively mature males were found.

Remarkable is the strong decline in the number of active males when larger sizes are reached. In Curaçao of 279 bluehead males only a minority of about 7 per cent possessed ripe testes; the majority had notably small gonads (see Chapter XII).

Gonad weight and total length

Since gonad weight has been used often as a reference for relating gonadal activity to body length, the results obtained in the seven Caribbean species will be presented here shortly.

In scatter diagrams (Fig. 21) the relationship between weight of the gonads and total length of the body is given of females and males in gonadal stages II to VI. Very small, not clearly differentiated or degenerating gonads are not included in these graphs.

The ovary weights in most species show an evident trend from the lower left to the upper right, indicating an association between greater ovary weight and larger sizes. However, although the largest weights indeed were only found in the larger females, the points are not clustered around a sharp straight line. (Therefore, we refrained from the calculation of correlation coefficients). Part of this variation is due to the fact that some have just spawned while others still have to spawn. Moreover, the large spread in the data also reflects the general trend that at attaining those sizes, at which in most species colors start to change, a considerable portion of the fishes proved to have relatively small gonads. These two processes may as well explain the fairly even scattering of the observations for

He. martinicensis. It is noteworthy that in *H. bivittatus* and *H. garnoti* – species in which females with normal, functional ovaries were found among the large specimens of the terminal color phase – the association between ovary weight and total length is most pronounced.

The testes weight on the average was never found to be as high as that of the ovary. A tendency towards an association between greater testis weight and larger size is shown in most species. As in the ovaries, the rather great variability found reflects the diversity in activity stage of the gonad on the moment of dissection (cf. Table 18).

Remarkable is the situation in the two species in which two types of males occur (first adult color phase and terminal color phase males). In *H. bivittatus* two positive trends can be noticed. From 6 to 9 cm TL there is an association between larger weight and length; around 10 to 11 cm body length testes are very small, then a new increase in weight develops. In *Th. bifasciatum*, on the other hand, a positive trend can only be observed in the first adult males. In large, bluehead males most testes had a very low weight. This is considered to be senescence (Chapter XII).

Summary

1. In the most abundant species, *Th. bifasciatum* and *H. bivittatus*, more than 40 per cent of the first adult phase females had active ovaries (slightly lower percentages were found in Puerto Rico). In the other five species a smaller portion of the (first adult phase) females – 16 to 31 per cent – had active gonads on the moment of dissection.

2. Ovarian activity declines at the end of the first adult phase in those species, in which females are restricted to the smaller sizes. However, in *H. bivittatus*, roughly a third and in *H. garnoti* roughly a quarter of the females of larger sizes and in intermediate or terminal phase colors, had active ovaries. In *H. garnoti* even a relatively

smaller portion of active females occurred in the first adult phase, as compared with the larger phases.

3. A relatively large number of fully developed, active testes was found whenever males occurred in the small, first adult phase. In *Th. bifasciatum* even almost all testes of yellow phase males were very functional.

4. A relatively large portion of non-functional gonads was found in medium-sized fish in intermediate colors; yet, part of the gonads of these fish were very functional; change of color does not run parallel to gonad inactivity in all wrasses.

5. Large fish with terminal colors almost invariably had relatively small testes; only a minority possesed active testes, also in those species, in which males are restricted to the larger sizes.

Point 4 and 5 will be further discussed in Chapter XII.

In literature indications concerning the activity condition of the gonads are scanty. The presence of fully developed, functional testes in small, first adult phase fish has been explained mostly as preliminary happenings of a protogyn species in which sometimes the males may mature before the alleged male coloration has been developed (*L. bimaculatus*, LÖNNBERG e.a., 1937; *Th. bifasciatum*, LONGLEY e.a., 1941); *St. strigiventer*, RANDALL, 1955). SOLJAN (1930a, b), discussing the two types of males in *Crenilabrus ocellatus*, reported that four of the small males, that acted as "Bystander der Befruchtung" had fully developed testes; all the females of similar colors proved to be full of eggs.

During the period covered a variety of side observations were made which unfortunately cannot be evaluated because they do not fit the purpose of the present study. An exception should be made for the relationship between gonadal activity and time of the year, and lunar phase.

GONADAL ACTIVITY AND TIME OF THE YEAR

Alternation of the non-breeding season with a period of definite spawning is a widespread phenomenon in fishes. Usually gonads decrease strongly in the non-breeding season. Very generally speaking it can be said that the length of the period of functional activity of the gonads increases as the fishes live closer to the equator. Even in subtropical waters many species show a brief annual hiatus between successive breeding seasons (HARRINGTON, 1959).

Labrids also show this general pattern. Wrasses of more temperate regions have seasonal spawning periods, with a decline in gonadal activity during autumn and

TABLE 28

PERCENTAGES OF FISH WITH "ACTIVE" GONADS PER MONTH
(December 1962/November 1963)

"active" = nearly mature, mature, or just spent; number of specimens collected in italics

Species	Dec.	Jan.	Feb.	March	April	May	June	July	Aug.	Sep.	Oct.	Nov.
Thalassoma bifasciatum												
all specimens	71	11	—	42	58	79	61	33	32	28	36	56
	14	*9*	—	*200*	*106*	*34*	*88*	*464*	*420*	*364*	*386*	*156*
color phase 1	83	11	—	48	70	84	71	39	39	35	48	69
specimens	*12*	*9*	—	*163*	*86*	*31*	*75*	*392*	*337*	*291*	*293*	*128*
Halichoeres bivittatus												
all specimens	40	30	19	33	54	14	76	60	64	50	35	25
	5	*20*	*25*	*298*	*56*	*14*	*55*	*113*	*155*	*241*	*280*	*119*
color phase 1	50	22	0	31	49	0	75	72	68	58	36	27
specimens	*2*	*9*	*6*	*244*	*45*	*2*	*24*	*95*	*145*	*207*	*244*	*97*
Halichoeres garnoti	100	—	—	—	100	33	—	17	44	42	24	18
	3	—	—	—	*2*	*15*	—	*36*	*48*	*105*	*90*	*33*
Halichoeres maculipinna	—	—	33	38	50	0	50	25	38	11	10	30
	—	—	*3*	*16*	*4*	*4*	*2*	*8*	*8*	*36*	*30*	*10*

winter. QUIGNARD (1966) summarized data from the literature on this subject for the Atlantic and Mediterranean labrids. For instance, *Labrus bimaculatus* spawns in the North Sea during May and June but along the Mediterranean coast off Provence from March until July; *Ctenolabrus rupestris* is mature from April until June in the Golf of Lion but from January until June along the Algerian coast.

In the Caribbean labrids functional gonads proved to be present the whole year through. Of four species the percentages of fish with "active" gonads per month are listed in Table 28. For *Th. bifasciatum* and *H. bivittatus* the analysis has also been made for the first adult specimens only, excluding the intermediate and terminal phases with relatively high portions of small, inactive gonads. Table 28 reveals that individuals with (nearly) mature or spent gonads (stages IV–VI) were present in the samples without any break. For the other three species no data are included in Table 28, the number of specimens per months being too diverse and small. Yet, here functional gonads have also been found throughout the year.

The histological aspect of the gonads confirms the existence of non-intermittent reproduction activities. Especially in the ovaries, within one specimen a great variety of developmental stages proved to be present, typical for fish in which a number of successive spawnings will occur (Table 19, 20).

Though mature gonads have been found throughout the year, the height of the percentages fluctuates. The portion of real functional gonads in phase 1 of *Th. bifasciatum* is significantly higher during November and December and during April until June (χ^2-test, p = 5%). Immediately after these periods of increased maturity significantly lower portions have been found, namely during January and during July until September. In *H. bivittatus* significantly higher percentages have been found during June until September, and lower portions during January, February, May and November.

These periods of increased and diminished gonadal activity may be vague reminiscences of the limited spawning periods of labrids in more temperate regions.

The periods of greatest sexual activity of *bifasciatum* and *bivittatus* partly coincide. Also during the rest of the year, repeatedly on the same day and the same spot very mature specimens of different

TABLE 29a

TOTAL LENGTH FREQUENCY DISTRIBUTION OF SAMPLES OF *Thalassoma bifasciatum* PER MONTH

(December 1962/November 1963)

Percentages of total number per month in italics

Total length (cm)	Dec.	Jan.	Feb.	March	April	May	June	July	Aug.	Sep.	Oct.	Nov.	*Total*
2	—	—	—	—	—	—	—	2	—	—	—	—	2
								(0.3)					*(0.1)*
3	1	—	—	3	—	—	—	10	15	—	—	1	30
	(3.3)			*(1.3)*				*(1.7)*	*(3.1)*			*(0.6)*	*(1.1)*
4	8	7	8	10	5	2	6	32	26	21	21	8	154
	(26.7)	*(14.9)*	*(12.5)*	*(4.4)*	*(4.0)*	*(2.7)*	*(4.9)*	*(5.3)*	*(5.4)*	*(5.8)*	*(5.4)*	*(5.1)*	*(5.8)*
5	8	13	14	40	26	21	26	119	65	80	69	22	503
	(26.7)	*(27.7)*	*(21.2)*	*(17.5)*	*(20.8)*	*(28.4)*	*(21.1)*	*(19.9)*	*(13.5)*	*(22.2)*	*(17.9)*	*(14.1)*	*(18.9)*
6	5	16	13	52	48	18	51	211	123	114	95	45	791
	(16.7)	*(34.0)*	*(22.0)*	*(22.8)*	*(38.4)*	*(24.3)*	*(41.5)*	*(35.2)*	*(25.6)*	*(31.7)*	*(24.6)*	*(28.9)*	*(29.7)*
7	2	4	6	58	18	13	19	112	125	77	102	36	572
	(6.7)	*(8.5)*	*(9.4)*	*(25.4)*	*(14.4)*	*(17.6)*	*(15.5)*	*(18.7)*	*(26.0)*	*(21.4)*	*(26.4)*	*(23.1)*	*(21.4)*
8	3	2	8	29	18	9	13	61	71	33	47	30	324
	(10.0)	*(4.3)*	*(12.5)*	*(12.7)*	*(14.4)*	*(12.2)*	*(10.6)*	*(10.2)*	*(14.8)*	*(9.2)*	*(12.2)*	*(19.2)*	*(12.2)*
9	2	3	6	16	8	8	7	27	34	19	38	10	178
	(6.7)	*(6.4)*	*(9.4)*	*(7.0)*	*(6.4)*	*(10.8)*	*(5.7)*	*(4.5)*	*(7.1)*	*(5.3)*	*(9.8)*	*(6.4)*	*(6.7)*
10	1	2	3	16	1	2	1	24	21	12	10	3	96
	(3.3)	*(4.3)*	*(4.7)*	*(7.0)*	*(0.8)*	*(2.7)*	*(0.8)*	*(4.0)*	*(4.4)*	*(3.3)*	*(2.6)*	*(1.9)*	*(3.6)*
11	—	—	1	4	1	1	—	1	—	4	4	1	17
			(1.6)	*(1.8)*	*(0.8)*	*(1.4)*		*(0.2)*		*(1.1)*	*(1.0)*	*(0.6)*	*(0.6)*
Total	*30*	*47*	*59*	*228*	*125*	*74*	*123*	*599*	*480*	*360*	*386*	*156*	*2667*
Mean TL	*6.25*	*6.26*	*6.46*	*6.79*	*6.41*	*6.58*	*6.26*	*6.33*	*6.61*	*6.41*	*6.67*	*6.65*	*6.49*
S	*1.81*	*1.55*	*1.84*	*1.68*	*1.35*	*1.57*	*1.25*	*1.48*	*1.57*	*1.47*	*1.50*	*1.42*	

TABLE 29b

TOTAL LENGTH FREQUENCY DISTRIBUTION OF SAMPLES OF *Halichoeres bivittatus* PER MONTH
(December 1962/November 1963)

Percentages of total number per month in italics

Total length (cm)	Dec.	Jan.	Feb.	March	April	May	June	July	Aug.	Sep.	Oct.	Nov.	*Total*
3	—	—	—	1	—	—	3	1	—	—	—	—	5
				(0.3)			*(3.4)*	*(0.5)*					*(0.3)*
4	3	—	1	20	—	—	16	4	2	—	1	2	49
	(4.9)		*(0.8)*	*(5.8)*			*(18.2)*	*(2.1)*	*(0.9)*		*(0.4)*	*(1.7)*	*(2.7)*
5	3	2	7	29	12	—	10	4	5	8	16	6	102
	(4.9)	*(6.1)*	*(5.6)*	*(8.4)*	*(9.3)*		*(11.4)*	*(2.1)*	*(2.4)*	*(3.4)*	*(5.7)*	*(5.2)*	*(5.5)*
6	2	3	11	43	18	—	1	7	10	19	55	24	193
	(3.3)	*(9.1)*	*(8.8)*	*(12.4)*	*(14.0)*		*(1.1)*	*(3.7)*	*(4.7)*	*(8.0)*	*(19.5)*	*(20.9)*	*(10.5)*
7	5	5	18	53	23	—	3	15	16	47	72	29	286
	(8.2)	*(15.2)*	*(14.4)*	*(15.3)*	*(17.8)*		*(3.4)*	*(8.0)*	*(7.5)*	*(19.7)*	*(25.5)*	*(25.2)*	*(15.5)*
8	5	4	25	54	26	2	9	46	47	52	59	19	348
	(8.2)	*(12.1)*	*(20.0)*	*(15.6)*	*(20.2)*	*(8.0)*	*(10.2)*	*(24.5)*	*(22.1)*	*(21.8)*	*(21.0)*	*(16.5)*	*(18.9)*
9	9	4	4	53	12	6	15	49	45	57	33	12	299
	(14.8)	*(12.1)*	*(3.2)*	*(15.3)*	*(9.3)*	*(24.0)*	*(17.1)*	*(26.1)*	*(21.1)*	*(23.9)*	*(11.7)*	*(10.4)*	*(16.2)*
10	13	2	19	21	13	3	16	25	38	20	22	12	204
	(21.3)	*(6.1)*	*(15.2)*	*(6.0)*	*(10.1)*	*(12.0)*	*(18.2)*	*(13.3)*	*(17.8)*	*(8.4)*	*(7.8)*	*(10.4)*	*(11.1)*
11	8	3	19	22	12	2	9	15	25	13	11	6	145
	(13.1)	*(9.1)*	*(15.2)*	*(6.3)*	*(9.3)*	*(8.0)*	*(10.2)*	*(8.0)*	*(11.7)*	*(5.4)*	*(3.9)*	*(5.2)*	*(7.9)*

Total length (cm)	Dec.	Jan.	Feb.	March	April	May	June	July	Aug.	Sep.	Oct.	Nov.	*Total*
12	8	7	8	23	8	9	5	9	8	4	9	3	101
	(*13.1*)	(*21.2*)	(*6.4*)	(*6.6*)	(*6.2*)	(*36.0*)	(*5.7*)	(*4.8*)	(*3.8*)	(*1.7*)	(*3.2*)	(*2.6*)	(*5.5*)
13	5	2	4	9	4	3	1	10	7	5	4	1	55
	(*8.2*)	(*6.1*)	(*3.2*)	(*2.6*)	(*3.1*)	(*12.0*)	(*1.1*)	(*5.3*)	(*3.3*)	(*2.1*)	(*1.4*)	(*0.9*)	(*3.0*)
14	—	1	5	10	1	—	—	3	7	10	—	—	37
		(*3.0*)	(*4.0*)	(*2.9*)	(*0.8*)			(*1.6*)	(*3.3*)	(*4.2*)			(*2.0*)
15	—	—	1	3	—	—	—	—	3	4	—	1	12
			(*0.8*)	(*0.9*)					(*1.4*)	(*1.7*)		(*0.9*)	(*0.6*)
16	—	—	1	3	—	—	—	—	—	—	—	—	4
			(*0.8*)	(*0.9*)									(*0.2*)
17	—	—	1	1	—	—	—	—	—	—	—	—	2
			(*0.8*)	(*0.3*)									(*0.1*)
18	—	—	1	1	—	—	—	—	—	—	—	—	2
			(*0.8*)	(*0.3*)									(*0.1*)
19	—	—	—	1	—	—	—	—	—	—	—	—	1
				(*0.3*)									(*0.05*)
Total	*61*	*33*	*125*	*347*	*129*	*25*	*88*	*188*	*213*	*239*	*282*	*115*	*1845*
Mean TL	*9.41*	*9.33*	*9.20*	*8.35*	*8.29*	*10.76*	*7.83*	*8.99*	*9.25*	*8.65*	*7.76*	*7.78*	*8.55*
S	*2.41*	*2.54*	*2.70*	*2.80*	*2.21*	*1.61*	*2.80*	*2.02*	*2.08*	*2.14*	*1.79*	*1.96*	

species have been encountered. Consequently, the moment of sexual maturity per se can not function as a seasonal isolating mechanism (cf. Chapter VIII).

FEDDERN (1965) also reported that in *Th. bifasciatum* spawning occurs throughout the year. On account of egg diameter he concluded that (in Florida waters) there are periods of intensive spawning and periods of diminished spawning, the former being about one and one-half to two months apart. RANDALL (1965) reported ripe females of *Hemipteronotus novacula* in April, of *He. splendens* in December. No further information has been published on gonad activity of Caribbean wrasses in relation to time of the year.

Though many factors influence growth, it may be assumed that definite spawning periods will be reflected by marked fluctuations in mean body length. In Table 29 the frequency distribution of total length groups per month is given of *Th. bifasciatum* and *H. bivittatus*. The mean TL and the standard deviation per month are also included. Significant differences in the frequency of the number of individuals falling in a certain size class are observed in some months. Relatively more small fish were collected of *Th. bifasciatum* during July, August, September and October, of *H. bivittatus* during March, June and October. Relatively more large fish were collected of *Th. bifasciatum* during March and during July to October, of *H. bivittatus* during March and during July to September. Yet, in *Th. bifasciatum* no clear shift in the mean total length can be recognized (Student's *t* test). In *H. bivittatus* significant differences have been found between the means of the months February–March, April–May, May–June (note the small sample size in May) and June–July (Student's *t* test). Yet, rather continuously young new fish must have been added to the population.

Of the other five Caribbean species no data are listed in Table 29, since the numbers per months were considered too small in several cases. Of *H. garnoti* only during six months ten or more specimens were caught. For these months, March and June/November 1963, no clearly different mean total lengths have been found. Of *He. martinicensis* only data are available of a three month period, as only at the end of the field investigations this species has been collected. The seven specimens collected during September 1963 were on the average 9.2 cm long, while in October and November mean TL's of 9.5

and 9.1 cm have been found, in 81 and 37 specimens respectively. Thus, in the trimester of investigation no real shift in the mean length is visible either.

Whether the unlimited spawning seasons are to be explained by the slight annual fluctuation in water temperature or the continuity of light intensity, is still open to investigation.

GONADAL ACTIVITY AND LUNAR MONTH

Striking cases of a conspicuous correlation of spawning and phases of the moon have been reported for various inhabitants of the sea. Since the day of collection and the maturity stage of every specimen studied were noted, possible lunar influence could be evaluated.

The actual spawning of labrid fish lasts only a few seconds and consequently observations are inadequate. RANDALL, who for years has regularly been observing wrasses in their natural environment, only accidentally noticed spawning labrids. Scanning of his field notes gave a slight suggestion of two peaks of spawning intensity within one lunar month, one during full moon, the other during new moon (RANDALL & RANDALL, 1963). FEDDERN (1965) elaborated these data further and provided more information by measuring diameters of eggs of *Th. bifasciatum*, collected during 18 collecting trips in 17 months. He concluded that each spawning period lasted for a week or more; the trend lines indicated that in seven months four spawning periods occurred (though one may wonder if the relative low number of collecting trips in relation to the period studied justifies definite conclusions).

During collecting it has been noticed that on certain days most females are either very ripe indeed, or have e.g. developing stage III gonads, suggesting some synchronization in maturity fluctuations.

To obtain more precise information on this phenomenon all days of collection have been converted into days of the lunar month. The day of full moon was constantly counted as day 15, the day before full moon as day 14, the day after full moon as day 16, etc. Due to fluctuations in the number of days per moon quarter, new moon is either on day 29, 30, 00 or 01; first quarter on day 6, 7 or 8, last quarter on day 20, 21 or 22.

For all seven species per three days of the lunar month, of the total number of females collected during that period the percentage with active ovaries (stage IV, V, or VI – i.e. nearly mature, mature or just

spent) has been calculated. The results are given in Table 31. Moreover, similar percentages are given in Table 30 for *Th. bifasciatum*, for females and males in first adult colors and males in terminal bluehead colors separately. The fluctuations in percentage active gonads per moon phase are further illustrated in Figs. 22 and 23.

For most species the results are based on data of at least 12 lunar months. The use of living fishes for experiments, and interruptions in collecting because of bad weather, caused some gaps in the data. Since *He. martinicensis* was only detected during the last period of my stay in Curaçao, only three successive moon months could be studied.

Table 30 and Fig. 22 show that on the day around and right after full moon a great majority of females was ready to spawn. Further, a top in ovulation activity around new moon, as well as around first quarter was found. Significantly lower are the percentages right

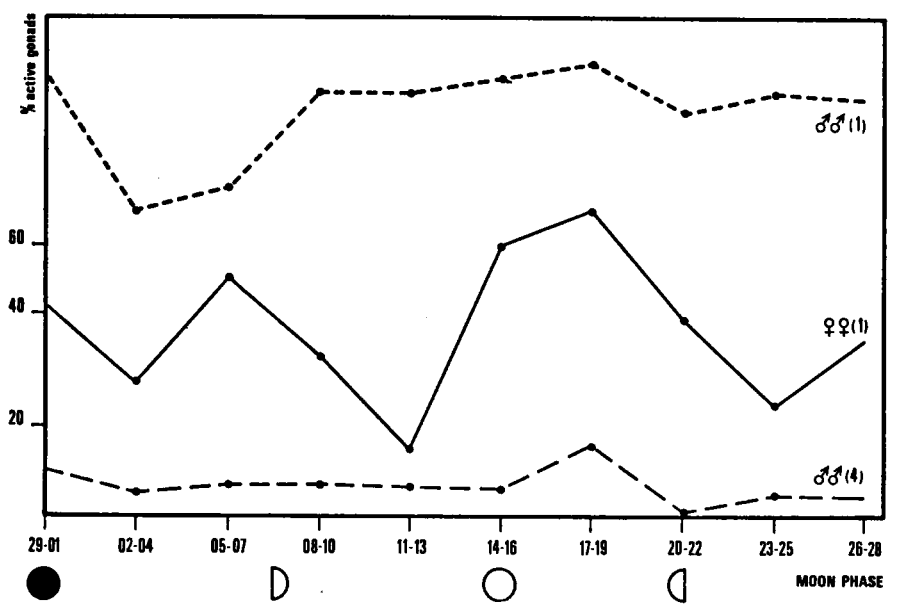


Fig. 22. Fluctuations in the percentages of individuals with active gonads (i.e. nearly mature, mature, or spent), per moon phase, for *Thalassoma bifasciatum*, for females and males in color phase 1 and males in bluehead phase 4 separately. (cf Table 30)

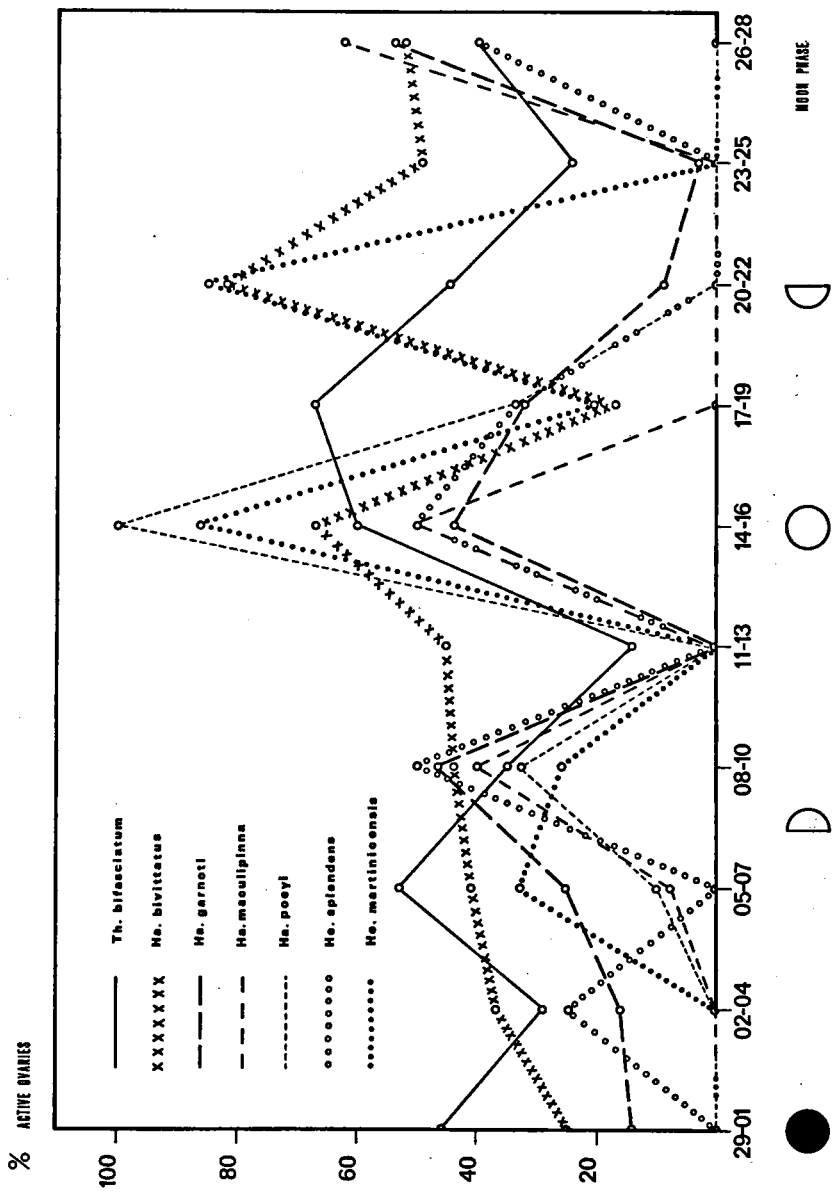


Fig. 23. Fluctuations in the percentages of specimens with active ovaries (i.e. nearly mature, mature, or spent), per moon phase, for seven Caribbean labrid species. (cf Table 31)

TABLE 30

PERCENTAGES OF "ACTIVE" GONADS PER MOON PHASE
in *Thalassoma bifasciatum* from Curaçao

"active" = nearly mature, mature, or spent

	Females color phase 1 (yellow phase)		Males color phase 1 (yellow phase)		Males color phase 4 (bluehead phase)	
Phase of the moon	% active gonads	total number	% active gonads	total number	% active gonads	total number
29–00–01 ●	46.2	132	97.2	36	10.0	20
02–03–04	28.9	45	66.7	9	4.8	21
05–06–07	52.7	112	72.0	25	6.9	29
08–09–10 ◗	36.2	133	92.3	39	6.7	30
11–12–13	14.2	106	92.1	38	5.6	18
14–15–16 ○	59.7	196	96.3	54	6.2	48
17–18–19	67.3	214	100.0	48	15.6	32
20–21–22 ◖	43.9	107	88.9	27	0.0	18
23–24–25	24.0	96	93.5	46	4.6	44
26–27–28	39.7	58	92.3	13	4.4	23

after new moon and just before full moon and new moon ($p = 0.001$). But, then still 14 to 30 per cent had ovaries full of mature ova.

The majority of the males in the yellow, first adult phase are pretty well ready to spawn during the whole lunar month. In agreement with RANDALL's impression, the highest percentages have been found in the periods of new and full moon. Right after new moon there is a significant drop ($p = 0.001$).

In terminal phase *bifasciatum* males the majority of the testes are small and not very functional anymore. A minority, however, has a significantly higher portion of active testes right after full moon – synchronized with the highest percentages of active gonads in both female and male yellow phase fish. This can hardly be considered plain coincidence.

In the other species around full moon a large majority of the females also had active ovaries. A relatively large activity has moreover been found around new moon in *H. garnoti*, *H. maculipinna*, *He. splendens* and *He. martinicensis*, and around first quarter in *H.*

TABLE 31

PERCENTAGES OF "ACTIVE" OVARIES PER MOON PHASE
in Caribbean species of *Thalassoma*, *Halichoeres* and *Hemipteronotus*

(Number of lunar months on which the data are based in parentheses)
"active" = nearly mature, mature, or spent

Phase of the moon	*Th. bifasciatum* (16)		*Ha. bivittatus* (16)		*Ha. garnoti* (10)		*Ha. maculipinna* (9)		*Ha. poeyi* (11)		*He. splendens* (5)		*He. martinicensis* (3)	
	active ovaries	total number	active ovaries	total number	active ovaries	total number	active ovaries	total number	active ovaries	total number	active ovaries	total number	active ovaries	total number
29–00–01 ●	46	132	25	77	14	29	0	7	0	4	0	1	0	14
02–03–04	29	45	37	79	16	19	0	3	0	3	25	4	0	0
05–06–07	53	112	41	116	25	12	8	25	10	10	0	2	33	12
08–09–10 ◗	35	133	44	138	47	15	40	5	33	3	50	2	26	19
11–12–13	14	106	45	62	0	3	0	0	0	1	0	2	0	4
14–15–16 ○	60	196	67	102	44	18	50	6	100	4	50	4	86	7
17–18–19	67	214	17	120	32	19	0	4	33	3	33	3	20	5
20–21–22 ◖	44	107	83	42	9	22	0	1	0	2	0	1	84	7
23–24–25	24	96	49	104	3	38	0	2	0	4	0	1	0	2
26–27–28	40	58	52	114	53	19	63	8	0	1	40	5	0	15
Total		*1199*		*954*		*194*		*61*		*35*		*25*		*85*

garnoti, *H. maculipinna*, *H. poeyi*, *He. splendens* and *He. martinicensis*.

In *H. bivittatus* the various percentages deviate less clearly, though some peak activity can be noticed around full moon and last quarter.

In *He. martinicensis* – deviating from the other species in its living more strictly together on one spot – around new moon the gonads were in the preparatory stages III and IV, and remarkably ready to spawn around full moon. The only male collected on moon day 15 contained large, very mature testes; after full moon only flabby, clearly rather drastically emptied testes were found. Only of day 6 data are obtained during two different lunar months. On both occasions, the females collected had ovaries in stage IV, while the males had testes of average sizes. These findings certainly do not contradict some synchronization in gonadal activity rhythm.

In short, these data suggest three peaks of reproduction activities within one lunar month, with a most pronounced top around full moon in all species. (RANDALL e.a. mentioned one peak during full moon, and another during new moon). Propagation, though, may continue in the periods in between. In which way fluctuations in intensity of the light of the moon may influence labrids with their remarkable sleeping-habits is still an intriguing problem.

It is relevant to mention here on which days of the moon month sexual behavior has been observed. (The actual spawning was seldom witnessed in spite of hours of shutter-peeping activity.)

Persistent pursuing by a large, bluehead *Th. bifasciatum* of a bright yellow specimen occurred at exactly the day of new moon (April 23rd, 1963). One day later chasing behavior was seen in a group of *He. splendens* specimens, while then a large, pastel colored *H. bivittatus* pursued a smaller phase 1 Slippery Dick. Yet, also chasing by a bluehead of a yellow congener was seen four days after new moon (July 25th, 1963). Active group dancing was observed for both *Th. bifasciatum* and *H. bivittatus* at the moment of first quarter (August 29th, 1963).

In literature only a few actual dates of maturity could be found. LONGLEY e.a. (1941) described four mature males and one mature female for *H. bivittatus* for July 26th, and 27th, 1929; these were moon day 20 and 21. The only occasion FEDDERN (1965) mentioned the actual collecting date of a ripe female was April 9th, 1963, moon day 16, the day after full moon. RANDALL, shooting fish right after he observed it in the spawning act, collected two mature females of *Hemipteronotus novacula* on April 29th, 1964, moon day 18, and one mature female of *He. splendens* on December 29th, 1961, moon day 22, one day before last quarter. Of *He. martinicensis* he shot three ripe females on March 15th, 1964, moon day 16.

TABLE 32

SEX RATIO IN RELATION TO THE LUNAR MONTH

New moon = day 29–01; First quarter = day 6–8; Full moon = moon day 15; Last quarter = day 20–22

	Phase of the moon on the day of collection																														*Total number*
	00	01	02	03	04	05	06	07	08	09	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	
																Thalassoma bifasciatum																
females	67	48	28	14	10	33	31	58	37	27	68	13	79	35	67	46	96	39	83	109	—	106	3	51	57	5	33	18	11	17	4	1293
males	28	23	20	7	5	9	35	26	16	30	31	89	45	13	58	22	80	17	34	46	—	45	3	40	51	6	26	13	3	1	2	833
total	*98*	*74*	*57*	*24*	*15*	*42*	*78*	*95*	*60*	*64*	*105*	*109*	*152*	*63*	*141*	*71*	*190*	*68*	*124*	*157*	—	*170*	*6*	*100*	*115*	*13*	*70*	*41*	*19*	*32*	*10*	*2363*
																Halichoeres bivittatus																
females	—	23	19	34	23	32	54	34	43	23	78	6	29	25	19	26	59	49	76	7	—	41	1	63	32	12	55	45	10	28	26	972
males	—	12	6	9	12	7	30	9	4	9	34	—	8	2	7	13	16	20	17	3	—	13	3	24	1	4	17	12	1	7	1	301
total	—	*37*	*25*	*44*	*45*	*44*	*99*	*55*	*48*	*45*	*118*	*7*	*41*	*28*	*36*	*45*	*83*	*77*	*109*	*11*	—	*56*	*4*	*93*	*41*	*17*	*77*	*59*	*12*	*37*	*40*	*1433*
																Halichoeres garnoti																
females	—	10	17	2	—	6	6	8	—	7	8	2	2	—	4	8	7	11	9	3	—	21	1	16	9	13	11	8	—	19	—	208
males	—	—	2	2	1	—	7	4	—	1	4	—	1	—	2	5	5	1	2	3	—	4	1	9	3	—	1	—	—	4	—	62
total	—	*10*	*20*	*5*	*1*	*7*	*19*	*12*	*2*	*12*	*17*	*3*	*3*	—	*8*	*17*	*14*	*13*	*12*	*9*	—	*34*	*3*	*29*	*13*	*17*	*17*	*10*	—	*24*	—	*331*
																Halichoeres maculipinna																
females	—	3	2	1	1	15	4	6	3	1	2	—	—	—	1	2	3	4	—	—	1	—	—	—	—	3	5	3	—	3	—	63
males	—	1	1	—	1	—	3	4	—	1	—	—	—	—	—	1	1	—	—	1	—	—	—	1	1	2	2	3	—	1	—	24
total	—	*8*	*5*	*1*	*2*	*15*	*8*	*10*	*4*	*4*	*6*	—	—	—	*5*	*5*	*4*	*5*	—	*1*	*1*	—	—	*2*	*1*	*7*	*7*	*10*	—	*4*	—	*115*
																Halichoeres poeyi																
females	—	—	3	—	—	4	2	5	2	—	1	1	—	—	—	3	1	2	1	—	—	2	—	1	—	3	—	—	1	4	—	36
males	—	—	1	1	—	—	—	—	—	—	—	—	1	1	—	—	—	1	1	—	1	1	—	1	—	—	—	—	—	—	—	9
total	—	—	*5*	*1*	—	*4*	*2*	*6*	*2*	—	*1*	*1*	*1*	*1*	*1*	*3*	*1*	*3*	*3*	—	*1*	*3*	—	*3*	—	*4*	—	—	*1*	*5*	—	*52*
																Hemipteronotus splendens																
females	—	1	1	1	—	2	2	—	—	—	2	—	2	—	1	—	2	1	3	—	—	1	—	1	—	—	—	5	—	—	—	25
males	—	2	—	—	—	—	2	2	—	2	4	—	1	—	—	—	1	2	2	—	1	—	—	1	—	—	1	3	—	—	—	24
total	—	*4*	*1*	*3*	—	*2*	*4*	*4*	—	*2*	*10*	—	*5*	—	*3*	*1*	*5*	*3*	*5*	—	*1*	*2*	—	*5*	—	*2*	*2*	*10*	—	*1*	—	*75*
																Hemipteronotus martinicensis																
females	—	14	—	—	—	—	12	—	—	14	5	—	4	—	7	—	—	1	4	—	1	7	—	2	—	—	9	6	—	—	—	86
males	—	3	—	—	—	—	6	—	—	2	3	—	—	—	1	—	—	1	—	—	—	3	—	4	—	—	2	6	—	—	—	31
total	—	*22*	—	—	—	—	*20*	—	—	*16*	*8*	—	*5*	—	*9*	—	—	*2*	*4*	—	*1*	*10*	—	*6*	—	—	*11*	*12*	—	—	—	*126*

It has been remarked above, how on some occasions the samples proved to contain an unusually great portion of mature males. To check this further the numbers of females and of males collected per moon day have been calculated. The results are presented in Table 32.

In *Th. bifasciatum* on moon day 11 the males strongly outnumbered the females (89 to 13; including data on one occasion on which of a total of 84 specimens 74 proved to be very mature males, cf Chapter VIII). On moon days 14 and 16, and 23 to 26 the numbers of both sexes were about equal. On the other moon days the sex distribution did not differ from the overall sex ratios given in Tables 24 and 25, i.e. females were in the majority.

In *H. bivittatus* on all moon days fewer males than females were collected. Of this species special gatherings of males have never been encountered. In *H. garnoti* the females did not outnumber the males on days 15 and 16, while the other days females prevailed more strongly. In *He. martinicensis* only on moon day 27 similar quantities of six females and six males have been found. (In the last five species of Table 32 the low numbers are too small to justify definite conclusions.)

These data suggest that during periods of top sexual activities temporary concentrations of males may occur, especially in *Th. bifasciatum*, the only species of which actual aggregate spawning runs were observed. (RANDALL & RANDALL, 1963, reported similar facts for sparid fish).

To obtain correct information on the true sex ratios in wrasses, collecting on various (moon) days, on various localities and if possible, at various times of the day is recommended.

XII. NON-FUNCTIONAL GONADS, IMMATURES AND SENESCENCE; INTERSEXES AND SEX REVERSAL

Present Investigations

In Chapter X it was mentioned that about 12 per cent of the material contained small, non-functional gonads. Their frequency distribution has been plotted in the histograms, Fig. 12 to 20, under the headings: "no gonads," "intersex," and "indistinct sex." Table 22 gives the exact numbers found for the three categories; Table 23 the percentages, and Table 25 the mean total lengths of this miscellaneous group, per species, per color phase.

The group of sex-indifferentiates includes both fish with immature gonads and with gonads in reduction, two essentially different stages that could often only be distinguished by histological examination, though the former are more firm, the latter more loose, both externally and internally. A minority of the small gonads appeared to be intersexual stages; these are of paramount importance for our study on the possibility of sex reversal in labrid fishes.

Immature gonads

Gonads in early stages of development are to be expected in young specimens. Since the very juveniles do not mingle with the larger, adult fish and do not react to the sea urchin bait, no wrasses smaller than 3 cm have been collected with the hoop net method. Conse-

quently, data on the onset of gonad differentiation cannot be included.

From 3 to 5 cm body length the frequency of the specimens in the samples increased markedly. The histograms illustrate that in the first adult phases at small size sex indifferentiates prevail. Histological inspection of the small gonads of these small fish confirmed their immature nature. This indicates that the change over from juvenile to adult way of life depends on the attainment of a certain body length rather than on the development stage of the gonads.

Yet, maturing of the reproductive organs may already start at a rather small size. Only in the smallest size groups do immatures outnumber the fish of similar colors in which classification into female or male was already possible (Table 25).

For instance, a *Halichoeres bivittatus* specimen of 5.4 cm TL contained ovaries in developing stage II–III (Plate II-b); a 5.7 cm TL female was in stage III; the large ovaries of a *bivittatus* female of 5.8 cm TL proved to be in stage IV with numerous eggs in which yolk formation was in an advanced stage, while other specimens of 5.8 cm TL had mature or just spent ovaries. In *Thalassoma bifasciatum* only a few small, yellow phase fish had still immature gonads. A specimen of 4.2 cm TL had developing stage II–III ovaries; several specimens of just about 4.8 cm TL had already mature stage V gonads, such as a male of 4.9 cm TL, with sperm in large quantities both in the tubuli and the ducts (Plate V-a).

Young ovaries

In species, in which males are restricted to larger sizes, all small first adult phase immatures proved to be young females. In *Th. bifasciatum* and *H. bivittatus* the majority of the immature gonads were young ovaries. As said, with increasing body length the proportion of the immatures strongly decreases; ovaries in the first developing stages I and II have hardly been found at the larger sizes of the first adult phases.

For instance, seven species of *H. bivittatus* – in phase 1 colors and total lengths ranging from 4.8 to 5.4 cm – possessed thin, though firm threads of gonads, classified as size *r*. The histological slides showed ovaries in early stages of development, full of cell nests of still basophilic oocytes and a minority of larger oocytes with the characteristic large nucleolus (Plate I-a).

Young testes

Two categories of young testes have been found. In *Th. bifasciatum* and *H. bivittatus* – in which species the occurrence of males in the first adult phase is a normal phenomenon – among the young, small fish in these colors specimens with young, just developing testes have been found. These young testes have a clearly metamere structure and no special irregularities.

For instance, the thin gonads of a 4.3 cm TL yellow phase specimen of *Th. bifasciatum* proved to be a young, immature testis in gonadal stage I.

Moreover, a remarkable amount of young, developing testes have been found in larger fish of intermediate and terminal colors, in all seven species. The often rather thick walls of the gonad and of the gonadal ducts (Plate V-c, f) and the presence of various yellowish or pink indefinite spots (Plate VI-a, c,d) are worth notice. Curious is also the presence of thick trabeculae, characteristic of ovaries. Often the whole structure of such testes is loose and somehow disordered. In some testes remnants of ovary structures have been found (see intersexes).

For instance, a *H. garnoti* specimen, 12.4 cm TL, in the colors of the last intermediate phase 4, contained small gonad threads that appeared to be full of developing, young testis tissues. Scattered among the areas of spermiogenesis were the described islets and fat tissue vacuoles (Plate VI-c).

Gonads in reduction

The above mentioned cases of young testes in larger fish coincide with the occurrence of ovaries in reduction and intersexual stages. Moreover, (local) reduction in testis activity has been found in very large, terminal phase males.

Ovaries in reduction

At the end of the first adult phase an increasing number of fish is

found with small, in-active gonads. Especially the larger females in this phase possess ovaries in total regression. On gross inspection these thin and slack gonads hardly can be classified as ovaries. Histological slides reveal that the recruitment stock of young oocytes as well as oogonia in various advanced stages of maturation are affected by overall resorption.

For instance, a yellow phase *Th. bifasciatum*, TL 8.5 cm, contained small gonads, classified as size *3*, activity stage VII (= regressing). The histological slides showed all over phagocytosis and relatively much connective tissue, pigments and capillaries (Plate IV-b).

First signs of reduction were encountered in a yellow phase *bifasciatum* of TL 7.6 cm. Macroscopically the ovaries were characterized as estimated size *3*, activity stage VI (= spent). However, granulose spots occurred, scattered among normal ovarian tissue characteristic of a just spent ovary. Some oogonia were already surrounded by the high follicle epithelium of the resorption process. Some nicely and strictly arranged strings of cells were present that might well be the very first stages of new germ epithelium (Plate IV-f).

There is some overlap as some larger first adult phase females still have immature ovaries, while others already show resorption. Yet, in general the total lengths of females with regressing ovaries differs from those with immature ovaries.

In *Th. bifasciatum*, for instance, most immature ovaries (stage I, II) were found up to 5.5 cm TL. The occurrence of regressing ovaries (stage VII) increased after a length of about 7 cm had been reached. In *H. bivittatus* most immature gonads were found in fish smaller than 6.5 cm, while regressing ovaries became more abundant after about 8 cm.

In most species females are limited to the first adult phase; then, ovaries in reduction are only found at the end of this phase. In *H. bivittatus* and *H. garnoti*, however, specimens with regressing ovaries have also been found among larger fish in intermediate colors.

No visible gonads

In a number of fish hardly any gonads could be detected. Among these were some very young specimens such as two orange *H. garnoti* juveniles and some first adult phase specimens of *H. bivittatus*,

smaller than 6 cm TL. However, most specimens without visible gonads were larger fishes in the first adult phase, intermediate and even terminal phase colors.

A minority of the freshly caught fish had to be stored at minus 20°C for some hours, to three days at a maximum. The deep freezing had some effect, especially on small flaccid gonads. This may explain the apparent absence of gonads at larger sizes in some of the animals dissected.

Testes in reduction – senescence

Males with testes with decreased fertility have been found among the larger fishes in terminal colors in all species; fully functional testes that occupy great part of the abdominal cavity are rather exceptional in large fish. This is illustrated in Table 27, where the percentages of males with active gonads (i.e. (nearly) mature or spent) are listed per color phase. Even in species in which males are restricted to the intermediate and terminal color phases, merely a minority of the males possessed active testes. The percentages are low, due to the small testes in the most large males. The histograms moreover indicate that at the end of the terminal phase numerous fish with small, non-functional gonads occur.

This phenomenon has been found most clearly in *Th. bifasciatum*; only a few bluehead phase males had large, active testes. The conspicuous difference of large, heavy testes in the small, first adult phase males and small testes in the bluehead males is shown in Fig. 21, in which testis weight per total length is plotted. After color change, the testis weight remains low.

In *H. bivittatus* numerous functional males occur also among the first adult phase, next to males found at larger sizes. In this species, however, some testes of the largest males were relatively very small and in-active, yet some were large and functional. Fig. 21 shows that after a decline in testis activity at intermediate sizes, again an association between larger testis weight and larger total length can be noticed, be it rather diffuse.

Often, the testes in large fishes are surrounded by superfluous adipose tissue (Plate V-e). On histological inspection they show only a few places of real spermiogenesis. Mature sperm occurs in tubuli and ducts but in relatively small quantities, while scattered through the whole gonad places of infiltration of connective tissue occur; some parts may be totally necrotic.

This type of reduction is different from the overall reduction in regressing ovaries. Reduction in testis function mostly is only topical; here and there places of normal testis activity are found.

Plate VI-b shows a section of the testis of a large, terminal color phase *H. bivittatus* specimen, 18.2 cm TL. Parts of the small gonad were clearly necrotic. A terminal bluehead phase specimen of *Th. bifasciatum*, 11.7 cm TL, contained small testes, externally classified as stage VII. Great parts of the gonads were occupied by loose tissue without spermiogenesis; relatively little young, recruitment stock is present. Here and there areas of maturing and mature sperm are found; there are scattered islets of lymphocyte tissue (Plate VI-e).

The present author considers this phenomenon in very large wrasses as a form of senescence. Senescence characterizes most large bluehead *Th. bifasciatum* males and some large males of the terminal phases of the other species.

Especially in the former species one may wonder to what purpose the bright terminal colors do exist. Perhaps here the bluehead colors are just a relict, remainder of a situation in which a colorful terminal phase had a biological meaning for the nestbuilding, territory defending and courting male (cf. Chapter VIII).

Senescense of fishes has been mentioned before (COMFORT, 1956, in BROWN, 1957). Some fish have a limited reproductive life, but many have lived on sterilely for years after their fertile period under the protected conditions of aquarium life. Other fishes are known to die after their first and last spawning activities.

About the occurrence of regression of the gonads in fish living in their natural environment (not the regression due to limited spawning sesaons), not much has been published. Despite a widespread misconception that fishes do not show senescense, because their somatic growth continues, PRISCILLA RASQUIN & ETHEL HAFTER (1951) are of the opinion that teleosts follow the common vertebrate pattern of aging. In old specimens of *Astyanax mexicanus* they found in the testes infiltration of connective tissue and formation of calcified concretions, similar to the concretions found in the aging mammalian prostrate. Accumulation of fat in the interstitial tissue proved also characteristic for senile testes. LOUISE STOLL (1955) reported that in *Th. bifasciatum* the testes of the large bluehead males contained only a very few mature sperm while the testes of the smaller yellow males were twice as large and filled with large reservoirs of mature sperm. RANDALL (1963) remarked on some parrot fishes, Scaridae – which have much in common with the labrids – that the gonads of most large fish consisted only of slender reddish strands that could not be identified as ovaries or testes without histological observation. MACHTELD ROEDE (1965) considered the low state of reproductive activity in the large, terminal phase males of the labrid *Coris julis* as senescence. The data of the present study may confirm her conclusion.

Intersexes

Of the total of 521 specimens with non-functional gonads only part could be investigated histologically. Of these, a small minority of 26 specimens proved to have both female and male characteristics (Plates VII, VIII and IX).

Intersexes show characteristics of both immature and regressing gonads. As described in Chapter IX and illustrated in the plates, various types have been found, from mainly regressive ovaries with first starts of sperm production, via young testes with degenerating ovarian structures to maturing testicular tissues with scattered oocytes remains. In the last case the rather firm gonad is hard to distinguish from a young testis externally.

Most intersexes were found in *Th. bifasciatum* and *H. bivittatus* of which species the largest total numbers were available for investigation. Of the 17 intersexes found in the former species two were large specimens of the first adult phase, ten were specimens of intermediate size and colors, five were in the terminal color phase (Fig. 12, 13). Of the 6 intersexes found in *H. bivittatus* four were of intermediate size but still in first adult colors, and two had intermediate sizes and intermediate phase 2 colors (Fig. 14, 15). The two *H. maculipinna* intersexes were large fish in intermediate phase 3, and in terminal phase 4 colors (Fig. 17). In *He. splendens* and *He. martinicensis* each only one intersex was found, both being in terminal colors (Fig. 19, 20).

The results indicate that the occurrence of intersexual organs is not strictly related to a certain color phase, but clearly falls within the range in which color changes develop.

Among the freshly caught *H. garnoti*, killed immediately, no intersexes have been found. Yet, there is evidence that in this species intersexes also occur. Some of the gonads of fish used for growth experiments – the data on which have been excluded from Table 22 e.a. and from Fig. 12/20 – were examined histologically. Thus, a clearly intersexual gonad was detected in a *garnoti* specimen, kept during one month in a cage at the bottom of the sea in Curaçao. The fish, at the end of the experiment of 8.7 cm TL, was in the inter-

mediate phase 3 colors. The small gonad consisted of ovarian tissue in overall regression with scattered spots of first stages of spermiogenesis, resembling the situation pictured in Plates VII-c and VIII-b. This is an interesting finding as in *H. garnoti* actual males have only been found in fish of 9 cm and more TL, and only among fish in intermediate phase 3 and 4 or in terminal phase 5 colors.

Sex reversal

The impression was gained that the attainment of a new morphological pattern more or less coincides with a temporary reduction of gonadal activity. In *Th. bifasciatum* about 40% of the color intermediates were fish with non-functional gonads; even more were found relatively in the intermediate phases of *H. maculipinna* and *He. splendens*. In *H. garnoti* 60% of the last, largest intermediate phase were specimens with small gonads (Table 23). Yet, there is no strict relation between intermediate colors and low gonadal activity since very mature females and males have also been found with transitory colors (Table 22).

In *H. bivittatus* the percentages of fish with non-functional gonads was not actually larger in the intermediate phases. In this species – in which in contrast to the pronounced dichromatic species colors only slightly change during growth, and in which both females and males occur at all sizes, in all color phases – a relatively low number of intersexes has been found (6, to 17 in *Th. bifasciatum*).

The data on fish with non-functional gonads can roughly be summarized as follows:

- first adult color phase
  - at small size — immature gonads
  - at large size — ovaries in reduction
- intermediate color phase(s)
  - at all sizes — ovaries in reduction / intersexes / immature testes
- terminal color phase
  - at small size — immature testes
  - at all sizes — intersexes
  - at large size — testes in reduction

These data strongly support the supposition that the males in the large, terminal phase (may) have developed out of female fish. Indirect and direct arguments suggesting the occurrence of reversal of sex are:

— In some species females are restricted to the small first adult phase; males exclusively occur at larger sizes.

— In species in which sex and color are not clearly related, females are also in the majority at small size while males prevail at large sizes.

— In average-sized fish, more or less coinciding with color change in most species, numerous ovaries show all over regression; in this range of body length numerous fish with young, developing testes have been found.

— In average-sized fish intersexual gonads have been found, from mainly a regressive ovary with few areas of spermiogenesis to gonads with mainly testis tissue with a few oocytes remains.

— The testes of large fish frequently show ovarian-like features such as thick walls of gonad and ducts and thick trabeculae.

From the facts of the present study it can be concluded that in Labridae sex reversal occurs as a normal process, by which wrasses successively may act first as female, then as male.

In strictly protogynous species – *H. maculipinna, H. poeyi, He. splendens* and *He. martinicensis* – all males will be reversed males.

In those species, in which functional males already occur in the small, first adult color phase – *Th. bifasciatum, H. bivittatus* – part of the terminal phase males will consist of transformed females. Consequently, in the latter species the use of the notation "protogynous" has to be rejected.

The process of reversal of sex develops in the range of intermediate sizes in which – in most labrid species – color patterns change. Yet, sex reversal and alterations in morphology (also fin shape may be concerned) only partly run parallel; the former process may start before or after the latter.

Remarks

Frequently, yellowish or pink islets of indefinite, necrotic tissue have been found in testes of males of intermediate and large sizes (cf. Chapter IX, Plate VI-a, c, d). The present author is strongly inclined to consider these islets merely as only partly resorbed former ovarian tissue. Sometimes they contain structures reminiscent of oolemma's or atrophic yolk; once, a regressive oocyte occurred along the margin of a yellowish area; their situation along trabeculae also points to a formerly ovarian situation. Moreover, some sections of formerly mature eggs in resorption looked like preliminary stages of the islets. A few times still clearly recognizable eggs may be maintained amidst maturing male tissues (Plate IX). Probably it happens more often that eggs that had been almost mature or perhaps already ovulated at the moment of onset of sex reversal become partly resorbed. These may develop into the discussed areas.

These islets, though, can hardly be a main factor in producing color change and reversal of sex since these radical processes mostly start to develop in fish without any of these areas, and since certainly not all terminal phase fish do contain such islets. The morphology of the large fish was not any different, no matter whether none, a few or several islets were present in the testes. Neither, can they be a sign of senescence as they may occur in very functional, mature testes.

As to the influence of external causes on sex reversal in labrids the following points are of importance:
– The Caribbean fishes live in waters of about the same temperature the whole year through.
– Small, mostly female fish and large, mostly male fish frequent the same areas and feed more or less on the same diet.
– Fish with intermediate colors and gonads in reduction or in the process of sex reversal have been found throughout the whole year.

Consequently, in Labridae the transformation from female towards male hardly can be induced by external causes. It has to be considered as an internal process.

The total composition of the populations show a marked decline of numbers at the end of the first adult phase. An explanation could be that when a certain body length has been reached a portion of individuals stops growing. This is not confirmed by the growth studies (Chapter XIII).

A high mortality rate may occur when at the end of the first adult phase colors start to change. This point during growth is of paramount importance, as:

- the total numbers decrease drastically;
- color patterns are subjected to permanent changes;
- fin shape may change;
- ovaries are submitted to overall regression;
- intersexual gonads occur; sex reversal takes place;
- young testes develop;
- growth rates increase after a strong decline (Chapter XIII).

It may well be that at this critical point many individuals succumb.

The present study indicates that in Labridae changing of sex and morphology is clearly related to body length. When passing from one growth stage into the other, a change in the spectrum of gene activity most probably occurs. (The view now generally prevailing is that genes are not active simultaneously, but require activation before they can be effective). The moment of often radical changes in external features – more or less coinciding with sex reversal in many specimens, and with temporarily low growth rates – may be due to the fact that inactive genes have become active through influence of some factors that probably also are genic in nature. Further investigations on color, size, and sex in labrids should include genetic studies.

Remarkable is the low portion of intermediates (compared to the terminal phase fish).

Morphological changes in pigmentation are time consuming processes, developing gradually and slowly, so the factor time cannot account for the small numbers observed. The frequencies of the intermediates only concern a small range of a few centimeters of

body length, while the total numbers of terminal fish include a range of many more centimeters; this partly accounts for the greater number found in the terminal phases.

As it is improbable that many swimming intermediates could have escaped collecting, other factors may have influenced the relatively low number of intermediates. Labrids stay hidden under the sand not only during the night, but also at moments of fear, on days when the sea is polluted, after manipulations by the investigator, and in temperate regions during the cold season. Therefore it is not inconceivable that during the drastic physiological alterations during change in pigmentation and in gonadal organization, labrids are also apt to stay hidden under the sand during the day. This may explain why so few specimens in the process of color change and/or sex reversal have been met by earlier collectors and myself.

Conclusions

1. Only at the smallest sizes of the fish collected have immatures been found; most small wrasses had already developing gonads, hence the notation "first adult color phase."

2. Two categories young testes have been found. In *Th. bifasciatum* and *H. bivittatus* – where males already occur in the first adult phase – among the immatures at small size young testes have been found. Most young testes, however, have been found in fish of intermediate and large size, in all species.

3. Local forms of senescence are found in the relatively small testes of the largest males in terminal colors, especially in *Th. bifasciatum.*

4. In the seven Caribbean labrid species sex reversal from functional female towards functional male occurs as a normal process.

5. During the sex reversal the gonad is strongly reduced in activity. Consequently, temporary, functional hermaphroditism does not occur in Labridae, this in contrast to Serranidae and Sparidae.

6. The process of sex reversal runs frequently more or less parallel to alterations in color, and sometimes to changes in the shape of the fins.

7. Yet, changes in morphology cannot be considered as being

directly related to the development of male sex; testes and intersexual gonads may also be found among fish in the more plain, first adult color phase.

History

The occurrence of sex reversal as a spontaneous phenomenon in labrid fishes raises the question whether such a process can be considered normal, and how sex is determined in such fish. Some essential references on these topics will be reviewed below.

Intersexuality and sex reversal*

Intersexuality and sex reversal occur all through the animal kingdom. Numerous lower evertebrates are hermaphrodites throughout life, though reproduction preferably takes place by cross-fertilization In vertebrates complete separation of the sexes has in general been accomplished but numerous exceptions are known (see ARMSTRONG & MARSHALL, 1964).

Within living memory individuals with both male and female disposition have been known. Some centuries ago even trials were held on animals that showed intersexual behavior, e.g. egg-laying cocks and crowing hens were officially convicted. Also in mammals intersexes occur (cf. ARMSTRONG e.a.).

In man and higher vertebrates intersexuality is an abnormal condition, due to chromosomal aberrations or pathological conditions on hormonal and/or organic level. In lower vertebrates, however, intersexuality and sex reversal are not pathological per se. The generalization "all vertebrates are gonochorists" given in many textbooks, is certainly wrong.

* Definitions used (quoted from ATZ, in ARMSTRONG e.a., 1964):
intersexuality: the presence of both male and female characteristics, or of intermediate sexual characteristics, in a single individual.
hermaphroditism: the existence of both the male and the female sex in a single individual, i.e. the presence of recognizable ovarian and testicular tissue.
functional hermaphroditism: hermaphroditism in which the individual functions both as male and female during its lifetime.
gonochorism: the existence of one sex, either male or female, in the individual.
protogynous hermaphroditism: the individual functions first as a female, and later in life as a male.
synchronous hermaphroditism: the individual is capable of functioning as male and female at the same time.
protandrous hermaphroditism: the individual functions first as a male, and later in life as a female.

Much has been published on fishes in this respect. For a critical review see ATZ (in ARMSTRONG e.a., 1964) who points to many poor statistical procedures, faulty histological interpretations and uncontrolled genetic and environmental factors.

Intersexuality has been reported in cyclostomes, though the functional hermaphroditism in hagfishes has been doubted in later years. It is rare in elasmobranchs but in teleosts the incidence of various types of both normal and abnormal hermaphroditism seems to be higher than in any other vertebrate group. Since early days in food fish such as salmon, carp, cod and herring specimens containing both soft and hard roe have been observed, incidental cases of normally gonochoristic species.

In many bony fishes, however, sex reversal and intersexuality are the rule rather than the exception, especially among Cyprinodontiformes and Perciformes. Small freshwater cyprinodonts have been studied especially in this respect. These laboratory studies formed the main base of the scientist's opinions on genetic and endocrine sex determination and differentiation in fishes. However, more recently the reliability of the conclusions and hence the true significance of sex reversal in poeciliid fishes has been questioned. Spontaneous sex reversal in the swordtail, *Xiphophorus helleri*, reported by ESSENBERG (1926) was doubted by GORDON (1957) who wondered whether the external masculinizations were truly associated with functional reversal of sex and pointed to the fact that all commercially grown swordtails, used by most workers, possess some *X. maculatus* genes, which may account for the instability of sex, in contrast to wild-caught specimens (which show stable sex development and differentiation, VALLOWE, 1957). In a similar way KALLMAN (1970) argued that most investigations on *X. maculatus* are outdated. Spontaneous sex reversal in guppies, *Poecilia* (*Lebistes*) *reticulata*, seems to be related to fungal infestation (WURMBACH, 1951).

Definite proof, however, of sex reversal as a natural process has been reported for the synbranchiform fish *Monopterus albus* (LIU, 1944; LIEM, 1963), younger and smaller individuals (both laboratory and field specimens) showing female gonads, the larger ones being functional males.

In most families of the Perciformes functional sex reversal occurs, in many species taking place in practically all specimens. In Maenidae protogynous hermaphroditism has been described. According to ZEI (1949) and REINBOTH (1962a) regular change from female to male occurs in *Maena* (*Spicara*) *smaris* and *chryselis*; the larger males showing a different color, which led to taxonomic confusion.

In the Serranidae both the synchronous and the protogynous type of functional hermaphroditism are well-represented (see survey on 33 species in ATZ). In a number of serranid species the ovo-testes is only functional during the transitional phase from female towards male. At first, these have erroneously been reported as a proof of permanent hermaphroditism (already ARISTOTLE, OVID, PLINY and RONDELET mentioned intersexual sea basses). Notwithstanding the temporary, synchronous maturity of the ovarian and testicular parts of the gonad, self-fertilization is not frequent (ATZ, 1965).

In most serranid species the bisexual configuration is clearly visible on gross inspection (REINBOTH, 1962a). The basic structure is ovarian; the testicular part is limited to two bands on the ventro-lateral wall of each lobe. In the gonads of the groupers and their relatives, however, no localization of ovarian and testicular tissues occurs. In *Sacura margaritacea* (REINBOTH, 1963) the females are smaller than the males and they differ also in coloration and shape of the dorsal fin. Here, the testicular portion of the ovo-testes is small in the "female" phase, yet spermiogenesis

takes place. Later on, the testicular portion enlarges while the ovarian degenerates.

In Sparidae protogynous, protandrous as well as synchronous hermaphroditism occur (see survey on 18 species in ATZ). Unlike the serranid ovo-testis, in the sparid organ the ovarian and the testicular parts are clearly separated by connective tissue. OKADA (1965) described how *Mylio macrocephalus* starts bisexual, but then develops separate sexes, with a strong tendency for protandry.

As to our Labridae: the presence of small females and large males has repeatedly been reported, but the question of sex reversal has barely been touched upon in literature, some authors considering them as protogynous. Only a few well-authenticated reports on gonad transformation are on record.

LÖNNBERG e.a. (1937) considered *Labrus bimaculatus* as a protogynous species. In two specimens with intermediate colors the small gonad contained both eggs and sperm. Among 36 large specimens in terminal colors dissection showed only one intersex; the rest had normal testes. SORDI (1962) found in *Labrus merula* and *turdus* reversal of sex a common, natural process, in the former species occurring in about half of the specimens, in the latter in all. He concluded: "The presence of a few scattered residual oocytes in the gonads showing either initial or advanced spermatogenetic processes shows that the passage from the female to the [male] phase takes place through a total substitution of female with male sexual elements in all territories of the gonad."

KINOSHITA (1934) reported for the Japanese wrasse *Halichoeres poecilopterus* the first color intermediate. Externally the gonad seemed to be a testis, but histological investigation revealed egg-like cells distributed over the whole tissue. OKADA (1962) concluded after observations of external transformation of color and drastic changes of the gonad that this species, hatched out as a female, dies as a male, sex reversal being an common phenomenon.

BACCI & RAZZAUTI (1958) considered *Coris julis* as a protogynous species. REINBOTH (1957), examining a large number macroscopically and histologically, only found few specimens in obviously intersexual stages. He distinguishes "primary" and "secondary" males, i.e. fish that were already male at smaller size, and those that first had gone through a female stage. He considers the shape of the ductus efferens as an important item for distinguishing these two types of males. Specimens in a transitional stage from female towards male either show intermediate or already turquoise terminal phase colors.

Thalassoma pavo is another dichromatic labrid REINBOTH (1962) investigated. Dissection of 65 gonads did not give any concrete proof of sex reversal. Neither could he find any confirmation of his two types of male theory.

LOUISE STOLL (1955), investigating *Thalassoma bifasciatum*, supposed it to be protogynous, FEDDERN (1965) considers sex reversal but could not prove it. BÖHLKE & CHAPLIN (1968) mention that possibly the bluehead colored males are all sexually reversed females.

ATZ (1965) gives the reason why the wide-spread phenomenon of hermaphroditism in fishes has been unsufficiently known and investigated up to now: "Most hermaphroditic fish are marine, and marine fish are notoriously loath to exhibit sexual activity in cap-

tivity. Moreover, it has been nearly impossible to collect examples in all the different stages of sexual development, both ontogenetic and seasonal. As a result, we do not have a single reasonably complete sexual history of an hermaphroditic marine fish."

The present study is an attempt to do so.

Mechanisms of sex determination and differentiation

Generally, in the process of sex realization two agents are concerned, sex differentiation into female or male, and the development of secondary sexual characteristics. The former is often considered to be genetically determined, while the latter are said to have an endocrine origin. In the Labridae the situation is rather intricate since reversal of sex occurs as a normal phenomenon, and the mere fact of having testes does not imply in all species the occurrence of alleged secondary male sexual characteristics such as large size, terminal phase colors or elongate fins.

The mechanisms involved in inducing sex differentiation are still poorly understood. In higher vertebrates and many insects sex chromosomes have been found, different from each other in size as well as in genetic content; sex determination depends on the fertilization by an X or Y spermatozoon (or on a Z or W egg in birds). Studies of numerical aberrations of the sex chromosomes (XO, XXY) indicate that the presence of the Y chromosome causes the differentiation of the testis, which further induces male characteristics. No evidence, however, of particular genes on the Y chromosome or of concrete genes related to sex has yet been found. (For a survey of this subject see OHNO, 1967; LECHER & SIGNORET, 1969).

GORDON (in BROWN, 1957), summarizing sex determination in fish insists on a stable, genetical sex determining mechanism in fish. Morphologically recognizable sex chromosomes seem to be absent in fishes, yet sex-associated charactersistics have been mentioned and explained by supposing heterogamety.

In numerous breeding studies – performed in a taxonomically rather limited group – sex-associated characteristics have been studied and explained by alleged heterogamety. Thus SCHMIDT (1920) and WINGE (1927–1947) (cf. BACCI, 1957; BROWN, 1957) distinguish nine characteristics in guppies, *Lebistes reticulatus*, which are inherited only from father to son and suppose that these are located on an Y chromosome. GALLIEN (1948) concludes from hormone experiments that there must

be genes on some Y chromosome. However, it was indicated how little differentiation the sex chromosomes must have. In selective breeding experiments it was possible to accumulate sex-determining "genes" on a pair of autosomes (WINGE, 1934).

Breeding experiments also indicated the presence of an XX–XY sex mechanism in the Japanese *Oryzias latipes* (AIDA, 1921; 1930; 1936) and the goldfish *Carassius auratus* (YAMAMOTO e.a., 1968). The X and Y, however, share many gene loci and the Y can substitute for the X (OHNO, 1970; see also YAMAMOTO, 1961). Moreover, a considerable amount of crossing-over has been reported for "sex chromosomes" in fish (WINGE, 1923, AIDA, 1921, 1930; GORDON, 1947).

KOSSWIG e.a. (1930–1959) studying *Xiphophorus helleri* and *maculatus*, could not manage to demonstrate the existence of distinct sex chromosomes (cf. BACCI, 1965). They discussed the balance between a number of male and female autosomal genes as sex determining.

GORDON (1951) described for *X. maculatus* a WY–YY situation, in which the female is heterogametic. According to KALLMAN (1970) there seem to be not one but two sex determining chromosomes. In natural populations the females have the genotype WY, WX or XX, the males XY or YY, of which W and Y show crossing-over. He explains the erroneous results of former studies in which commercially available fishes were used by relaxation of selection; then crossing-over may tend to equalize the frequency of marked W and Y chromosomes.

Nor, in cytological studies have heteromorphic sex chromosomes in fishes been demonstrated until now. Recently the techniques of analyzing the karyotypes of somatic cells have been improved considerably and a great diversity of species, belonging to quite different groups, has been studied (OHNO & ATKIN, 1966; TAYLOR, 1967; OHNO e.a., 1967; MURAMOTO e.a., 1968; OHNO e.a., 1969; WOLF e.a., 1969).

A method was developed to express DNA values as percentages of the mammalian DNA content (placental mammals constitute one uniform group with regard to DNA contents) (OHNO e.a., 1964; ATKIN e.a., 1965). Accordingly, OHNO & ATKIN (1966) analyzed comparative DNA values and chromosome complements of eight species of fishes. They found fairly distinct categories, viz. the DNA value of the lungfish showed close kinship to that of Caudata; the trout resembled Crocodilia; the goldfish resembled Squamata and Aves, while the swordtail, sole and turbot with only about 20% of the typical complement in mammals, were regarded as the retainers of the original vertebrate genome. Investigations by OHNO e.a. (1968) and MURAMOTO e.a. (1968) revealed that so called advanced teleost fish such as the Percomorphi maintained the original diploid complement of 48 acrocentrics with little or no modification and increased the original DNA content only slightly.

These results support the suggestion by OHNO & ATKIN that during the course of vertebrate evolution a progressive increase in DNA values was accomplished not only by a regional duplication of chromosomal segments but also by polyploidization. Polyploidy, however, is incompatible with the well-established chromosomal sex-determining mechanism (OHNO, 1970). OHNO c.s. concluded that gene duplication by polyploidization must have occurred at the initial stages of vertebrate evolution,

while vertebrates were still aquatic or amphibious and the "sex chromosomes" were undifferentiated enough for the X and Y or the Z and W to be still nearly genetical equivalents of each other. Once the chromosomal sex-determining mechanism was firmly established, further polyploidization became impossible.*

These cytological investigations indicate that heteromorphic sex chromosomes hardly can be expected in Pisces. Consequently, it may be supposed that in teleosts all "sex genes" are scattered among the autosomes. Whether this in any way is related to the great diversity in sex realization in labrids (and in fish in general) remains an open question. Studies on proper genetic models should be started.

Endocrine aspects of sex differentiation are discussed in the following chapter.

* For comparison: In the class Reptilia chromosomal sex-determination is still in an initial stage. In the order Crocodilia no evidence can be found for morphologically distinguishable sex chromosomes (COHEN e.a., 1970). PENNOCK e.a. (1969) detected a very minute Y chromosome in lizards. In snakes diverse stages of heteromorphic sex chromosome differentiation have been found, ranging from absence of heteromorphism in either sex to striking differences in form and size of the sex chromosomes (BEÇAK e.a., 1969).

XIII. GROWTH AND HORMONE EXPERIMENTS

Of the fishes collected an at random selected number of approximately 1100 specimens was kept alive to study behavior and eventual color changes, and to experiment on color and growth. Those data not dealt with in the other chapters are discussed briefly below.

The fishes were kept in indoor tanks supplied with a continuous current of sea water pumped up directly from the sea. The tanks contained some centimeters of sand, pieces of living coral and stones, all from areas frequented by wrasses. The labrids were fed daily with canned dog food, supplemented with sea urchin meat or pieces of fresh fish.

During the first days of captivity the wrasses were shy and frightened, dashing away in the sand or hiding under stones. After some days they usually became more adjusted and started to swim around. In plain tanks only filled with sea water and without sand or stones, the fish stayed obviously more and longer scared. It was better not to keep too many labrids together in a small tank; in the large outdoor tanks they did not seem to behave differently from the wrasses observed in the sea.

It had a soothing effect when newly caught wrasses were placed in glass tanks next to a glass tank in which already adapted labrids were kept, or to place an adapted labrid among the newcomers. When fed, the adapted animal reacted immediately on the bait and this stimulated the fresh fish to start picking at the food. *Th. bifasciatum* was sooner adjusted than specimens of *H. bivittatus* which remained shy for a longer time and were more scared when fed for the first time. Placing one or two Blueheads among the Slippery Dicks proved to quiet them down.

The mortality was at first considerable, especially the first days of captivity. Fast, gracious twirlings around were hardly displayed; the fish appeared to take longer rests on the bottom than those observed in the sea; they seemed to suffer from being deprived of their free rambling life. The state of depression caused by captivity is also reflected in the reproductive organs. Gonads of wrasses kept for more than a few

days in small tanks never had the same prosperous aspect and size of freshly collected labrids killed the same day.

The captivity stress makes wrasses not very appropriate for experimental studies. Nevertheless some research has been performed. Unexpected mishaps repeatedly impeded the continuation of the experiments. This, together with the stress reaction on captivity – with as utmost consequence for many an early death – made it seldom possible to continue experiments for long. Hence the results are only few and not absolutely reliable.

During the first days in captivity the colors are pale and dull, faded to inconspicuous shades. Later on, reversible fluctuations of the body hues could be observed, especially when the fish were fed.

In subsequent studies a total of about 500 wrasses of diverse body lengths were kept for weeks, sometimes even for months. Nevertheless, only a very few spontaneous cases of color change from one phase towards the succeeding phase have been observed. These have been described in Chapter VI.

Growth studies

The present author tried to read the rings in scales and otoliths as a check on age. However, no real fluctuations could be distinguished, making the interpretation so hazardous that this method was rejected. Growth being an interesting item in discussing bodylength and sex, growth rates of different size and color groups were studied in about 400 specimens.

Increase in length not necessarily concurs with increasing age. Often fish of the same size prove to be of different ages. Growth rate is strongly influenced by environmental factors such as temperature and food supply; yet, the growth rate potentials are said to be genetically determined (Weatherly, 1966). Heredity also accounts for differences in growth rates between the sexes in many species of fish. *Xiphophorus* and *Lebistes* males attain a specific size while the females continue to grow after maturing (Margaret Brown, 1957). In many other species as well, females are larger than the males (this in contrast to the labrids).

In wrasses size is an important parameter: color, sex ratio and gonadal activity are clearly related to body length. No data are available on the growth rates of labrid species. Only Soljan (1930b) reported for *Crenilabrus ocellatus* different growth rates in the two types of males. Males born at the end of the spawning season would grow faster and develop into the large, brightly colored nestbuilding males. Males born early in the spawning season would grow more slowly, stay smaller and keep the similar less colorful pattern as the female.

Of groups of fish of approximately similar length, total length and some other body sizes were measured before and after a certain period of time. In a number of experiments the fish were, after remeasuring, put back for a second growth observation. As the number of specimens in all experiments was strongly decreased on the moment of remeasuring, these fish were supplemented by newly caught fish of approximately the same size.

At the same time, experiments were performed under slightly different environmental conditions. That is, during a certain period fish of similar size groups were put in glass aquaria or in large, but shallow concrete tanks inside the laboratory. In Curaçao also three large concrete outdoor tanks were available. For remeasuring, the water had to be let out of the tanks and the wrasses caught and dug out of the sand on the bottom. This had the disadvantage that some labrids escaped remeasuring.

Moreover, in Puerto Rico two large cages (3.5 × 1.5 × 1.25 m), in Curaçao one cage (1.5 × 1.0 × 1.25 m) were made for use on the bottom of the sea.

They were made of chicken wire; those of Puerto Rico of wire of two different mesh-sizes, tested in connection with the size of the objects of study. After the cages were placed on the sea bottom, a thick layer of sand was put on the bottom via a door at the top of the cage, large enough to enable a human being to go in and out. Big pieces of coral and stones, together with sea urchins and other coral inhabitants simulated normal field conditions. Through a small hatch the fishes were brought inside. Though the fish were picking at the corals, rocks and sand just as wrasses under normal conditions, the caged fish were fed every two days (canned dog food and cut fish meat).

Unfortunately, there was heavy growth of algae on the wire, thus reducing light intensity and no doubt, also reducing water circulation. As wrasses need fresh and clear water the rather great mortality, especially of *Th. bifasciatum* may have been caused by this factor. Several times the wire was scrubbed, but this again influenced temporarily the clarity of the water.

When at the end of the experiment the heavy cages were lifted – in Puerto Rico by the aid of the 65 ft. research vessel of the institute – the sand on the bottom fell through the meshes, so there were no difficulties in finding the wrasses again.

The recults obtained for *Th. bifasciatum* and *H. bivittatus* are represented in Tables 33 and 34. Of the other species too few specimens could be remeasured to give reliable information. In Fig. 24 per size group studied the average increment in mm per total length

TABLE 33

GROWTH STUDIES IN *Thalassoma bifasciatum*

* all or (*) some specimens in terminal phase 4 colors.

Place	Start of experiment	N	Mean sizes at start of the study (cm) TL ± s	SL ± s	head ± s	Da ± s
CURAÇAO indoor tank	18.VII	4	3.04 ± 0.12	2.43 ± 0.11	0.81 ± 0.02	0.51 ± 0.03
	18.VII	4	3.91 ± 0.13	3.18 ± 0.09	1.03 ± 0.03	0.65 ± 0.03
	8.VI	3	4.44 ± 0.19	3.72 ± 0.18	1.14 ± 0.04	0.68 ± 0.03
	18.VII	12	5.17 ± 0.33	4.28 ± 0.30	1.37 ± 0.10	0.83 ± 0.06
CURAÇAO outdoor tanks	16.XII	3	4.25 ± 0.21	3.73 ± 0.23	1.05 ± 0.01	0.69 ± 0.03
	18.VII	10	4.52 ± 0.32	3.71 ± 0.26	1.17 ± 0.11	0.74 ± 0.05
	24.I	5	5.24 ± 0.24	4.55 ± 0.25	1.28 ± 0.09	0.92 ± 0.08
	5.VI	13	5.44 ± 0.30	4.40 ± 0.21	1.36 ± 0.07	0.82 ± 0.06
	18.VII	23	5.67 ± 0.30	4.67 ± 0.27	1.46 ± 0.08	0.89 ± 0.05
	16.XII	4	5.92 ± 0.26	5.22 ± 0.24	1.45 ± 0.05	1.03 ± 0.08
	12.I	5	6.09 ± 0.15	5.28 ± 0.15	1.51 ± 0.06	1.08 ± 0.09
	3.II	8	6.32 ± 0.32	5.52 ± 0.27	1.60 ± 0.08	1.16 ± 0.06
	18.VII	16	6.34 ± 0.13	5.26 ± 0.13	1.65 ± 0.06	1.00 ± 0.05
	4.VI	13	6.36 ± 0.24	5.29 ± 0.21	1.59 ± 0.06	0.98 ± 0.06
	12.I	1	6.79	5.90	1.66	1.09
	14.VII	5	7.46 ± 0.23	6.20 ± 0.18	1.93 ± 0.05	1.22 ± 0.04
	7.VI	6	7.53 ± 0.35	6.34 ± 0.34	1.92 ± 0.11	1.17 ± 0.06
	6.VI	3*	8.70 ± 0.03	7.29 ± 0.06	2.24 ± 0.08	1.40 ± 0.07
	16.VII	1*	8.94	—	2.23	1.48
	25.I	5*	9.98 ± 0.90	8.93 ± 0.90	2.50 ± 0.23	1.97 ± 0.14
PUERTO RICO cages in sea	25.II	4	4.70 ± 0.35	3.84 ± 0.29	1.19 ± 0.09	—
	25.II	11	6.10 ± 0.38	5.15 ± 0.39	1.55 ± 0.11	—
	25.II	4	7.99 ± 0.29	6.72 ± 0.24	2.02 ± 0.10	—
	25.II	5*	8.34 ± 0.45	7.01 ± 0.39	2.14 ± 0.12	—
	25.II	5*	9.89 ± 0.62	8.56 ± 0.37	2.61 ± 0.10	—
CURAÇAO cage in sea	23.VII	14	5.88 ± 0.28	4.88 ± 0.25	1.51 ± 0.06	0.92 ± 0.05
	23.VII	6*	8.98 ± 0.59	—	2.25 ± 0.17	1.46 ± 0.13

End of experiment	N	Mean sizes at the end of the study (cm) TL ± s	SL ± s	head ± s	Da ± s	Experiment in number of days	Gain (cm)/ per 30 days
21.VIII	2	3.75	3.06	1.03	0.65	35	0.61
21.VIII	2	4.99	4.14	1.26	0.81	35	0.93
16.VII	2	4.91	4.04	1.27	0.83	39	0.36
21.VIII	8	5.45 ± 0.37	4.53 ± 0.29	1.45 ± 0.12	0.87 ± 0.06	35	0.24
9.I	2	4.54	4.02	1.21	0.84	25	0.35
21.VIII	8	5.04 ± 0.47	4.13 ± 0.38	1.32 ± 0.11	0.79 ± 0.06	35	0.45
1.II	5	5.49 ± 0.34	4.75 ± 0.35	1.38 ± 0.10	0.99 ± 0.08	9	0.83
12.VII	6	5.72 ± 0.20	4.68 ± 0.25	1.50 ± 0.06	0.88 ± 0.06	38	0.22
21.VIII	5	5.84 ± 0.26	4.83 ± 0.32	1.52 ± 0.04	0.93 ± 0.05	35	0.15
9.I	4	6.19 ± 0.20	5.44 ± 0.17	1.57 ± 0.09	1.14 ± 0.08	25	0.32
1.II	4	6.32 ± 0.18	5.47 ± 0.17	1.58 ± 0.06	1.19 ± 0.02	21	0.33
26.IV	3(*)	6.71 ± 0.30	5.84 ± 0.24	1.74 ± 0.06	1.08 ± 0.04	81	0.15
21.VIII	5	6.56 ± 0.19	5.50 ± 0.15	1.71 ± 0.06	1.06 ± 0.08	35	0.19
12.VII	9	6.67 ± 0.28	5.55 ± 0.21	1.72 ± 0.05	1.04 ± 0.06	39	0.24
1.II	1	6.81	5.96	1.71	1.18	21	0.04
21.VIII	4(*)	7.79 ± 0.28	6.51 ± 0.26	1.96 ± 0.10	1.27 ± 0.06	39	0.25
12.VII	3	7.62 ± 0.47	6.39 ± 0.39	2.00 ± 0.10	1.24 ± 0.07	36	0.08
13.VII	1*	9.00	7.56	2.34	1.53	38	0.24
21.VIII	1*	9.27	—	2.42	1.56	37	0.27
1.II	4*	9.93 ± 0.87	8.85 ± 0.82	2.52 ± 0.20	1.99 ± 0.11	8	—
5.IV	1	5.48	4.47	1.35	—	39	0.60
5.IV	4	6.38 ± 0.10	5.34 ± 0.16	1.62 ± 0.06	—	39	0.22
5.IV	3(*)	8.13 ± 0.56	6.83 ± 0.50	2.06 ± 0.19	—	39	0.11
5.IV	3*	8.86 ± 0.27	7.53 ± 0.35	2.28 ± 0.06	—	39	0.40
5.IV	2*	10.24	8.74	2.84	—	39	0.27
27.VIII	4	6.24 ± 0.33	5.18 ± 0.28	1.56 ± 0.11	1.01 ± 0.14	36	0.30
27.VIII	2	9.60	—	2.42	1.64	36	0.52

TABLE 34

GROWTH STUDIES IN *Halichoeres bivittatus*

Place	Start of experiment	N	Mean sizes at the start of the study (cm) TL ± s	SL ± s	head ± s	Da ± s
CURAÇAO indoor tank	16.VII	3	3.51 ± 0.19	2.90 ± 0.15	0.97 ± 0.05	0.66 ± 0.04
	8.VI	7	4.06 ± 0.34	3.32 ± 0.29	1.12 ± 0.06	0.68 ± 0.06
	16.VII	4	5.18 ± 0.21	4.27 ± 0.21	1.39 ± 0.06	0.88 ± 0.05
	8.VI	7	8.79 ± 0.46	7.38 ± 0.43	2.28 ± 0.14	1.45 ± 0.09
	16.VII	8	9.39 ± 0.49	7.86 ± 0.38	2.47 ± 0.14	1.58 ± 0.11
CURAÇAO outdoor tanks	12.VII	5	4.49 ± 0.19	3.74 ± 0.19	1.25 ± 0.06	0.74 ± 0.09
	16.XII	5	4.87 ± 0.32	4.25 ± 0.26	1.29 ± 0.08	0.85 ± 0.09
	4.VI	19	4.93 ± 0.36	4.06 ± 0.29	1.30 ± 0.10	0.79 ± 0.06
	12.VII	9	5.50 ± 0.34	4.52 ± 0.31	1.48 ± 0.09	0.89 ± 0.06
	3.I	4	5.55 ± 0.45	4.87 ± 0.39	1.49 ± 0.11	1.01 ± 0.09
	16.I	3	5.57 ± 0.39	4.86 ± 0.33	1.49 ± 0.08	1.00 ± 0.07
	1.II	3	5.84 ± 0.41	5.13 ± 0.35	1.49 ± 0.07	1.10 ± 0.07
	16.I	4	6.63 ± 0.44	5.77 ± 0.35	1.76 ± 0.13	1.20 ± 0.10
	16.XII	9	6.94 ± 0.78	6.15 ± 0.72	1.80 ± 0.18	1.20 ± 0.16
	25.IV	2	7.02	5.79	2.00	1.18
	1.II	4	7.03 ± 0.13	6.27 ± 0.17	1.80 ± 0.09	1.28 ± 0.08
	4.VI	5	7.24 ± 0.45	6.05 ± 0.37	1.91 ± 0.04	1.17 ± 0.08
	12.VII	9	7.78 ± 0.40	6.63 ± 0.31	2.03 ± 0.12	1.27 ± 0.11
	16.I	10	8.63 ± 0.45	7.67 ± 0.41	2.24 ± 0.17	1.64 ± 0.13
	1.II	9	8.67 ± 0.43	7.69 ± 0.41	2.27 ± 0.23	1.66 ± 0.14
	16.XII	11	8.86 ± 0.45	7.98 ± 0.58	2.26 ± 0.15	1.59 ± 0.10
	3.I	5	9.05 ± 0.37	8.06 ± 0.32	2.35 ± 0.09	1.67 ± 0.08
	4.VI	10	9.85 ± 0.52	8.28 ± 0.37	2.52 ± 0.11	1.63 ± 0.08
	12.VII	13	10.07 ± 0.35	8.44 ± 0.29	2.61 ± 0.13	1.68 ± 0.09
	18.I	9	10.28 ± 0.34	9.11 ± 0.37	2.71 ± 0.11	1.98 ± 0.15
	1.II	8	10.35 ± 0.40	9.21 ± 0.39	2.67 ± 0.14	2.01 ± 0.12
	16.XII	15	10.43 ± 0.38	9.27 ± 0.32	2.69 ± 0.12	1.98 ± 0.18
	3.I	6	10.51 ± 0.47	9.30 ± 0.36	2.80 ± 0.17	2.02 ± 0.13
	16.I	9	12.02 ± 0.65	10.77 ± 0.64	3.08 ± 0.14	2.36 ± 0.17
	16.XII	17	12.15 ± 0.79	10.95 ± 0.76	3.14 ± 0.20	2.41 ± 0.20
	16.I	1	14.47	13.18	3.77	3.20
PUERTO RICO cages in sea	28.II	27	6.11 ± 0.61	5.07 ± 0.52	1.61 ± 0.16	—
	28.II	38	8.05 ± 0.44	6.71 ± 0.37	2.11 ± 0.14	—
	28.II	42	11.21 ± 0.61	9.48 ± 0.48	2.97 ± 0.18	—
CURAÇAO cage in sea	23.VII	3	6.45 ± 0.31	5.35 ± 0.29	1.66 ± 0.11	1.06 ± 0.09
	23.VII	3	7.78 ± 0.26	6.47 ± 0.24	2.03 ± 0.09	1.31 ± 0.11
	23.VII	12	8.61 ± 0.23	7.28 ± 0.23	2.22 ± 0.07	1.40 ± 0.06

End of experiment	N	Mean sizes at the end of the study (cm) TL ± s	SL ± s	head ± s	Da ± s	Experiment in number of days	Gain (cm)/ per 30 days
21.VIII	2	4.46	3.68	1.20	0.76	37	0.77
16.VII	4	5.18 ± 0.21	4.27 ± 0.21	1.39 ± 0.06	0.88 ± 0.05	39	0.86
21.VIII	3	5.77 ± 0.26	4.76 ± 0.22	1.53 ± 0.07	0.96 ± 0.05	37	0.48
16.VII	4	9.32 ± 0.54	7.78 ± 0.54	2.47 ± 0.17	1.59 ± 0.14	39	0.41
21.VIII	5	9.69 ± 0.51	8.08 ± 0.37	2.56 ± 0.19	1.66 ± 0.16	37	0.24
21.VIII	4	5.32 ± 0.26	4.48 ± 0.27	1.44 ± 0.04	0.93 ± 0.07	41	0.61
9.I	4	5.55 ± 0.45	4.87 ± 0.39	1.49 ± 0.11	1.01 ± 0.09	25	0.82
12.VII	9	5.26 ± 0.47	4.34 ± 0.37	1.44 ± 0.11	0.86 ± 0.08	39	0.25
21.VIII	8	6.13 ± 0.32	5.09 ± 0.25	1.62 ± 0.08	1.00 ± 0.04	41	0.46
16.I	4	5.75 ± 0.24	5.01 ± 0.22	1.55 ± 0.09	1.05 ± 0.06	14	0.43
1.II	3	5.84 ± 0.41	5.13 ± 0.35	1.49 ± 0.09	1.10 ± 0.07	17	0.48
25.IV	2	7.02	5.79	2.00	1.18	84	0.42
1.II	4	7.03 ± 0.13	6.27 ± 0.17	1.80 ± 0.09	1.28 ± 0.08	17	0.71
9.I	4	7.29 ± 0.57	6.46 ± 0.57	1.88 ± 0.12	1.31 ± 0.06	25	0.42
6.V	1	7.10	5.84	1.90	1.17	12	0.25
25.IV	2	7.81	6.73	2.10	1.27	84	0.28
12.VII	2	7.61	6.81	1.98	1.23	39	0.29
21.VIII	7	8.12 ± 0.51	6.78 ± 0.41	2.14 ± 0.14	1.34 ± 0.09	41	0.25
1.II	9	8.67 ± 0.43	7.69 ± 0.41	2.27 ± 0.23	1.66 ± 0.14	17	0.09
25.IV	6	8.99 ± 0.43	7.98 ± 0.39	2.46 ± 0.13	1.54 ± 0.13	84	0.11
9.I	5	9.05 ± 0.37	8.06 ± 0.32	2.35 ± 0.09	1.67 ± 0.08	25	0.23
16.I	4	9.15 ± 0.35	8.15 ± 0.32	2.45 ± 0.11	1.73 ± 0.06	14	0.21
12.VII	9	9.92 ± 0.46	8.30 ± 0.45	2.59 ± 0.15	1.63 ± 0.12	39	0.05
21.VIII	6	10.15 ± 0.46	8.51 ± 0.41	2.65 ± 0.18	1.76 ± 0.18	41	0.06
1.II	8	10.35 ± 0.40	9.21 ± 0.39	2.67 ± 0.14	2.01 ± 0.12	15	0.14
6.V	1	10.79	9.00	2.96	1.91	95	0.14
9.I	6	10.51 ± 0.47	9.30 ± 0.36	2.80 ± 0.17	2.02 ± 0.13	25	0.10
16.I	6	10.62 ± 0.40	9.42 ± 0.40	2.80 ± 0.05	2.04 ± 0.16	14	0.24
1.II	8	12.09 ± 0.78	10.73 ± 0.73	3.09 ± 0.17	2.42 ± 0.20	17	0.12
9.I	10	12.30 ± 0.72	11.00 ± 0.62	3.20 ± 0.18	2.48 ± 0.17	25	0.18
1.II	1	14.67	13.30	3.87	3.33	17	0.35
5.IV	26	6.59 ± 0.68	5.48 ± 0.58	1.79 ± 0.21	—	36	0.40
5.IV	27	8.55 ± 0.54	7.12 ± 0.46	2.31 ± 0.15	—	36	0.42
5.IV	19	11.37 ± 0.70	9.57 ± 0.61	3.07 ± 0.19	—	36	0.13
27.VIII	2	7.27	6.06	2.29	1.19	36	0.68
27.VIII	2	8.20	6.86	2.19	1.38	36	0.35
27.VIII	7	9.10 ± 0.26	7.63 ± 0.26	2.43 ± 0.12	1.55 ± 0.10	36	0.41

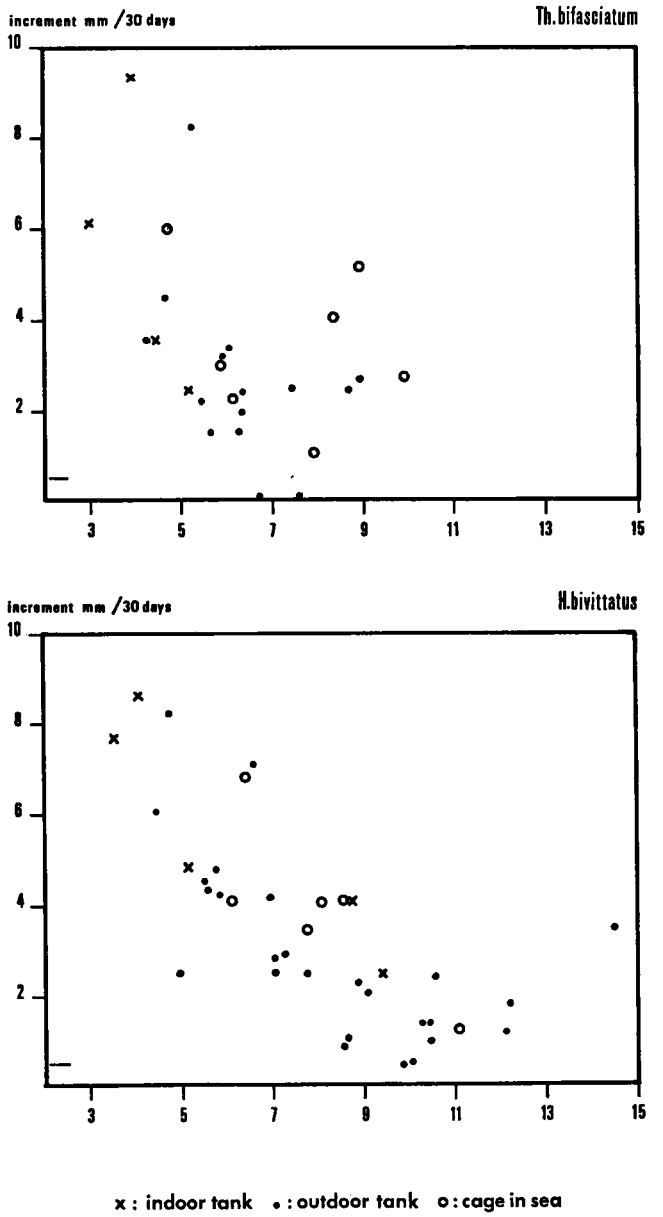


Fig. 24. Growth velocity. Increment in length (mm) per total length TL (cm) at the start of the growth experiment in *Thalassoma bifasciatum* and *Halichoeres bivittatus*; all results converted in gain of length per 30 days.

at the start has been given, all results converted in gain of length per 30 days.

Though the graphs are a compilation of data of experiments under different environmental conditions and various periods, for both species the results tend to a certain general pattern. Apparently the artificial environment did not really interfere with growth, though, especially in *H. bivittatus*, the results obtained in the large outdoor tanks are all lower as compared with the other data. Yet, the overall trend is not essentially different.

The growth velocity slows down rapidly when the fish are growing larger. In this respect the results do not deviate from the general situation that average growth rates are lower in fish after sexual maturity has been reached (MARGARET BROWN, 1957).

The increment in length is almost zero at the length at which color change starts. Interesting is the rather unusual finding that after this critical period (cf. Chapter XII), there is again an increase in growth rate. In *Th. bifasciatum* this effect is intensified because of the differential growth of the caudal fin, but this trend has also been found when the standard length data were analyzed. A similar, though less pronounced increase of growth rates at larger sizes has been noted in *H. bivittatus*. Thus, an essential part of growth is realised after color changes have taken place. These results emphasize that at the point where color changes are developing an overall internal reorganisation seems to take place; during the occurrence of color change and sex reversal, growth is temporarily minimized.

Figure 25, in which the data from Tables 33 and 34 are summarized, is an illustration of the allometries discussed in Chapter VII. Again, the results proved hardly to mutually deviate, notwithstanding the different environmental conditions during the experiments, so it may be assumed that they represent the natural, normal progress.

HORMONE EXPERIMENTS

To investigate possible mechanisms causing the striking alterations in color during growth, some endocrinological experiments have been performed.

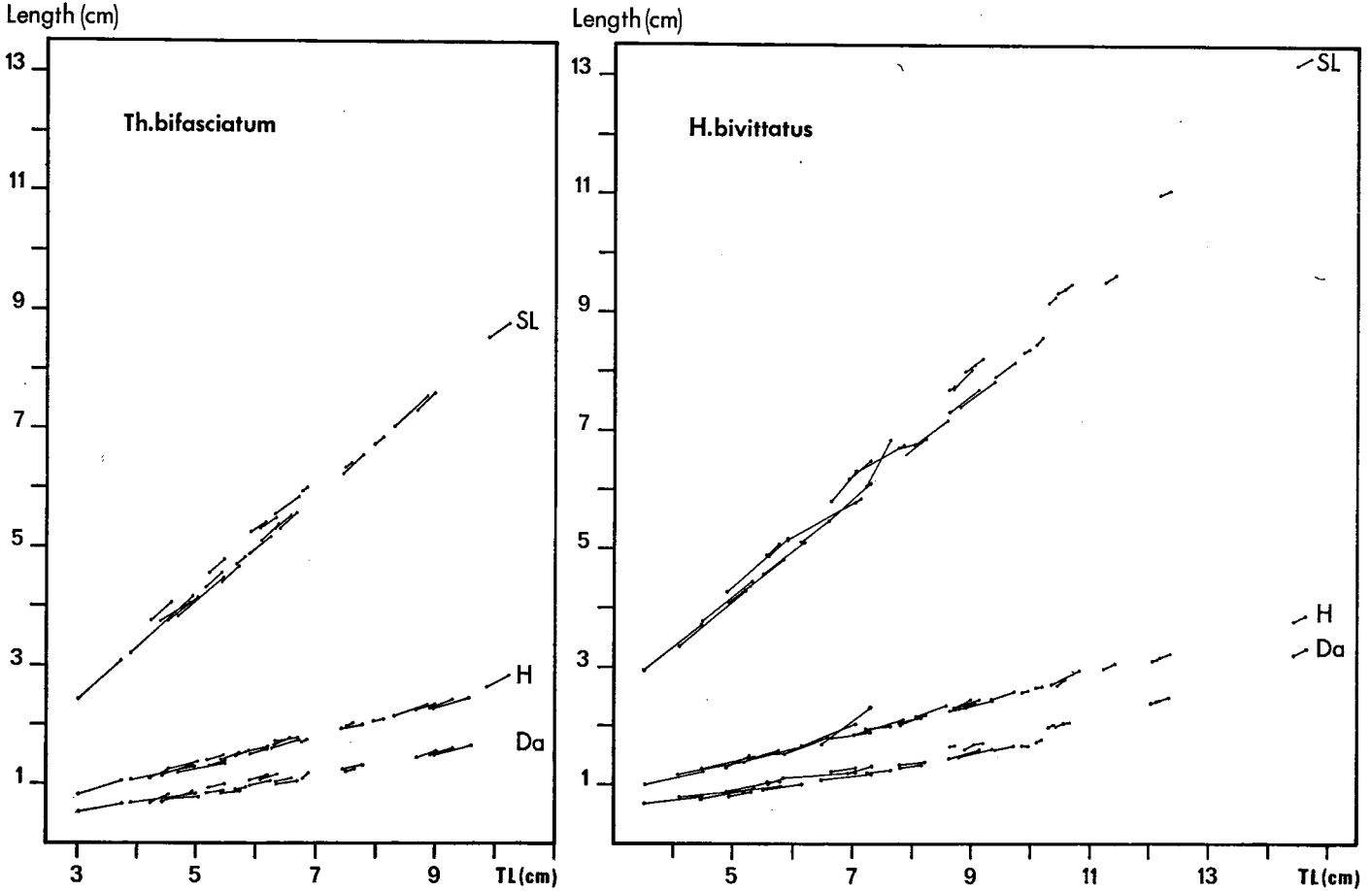


Fig. 25. Allometries of growth. Growth curves of standard length (SL), head length (H) and anal depth (Da), all relative to total length (TL), summarized from a number of growth experiments in *Thalassoma bifasciatum* and *Halichoe res bivittatus*.

History

Fishes possess a well-developed endocrine system, but several points of the endocrine control on reproduction still remain to be settled. (For reviews see DODD, 1960a, b; ATZ, 1964; OHNO, 1967). The gonads play a decisive role in the development of the morphogenesis of sex differentiation. It is generally assumed that this is achieved by hormones, produced by the gonads.

Definite proof has been given that secondary sexual characteristics depend on both gonadal hormones and on gonadotrope hormones from the pituitary. Yet, relatively few studies have been made on pituitary physiology. Only the gonadotropic activity of Cypriniformes pituitary has been the object of investigation; on Perciformes scanty information is available. Gonadectomies performed on various species of teleosts resulted in disappearance or complete absence of secondary sexual characteristics as well as in change of sexual behavior. In various procedures it has been shown that fishes are sensitive to mammalian or synthetic sex steroids.

Cypriniformes and Cyprinodontiformes have been frequently used as test animals. ESSENBERG (1926) working on Poeciliidae postulated that in *Xiphophorus* and *Lebistes* sex differentiation is not genetically determined but directed by hormones. In these fishes the gonopodium and certain pigment formations of the male form well-marked secondary sexual characteristics. Mammalian testosterone stimulated the development of these features in many cases (GALLIEN, 1948; GAISER, 1952). However, sometimes atypical fin formations were induced, the typical male pigmentation did not always appear, and also estrogen and chorionic gonadotropin induced masculinisation of female swordtails. In the gobid fish *Pterogobius zonoleucus* intraperitoneal injections of androgens gave rise to marked elongation of dorsal spines and the enlargement of urogenital papillae (EGAMI, 1959).

Next to side effects on morphology also drastic changes of the gonads have been reported, such as development of testicular tissue and regression and absorption of ovarian tissue in females after testosterone treatment; pregnant females of life-bearing species absorbed the eggs or aborted (cf. ATZ, 1964). In a few cases even complete sex reversal could be achieved by hormone treatment. Mostly this has been from female sex towards the male sex. Only in a few cases has a sex reversal in the opposite direction been reported (BALDWIN e.a., 1939; YAMAMOTO e.a., 1968). As mentioned in Chapter XII, most experiments were performed on fish from commercial stocks, in which sex is inbalanced due to some hybridization and fungal infestation. This reduces the reliability of the results. Moreover, these species are rather remote from the Labridae.

On members of the Perciformes, in which (functional) hermaphroditism and reversal of sex have been reported as common, natural phenomena, relatively few endocrinological experiments have been performed. The normally hermaphroditic *Serranus hepatus* was used for the first experiment. After being kept in sea water to which estrone had been added, both the ovarian and the testicular portions of the gonad appeared to be stimulated (PADOA, in ATZ, 1964). REINBOTH (1962) found that neither injections of testosterone nor estradiol to three *Serranus* species had any specific masculinizing or feminizing effect. Testosterone even had a rather paradoxical effect as spermiogenesis became only slightly intensified while many oocytes

started to develop. The intramuscular injections of pituitary suspensions by REINBOTH & SIMON (1962) on *S. cabrilla* did not show any effect. In the protandrous sparid *Sparus auratus* REINBOTH tried the effect of estrogen on sexually still indifferentiated specimens; both the female as the male development were suppressed. In the protogyn maenid fish *Maena maena* however, testerone treatment resulted in external and internal masculinization; colors and gonads changed drastically, resembling the transformation process of the natural sex reversal in this species. OKADA (1965b) found after subcutaneous implantation of testosterone in immature specimens of the sparid *Mylio macrocephalus*, marked stimulation of the testicular part.

Several labrid species have been used for experiments. KINOSHITA (1935–1938) studied in *Halichoeres poecilopterus* the effects of gonadectomy upon color. When in large terminal colored fish both testis lobes were removed, the fish rapidly lost its bright blue coloration and adapted a pattern, similar to that of the first adult phase of this species. Iridophores, melanophores and erythrophores degenerated and finally disappeared, while xanthophores appeared gradually (the reverse of the processes that normally take place during color change towards the terminal phase). In three unilateral castrated males the terminal pattern faded away less intensively. Castration of small, first adult color phase males caused retardation of the appearance of the characteristic terminal pattern. In ovariotomized females no change in coloration took place, neither did ovary transplantation provoke any alteration of color. He concluded that the color of the "female" (= the first adult phase) should be a fundamental one, while the brighter "male" color should depend upon endocrinal substances, elaborated in the testis. Later, OKADA (1965a) discussed that, since in *H. poecilopterus* about 14% of the alleged "female" phase are functional males, it cannot be just the mere fact of having testes, that caused the color difference. Yet, OKADA with testosterone induced a change in the pigmentation pattern towards the terminal blue colors, though no sperm production resulted from such treatment.

LOUISE STOLL (1955) administered methyl testosterone to yellow, first adult phase specimens of *Thalassoma bifasciatum*. No matter whether the sex at the moment the experiment started had been female or male, after about four days a slight change in color became apparent. After another three days the entire head acquired blue hues, vague lateral black bars had appeared in the region of the pectoral fins and the tips of the pectorals had become darker. In males the androgenic hormone accelerated the production of mature sperm. Specimens that apparently had been of female sex on the moment of injection, had drastically reduced ovaries filled with degenerating eggs; all over the gonad all stages of spermatogenesis were found.

REINBOTH (1957) gave injections of testosterone to red-brown first adult phase specimens of *Coris julis*. After 13 days all specimens had developed external characteristics of the turquoise terminal phase. After three weeks the first dorsal spines had also become elongated. Oestradiol treatment, however, did not have any effect on the coloration.

Present investigations

Different types of sex hormones, both androgens and estrogens, have been injected into specimens of various sizes and color phases

of several species. The use of selfmade injection solutions (dissolving hormone powder via 96% alcohol in sesam oil) was rejected because of both the time taking procedure of preparation and some after-effects such as a high mortality rate and sore spots at the place of injection. Then use was made of commercial pre-prepared mammalian hormones, dissolved in oil (kindly presented by Organon). The injections were given intraperitoneally in the abdominal area after the wrasses had been placed first into water with a low concentration of an anaestetic that quieted them; controls were injected with aqua destillata. After the injections the fish were hiding and motionless for some hours; most of them soon recovered though. The controls were also at first more passive after the shadow treatment.

As there are no external features to distinguish males from females the sex of the treated fish was not known on the moment of injection. Only in very mature specimens did the ejected gonadal products reveal whether they possessed ovaries or testes.

After treatment with the pre-prepared solutions in a few cases the place of injection was also affected. After a dimenformon injection an open, sore spot developed in a *H. bivittatus* specimen of 14.8 cm TL (ZMA 104.109). Neo-hombreol induced an area provided with numerous capillaries in a *bivittatus* fish of 11.3 cm TL (ZMA 104.112), while in a *bivittatus* of 9.3 cm TL (ZMA 104.111) solid, little grains were present, encysted among the muscular tissue on the spot of treatment, 20 days after sustanon 100 injection.

Male hormones in various solutions and dosages have been given to fish in first adult phase and in terminal phase colors. Besides testosterone (shots of 0.5 and 1 mg), also "durabolin" (10 mg nandrolonfenylpropionate/1 cc oil), "sustanon 100" (a mixture of 3 testosterone esters, prepared for long term treatment) and "neo-hombreol" (10 mg testosterone propionate/1 cc oil) have been used (shots of 0.05–0.1 cc). In some groups the injections were repeated three times, with an interval of two days.

A total of 56 yellow, first adult phase specimens and 5 terminal phase specimens of *Th. bifasciatum* have been treated with androgens. Though a majority died within one to a few days after injection, nevertheless evidence for the influence of mammalian male hormone

on the color of the yellow phase of this species has been found. Externally, the shots did not influence fish that had been in terminal colors on the moment of treatment.

Of the yellow fish 18 survived longer than a week; in 16 of these a change of color towards the intermediate pattern was noticed. Only 2 completely preserved their phase 1 appearance. First signs of color change always show on the head, which may develop bluish colors already two to three days after injection: after at least 7 days, vague darkish cross bars become apparent. The alterations never went further than an intermediate phase 3 pattern; a complete color change towards the extreme terminal bluehead phase has not been produced. A distinct influence on the shape of the caudal fin could not be established. All types of male hormones used induced the described color changes. The dosage used proved to be less relevant. Dissection revealed that also in fishes, that must have been functional females on the moment of injection, color changes had started within a few days.

Histologically, the injected male hormones proved to have had a distinct influence on the *bifasciatum* gonads. Ovarian tissue was in reduction; spermiogenesis was stimulated. Most of the injected fish had gonads that were extra provided with capillary blood vessels. In males the shots had stimulated the testicular tissues; their testes were full of spermiogenesis and mature sperm was present everywhere.

In two females, of 4.1 and 4.7 cm TL (ZMA 104.103, 104.104), who died one day after injections of testosterone the gonads had still the normal aspect of a functional ovary. Females, however, exposed to mammalian male hormones for a longer period, had ovaries in various stages of regression. For instance, 15 days after 0.1 cc sustanon 100 treatment a specimen of then 6.3 cm TL (ZMA 104.105) showed vague indications of change of color; a 7.9 cm TL *bifasciatum* had an already real bluish head (ZMA 104.106); both contained ovaries in overall regression full of loose, strange networks. In a fish of 9.0 cm TL (ZMA 104.107) 8 days after twice repeated durabolin shots (0.1 cc), the head had slightly changed towards bluish hues; the ovary proved to have been really functional, but now was in full reduction; scattered very folded, distorted oolemma's were present; basophilic oocytes were in full regression while among the loose tissue clusters of primordial cells were visible. A specimen of 7.6 cm TL (ZMA 104.108), dissected 9 days after a neo-hombreol injection, showed a similar histological picture; both the head and the ventral part had developed bluish hues.

In some specimens intersexual gonads have been found, namely a regressing ovary containing numerous primordial cells and various stages of spermatogenesis, generally developing from the walls of the (ex-)ovigerous lamellae inwards.

For instance, a first adult phase *bifasciatum* specimen of 7.5 cm TL 5 days after 1 mg testosterone treatment had very small gonads with typical ovarian features

such as thick walls and thick efferent ducts; the more advanced stages of egg development were regressing but the smaller, basophilic oocytes had a rather normal appearance; first stages of sperm formation were invading from the margins of the lamellae (Plate X-b).

The results indicate that color changes are more easily and more rapidly induced in the larger fish of the first adult phase. The somehow fluctuating effects found in fish that had been given a similar treatment may be attributed to the various physiological stages of the wrasses on the moment of injection. Fish, that normally were already near the moment to start sex and color change, may have been more apt to react to administered exogenous male hormones.

Interesting for our discussion on the possible relation between color and sex, is the finding that colors were often found to change, while the gonads were still in clearly ovarian stages and testis tissue was not yet recognizable.

In *Th. bifasciatum* twice a remarkable reaction was seen. A large, terminal phase fish was, one day after treatment with 1 mg testosterone, very actively dancing up and down along the glass wall of its tank, inviting and chasing the two smaller, yellow, also injected specimens present. In another experiment two days after shots of 0.1 cc durabolin a similar reaction was observed. It was not displayed by control fish. Thus, the mammalian male hormones seemed to have stimulated spawning behavior (seldom displayed in captivity).

The various androgens did not cause visible alterations of color in any of the 77 specimens of *H. bivittatus* nor in the 10 specimens of *H. garnoti* treated. Histologically, similar pictures have been found as described for *Th. bifasciatum.*

The hormones immediately affected large, yolk containing maturing eggs; the basophilic oocytes started to regress some days after treatment. This is illustrated in Plate XI-a, showing a section of an ovary of a *bivittatus* specimen of 9.3 cm TL, in first adult phase colors, dissected 4 days after treatment with durabolin (0.07 cc).

Some days after treatment ovaries showed overall regression with resorption of yolk and picnotic nuclei in formerly actually functional ovaries. The regressing ovary of a *bivittatus* specimen of 9.5 cm TL and in intermediate phase 3 colors, contained numerous lobes consisting of loose tissue, bordered with numerous small, basophilic oocytes (Plate X-a, d). Numerous vacuoles characterized the ovary in regression of a *garnoti* female of 9.4 cm TL, in intermediate phase 2 colors (Plate XI-d).

Repeatedly, intersexual stages were found. Plate X-c, e, f shows the gonads of *bivittatus* specimens, treated with 0.05 cc sustanon, such as a specimen of 9.7 cm TL

(ZMA 104.110). First stages of spermiogenesis may develop among numerous resorbing granulosa cells and distorted oolemma's, while the basophilic oocytes are still normal (Plate XI-a). Plate XI-b illustrates how often testicular tissue develops from the margins of the lamellae, invading the formerly ovarian tissue.

A number of injected fish on dissection proved to contain very active testes, full of mature sperm (most probably already male on the moment of injection).

In all three species the effects of sustanon 100 seemed to be more extreme as compared with the other androgens used; labrids are also sensitive to the inbuilt long-term action of this preparation. The induced results are not essentially different from the various stages that normally occur during the process of spontaneous sex reversal (Chapter XII).

In seven series of experiments a total of 49 wrasses were injected intraperitoneally with mammalian female hormones; 42 individuals were in terminal colors (19 *bifasciatum*, 17 *bivittatus* and 6 *garnoti* specimens), while 7 first adult phase *bifasciatum* fish were included. In two series 1 mg oestradiol was injected; in two 0.1 cc "di-pro oleosum" (2.5 mg oestradiolbenzoate + 12.5 mg progesteron/1 cc oil) and in three series 0.05 to 0.1 cc "dimenformon" (1 mg oestradiol-benzoate/1 cc oil) was given (0.05 cc in specimens up to 8 cm TL; 0.1 cc in larger fish).

Of the first oestradiol experiment all specimens died after one day. In a second series on the 4th day after injection in 4 terminal phase *bifasciatum* specimens, the head had become less deep and bright blue; then the experiment was interrupted.

Injections of di-pro oleosum had remarkable effects. Longer than in any other series the 9 wrasses treated stayed very quiet; for more than 24 hours they were resting on their sides breathing very slowly, in an abnormal position for resting or sleeping labrids; then they started a more normal life again. After five days they even were overactively dancing and swimming around as often observed in free living labrids but rarely in captivity and showed great interest in food.

Three pastel colored specimens of *bivittatus* and two terminal phases of *garnoti* did not show any alterations of colors after injection. But 6 days after di-pro oleosum injections of three bluehead *bifasciatum* individuals, one was losing the characteristic features of

its bluehead pattern. The head had become very pale blue, the two dark vertical bars were only vaguely outlined and the posterior part of the body was faded yellowish; the overall impression was no longer that of phase 4, but of intermediate phase 3. The other two blueheads were at that time still in terminal colors. But two weeks after the shots had been given one was also paling towards a phase 3 appearance, though less extremely pronounced. Because of difficulties with the sea water-pump these two paling specimens died and when found it was too late to investigate their small gonads.

After 5 weeks the three specimens of *bivittatus* and one *bifasciatum* were still alive, and then put to death; none of these had lost any of the terminal colors. All had very small gonads. While the total body weight of the Bluehead was 9.2 g, the gonads weighed 0.16 mg; the three Slippery Dicks had a body weight of 9.1, 21.5 and 25.8 g and gonads of only 0.10, 0.20 and 0.14 mg respectively.

The histological aspect of their thin threads of gonads was interesting. Two *bivittatus* specimens of 13 and 14 cm TL both contained small testes threads showing sperm in all stages; among which a relatively greater quantity of youthful spermatogenesis as compared with normal, non-treated fish of this length. The gonads of the third *bivittatus* specimen, 13 cm TL, contained young ovarian tissue in the midst of young spermatogeneous tissue. A similar histological appearance showed the *bifasciatum* fish, 11.3 cm TL, that outwardly had not changed. The gonads proved to consist partly of testicular tissue, full of various stages of spermiogenesis, and partly of young ovarian tissue, full of large, though still basophilic oocytes (Plate XI e).

Since in *Th. bifasciatum* normally no females occur among fish of larger size, in advanced intermediate and terminal colors, the finding of numerous oocytes in a bluehead phase fish was surprising. Sex reversal then seems to be not a strictly irreversible process.

Less radical has been the influence of dimenformon. The shots did not effect the labrids externally. In some females the ovaries had on dissection a rather normal aspect, though there was more connective tissue and loose tissue with large, primordial cells than in normal, non-treated ovaries.

For instance, the ovaries of a terminal phase *H. bivittatus*, TL 14.8 cm (in this species females occur up to the final terminal phase) (ZMA 104.109) contained many pinkish, loose areas; scattered around were new, young oocytes and also yellowish islets, as often found in terminal phase testes. Most of the treated fish, however, had small, but very functional, active testes, full of mature sperm. Here numerous loose areas and yellowish islets were also found. For instance, a *H. bivittatus*, TL 13.7 cm, had testes where the pink areas were rather pronounced (Plate XI c).

These hormone experiments confirm the results of other scientists that labrids may react to mammalian hormones. Next to the gonads color patterns may be influenced, be it only in *Th. bifasciatum.*

However, the chemical nature and the influence of the natural gonadal hormones is still a point of discussion. It has not been possible to localize the possible site of formation. In female fish pre- and post ovulatory corpora lutea have been considered as responsible for endocrine activity (BRETSCHNEIDER e.a., 1941, 1947). It cannot be denied that for various species such spots have been described; the endocrine function, yet, is entirely speculative (cf ATZ, 1964). In the present study (Chapter IX) such formations could not be detected in the labrids, freshly caught in the sea.

In a variety of teleost testes endocrine interstitial cells (Leydig cells) have been described. Because of their development during periods that nuptial colors are shown, these cells were considered as being the source of male hormones (COURRIER, 1921; CRAIG-BENNETT, 1931). Others have denied this; in many species the absence of such tissue was reported (cf. NANCY HENDERSON, 1962). KINOSHITA (1935) reported interstitial cells in the terminal phase of the labrid *Halichoeres poecilopterus.* REINBOTH (1957, 1962), however, after thorough histological observations, failed to discover such cells in labrid (and sparid) testes. Neither could the present author detect such spots.

On the other hand, in the testes of large males frequently certain islets of indefinite, necrotic tissue have been found (not mentioned elsewhere). It has been a privilege to discuss these areas with Professor L. H. BRETSCHNEIDER, who did not consider them to be of a similar nature as the spots he described for *Rhodeus.* It has been mentioned above (Chapter IX, XII), that the present author considers the yellowish or pink islets merely as only partly resorbed areas of formerly ovarian structures in testes of males (that are reversed females). Their inorganic structure and the fact that these islets only characterize part of the large males, while terminal colors may occur in males without such areas in their gonads or even in some species in large females, renders doubtful any endocrine influence of the islets on morphology.

Thus, suggestions are only speculative at present. The true phy-

siological rôle of the gonads in sex differentiation cannot be explained yet; further histochemical and bioassay tests will be needed.

Conclusions

1. Mammalian male hormones have no influence on first adult phase colors in *H. bivittatus* and *H. garnoti*, but in yellow phase *Th. bifasciatum* induce a development towards the bluehead pattern. Histologically, in all three species reduction of ovarian tissue, induction of testis tissue and stimulation of spermiogenesis has been found.

2. Mammalian female hormones have no influence on terminal phase colors in *H. bivittatus* and *H. garnoti*; after treatment with dipro oleosum in some *Th. bifasciatum* specimens colors faded from the extreme bluehead phase 4 towards intermediate phase 3; the other two types of hormones did not affect the fish externally. Both ovarian and testicular activity seemed to be stimulated, although testes with various necrotic areas have also been found; the development of oocytes in testes of large, terminal fish is spectacular.

3. The first adult phase color pattern (in *Th. bifasciatum*) is more easy to influence than the terminal colors; the ovary is more sensitive to induction of a sex reversal than the testis; yet, both color and sex change proved to be not strictly irreversible.

4. No clear, strict relation between change of color and of sex has been found.

5. In various experiments, sex hormones proved to react upon secondary sexual characteristics; in the labrids, however, the effect on morphology was none or minor, in comparison with the radical changes of the gonads. The induced stages of sex reversal did not essentially differ from those found in fish in which spontaneous reversal of sex had taken place.

6. The possible site of formation of possible natural gonadal hormones could not be localized. In freshly caught females no corpus luteum-like structures have been found, nor Leydig cells in the males; the indefinite, necrotic islets that may be scattered among testes of large males merely are partly resorbed, non-functional areas of formerly ovarian structures.

XIV. CONCLUDING REMARKS AND SUMMARY

In the preceeding chapters various aspects of the biology of seven Caribbean labrid species have been discussed. Here, only the facts most pertinent to our investigation on the possible relation between color, size, and sex will shortly be reviewed.

In the present study the alleged relation between color and sex has been unsettled. For a long time the successive color phases – that characterize numerous labrid species – were considered as sex-specific coloration: the small, first adult phase being the females, the large, colorful terminal phase the males.

However:

= In some species males with functional, mature testes occur already in the first adult phase (alleged female phase);

= In some species females with normal, functional ovaries still occur in the larger intermediate and large terminal phases (alleged male phase);

= Color may start to change from the first adult phase pattern towards the terminal phase coloration in fish that are still females (though often in regression);

= Reversal of sex, from female into male, may start in fish that are still in first adult phase colors;

= Intermediate colors more or less coincide with a reduction in gonadal activity; yet, very mature females and males have also been found with these transitional colors.

These results, based on large samples of freshly caught fish, led to the conclusion that there is no clear relation between color phase and sex. Color change and sex reversal only partly coincide; in species in which males already occur at small size only part of the large males are reversed females, though morphological transformation takes place in all larger specimens.

Yet, it cannot be denied that:

= In some species females are restricted to the small, first adult phase, while males exclusively occur at larger sizes;

= Even when sex and color are not clearly related, females prevail in the first adult phase, while the majority of the large terminal phase is male in all species;

= Exogenous mammalian sex hormones do have an influence, both on color (only in *Thalassoma bifasciatum*) and on the gonads (in all species); sex reversal in both directions could be induced.

The former points render doubtful a direct influence of the gonads on color; it cannot be the mere fact of having testicular tissue that causes the lasting changes of pigmentation patterns. The latter points, however, suggest some interaction.

At present, the only justifiable conclusion is that basically growth seems to play a decisive role in governing changes in morphology. Terminal colors, and in some species, elongate fins, only in strictly protogynous species can be considered secondary sexual characteristics of the male. In species in which only part of the terminal phase fish are reversed females these merely are neutral features in large specimens.

The author has had to restrict herself mainly to examining gonads to obtain information on the true sex ratios. The distribution of females and males in the successive color phases being defined, it should be worthwhile to extend the investigations by searching histochemical and genetical backgrounds of the intricate interaction of color, size, and sex in the various labrid species.

Summarizing the results on behavior and on sex and morphology leads to the following speculative remark. The gregarious wrasses often frequent the same rocky sand areas, where they form heterospecific crowds. With the exception of *Hemipteronotus martinicensis*, living in homospecific groups, and with some restriction for *Hemipteronotus splendens* and *Halichoeres poeyi* which also frequent seagrass areas, environmental factors are not really different.

Abundance is regulated by the genetic composition in combination with environmental factors. Populations with greater genetic variability have larger population sizes (cf AYALA, 1968). Is it mere coincidence that the most abundant species *Thalassoma bifasciatum*, *Halichoeres bivittatus* and *Halochoeres garnoti* are the species in which sex, color, and size are not clearly related? Is the greater diversity of sex realization – be it with two color types of males, be it that female sex is not restricted to one size/color group – an indication of the greater genetic variability of these species? Speculating further we may assume that the abandoning of a strict protogynous propagation and the assumption of a sex relation that approximates the gonochorism of the higher vertebrates is selectively advantageous.

SUMMARY

1. Color changes ascribed to size, sex, gonadal activity, and behavior have been studied in seven Caribbean labrid species (wrasses): *Thalassoma bifasciatum* (Bloch), *Halichoeres bivittatus* (Bloch), *Halichoeres garnoti* (C. & V.), *Halichoeres maculipinna* (M. & Tr.), *Halichoeres poeyi* (St.), *Hemipteronotus splendens* (C.), and *Hemipteronotus martinicensis* (C. & V.).

With the aid of a hoopnet approximately 5500 labrids were collected in Curaçao (during 13 months) and in Puerto Rico (during 2 months). A minority was kept alive for experiments. The remaining 4474 specimens were immediately killed, transported on ice to the laboratory and subsequently studied. The major portion was examined immediately; some 20 per cent was stored briefly (< 3 days) at minus 20°C. [Chapters I, II and V]

2. Next to fast, reversible shadings of color due to changes in affective behavior, color patterns may change during growth. The first category – due to aggregations and dispersions of the pigment within the chromatophores – especially occurs in small *Th. bifasciatum, H. bivittatus* and *H. maculipinna* specimens. The second category, morphological color changes – in which the number of chromatophores may alter as well as the amount of pigment they contain – formed one of the topics of this study. The latter transitions are slowly developing processes of a rather irreversible character. Detailed color descriptions of all seven species have been given after thorough observation of the wrasses in their natural surroundings and of fish freshly caught and killed. In six out of the seven species a number of color phases could be distinguished, indicated as "first adult phase," "intermediate phase(s)" and "terminal phase," successively. [Chapter VI]

3. No general rule can be given concerning the color patterns of Labridae during their lifespan. There is no salient change of color in *H. poeyi*, and only a shading from dark, contrasting colors towards soft, pastel hues with no actual changing of the basic pattern in *H. bivittatus*. In the other five species the changes are conspicuous, varying from local alterations in some parts of the body (*He. splendens*) to more radical ones involving all parts of the body (*Th. bifasciatum, H. garnoti*). [Chapter VI]

4. The first adult phase in general is more dull and plain in contrast to the rich, often brilliant hues of the terminal phase. First adult phases are frequently characterized by reddish-brown hues and longitudinal stripes. These colored bands are found in *Th. bifasciatum, H. bivittatus* and *H. maculipinna*; the back of *H. garnoti* is plain red-brown. In some species small, dark spots occur in the first adult phase only, such as the tiny black spot at the base of the last dorsal ray in *H. bivittatus*, or the blackish area on the opercle in *He. martinicensis*. [Chapter VI]

5. The terminal phase is mainly green or green and blue in *Th. bifasciatum, H. bivittatus, H. maculipinna, He. splendens*. Character-

istic are dark cross bars (*bifasciatum, garnoti*) or conspicuous large, black side spots (*maculipinna, splendens*). In *Th. bifasciatum* and *H. garnoti* the pectorals have black tips; a dark spot in the axil of the pectorals is developed in *He. martinicensis*. [Chapter VI]

Comparable color patterns can be found in the successive phases of other dichromatic labrid species.

6. Morphological changes of color are strongly related to size. First adult phase colors occur up to a certain average body length; terminal phase colors occur in large fish only. There is a small overlap in which the fish may display all possible adult color phases. [Chapter X]

7. Fishes in first adult phase colors considerably outnumber the large, terminal phase individuals. A high mortality rate at the end of the first adult phase may explain the extreme decline in numbers.

Only a small percentage of the samples consisted of individuals in intermediate colors. Since morphological color changes develop gradually – in captivity periods of some weeks were involved – the factor time cannot account for the extra low numbers of intermediates collected. It may be that fish in which pigmentation and often at the same time gonad function are changing drastically, stay hidden under the sand during day time and so escape collection and observation. [Chapters X and XII]

8. On gross inspection the paired, elongated gonads can be classified either as ovaries or testes or as a miscellaneous group of indistinct sex. Macroscopically eight stages of gonadal activity have been distinguished of which both macroscopical and histological characteristics were described. Intersexes can only be recognized histologically. [Chapter IX]

9. Per species the total number of females is much higher than that of the males; only in *He. splendens* about the same number was counted for both sexes. Per color phase the proportion males to females is divergent; here striking hetero-specific differences have been found. [Chapter X]

10. In *H. poeyi* – in which no striking changes of color occur during growth – females are on the average smaller than males. In *H. maculipinna*, *He. splendens* and *He. martinicensis* females exclusively occur in the small, first adult phase; males occur in the larger intermediate phases and especially in the large terminal phase. These facts agree with the prevailing opinion that color dichromatism in labrids would represent a sexual dimorphism. [Chapter X]

11. In the extremely dichromatic *Th. bifasciatum* a relation between male sex and size-and-color is absent. Females are restricted to the small, yellow first adult phase. Males, however, occur in all size and color groups. Both small, yellow phase and large, bluehead phase males may have functional, active testes; curiously, the highest percentages of very mature, active males are found in the former group. [Chapter X, XI]

12. In *H. bivittatus* a clear relation between both sexes and size-and-color is absent. Though females prevail among the smaller adult fish, some females with functional ovaries have been found among larger fish of intermediate colors and even among the large, terminal phase. About a third of the first adult phase consists of functional males; moreover males occur at larger sizes. [Chapter X]

13. In *H. garnoti* a relation between female sex and size-and-color is not obvious. Though the majority of females is of smaller size, some females with functional ovaries have been found among the larger intermediates and even among fish in the large terminal phase. Males are limited to the larger phases. [Chapter X]

14. Sex reversal may occur in all species. In truly protogynous species all large males are reversed females; in species in which males already occur among the first adult phase, part of the large, terminal phase males are transformed females. Various indications of the existence of reversal of sex have been found. Females prevail at small sizes, males at large sizes, in all species. Overall regression of ovaries takes place in fishes of intermediate sizes. In intermediate and large sized fish numerous immature testes are found; testes

of large males often have female features such as thick walls and trabeculae; often there are necrotic areas that vaguely resemble ovarian structures. A minority of larger fish contained small intersexual gonads in various stages from mainly a regressive ovary with a few young spermogenous centers to mainly a testis with a few remains of oocytes. In contrast to Serranidae and Sparidae a temporary functional intersexuality does not exist in Labridae. [Chapter XII]

15. Thus, color and size are strongly related in all species, yet the relation between color and sex is rather variable and not very obvious. In some species numerous males are found in the alleged "female" phase, the first adult color phase; in some species some females occur in the alleged "male" phase, the terminal color phase. Further, color changes may start in fish that are still functional females, and intersexual gonads with areas of spermiogenesis may develop in fish that are still in the first adult phase colors. [Chapter XIV]

ADDITIONAL INFORMATION

16. The seven species, restricted to the Atlantic coasts of tropical America, frequent clear, shallow rocky places and reef sand areas; *H. poeyi* and *He. splendens* may also occur among sea grass beds. They often form loose, heterospecific aggregations. Only *He. martinicensis*, exclusively found at one strictly located spot, forms a homospecific colony. [Chapter IV]

17. The elongate labrids are agile fishes, dashing around with swift turns and movements achieved mainly by synchronous flapping of the pectoral fins. Smaller adults of the very common species *Th. bifasciatum* and *H. bivittatus* often are playing around in turbulent waters around projecting pieces of rocks and coral. Vision seems to be an important factor in their spatial orientation. *He. martinicensis* specimens often stand in almost perpendicular position, head upwards, some meters above small sand hills. [Chapter VIII]

18. Wrasses may take long rests on the bottom, especially large *Th. bifasciatum*, *H. bivittatus* and *H. garnoti* specimens that at times defend their (temporary) territory by agressively chasing other wrasses away, imposingly unfolding the dorsal fin. [Chapter VIII]

19. During the night wrasses disappear under the sand or hide in crevices in rocks and coral to sleep. Then the metabolism slows down towards a state of suspended

animation. During daytime they dive into the sand when frightened. On cloudy days the numbers visible are considerably lower, most probably also because of their hiding mechanism. [Chapter VIII]

20. Wrasses feed by picking with their fleshy lips and strong canine-like front teeth at sand bottom, rocks and coral; small *Th. bifasciatum* and *H. bivittatus* specimens moreover may be cleaning away ectoparasites of other fishes. In intestines of *Th. bifasciatum* and *H. bivittatus* juveniles mainly copepods were found; in smaller adults mainly crustaceans, in larger specimens small molluscs were also noticed. Being not over-particular in their choice of food may account for a low food competition and explain the occurrence of heterospecific groups. [Chapter VIII]

21. In *Th. bifasciatum* both group spawning of yellow colored fish as well as individual pair spawning of a large bluehead colored male and a smaller yellow colored female occurs; incidentally, concentrations of very mature yellow phase males have been met. For the *Halichoeres* and *Hemipteronotus* species only individual pair spawning has been observed. Spawning occurs by a fast upward movement resulting in release of the pelagic eggs and sperm near the water surface. In the seven Caribbean species no nest building or care for the offspring have been observed. [Chapter VIII]

22. The species differ a.o. in coloration, fin formulae, and number of canine teeth. No reason was found to reconsider the taxonomy. Morphometric differences between *Thalassoma* and *Halichoeres* species are small; *Hemipteronotus* is more compressed and has a steeper head. Per species no differences have been found between specimens from Curaçao and Puerto Rico. No essential morphological differences could be detected between females and males of the same size-and-color group. In all species some slightly positive allometric growth is found next to isometric relations; only the eye shows negative allometry. Allometry accounts for some slight, not significant differences found between females and males of different color phases, which obviously contributed to the older discussions on "specific" differences. [Chapter VII]

23. In *Th. bifasciatum* at about 6 cm TL the caudal fin starts to change during further growth from slightly convex to deeply forked, due to increasing exsertion of the outer rays. This change is more strongly associated with size than with color. In young *He. splendens* the first two dorsal spines are slightly prolonged. In both *Hemipteronotus* species there is a great increase in length of the first ventral ray in relation to increasing body length. In *Halichoeres* species no essential differences in the shape of the fins develop during its lifespan. [Chapter VII]

24. Growth studies, performed in indoor tanks, large outdoor tanks and huge cages on the bottom of the sea, show a decline in growth rates during the first adult phase; increment in length is almost nil during color change; then, there is a remarkable increase in growth rates. The growth studies further illustrate the allometries as discussed in the chapter on morphometry. [Chapter XIII]

25. Injections of male mammalian hormones applied to yellow phase *Th. bifasciatum* induced changes towards bluehead, terminal colors; in *H. bivittatus* and *H. garnoti* there was no clear influence on the color pattern. In all three species ovarian

tissues became regressive while spermiogenesis was induced in females and stimulated in males. One type of female mammalian hormones resulted in paling of the terminal colors of *Th. bifasciatum* towards intermediate hues. In the large, terminal phase males both oviogenesis and sperm production were stimulated. [Chapter XIII]

26. Ovulated eggs strongly increase in size due to liquid uptake. In the ovaries of freshly caught labrids no atretic "corpora-lutea" have been found. [Chapter IX]

27. Local forms of senescence are found in the relatively small testes of the largest males in terminal colors, especially in *Th. bifasciatum.* There are only a few spots of spermiogenesis; parts of the gonad are loose and not overactive, yet mature sperm occurs. [Chapter XII]

28. No special spawning season occurs; throughout the year individuals with mature gonads are present; the histological texture is characteristic for fish with successive spawning periods. Moreover, the frequency distribution of the total length of the fish per month does not reveal clear shifts and juveniles have been found every time of the year. [Chapter XI]

29. Fluctuations of percentages of fish with active gonads (nearly mature, mature or just spent) within one lunar month have been found. There is a pronounced top around full moon in all species; there are peaks around new moon and first quarter in most species. [Chapter XI]

The species in which sex and size are less strictly correlated are abundant and widely spread. Especially the existence of two types of males – functional males of small size and (often less fertile) large, terminal phase males – coincides with a great abundance (*Th. bifasciatum, H. bivittatus*; cf Mediterranean *Coris julis*). As these species are the most fit in Darwinian sense, the deviation from a basic protogynous propagation pattern might be of selective advantage. The Labridae may form an interesting interphase in the evolution from a protogynous hermaphroditism towards gonochorism.

XV. REFERENCES

ABOLINS, L., 1957. Sexual differences of carotenoid content in the skin of Labrus mixtus Kroeyer. *Acta Zool. Stockh. 38*: 223–238.

ABOLINS, L. & ABOLINS-KROGIS, A. 1957. Studies on skin carotenoids of Crenilabrus pavo. *Publ. Staz. Zool. Napoli 29*: 389–406.

AIDA, T., 1921. On the inheritance of color in a freshwater fish Aplocheilus latipes (Temm. and Schl.), with special reference to sex-linked inheritance. *Genetics 6*: 554–573.

AIDA, T., 1930. Further genetical studies of Aplocheilus latipes. *Genetics 15*: 1–16.

AIDA, T., 1936. Sex reversal in Aplocheilus latipes and a new explanation of sex differentiation. *Genetics 27*: 136–153.

AL-HUSSAINI, A. H., 1947. The feeding habits and the morphology of the alimentary tract of some Teleosts... *Publ. Mar. Biol. Staz. Al-Ghardaqa 5*: 1–61.

AL-HUSSAINI, A. H., 1949. On the functional morphology of the alimentary tract of some fish in relation to differences in their feeding habits... *Quart. J. Micr. Sci. 90*: 109–139.

ALMY Jr., CH. C. & CARRIÓN-TORRES, G., 1963. Shallow-water stony corals of Puerto Rico. *Carib. J. Science 3* (2 & 3): 133–162.

ARMSTRONG, C. N. & MARSHALL, A. J., 1964. *Intersexuality in vertebrates including man*. Academic Press, London/New York, 479 pp.

ARTEDI, P., 1738. *Ichthyologia*. (Wishoff, Leiden), *1–5*; *3*, 84 pp.

ARTEDI, P., 1792. *Ichthyologiae III*. (Crypeswaldiae), 721 pp.

ATKIN, N. B. & MATTINSON, G. & BEÇAK, W. & OHNO, S., 1965. The comparative DNA content of 19 species of placental mammals, reptiles and birds. *Chromosoma 17*: 1–10.

ATZ, J. W., 1964. Intersexuality in fishes. In ARMSTRONG & MARSHALL, *Intersexuality in vertebrates including man*: 145–232.

ATZ, J. W., 1965. Hermaphroditic fish. *Science 150*: 789–797.

ATZ, J. W. & PICKFORD, GRACE E., 1959. The use of pituitary hormones in fish culture. *Endeavour 28* (71): 125–129.

AYALA, F. J., 1968. Genotype environment and population numbers. *Science 162*: 1453–1459.

BACCI, G., 1965. *Sex determination*. Pergamon Press, London, 306 pp.

BACCI, G. & RAZZAUTI, A., 1957. Falso gonocorisme in "Coris julis" L. *Rend. Acc. Naz. Lincei 23* (8): 181–189.

BACCI, G. & RAZZAUTI, A., 1958. Protogynous hermaphroditism in Coris julis L. *Nature 181*: 432–433.

BALDWIN, F. M. & GOLDIN, H. S., 1939. Effects of testosterone propionate of the female viviparous teleost, Xiphophorus helleri. *Proc. Soc. Exp. Biol. N.Y. 42*: 813–819.

BARBOUR, TH., 1905. Notes on Bermudian fishes. *Bull. Mus. Comp. Zool. Harvard 46*: 109–134.

BEAN, B. A., 1905. Fishes of the Bahama Islands. In SHATTUCK, *The Bahama Islands*, Macmillan Co., New York: 293–325.

BEAN, T. H., 1890. Notes on fishes collected at Cozumel, Yucatán... *Bull. U.S. Fish Comm.* (for 1888) *8*: 193–206.

BEAN, T. H., 1960a. Description of new Bermudian fishes. *Proc. Biol. Soc. Wash. 19*: 29–33.

BEAN, T. H., 1906b. A catalogue of the fishes of Bermuda... *Publ. Field Mus. Chicago (Zool.) 7* (2): 21–89.

BEAN, T. H., 1912. Description of new fishes of Bermuda. *Proc. Biol. Soc. Wash. 25*: 121–126.

BEAN, T. H. & DRESEL, H. G., 1884. A catalogue of fishes received from the Public Museum of the Institute of Jamaica. *Proc. U.S. Nat. Mus. 7*: 151–160.

BEAUFORT, L. F. DE, 1940. *The fishes of the Indo-Australian Archipelago, 8*. Brill, Leiden, xv + 508 pp.

BEÇAK, W., 1965. Constituição cromossômica e mecanismo de determinção do sexo em ofídios sul-americanos. I. Aspectos cariotípicos. *Mem. Inst. Butantan 32*: 37–78.

BEÇAK, W., 1966. Idem. II. Crossomos sexuais e evoluçao do cariótipo. *Mem. Inst. Butantan 33*: 775–798.

BEÇAK, W. & BEÇAK, MARIA L., 1969. Cytotaxonomy and chromosomal evolution in Serpentes. *Cytogenetics 8*: 247–262.

BEÇAK, W. & BEÇAK, MARIA L. & NAZARETH, H. R. S., 1962. Karyotypic studies of two species of South-American snakes... *Cytogenetics 1*: 305–313.

BEEBE, W. & HOLLISTER, GLORIA, 1935. The fishes of Union Island, Grenadines... *Zoologica N.Y. 19* (6): 209–224.

BEEBE, W. & TEE-VAN, J., 1928. The fishes of Port-au-Prince Bay, Haiti. *Zoologica N.Y. 10* (1): 1–279.

BEEBE, W. & TEE-VAN, J., 1933a. Nomenclatural notes on the shore fishes of Bermuda. *Zoologica N.Y. 13* (7): 133–158.

BEEBE, W. & TEE-VAN, J., 1933b. *Field book on the shore fishes of Bermuda*. Putnam, New York, 337 pp.

BLAIR, W., 1951. Interbreeding of natural populations of vertebrates. *Amer. Nat. 85*: 9–30.

BLOCH, M. E., 1791. *Naturgeschichte der ausländischen Fische..., 5*, 152 pp.

BLOCH, M. E., 1792. *Naturgeschichte der ausländischen Fische..., 6*, 126 pp.

BLOCH, M. E. (ed. J. G. SCHNEIDER), 1801. *Systema ichthyologiae*. Berlin, 584 pp.

BLOSSER, CH. B., 1909. Reports on the expedition to British Guiana of the Indiana University and the Carnegie Museum, 1908. *Ann. Carn. Mus. 6* (1): 295–300.

BODMER, W. F. & EDWARDS, A. W. F., 1960. Natural selection and the sex ratio. *Ann. Human. Genet. 24*: 239–244.

BÖHLKE, J. E. & CHAPLIN, CH. C. G., 1968. *Fishes of the Bahamas and adjacent tropical waters*. Acad. Nat. Sci. Phila.; Livingston Publ., xxx + 771 pp.

BONAPARTE, C. L., 1832. *Pesci*. Iconografia della fauna italica... *3*, 532 pp.

BREDER, C. M., 1926. The locomotion of fishes. *Zoologica N.Y. 4*: 159–297.

BREDER, C. M. 1927. Scientific results of the first oceanographic expedition of the "Pawnee." I – Fishes. *Bull. Bingham Oceanogr. Coll. 1* (1): 1–90.

BREDER, C. M., 1948. *Field book of marine fishes from Labrador to Texas*. Putnam, New York, 332 pp.

BRETSCHNEIDER, L. H. & DUYVENÉ DE WIT, J. J., 1941. Histo-physiologische Analyse der sexuell-endokrinen Organisation des Bitterlingweibchens (Rhodeus amarus). *Ztschr. Zellforsch. mikr. Anat. 31*: 227–349.

BRETSCHNEIDER, L. H. & DUYVENÉ DE WIT, J. J., 1947. *Sexual endocrinology of non-mammalian vertebrates*. Elsevier, 146 pp.

BROCK, V. & YAMAGUCHI, Y., 1954. The identity of the parrot fish Scarus ahula, the female of Scarus perspicillatus. *Copeia 1954* (2): 154–155.

BROWN, MARGARET E., 1957. *The physiology of fishes. I & II.* Academic Press, New York, 447 + 526 pp.

BUISONJÉ, P. H. & ZONNEVELD, J. I. S., 1960. De kustvormen van Curaçao, Aruba en Bonaire. *Nieuwe West-Indische Gids 40*: 121–144.

CALDWELL, D. K., 1959. Observations on tropical marine fishes from the northeastern Gulf of Mexico. *Quart. J. Fla. Acad. Sci. 22* (1): 69–74.

CANESTRINI, G., 1868. Intorno di Labroidi del Mediterranea. *Ann. Soc. Nat. Modena 3*: 104–144.

CAPORIACCO, L. DI, 1921. Revisione delle specie mediterranean della famiglia Labridae. *Att. Soc. Ital. Sc. Nat. Milano 60* (1): 49–101.

CASTELNAU, F. DE, 1855. *Animaux nouveaux ou rares... de l'Amérique du Sud, de Rio de Janeiro à Lima, et de Lima au Para; ... Poissons, 7* (3): xii + 100 pp.

CERVIGÓN, F. M., 1966. *Los peces marinos de Venezuela* I + II. Caracas; Estación Investig. Marinas Margarita, 951 pp.

COHEN, M. M. & GANS, C., 1970. The chromosomes of the order Crocodilia. *Cytogenetics 9*: 81–105.

COPE, E. D., 1870. Contribution to the ichthyology of the Lesser Antilles. *Trans. Am. Phil. Soc. 14*: 445–483.

COURRIER, R., 1921. Sur l'existence d'une glande interstitielle dans les testicules des poissons. *C. R. Soc. Biol., Paris 85*: 939–941.

CRAIG-BENNETT, A., 1931. The reproductive cycle of the three-spined stickle back, Gasterosteus aculeatus. *Phil. Trans. Roy. Soc. London (B) 219*: 197–280.

CUVIER, G. & VALENCIENNES, A., 1839. *Histoire naturelle des poissons, 13 & 14.* Levrault, Paris, 505 + 464 pp.

DANOIS, E. D. LE, 1913. Contribution à l'étude systématique et biologique des poissons de la Manche occidentale. *Ann. Inst. Oceanogr. 5* (5): 1–214.

D'ARCY THOMPSON, W., 1947. *A glossary of Greek fishes.* Oxford Univ. Press, viii + 302 pp.

DODD, J. M., 1960a. Reproductive endocrinology in cyclostomes and elasmobranchs. *Symp. Zool. Soc. London 1*: 77–103.

DODD, J. M., 1960b. Genetic and environmental aspects of sex determination in cold-blooded vertebrates. In: Sex differentiation and development. *Mem. Soc. Endocr. 7*: 17–44.

EDWARDS, A. W. F., 1960. Natural selection and sex ratio. *Nature 188*: 960.

EGAMI, N., 1959. Effects of testosterone on the sexual characteristics of the gobiid fish, Pterogobius zonoleucus. *Ann. Zool. Jap. 32* (3): 123–128.

EIBL-EIBESFELDT, I., 1955. Ueber Symbiosen, Parasitismus und andere besondere zwischenartliche Beziehungen tropischer Meeresfische. *Ztschr. Tierpsych. 12* (2): 203–219.

ESSENBERG, J. M., 1926. Complete sex reversal in viviparous teleosts. *Biol. Bull. 51*: 98–109.

EVERMANN, B. W. & MARSH, M. C., 1902. The fishes of Porto Rico. *Bull. U.S. Fish. Com. 20*: 51–350.

FACCIOLA, L., 1916. Labroidi del mar di Messina. *Monit. Zool. Italiano 27*: 140–152.

FEDDERN, H. A., 1963. Color pattern changes during growth of Bodianus pulchellus and B. rufus. (Pisces: Labridae). *Bull. Marine Sci. Gulf Caribb. 13* (2): 224–241.

FEDDERN, H. A., 1965. The spawning, growth and general behavior of the Bluehead Wrasse, Thalassoma bifasciatum (Pisces: Labridae). *Bull. Marine Sci. 15*: 896–941.

FIEDLER, K., 1964. Verhaltensstudien an Lippfischen der Gattung Crenilabrus (Labridae, Perciformes). *Ztschr. Tierpsychiat. 21*: 521–591.

FOWLER, H. W., 1919. Notes on tropical American fishes. *Proc. Acad. Nat. Sci. Phila. 71*: 128–155.

FOWLER, H. W., 1928. Fishes from Florida and the West Indies. *Proc. Acad. Nat. Sci. Phila. 80*: 451–473.

FOWLER, H. W., 1936. The marine fishes of West-Africa. *Bull. Amer. Mus. Nat. Hist. 70*: 1–1493.

FOWLER, H. W., 1942. Notes on marine fishes from Honduras. *Fish Culturist 22* (2): 9–12.

FOWLER, H. W., 1950. Results of the Catherwood-Chaplin West Indies expedition 1948. Part 3 – The fishes. *Proc. Acad. Nat. Sci. Phila. 102*: 69–93.

FOWLER, H. W., 1952. The fishes of Hispaniola. *Mem. Soc. Cub. Hist. Nat. 21* (1): 81–115.

FOWLER, H. W., 1953. The shore fishes of the Colombian Caribbean. *Caldasia 6* (27): 43–73.

FOX, D. L., 1953. *Animal biochromes and structural colours*. Cambridge Univ. Press, 379 pp.

FULTON, T. W., 1891. The comparative fecundity of sea-fishes. *Rep. Fish. Board Scot. 9*: 243–268.

GAISER, MARIE-LOUISE, 1952. Effects produits par l'administration prolongée de thiourée et de thyroxine chez Lebistes reticulatus. *C.R. Soc. Biol. Paris 146*: 496–498.

GALLIEN, L., 1948. Sur la structure des nageoires chez les femelles de Lebistes reticulatus Regan, masculinisées par la prégnéninolone. *C.R. Acad. Sci. Paris 226* (2): 1749–1751.

GERBE, Z., 1864. Observations sur la nidification des Crénilabres. *Rev. Mag. Zool.* (2) *16*: 255–258, 273–279, 337–340.

GILL, TH., 1863. Description of a new species of Choerojulis from North Carolina. *Proc. Acad. Nat. Sci. Phila. 15*: 205–207.

GOHAR, H. A. F. & LATIF, A. F. A., 1961a. The histology of the alimentary tract in representative scarid and labrid fishes from the Red Sea. *Publ. Mar. Biol. Sta. Al-Ghardaqa 11*: 95–126.

GOHAR, H. A. F. & LATIF, A. F. A., 1961b. The carbohydrases of some scarid and labrid fishes from the Red Sea. *Publ. Mar. Biol. Sta. Al-Ghardaqa 11*: 127–146.

GOHAR, H. A. F. & LATIF, A. F. A., 1961c. Gut lipase of some scarid and labrid fishes from the Red Sea. *Publ. Mar. Biol. Sta. Al-Ghardaqa 11*: 215–234.

GOHAR, H. A. F. & LATIF, A. F. A., 1963. Digestive proteolytic enzymes of some scarid and labrid fishes from the Red Sea. *Publ. Mar. Biol. Sta. Al-Ghardaqa 12*: 3–42.

GOODE, G. B., 1877. A preliminary catalogue of the reptiles, fishes and leptocardians of the Bermudas. *Am. J. Sci. Arts 14*: 287–298.

GOODE, G. B. & BEAN, T. H., 1879. Catalogue of a collection of fishes obtained in the Gulf of Mexico... *Proc. U.S. Nat. Mus. 2*: 333–345.

GOODE, G. B. & BEAN, T. H., 1882. A list of the species of fishes recorded as occurring in the Gulf of Mexico. *Proc. U.S. Nat. Mus. 5*: 234–240.

GOODRICH, DOROTHY H. B. & BIESINGER, I., 1953. The histological basis of color patterns in three tropical marine fish with observations on regeneration and the production of the blue color. *J. Morph. 93* (3): 465–488.

GORDON, M., 1946. Interchanging genetic mechanisms for sex determination in fishes under domestication. *J. Heredity 37*: 307–320.

GORDON, M., 1947. Genetics of Platypoecilus maculatus. IV. *Genetics 32*: 8–107.

GORDON, M., 1951. Genetics of Platypoecilus maculatus. V. *Zoologica N.Y. 36*: 127–134.

GORDON, M., 1957. Physiological genetics of fishes. In BROWN, *Physiology of fishes, 2*. Acad. Press, New York: 431–501.

GOURRET, P., 1893. Famille des Labroïdes. *Ann. Musée Hist. Nat. Marseille 4*: 1–86.

GRAY, J. E., 1854. *Catalogue of fish collected and described by L. T. Gronow, now in the British Museum*. London, 196 pp.

GRONOVIUS, L. TH., 1781. *Zoophylacium Gronovianum – I. Animalia quadrupeda, amphibia atque pisces*. [1763–1781] xv + 380 pp.

GÜNTHER, A., 1862. *Catalogue of the fish in the British Museum, 4*. London, 534 pp.

HAGSTRÖM, B. E. & WENNERBERG, CHR., 1964. Hybridization experiments with wrasses (Labridae). *Sarsia 17*: 47–54.

HAMILTON, H. L., 1941. The biological action of rotenone on fresh-water animals. *Iowa Acad. Sci. 48*: 467–479.

HARRINGTON, R. WH., 1959. Effects of four combinations of temperature and day length on the ovogenetic cycle of a low-latitude fish, Fundulus confluentus Goode & Bean. *Zoologica N.Y. 44* (4): 149–168.

HEFFORD, A. E., 1910. Notes on teleostean ova and larvae observed at Plymouth in spring and summer 1909. *J. Mar. Biol. Ass. U.K. 9* (1): 1–58.

HEINCKE, F., 1898. Naturgeschichte des Herings. *Abh. Deutsch. Seefischer. Ver. 2* (1) (1 + 2).

HENDERSON, NANCY E., 1962. The annual cycle in the testis of the eastern brook trout, Salvelinus fontinalis (Mitchill). *Canad. J. Zool. 40*: 631–645.

HENDERSON, NANCY E., 1963a. Influence of light and temperature on the reproductive cycle of the eastern brook trout, Salvelinus fontinalis (Mitchill). *J. Fish. Res. Bd. Canada 20*: 859–897.

HENDERSON, NANCY E., 1963b. Extent of atresia in maturing ovaries of the eastern brook trout, Salvelinus fontinalis (Mitchill). *J. Fish Res. Bd. Canada 20*: 899–908.

HERALD, E., 1961. *Living fishes of the world*. Doubleday, New York, 304 pp.

HERTER, K., 1953. *Die Fischdressuren und ihre sinnesphysiologischen Grundlagen*. Akad. Verlag, Berlin, vi + 326 pp.

HICKLING, C. F. & RUTENBERG, E., 1936. The ovary as an indicator of the spawning, period in fishes. *J. Marine Biol. Ass. U.K. 21*: 311–318.

HISAW, F. L. & HISAW Jr. F. L., 1959. Corpora lutea of elasmobranch fishes. *Anat. Rec. 135* (4): 269–273.

HOBSON, E. S., 1965. Diurnal-nocturnal activity of some inshore fishes in the Gulf of California. *Copeia 1965* (3): 291–302.

HOLST, E. VAN, 1935. Ueber den Lichtrücken Reflex bei Fischen. *Publ. Staz. Zool. Nap. 15*: 143–158.

HUBBS, C. L. & LAGLER, K. F., 1947. *Fishes of the Great Lakes Region*. Cranbrook Inst. Bull. 26, Cranbrook, Michigan, 186 pp.

JACOBSHAGEN, E., 1937. Mittel und End-darm (Rumpfdarm). In BOLK, *Hand. Vergl. Anat. Wirbeltiere, 3*: 563–724.

JAMES, MARIAN F., 1946. Histology of gonadal changes in the bluegill, Lepomis macrochirus Rafinesque and the largemouth bass, Huro salmoides (Lacépède). *J. Morph. 79*: 63–92.

JAMES, MARIAN F., 1946. Hermaphroditism in the Largemouth bass. *J. Morph. 79*: 93–96.

JORDAN, D. S., 1884. List of fishes collected at Key West, Florida... *Proc. U.S. Nat. Mus. 7*: 103–150.

JORDAN, D. S., 1885. *A catalogue of the fishes known to inhabit the waters of North America north of the Tropic of Cancer*. Ann. Rep. Comm. Fish & Fisheries, 1884, Washington; 185 pp.

JORDAN, D. S., 1886a. Notes on fishes collected at Beaufort North Carolina... *Proc. U.S. Nat. Mus. 9*: 25–30.

JORDAN, D. S., 1886b. List of fishes collected at Havana, Cuba... *Proc. U.S. Nat. Mus. 9*: 31–55.

JORDAN, D. S., 1886c. Notes on typical specimens of fishes described by Cuvier and Valenciennes... *Proc. U.S. Nat. Mus. 9*: 525–546.

JORDAN, D. S., 1886d. A preliminary list of the fishes of the West-Indies. *Proc. U.S. Nat. Mus. 9*: 554–608.

JORDAN, D. S., 1890. A review of the Labroid fishes of America and Europe. *Rep. U.S. Fish Comm.* (for 1887) *15*: 559–699.

JORDAN, D. S. & EVERMANN, B. W., 1896. A check-list of the fishes and fish-like vertebrates of North and Middle America. *Rep. U.S. Comm. Fish.* (for 1894–1895) *21*: 207–590.

JORDAN, D. S. & EVERMANN, B. W., 1898. The fishes of North and Middle America. *Bull. U.S. Nat. Mus. 47* (2): 1241–2183.

JORDAN, D. S. & GILBERT, CH. H., 1878. Notes on fishes of Beaufort Harbor, North-Carolina. *Proc. U.S. Nat. Mus. 1*: 365–388.

JORDAN, D. S. & GILBERT, CH. H., 1882a. Notes on fishes observed about Pensacola, Florida and Galveston, Texas... *Proc. U.S. Nat. Mus. 5*: 241–289.

JORDAN, D. S. & GILBERT, CH. H., 1882b. Notes on a collection of fishes from Charleston, South Carolina. *Proc. U.S. Nat. Mus. 5*: 580–620.

JORDAN, D. S. & GILBERT, CH. H., 1883. Synopsis of the fishes of North America. *Bull. U.S. Nat. Mus. 16*: lvi + 1018 pp.

JORDAN, D. S. & HUGHES, ELISABETH G., 1886. A review of the genera and species of Julidinae found in American waters. *Proc. U.S. Nat. Mus. 9*: 56–70.

JORDAN, D. S. & RUTTER, C., 1897. A collection of fishes made... in Kingston, Jamaica. *Proc. Acad. Nat. Sci. Phila. 49*: 91–133.

JORDAN, D. S. & THOMPSON, J. C., 1905. The fish fauna of the Tortugas archipelago. *Bull. U.S. Bur. Fish* (for 1904) *24*: 231–256.

KALLMAN, K. D., 1970. Sex determination and the restriction of sex-linked pigment patterns to the X and Y chromosomes in populations of a poeciliid fish, Xiphophorus maculatus... *Zoologica N.Y. 55* (1): 1–16.

KALMUS, H. & SMITH, C. A. B., 1960. Evolutionary origin of sexual differentiation and the sex-ratio. *Nature 186*: 1004–1006.

KINOSHITA, Y., 1934. On the differentiation of the male colour-patterns, and the sex ratio in Halichoeres poecilopterus. *J. Sci. Hiroshima Univ. (B) 1, 3*: 65.

KINOSHITA, Y., 1935. Effects of gonadectomies on the secondary sexual characters in Halichoeres poecilopterus (Temminck & Schlegel). *J. Sci. Hiroshima Univ.* (*B*) *1*, *4*: 1–14.

KINOSHITA, Y., 1938. On the secondary sexual characters... in Chloea sarchynnis Jordan and Snyder. *J. Sci. Hiroshima Univ.* (*B*) *1*, *6*: 5–20.

KINOSHITA, Y., 1939. Studies on the sexuality of genus Sparus (Teleostei). *J. Sci. Hiroshima Univ.* (*B*) *1*, *7*: 25–37.

KOSSWIG, C., 1964. Polygenic sex determination. *Experientia 20*: 190–199.

LACÉPÈDE, B. G. DE, 1802. *Histoire naturelle des poissons*, *3*. Plassan, Paris, 558 pp.

LAVENDA, N., 1949. Sexual differences and normal protogynous hermaphroditism in the Atlantic see bass Centropristes striatus. *Copeia 1949* (3): 185–194.

LECHER, P. & SIGNORET, J., 1969. Données actuelles sur les chromosomes sexuels des mammifères. *Ann. biol.* (*Paris*) *8* (3–4): 167–198.

LETACONNOUX, R., 1949. Note sur les caractères sexuels secondaires du Callionymus lyra. *J. Conseil Copenhague 16*: 59–62.

LIEM, K. F., 1963. Sex reversal as a natural process in the synbranchiform fish Monopterus albus. *Copeia 1963* (2): 303–312.

LINTON, E., 1907. Notes on parasites of Bermuda fishes. *Proc. U.S. Nat. Mus. 33*: 85–126.

LIST, H. J., 1887a. Ueber die Bastardierungsversuche bei Knochenfischen (Labriden). *Biol. Zentrallbl. 7*: 20–21.

LIST, H. J., 1887b. Ueber die Variation der Laichzeit bei Labriden. *Biol. Zentrallbl. 7*: 64.

LIU, C. K., 1944. Rudimentary hermaphroditism in the symbranchoid eel, Monopterus javanensis. *Sinensia 15*: 1–18.

LO BIANCO, S., 1888. Notizie biologiche riguardanti specialmente il periodo di maturità sessuale degli animali del golfo di Napoli. *Mitth. Zool. St. Neapel 8*: 385–440.

LO BIANCO, S., 1909. Notizie biologiche riguardanti specialmente il periodo di maturità sessuale degli animali del golfo di Napoli. *Mitth. Zool. St. Neapel 19*: 513–761.

LONGLEY, W. H., 1914. Report upon color of fishes of the Tortugas reefs. *Carn. Inst. Wash. Year Book 13*: 207–208.

LONGLEY, W. H., 1915. Coloration of tropical reef fishes. *Carn. Inst. Wash. Year Book 14*: 208–209.

LONGLEY, W. H. & HILDEBRAND, S. F., 1941. Systematic catalogue of the fishes of Tortugas, Florida. *Papers Tortugas Lab. 34* (Publ. Carn. Inst. 535): 1–331.

LÖNNBERG, E. & GUSTAFSON, G., 1937. Contribution to the life-history of the Striped Wrasse, Labrus ossifagus Lin. *Arkiv Zoologi 19A* (7): 1–16.

LORENZ, K., 1965. *Over agressie bij dier en mens*. Ploegsma, Amsterdam, 283 pp.

MAES, R., 1930. La vision des formes chez les poissons. *Ann. Soc. Roy. Zool. Belg. 60*: 103–130.

MATTEWS, J. D., 1887. Note on the ova, fry and nest of the Ballan Wrasse (Labrus maculatus). *App. 5th Ann. Rep. Fish. Board Scotland*: 245–247.

MATTHEWS, S. A., 1938. The seasonal cycle in the gonads of Fundulus. *Biol. Bull. Woods Hole 75*: 66–74.

MCERLEAN, A. J., 1963. A study of the age and growth of the Gag, Mycteroperca microlepis... *Fla. State Bd. Cons., Tech. Ser. 41*: 1–29.

MEEK, S. E. & HILDEBRAND, S. F., 1928. The marine fishes of Panama, III. *Publ. Field Mus. Nat. Hist. 249 (Zool.) 15*: xxi–xxxi +709–1045.

METZELAAR, J., 1919. *Over Tropisch Atlantische visschen.* Kruyt, Amsterdam, 314 pp. [= Report on the fishes...; in *Rapport betreffende... de Visscherij... in de kolonie Curaçao...* door J. BOEKE, II.]

MITTWOCH, URSULA, 1967. *Sex chromosomes.* Acad. Press, New York/London, 306 pp.

MOE, M. A., 1966. Tagging fishes in Florida offshore waters. *Fla. Bd. Conserv., Tech. Ser. 49*: 1–40.

MOE, M. A., 1967. Prolonged survival and migration of three tagged reef fishes in the Gulf of Mexico. *Trans. Am. Fish. Soc. 96*: 228–229.

MOREAU, E., 1881. *Histoire naturelle des poissons de la France, 3.* Masson, Paris, 697 pp.

MOWBRAY, L. L., 1931. Notes on two species of the genus Iridio. Iridio bivittatus and Iridio radiatus. *Fauna bermudensis 1*, [1 p.].

MÜLLER, J. & TROSCHEL, F. H., 1848. Fishes. In R. H. SCHOMBURGK, *The history of Barbados...* 665–678 [n.v.].

MURAMOTO, J. & OHNO, S., 1968. On the diploid state of the fish order Ostariophysi. *Chromosoma 24* (1): 59–66.

NEU, W., 1935. Beitrag zur Bewegungsphysiologie der Lippfische (Labridae). *Acta Adriatica 1* (6): 1–14.

NICOL, J. A. C., 1968. *The biology of marine animals* (2nd ed.). Pitman, London, 699 pp.

NICHOLS, J. T., 1915. Fishes new to Porto Rico. *Bull. Amer. Mus. Nat. Hist. 34* (7): 141–146.

NICHOLS, J. T., 1920. A contribution to the ichthyology of Bermuda. *Proc. Biol. Soc. Wash. 33*: 59–64.

NICHOLS, J. T., 1921. A list of Turk Island fishes... *Bull. Amer. Mus. Nat. Hist. 44* (3): 21–24.

NICHOLS, J. T., 1930. The fishes of Porto Rico and the Virgin Islands. *Sci. Survey P. Rico and Virgin Isl. 10* (3): 299–399.

OHNO, S., 1967. *Sex chromosomes and sex-linked genes.* Springer, Berlin/New York, 192 pp.

OHNO, S., 1970. *Evolution by gene duplication.* Springer, Berlin/New York, 160 pp.

OHNO, S. & ATKIN, N. B., 1966. Comparative DNA values and chromosome complements of eight species of fish. *Chromosoma 18*: 455–466.

OHNO, S. & BEÇAK, W. & BEÇAK, M. L., 1964. X-autosome ratio and the behavior pattern of individual X-chromosomes in placental mammals. *Chromosoma 15*: 14–30.

OHNO, S. & MURAMOTO, J. & CHRISTIAN, L. & ATKIN, N. B., 1967. Diploid-tetraploid relationship among old-world members of the fish family Cyprinidae. *Chromosoma 23*: 1–9.

OHNO, S. & MURAMOTO, J. & STENIUS, C. & CHRISTIAN, L. & KITTRELL, W. A., 1969. Microchromosomes in Holocephalian, Chondrostean and Holostean fishes. *Chromosoma 26*: 35–40.

OHNO, S. & WOLF, U. & ATKIN, N. B., 1968. Evolution from fish to mammals by gene duplication. *Hereditas 59* (1): 168–187.

OKADA, YO. K., 1955. *Fishes of Japan.* Maruzen, Tokyo, 343 pp.

OKADA, YO. K., 1962. Sex reversal in the Japanese wrasse, Halichoeres poecilopterus. *Proc. Japan. Acad. 38*: 508–513.

OKADA, YO. K., 1965a. A further note on sex reversal in the wrasse Halichoeres poecilopterus. *Proc. Japan Acad. 40*: 533–535.

OKADA, YO. K., 1965b. Bisexuality in sparid fish. I & II... *Proc. Japan. Acad. 41*: 294–304.

OLIVER, M. & MASSUTI, M., 1952. El rao, Xyrichthys novacula (Fam. Labridae). Notas biológicas y biométricas. *Bd. Inst. Esp. Oceanogr. Madrid 48*: 1–14.

OSORIO, B., 1909. Contribuição para o conhecimento da fauna bathypelagica visinha das costas de Portugal. *Mem. Mus. Bocage, Lisboa, 1.*

PARR, A. E., 1930. Teleostean shore and shallow-water fishes from the Bahamas and Turks Island. *Bull. Bingham Ocean. Coll. 3* (4): 1–148.

PENNOCK, L. A. & TINKLE, D. W. & SHAW, MARGERY W., 1969. Minute Y chromosome in the lizard genus Uta (family Igvanidae). *Cytogenetics 8*: 9–19.

PICKFORD, GRACE E. & ATZ, J. W., 1957. *The physiology of the pituitary gland of fishes.* N.Y. Zool. Soc., 613 pp.

POEY, F., 1860. Poissons de Cuba. *Mém. Hist. nat. Cuba 2*: 115–336.

POEY, F., 1867. Peces Cubanos especies nuevas. *Repert. fis. nat. Cuba 2*: 229–245.

POEY, F., 1868. Synopsis piscium Cubensium. *Repert. fis. nat. Cuba 2*: 279–484.

POEY, F., 1875. Enumeratio piscium Cubensium. *Anal. Soc. Esp. Hist. Nat. 4*: 75–161.

POLDER, J. J. W., 1961. Cyclical changes in testis and ovary related to maturity stages in the north sea herring, Clupea harengus L. *Arch. néerl. zool. 14*: 45–60.

POLDER, J. J. W., 1964. On the occurrence and significance of atretic follicles ("preovulatory corpora lutea") in ovaries of the bitterling, Rhodeus amarus Bloch. *Proc. Kon. Ned. Akad. Wetensch. (C) 67*: 218–222.

POLDER, J. J. W., 1971. On gonads and reproductive behaviour in the cichlid fish Aequidens portalegrensis (Hensel). *Neth. J. Zool. 21* (3): 265–365.

QUIGNARD, J. P., 1962. La reproduction chez les Labrides, le nid, l'oeuf et la larve de Symphodus cinereus (Bonn). *Naturalia Monspel. (Zool.) 4*: 52–59.

QUIGNARD, J. P., 1966. Recherches sur les Labridae (poissons téléostéens Perciformes) des côtes Européennes. *Naturalia Monspel. (Zool.) 5*: 1–247.

QUIGNARD, J. P., 1967. Le nid, l'oeuf et la larve du labridé Symphodus (Crenilabrus) mediterraneus (Linné, 1758). *Rev. trav. Inst. Pêches Marit. 31* (4): 359–362.

RANDALL, J. E., 1955a. Stethojulis renardi, the adult male of the labrid fish Stethojulis strigiventer. *Copeia 1955* (3): 237.

RANDALL, J. E., 1955b. Fishes of the Gilbert Islands. *Atoll. Res. Bull. 47*: 1–243.

RANDALL, J. E., 1958. A review of the Labrid fish genus Labroides... *Pacif. Sci. 12*: 327–347.

RANDALL, J. E., 1961a. A contribution to the biology of the Convict Surgeonfish of the Hawaiian Islands, Acanthurus triostegus sandvicensis. *Pacif. Sci. 15*: 215–272.

RANDALL, J. E., 1961b. Tagging reef fishes in the Virgin Islands. *Gulf Caribb. Fish. Inst. 14*: 201–241.

RANDALL, J. E., 1962. Fish service stations. *Sea Frontiers 8*: 40–47.

RANDALL, J. E., 1963. Notes on the systematics of parrot fishes (Scaridae) with emphasis on sexual dichromatism. *Copeia 1963* (2): 225–237.

RANDALL, J. E., 1965. A review of the razorfish genus Hemipteronotus (Labridae) of the Atlantic Ocean. *Copeia 1965* (4): 487–501.

RANDALL, J. E., 1967. Food habits of reef fishes of the West Indies. *Studies in tropical oceanography 5*: 665–847.

RANDALL, J. E., 1968. *Caribbean reef fishes.* T.H.F. Publications, Jersey City, 318 pp.

RANDALL, J. E. & BÖHLKE, J. E., 1965. Review of the Atlantic labrid fishes of the genus Halichoeres. *Proc. Acad. Nat. Sci. Phila. 117*: 235–259.

RANDALL, J. E. & BROCK, V. E., 1960. Observations on the ecology of epinepheline and lutjanid fishes of the Society Islands, with emphasis on food habits. *Trans. Amer. Fish. Soc. 89*: 9–16.

RANDALL, J. E. & RANDALL, HELEN A., 1960. Examples of mimicry and protective resemblance in tropical marine fishes. *Bull. mar. sci. Gulf Caribb. 10* (4): 444–480.

RANDALL, J. E. & RANDALL, HELEN A., 1963. The spawning and early development of the Atlantic parrot fish, Sparisoma rubripinne, with notes on other scarid and labrid fishes. *Zoologica N.Y. 48*: 49–60.

RASQUIN, PRISCILLA, 1958. Studies on the control of pigment cells and light reactions in recent teleost fishes. *Bull. Amer. Mus. Nat. Hist. 115*: 7–68.

RASQUIN, PRISCILLA & HAFTER, ETHEL, 1951. Age changes in the testis of the teleost, Astyanax mexicanus. *J. Morphol.* 89 (3): 397–404.

RASTOGI, R. K., 1968. Studies on the fish oogenesis I... *Cytologia 33*: 357–369.

REINBOTH, R., 1957. Sur la sexualité du téléostéen Coris julis (L). *C.R. Acad. Sci. Paris 245*: 1662–1665.

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

REINBOTH, R., 1962a. Morphologische und funktionelle Zweigeschlechtlichkeit bei marinen Teleostiern. (Serranidae, Sparidae, Centracanthidae, Labridae). *Zool. J. Physiol. 69*: 405–480.

REINBOTH, R., 1962b. The effects of testosterone on female Coris julis (L), a wrasse with spontaneous sex-inversion. *Gen. Comp. Endocrin. 2* (6): 629.

REINBOTH, R., 1963. Natürlicher Geschlechtswechsel bei Sacura margaritacea (Hilgendorf) (Serranidae). *Annot. zool. Jap. 36* (4): 173–178.

REINBOTH, R. & SIMON, N., 1962. Die Wirkung von Hypophysen-Homogenaten auf der Gonadenreifung bei Teleostiern. *Verh. Deutsch. Zool. Gesell. Wien. 1962*: 159–168.

RISSO, A., 1810. *Ichthyologie de Nice, ou Histoire naturelle des poissons du département des Alpes-Maritimes.* (re-edit. 1966; Asher, Amsterdam).

RISSO, A., 1826. *Histoire naturelle des principales productions de l'Europe méridionale...* Paris *3*: 299–335.

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

ROOS, P. J., 1964. The distribution of reef corals in Curaçao. *Stud. Fauna Curaçao Caribb. Isl. 20*: 1–51.

ROOS, P. J., 1967. *Growth and occurrence of the reef coral Porites astreoides Lamarck in relation to submarine radiance distribution.* Thesis, Amsterdam, 72 pp.

ROOS, P. J., 1971. The shallow-water stony corals of the Netherlands Antilles. *Stud. Fauna Curaçao Caribb. Isl. 37*: 1–108.

ROSÉN, N., 1911. Contributions to the fauna of the Bahamas, part. 2. *Acta Univ. Lunds 7* (5): 1–71.

RÜPPELL, E., 1835. *Neue Wirbeltiere zu der Fauna von Abyssinien gehörig.* Frankfurt, 148 pp.

SADOV, I. A., 1957. Changes in the size of the nuclei during the period of growth and maturing of the ovocytes of the sturgeon, the sevryoga and the sterlet. *Dokl. Akad. Nauk. SSSR.* [Transl.] *Biol. Sci. 112*: 57–60.

SAMUEL, M., 1943. Studies on the corpus luteum in Rhinobatus granulatus Cuv. *Proc. Indian Acad. Sci. 18B* (6): 133–157.

SCHMIDT, J., 1920. Racial investigations, IV. The genetic behaviour of a secondary sexual character. *C.R. Trav. Lab. Carlsberg 14* (8): 1–12.

SCHULTZ, L. P., 1958. Review of the Parrotfishes Family Scaridae. *Bull. U.S. Nat. Mus. 214*: v + 143 pp.

SCUDO, F. M., 1967. The adaptive value of sexual dimorphism. I. Anisogamy. *Evolution 21*: 285–291.

SCUDO, F. M., 1969. On the adaptive value of sexual dimorphism. II. Unisexuality. *Evolution 23*: 36–49.

SIMPSON, G. G. & ROE, ANNE & LEWONTIN, R. C., 1960. *Quantitative Zoology.* Harcourt, New York, 440 pp.

SMITH, J. L. B., 1959. The identity of Scarus gibbus Ruppell, 1828 and of other parrotfishes of the family Callyodontidae... *Bull. Dept. Ichth. Rhodes Univ. 16*: 265–282.

SOLJAN, T., 1930a. Nestbau eines Adriatischen Lippfisches (Crenilabrus ocellatus Forsk.). *Ztschr. Morph. Ökol. Tiere 17*: 145–153.

SOLJAN, T., 1930b. Die Fortpflanzung und das Wachstum von Crenilabrus ocellatus Forsk., einem Lippfisch des Mittelmeeres. *Ztschr. Wiss. Zool. 137*: 150–174.

SOLJAN, T., 1931. Brutpflege durch Nestbau bei Crenilabrus quinquemaculatus Risso, einem adriatischen Lippfisch. *Ztschr. Morph. Ökol. Tiere 20*: 132–135.

SORDI, M., 1962. Ermafroditismo proteroginoco in Labrus turdus L. e in L. merula L. *Mon. Zool. Ital. 69* (3–4): 69–89.

STARCK, W. A. & DAVIS, W. P., 1966. Night habits of fishes of Alligator Reef, Florida. *Ichthyologica 38*: 313–356.

STARKS, E. C., 1913. The fishes of the Stanford expedition to Brazil. *Leland Stanford Univ. Publ., Univ. Ser.*: 1–77.

STEFANI, ROSA DE, 1955. Osservazioni sull'organizzazione della gonade dei Labridi. *Atti Ist. Veneto Lett. Arti 113*: 210–214.

STEINDACHNER, F., 1867. Ichthyologische Notizen (VI). *Sitzber. Akad. Wiss. Wien 56* (6): 307–376.

STEINDACHNER, F., 1868. Ichthyologischer Bericht über eine nach Spanien und Portugal unternommene Reise. *Sitz. ber. Akad. Wiss. Wien 57* (1): 351–424, 667–738.

STENGER, A. H., 1959. A study of the structure and development of certain reproductive tissues of Mugil cephalus Linnaeus. *Zoologica N.Y. 44*: 53–70.

STOLL, LOUISE M., 1955. Hormon control of the sexually dimorphic pigmentation of Thalassoma bifasciatum. *Zoologica N.Y. 40* (11): 125–132.

STORER, D. H., 1846. *A synopsis of the fishes of North America.* Metcalf, Cambridge, 298 pp.

STRASBURG, D. W. & HIATT, R. W., 1957. Sexual dimorphism in the labrid fish genus Gomphosus. *Pacific Sci. 11*: 133–134.

SUWOROW, J. K., 1959. *Allgemeine Fischkunde.* Deutsches Verlag Wissensch., Berlin, 581 pp.

SWAIN, J., 1882. A review of Swainson's genera of fishes. *Proc. Acad. Nat. Sci. Phila. 34*: 272–284.

SWAINSON, W., 1839. *The natural history of fishes, amphibians, and reptiles, or monocardian animals, 2*. London, 452 pp.

TAYLOR, K. M., 1967. The chromosomes of some lower chordates. *Chromosoma 21*: 181–188.

TEE-VAN, J., 1932. Color changes in the bluehead wrasse, Thalassoma bifasciatum (Bloch). *Bull. N.Y. Zool. Soc. 35*: 43–47.

TORTONESE, E., 1967. Coris julis (L), a common mediterranean wrasse: problems ot color-pattern and taxonomy. *Ichthyologica – the Aquarium J. 39* (1): 41–44.

VALLOWE, H. H., 1957. Sexual differentiation in the teleost fish Xiphophorus helleri as modified by experimental treatment. *Biol. Bull. Woods Hole 112*: 422–429.

VANDINI, RENATA Z., 1965. Il problema dei maschi primari di Coris julis. *Mon. Zool. Ital. 73*: 102–110.

VERRIER, M. L., 1933. Recherches sur les fovéa des poissons. Étude des yeux de Julis giofredi Risso. *C.R. Soc. Biol. 113*: 134–135.

VERRIER, M. L. & ESCHER-DESRIVIÈRES, J., 1937. Recherches sur la sensibilité lumineuse des poissons. *Bull. Soc. Zool. Fr. 62*: 126–136.

WEATHERLEY, A. H., 1966. Ecology of fish growth. *Nature 212*: 1321–1324.

WINGE, Ö., 1923. Crossing-over between the X and Y chromosomes in Lebistes. *J. Genet. 13*: 201–217.

WINGE, Ö., 1934. The experimental alteration of sex chromosomes into autosomes and vice versa, as illustrated by Lebistes. *C.R. Trav. Lab. Carlsberg 21*: 1–49.

WINN, H. E., 1955. Formation of a mucous envelope at night by parrot fishes. *Zoologica N.Y. 40*: 145–148.

WINN, H. E. & BARDACH, J. E., 1957. Behavior, sexual dichromatism and species of parrot fishes. *Science 125*: 885–886.

WINN, H. E. & BARDACH, J. E., 1959. Differential food selection by moray eels and a possible role of the mucous envelope of parrot fishes in reduction of predation. *Ecology 40*: 296–298.

WINN, H. E. & BARDACH, J. E., 1960. Some aspects of the comparative biology of parrot fishes at Bermuda. *Zoologica N.Y. 45*: 29–34.

WOLF, U. & RITTER, H., 1969. Polyploidization in the fish family Cyprinidae... *Humangenetik 7*: 240–244, 245–250.

WURMBACH, H., 1951. Geschlechtsumkehr bei Weibchen von Lebistes reticulatus bei Befall mit Ichthyophonus hoferi Plehn-Mulsow. *Roux Arch. EntwMech. Org. 145*: 109–124.

YAMAMOTO, T., 1961. Progenies of sex-reversal females mated with sex-reversal males in the medaka, Oryzias latipes. *J. Exp. Zool. 146*: 163–180.

YAMAMOTO, T. & KAJISHIMA, T., 1968. Sex hormone induction of sex reversal in the goldfish and evidence for male heterogamity. *J. Exp. Zool. 168*: 215–222.

YARRELL, W., 1836. *A history of the British fishes, 1*. London. [p. 275–301].

ZANEVELD, J. S., 1959. *Index to the vernacular names of the fishes of the Netherlands Antilles*. Carmabi-Curaçao, Publ. *16*: 24 pp.

ZEI, M., 1949. Typical sex-reversal in teleosts. *Proc. Zool. Soc. London 119*: 917–920.

ZUMPE, DORIS, 1963. Ueber das Ablaichen von Thalassoma bifasciatum (Bloch). *Aquarien-Terrarienztschr. (DATZ) 16*: 86–88.

Explanations of Plates I–XI

I. Sections of ovaries of labrids in first adult phase colors.

a. Very young ovary (stage I); *H. bivittatus*, 4.8 cm TL; 560 ×. — b. Oocytes and maturing eggs full of yolk (stage III-a); *Th. bifasciatum*, 5.6 cm TL; 224 ×. — c. Overall regression (stage VII); *Th. bifasciatum*, 7.2 cm TL; 350 ×. — d. Calyces in spent ovary (stage VI); *Th. bifasciatum*, 5.1 cm TL; 140 ×. — e. Calyx and maturing eggs with vacuoles in the cytoplasma (stage V–VI); *Th. bifasciatum*, 4.1 cm TL; 350 ×. — f. Mature, ovulated eggs (distorted by fixation) (stage V); *H. bivittatus*, 9.0 cm TL; 35 ×. — g. Mature ovary, partly spent (stage VI); *H. bivittatus*, 9.3 cm TL; 35 ×.

II. Sections of developing labrid ovaries.

a. Young ovary (stage II); *He. splendens*, 9.3 cm TL, color phase 1; 35 ×. — b. Developing ovary (stage II–III); *H. bivittatus*, 5.4 cm TL, color phase 1; 56 ×. — c. Recovering, developing ovary (stage III); *H. garnoti*, 10.7 cm TL, color phase 3; 35 ×. — d. Maturing ovary (stage IV); *H. poeyi*, 9.1 cm TL; 35 ×.

III. Sections of mature labrid ovaries.

a. Partly maturing, partly ovulated eggs (stage IV–V); *He. martinicensis*, 8.4 cm TL, color phase 1; 35 ×. — b. Partly spent ovary (stage VI); *He. martinicensis*, 9.2 cm TL, color phase 1; 35 ×. — c. Mature ovary (stage V); *H. garnoti*, 13.0 cm TL, color phase 5; 35 ×. — d. Mature ovary (stage V); *H. bivittatus*, 11.2 cm TL, color phase 3; 35 ×.

IV. Sections of labrid ovaries in regression (stage VII).

a. *He. martinicensis*, 9.3 cm TL, color phase 2; 35 ×. — b. *Th. bifasciatum*, 8.5 cm TL, color phase 1; 56 ×. — c. *H. bivittatus*, 8.7 cm TL; 140 ×. — d. *H. bivittatus*, 7.6 cm TL; 140 ×. — e. *H. garnoti*, 10.3 cm TL, color phase 3; 56 ×. — f. *Th. bifasciatum*, 7.6 cm TL, color phase 1; 140 ×.

V. Sections of labrid testes.

a. Mature testis full of spermatozoa (stage V); *Th. bifasciatum*, 4.9 cm TL, color phase 1; 224 ×. — b. Spent testis (stage VI; *Th. bifasciatum*, 9.5 cm TL, color phase 4; 35 ×. — c. Various stages of spermiogenesis (stage III); *H. garnoti*, 14.4 cm TL, color phase 5; 350 ×. — d. Very functional testis (stage V); *Th. bifasciatum*, 4.9 cm TL, color phase 1; 35 ×. — e. Adipose fat tissue; *Th. bifasciatum*, 10.6 cm TL, color phase 4; 56 ×. — f. Thick walls in functional testis; *H. garnoti*, 15.3 cm TL, color phase 5; 140 ×.

VI. Sections of testes in large labrids.

a. *H. bivittatus*, 10.5 cm TL, color phase 3; 56 ×. — b. Necrotic area; *H. bivittatus*, 18.2 cm TL, color phase 4; 56 ×. — c. Islets with vacuoles; *H. garnoti*, 12.4 cm TL, color phase 4; 140 ×. — d. Pinkish-yellowish islet in functional testis; *H. garnoti*, 13.9 cm TL, color phase 4; 140 ×. — e. *Th. bifasciatum*, 7.0 cm TL, color phase 3; 56 ×. — f. *Th. bifasciatum*, 11.7 cm TL, color phase 4; 56 ×.

VII. Sections of intersexual labrid gonads.

a. Strongly regressing ovary with all over developing spermiogenesis; *H. bivittatus*, 11.8 cm TL, color phase 3; 224 ×. — b. Reduced ovarian tissue full of vacuoles and some left over oocytes; sperm production develops everywhere; *Th. bifasciatum*, 8.6 cm TL, color phase 2; 140 ×. — c. Ovary in regression; first stages of testicular tissue; *Th. bifasciatum*, 8.3 cm TL, color phase 1; 140 ×.

VIII. Sections of intersexual labrid gonads.

a. Active testis, separated from ovarian part; *He martinicensis*, 10.6 cm TL, color phase 3; 56 ×. — b. Strongly reduced ovarian tissue with first stages of spermiogenesis; *H. bivittatus*, 11.2 cm TL, color phase 2; 224 ×. — c. A higher magnification view of the gonad of VIII-b; 350 ×. — d. Resorption of formerly mature eggs; very young testis tissue; *Th. bifasciatum*, 8.3 cm TL, color phase 2; 350 ×. — e. Remains of resorbed eggs; young and more advanced stages of spermiogenesis; *He. splendens*, 13.2 cm TL, color phase 3; 350 ×. — f. Spermiogenesis among remains of former eggs and clusters of primordial cells; *H. bivittatus*, 11.2 cm TL, color phase 1; 224 ×.

IX. Sections on intersexual labrid gonads.

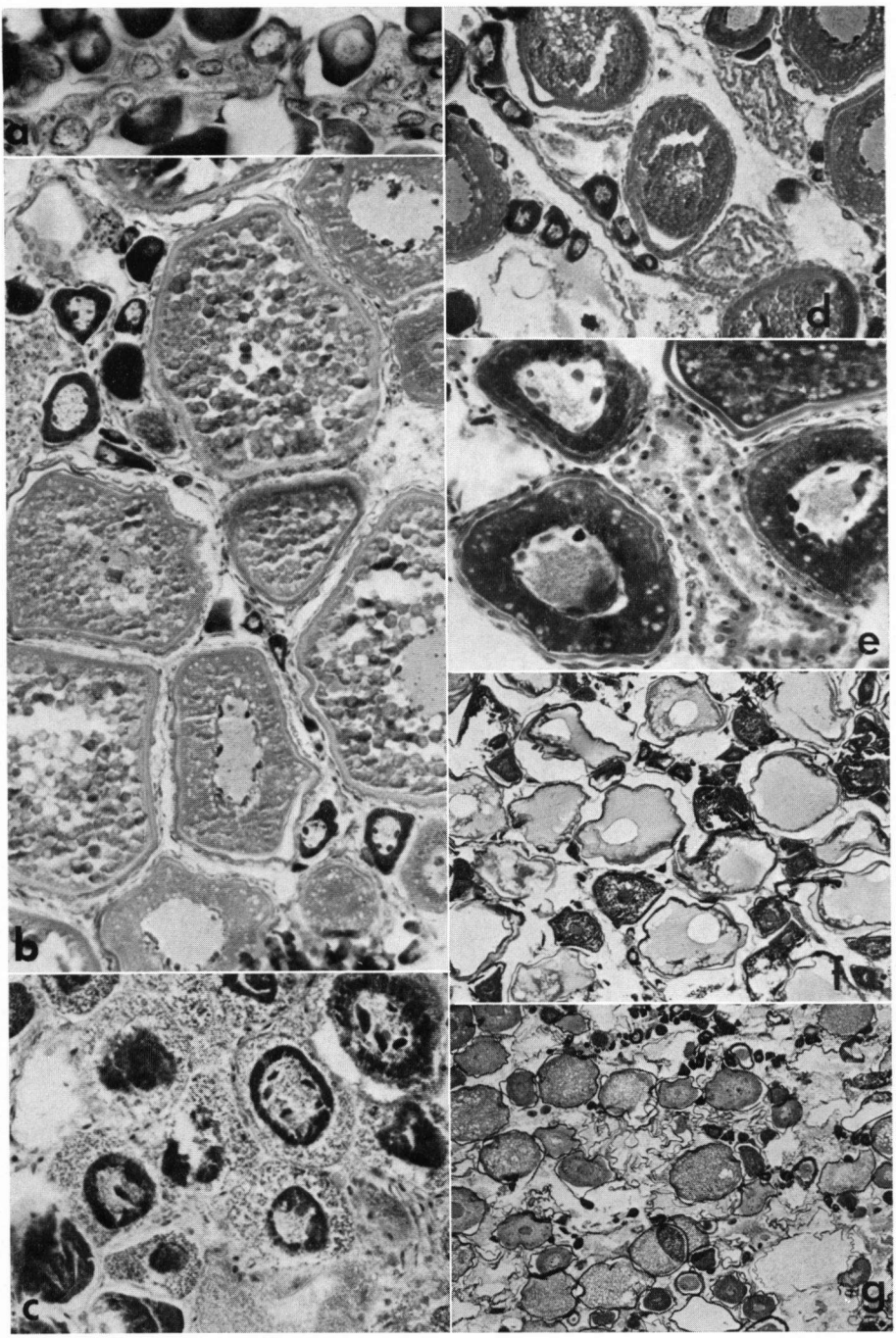
a. Left over egg among active testis; *H. maculipinna*, 14.3 cm TL, color phase 3; 140 ×. — b. Idem; *Th. bifasciatum*, 9.1 cm TL, color phase 3; 224 ×. — c. Idem; *H. bivittatus*, 6.1 cm TL, color phase 1; 56 ×. — d. Idem; same gonad as IX-c, e; 140 ×. — e. Idem; same gonad as IX-c, d; 35 ×.

X. Sections of labrid gonads after mammalian hormone treatment.

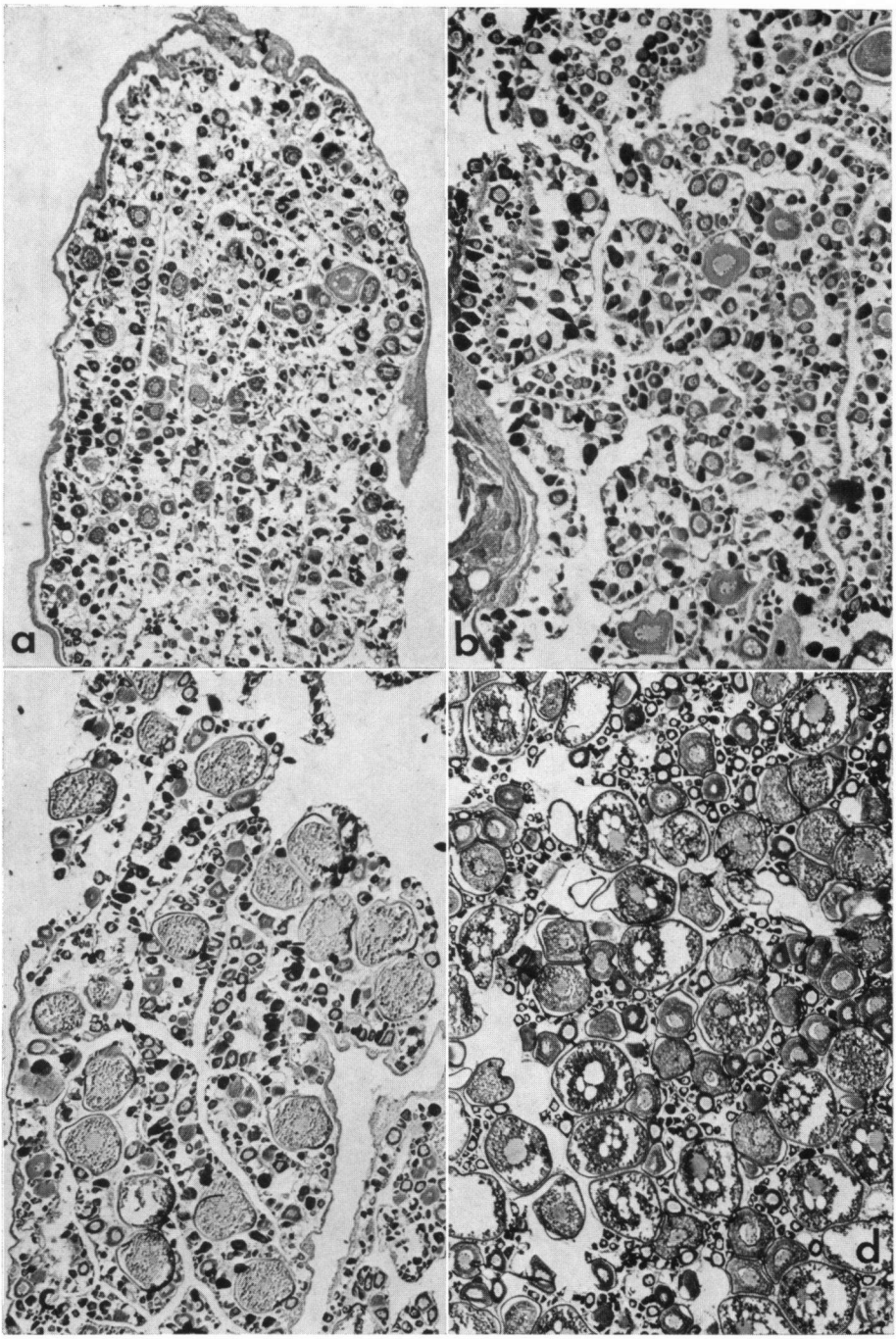
a. *H. bivittatus*, 9.5 cm TL, color phase 3; 7 days after sustanon 100 treatment; 140 × (loose regressing ovarian tissue full of vacuoles, bordered by small oocytes). — b. *Th. bifasciatum*, 7.5 cm TL, color phase 1; 5 days after testosteron treatment; 350 × (larger eggs in resorption; small oocytes still rather normal; first stages of spermiogenesis scattered around). — c. *H. bivittatus*, 11.3 cm TL, color phase 3; 19 days after sustanon 100 treatment; 224 × (resorption of larger eggs; various young stages of sperm production). — d. *H. bivittatus*, 9.5 cm TL, color phase 3; 7 days after sustanon 100 treatment; idem as X-a; 56 ×. — e. *H. bivittatus*, 9.7 cm TL, color phase 1; 14 days after sustanon 100 treatment; 224 × (ZMA 104.110) (clearly intersexual stage). — f. *H. bivittatus*, 9.6 cm TL, color phase 1; 14 days after sustanon 100 treatment; 56 ×. (full of oolemma's of large eggs, full of spermiogenesis).

XI. Sections of labrid gonads after mammalian hormone treatment.

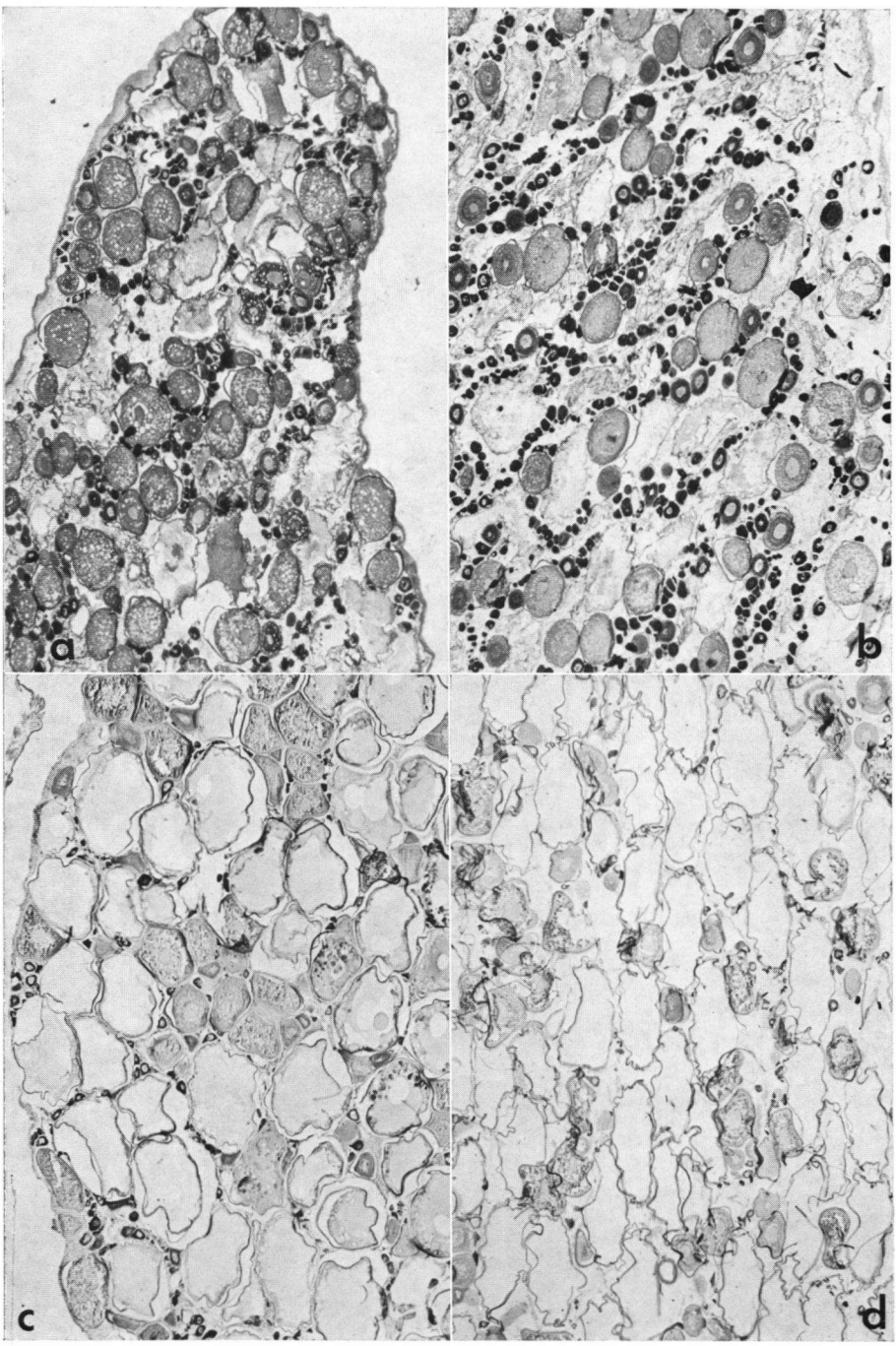
a. *H. bivittatus*, 9.3 cm TL, color phase 1; 4 days after durabolin treatment; 140 × (larger eggs in regression; basophilic oocytes still rather normal; first stages of spermiogenesis). — b. *H. bivittatus*, 9.6 cm TL, color phase 1; 16 days after durabolin treatment; 224 × (from the margin of the lamellae infiltrating young testicular tissue). — c. *H. bivittatus*, 13.7 cm TL, color phase 4; 6 days after dimenformon treatment; 224 × (large, loose pinkish necrotic areas in mature testis). — d. *H. garnoti*, 9.4 cm TL, color phase 2; 9 days after neo-hombreol treatment; 35 × (all over regression of ovary). — e. *Th. bifasciatum*, 11.3 cm TL, color phase 4; 5 weeks after di-pro oleosum treatment; 56 × (interesting case of numerous oocytes in testis of a bluehead specimen).



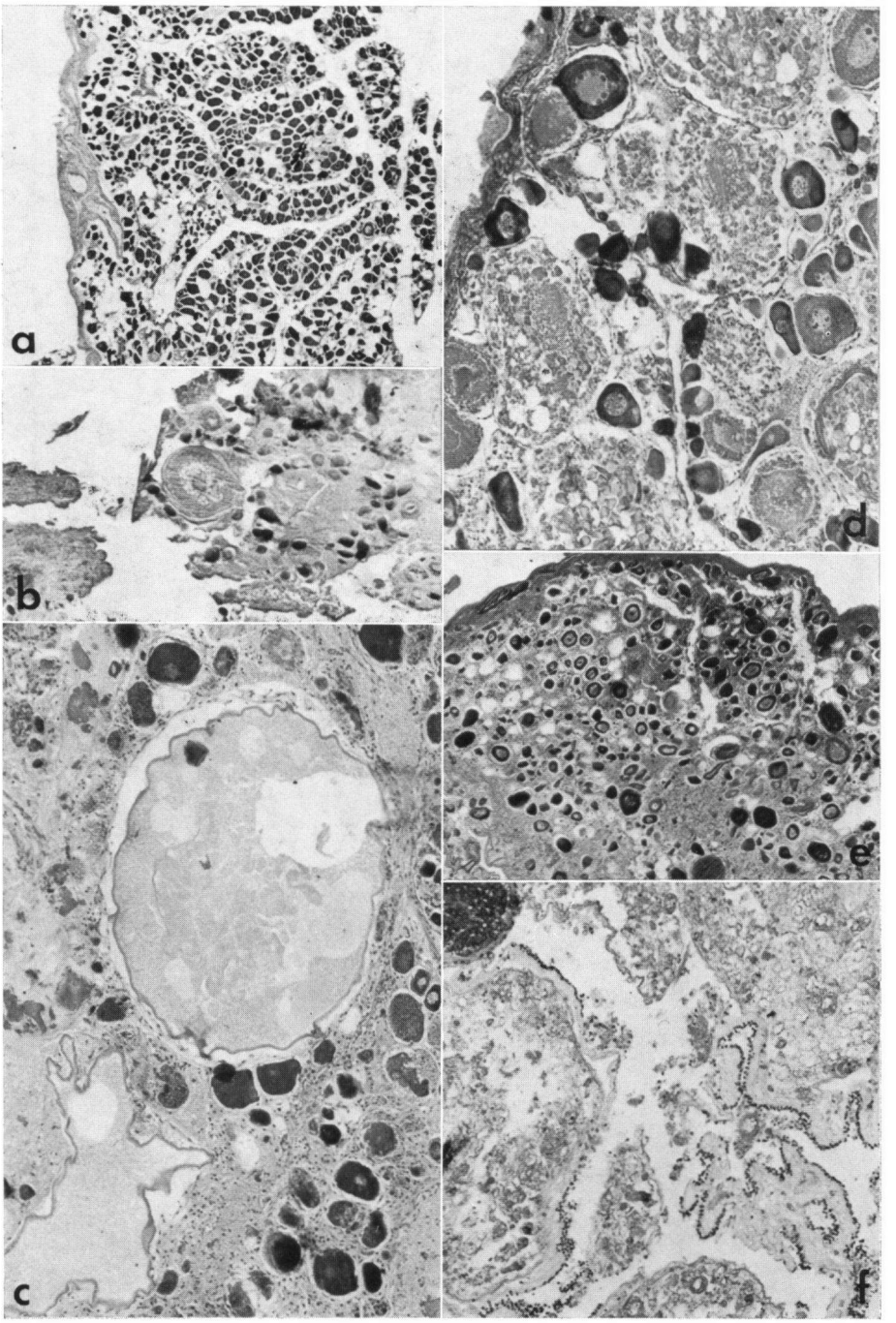
I. Sections of ovaries of labrids in first adult phase colors; various stages of development.



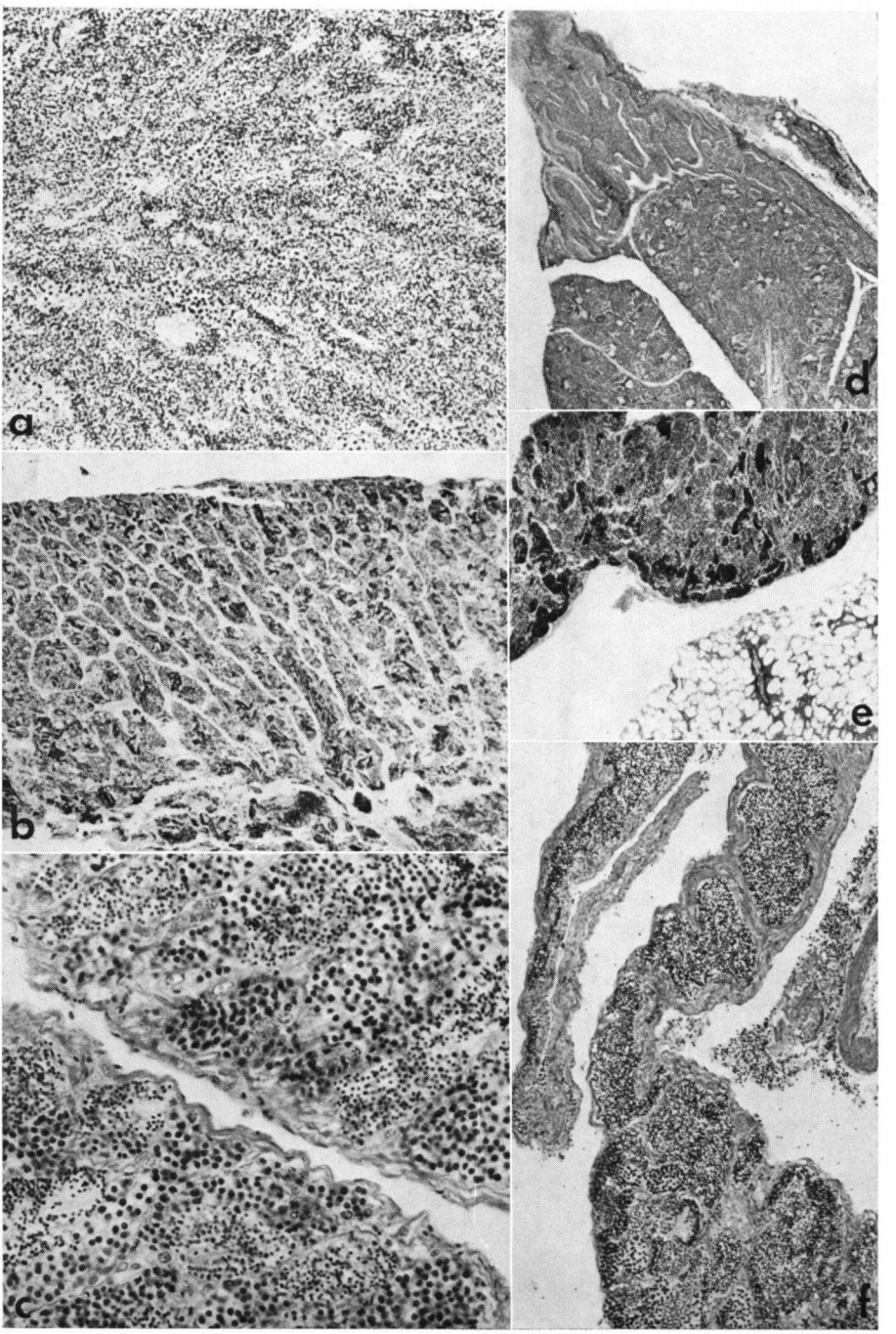
II. Sections of developing labrid ovaries.



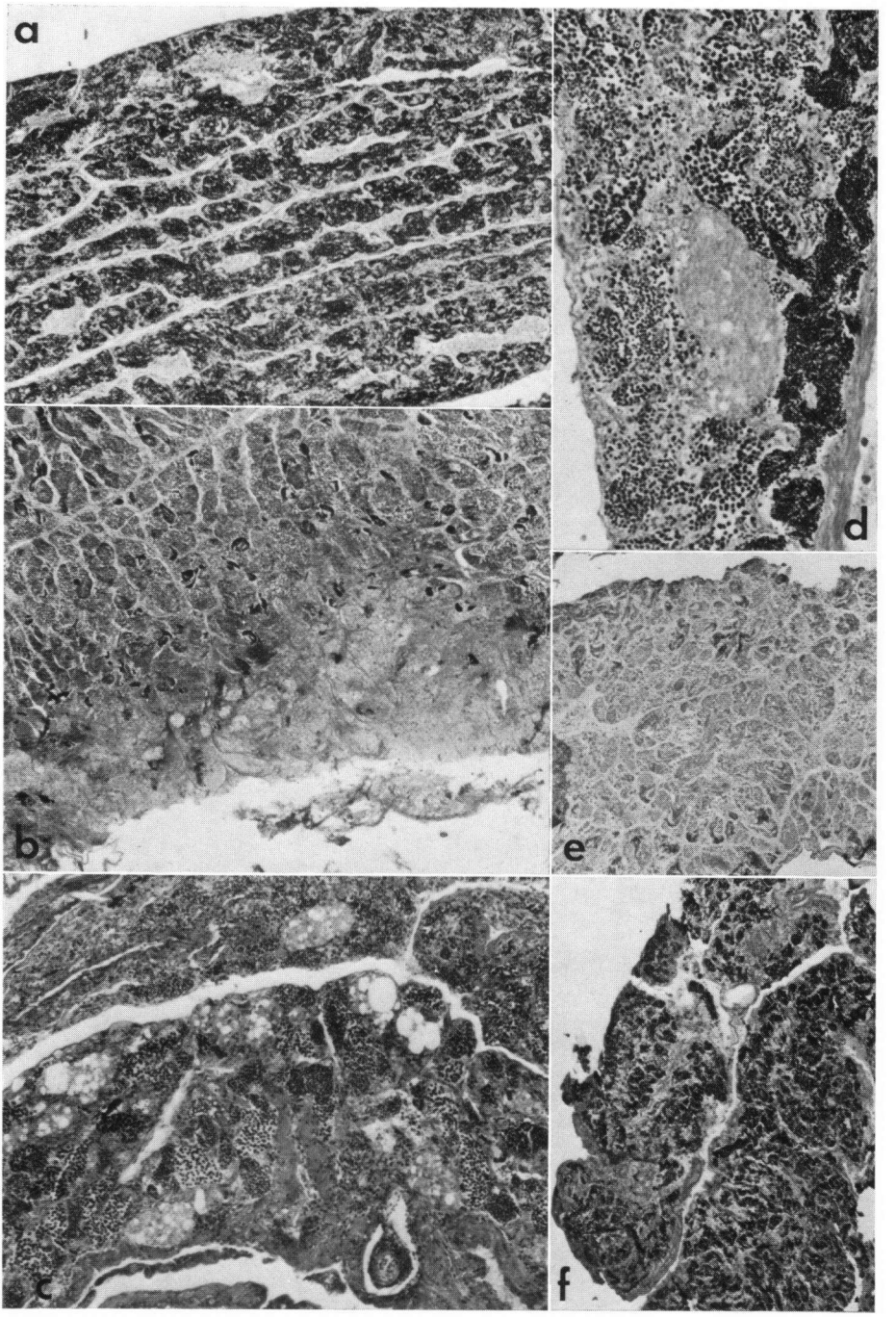
III. Sections of mature labrid ovaries.



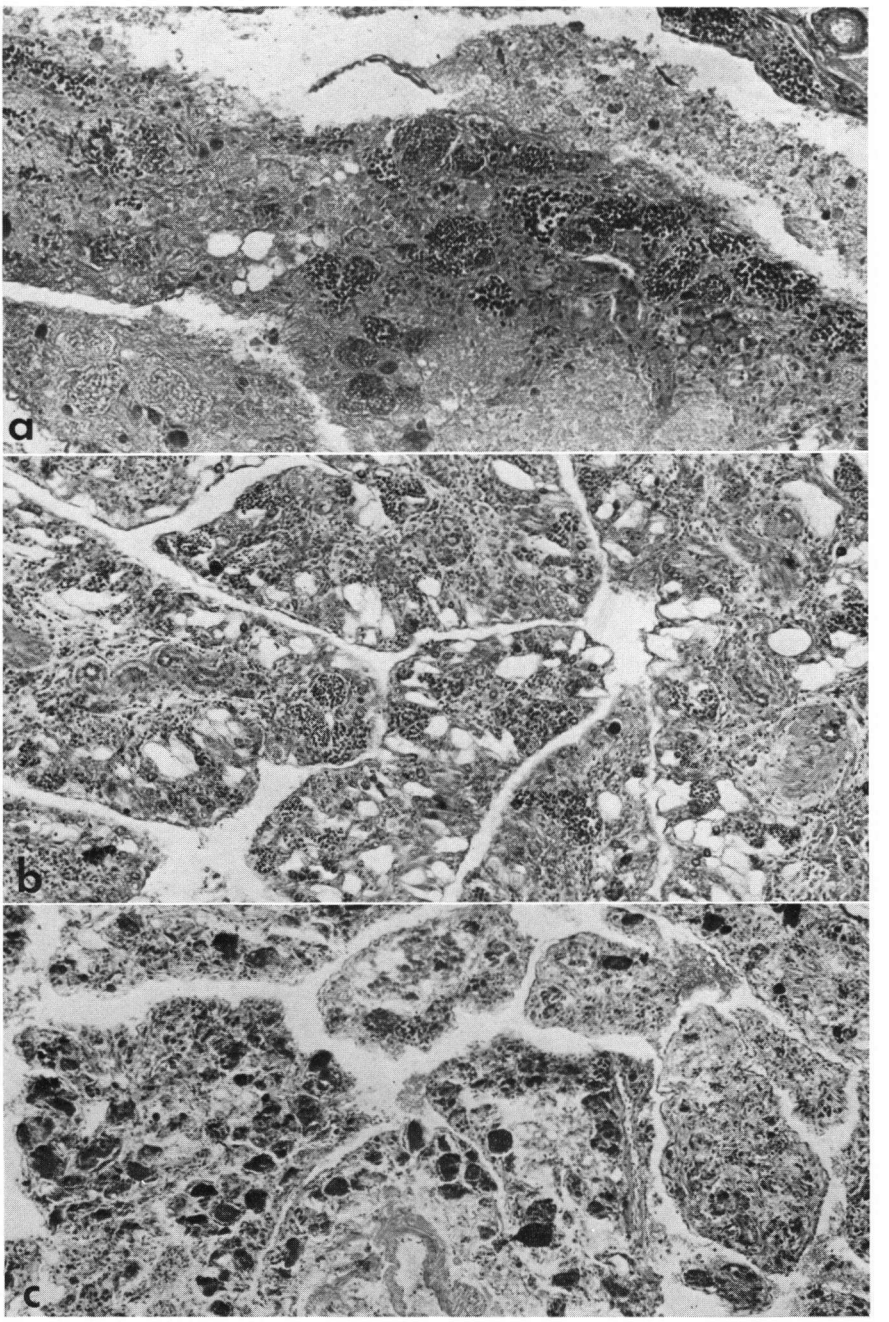
IV. Sections of labrid ovaries in regression (stage VII).



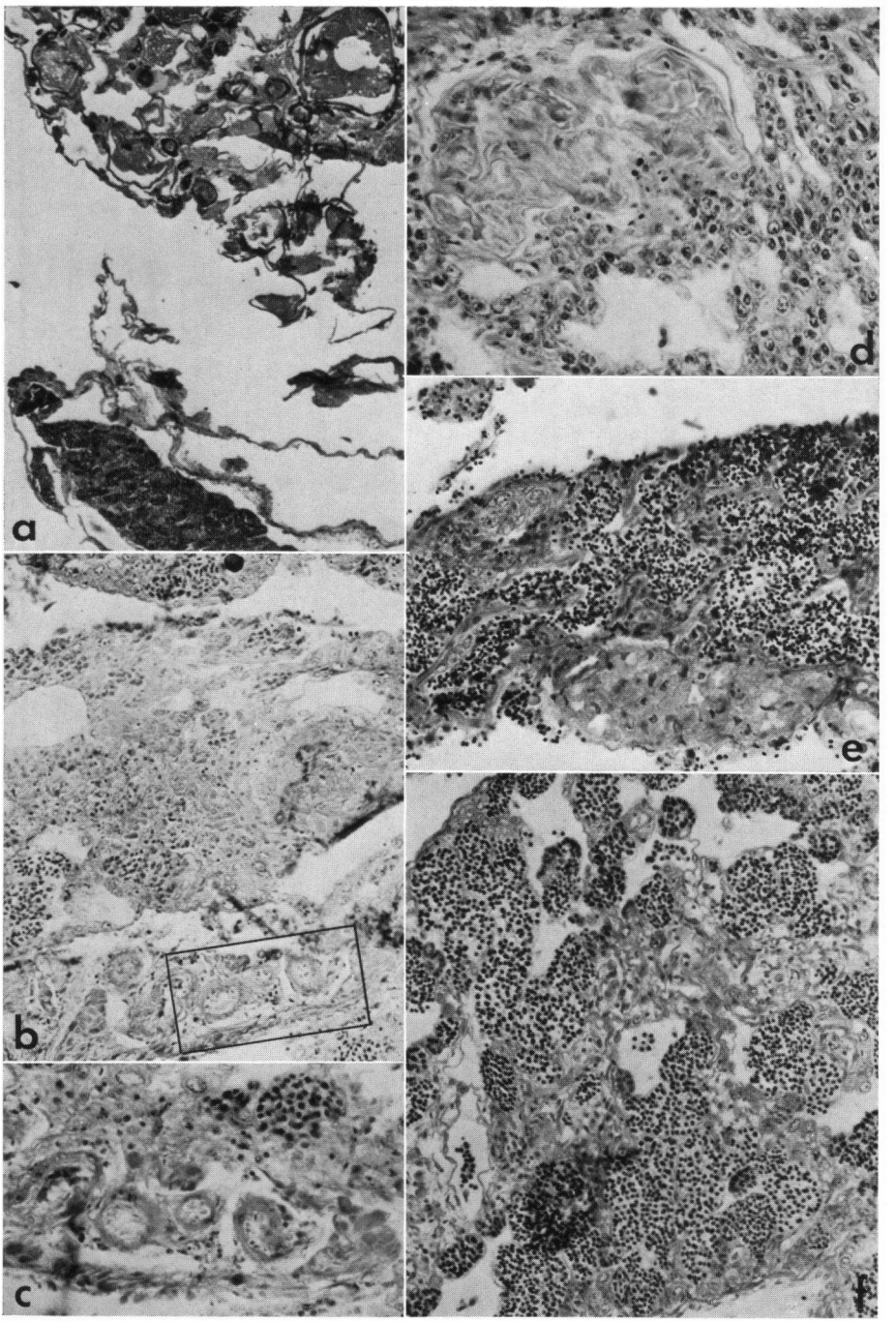
V. Sections of labrid testes.



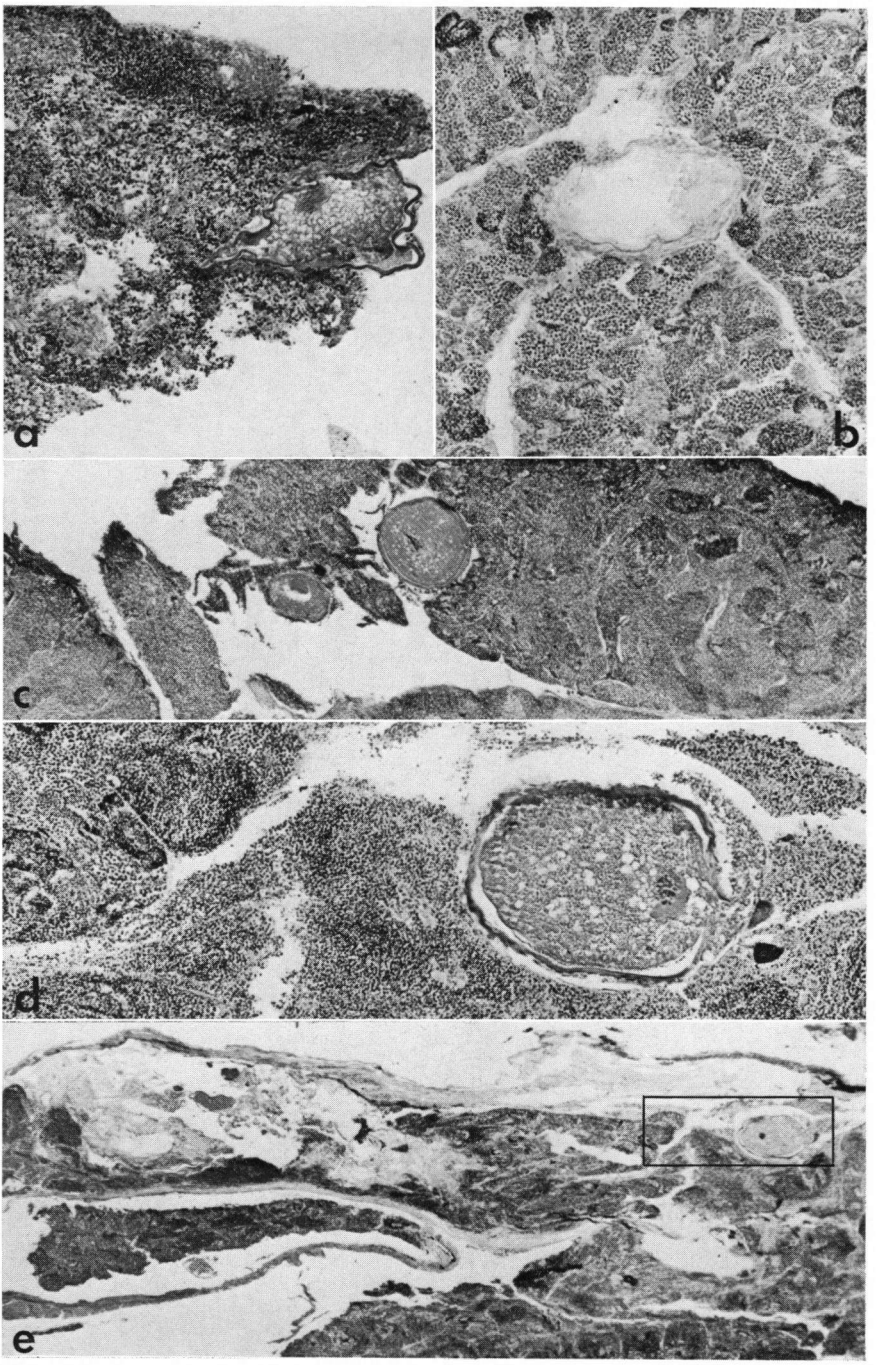
VI. Sections of testes in large labrids.



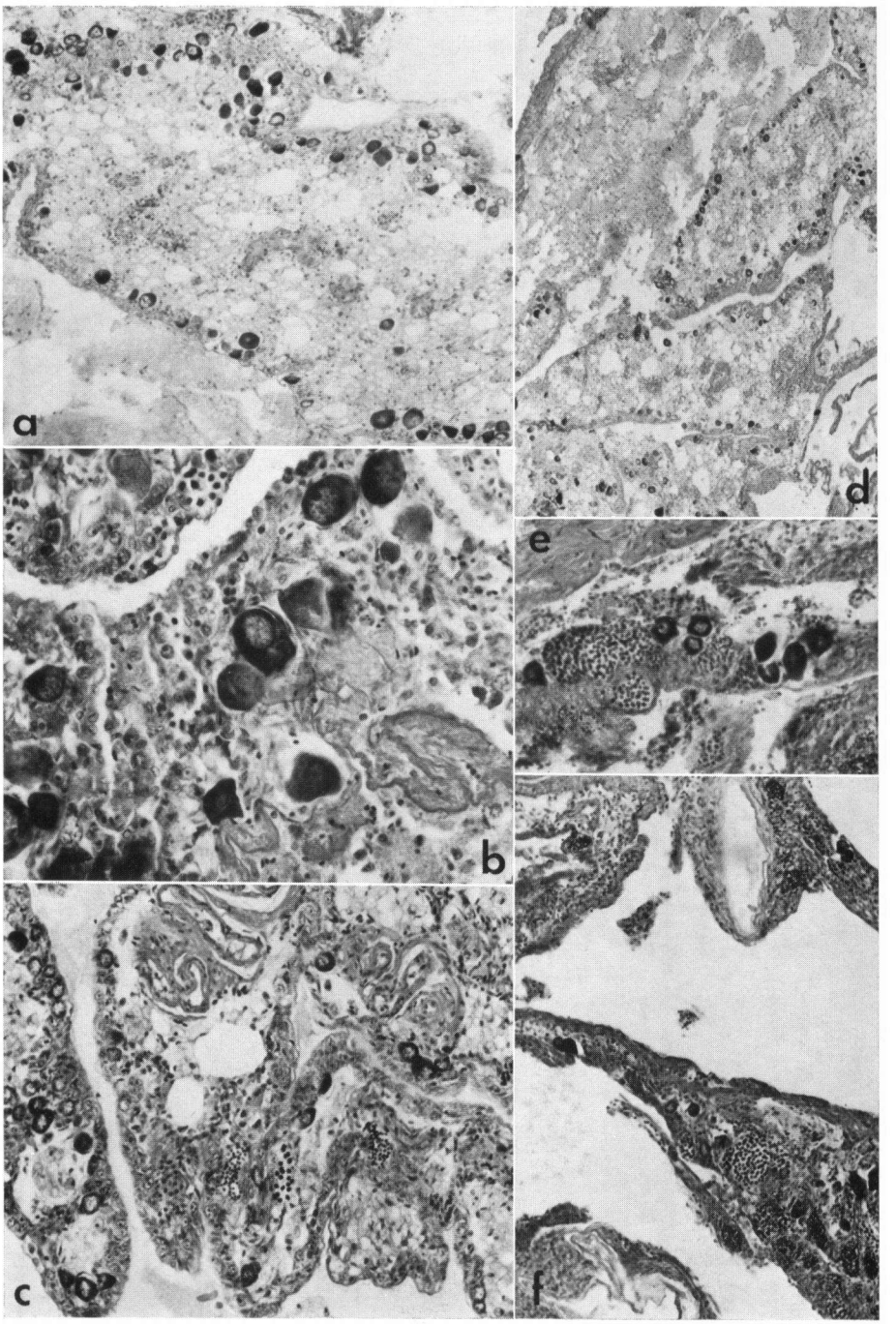
VII. Sections of intersexual labrid gonads.



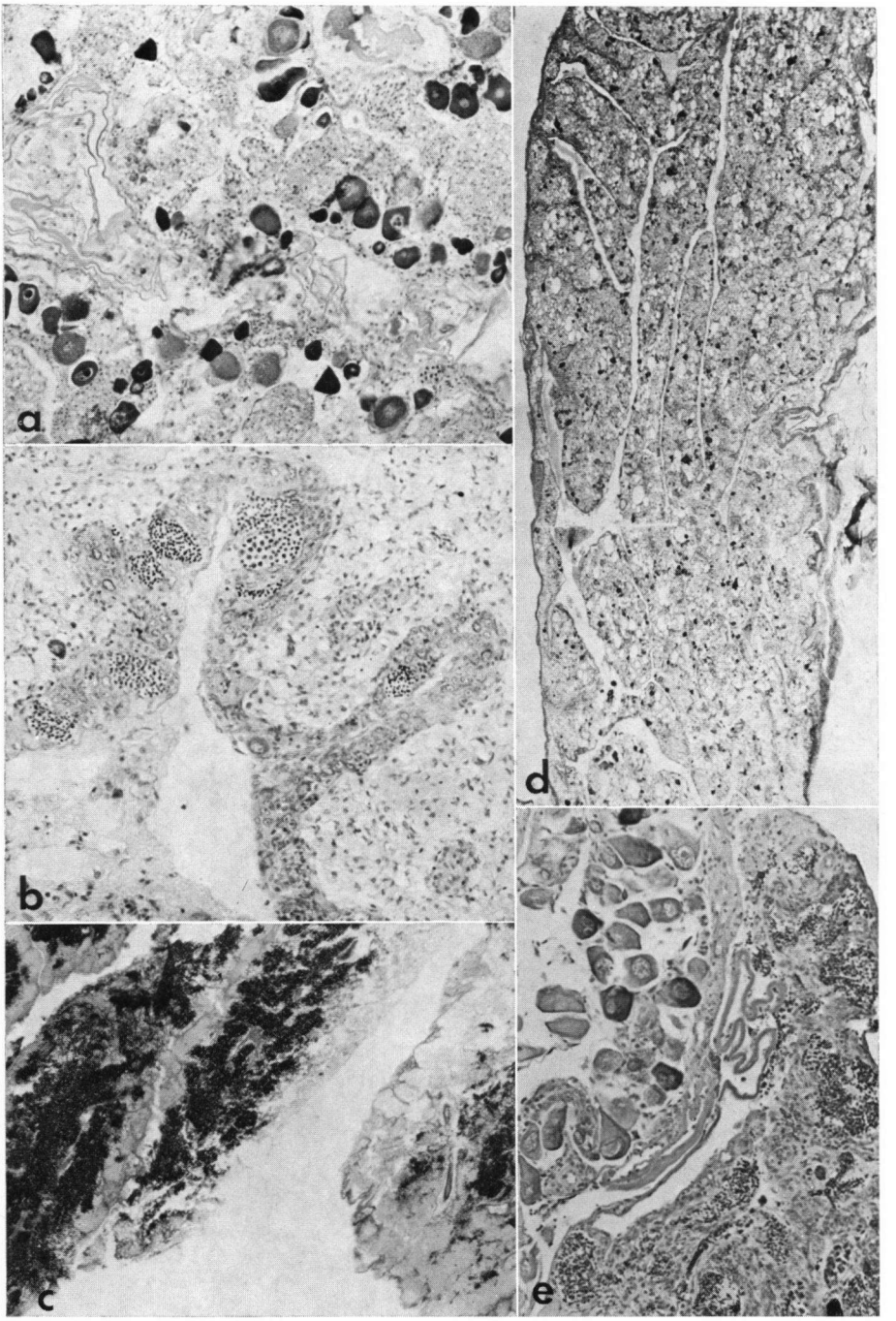
VIII. Sections of intersexual labrid gonads.



IX. Sections of intersexual labrid gonads.



X. Sections of labrid gonads after mammalian hormone treatment.



XI. Sections of labrid gonads after mammalian hormone treatment.