

THE REPRODUCTIVE BIOLOGY OF THE
PROTOGYNOUS HERMAPHRODITE *PIMELOMETOPON PULCHRUM*
(PISCES: LABRIDAE)

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ABSTRACT

Pimelometopon pulchrum, California sheephead, a labrid fish of the eastern Pacific Ocean, was collected the year round at Catalina Island, Calif., and comparative material was taken at Guadalupe Island, Mexico. Individuals at Guadalupe were dwarfed relative to those at Catalina. *Pimelometopon pulchrum* is a protogynous hermaphrodite, the ovarian elements undergoing massive degeneration as spermatogenic crypts proliferate in the gonads of transitional individuals. Sexual changes occur between breeding seasons. Individuals from both populations mature as females at age four; most of those at Catalina function as females for 4 yr and then change sex, at a length of around 310 mm. Sexual transformation occurs earlier on the average at Guadalupe; most individuals are male by age seven. In both populations, more rapidly growing fishes apparently change sex sooner than other individuals of the same age, and fishes that grow slowly may not change sex at all. Spawning appears to occur in July, August, and September in the Catalina population. Individuals probably spawn several times in a breeding season. The weight of active, prespawning ovaries increases at a rate approximately proportional to the third power of the length of the fish. Ovary weight increases in a linear fashion with age in the Catalina population. The rate of increase with age would be less in the Guadalupe population due to dwarfing.

The three coloration phases of *P. pulchrum* are described, two of which are found in adult individuals. The uniform coloration is made up mostly of mature female and immature fishes. About 5% of the mature uniform individuals were males at Catalina, and about 12% at Guadalupe. The bicolored phase is made up exclusively of males and late transitional individuals. Data from field transects revealed that there were about five uniform individuals to every bicolored male. Based on an estimated yearly survival rate of about 0.7, the mature sex ratio at Catalina was approximately two females for every male. The ratio at Guadalupe was closer to three females for every two males, due in part to the earlier sex changes seen there.

Sequential hermaphroditism, a phenomenon characterized by an individual changing from one sex to another at some point in its life history, is widespread in teleost fishes (Atz 1964; Reinboth 1970). In some species, individuals change from male to female (protandry) and in others the situation is the reverse (protogyny).

Most of the published information on the life histories of sequentially hermaphroditic species has dealt with the distribution of the sexes with size, sometimes correlated with a histological investigation of the gonads (Atz 1964; Reinboth 1970). However, in order to interpret the full implications of the sexual patterns seen in sequential hermaphrodites, data on the age distribution, age-specific fecundity, and the sexual transformation schedule of the population are needed (Warner in press).

There are a few protogynous fish species for which the information is nearly complete. For example, Moe (1969) provided excellent data on the life history pattern, gonadal transformation, and survival rate of the serranid *Epinephelus morio*. Natural sex reversal in the synbranchid *Monopterus albus* has been extensively studied both in the field and laboratory (Liem 1963, 1968; Chan 1971), but little is known about its age-specific fecundity and survival pattern. A similar situation exists for the labrid *Coris julis* (Reinboth 1957, 1962; Roede 1966), where again we lack information on the demography of the population. Among the Labridae, perhaps the most complete information exists on the seven Caribbean species of the genera *Thalassoma*, *Halichoeres*, and *Hemipteronotus* studied by Roede (1972). An unfortunate limitation was placed on Roede's work by the tropical location, which precluded age determination from growth rings on scales or otoliths.

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Pimelometopon pulchrum (Ayres), the California sheephead, is a labrid of the subfamily Bodianinae. It is confined to temperate waters, ranging from Monterey Bay, Calif., to Cabo San Lucas at the tip of Baja California, Mexico (Miller and Lea 1972). Individuals can reach a large size (over 800 mm standard length [SL]) and are commonly found off southern California along rocky shores at depths between 5 and 50 m. In this report, it is demonstrated that *P. pulchrum*, like many other labrids, is a protogynous hermaphrodite. In addition, data are presented on age and growth, on the distribution of the sexes in relation to color, size, and age, and on the observed patterns of fecundity and survival. The study embraces two widely separated populations, chosen to reflect how differences in the demography of the population might lead to the observed differences in the schedule of sexual transformation (discussed in Warner in press).

MATERIALS AND METHODS

Source of Materials and Times of Sampling

Pimelometopon pulchrum was taken by means of a hand spear while either skin diving or using scuba. The main collecting area was at Fisherman's Cove on the northeast shore of Santa Catalina Island, Calif., near the University of Southern California Marine Station (lat. 33°27'N, long. 118°29'W). A total of 341 individuals of *P. pulchrum* were processed from samples taken the year round at monthly intervals. Collections began in December 1969 and continued, with occasional gaps, until July 1971; monthly samples were between 20 and 30 individuals.

The other area sampled in this study was at Guadalupe Island, Mexico, located approximately 200 km west of Punta Baja, Baja California. Collections were made along the protected east side of the island, concentrating on an area 3 km from the southern tip known as Lobster Camp (lat. 29°01'N, long. 118°14'W). Year-round sampling at Guadalupe Island was not possible, and the 130 individuals taken there were from three expeditions, January 1970 (16 specimens), April 1970 (53 specimens), and May 1971 (61 specimens).

Supplemental collections were made at La Jolla, Calif., including a sample of large individuals from a spearfishing meet on 19 July 1970.

The standard length of each fish was measured,

and its coloration noted. Several dorsal spines were removed and frozen, and the gonads were fixed in bouin's fluid.

Age Determination Methods

Age determination by counting annular marks on the otoliths or scales was precluded in *P. pulchrum*. The otoliths are extremely small and difficult to locate, and the central portions of nearly all the scales were either clear or irregularly banded, indicating regeneration.

The bones and spines of *P. pulchrum* did show regular markings, and younger fish could be successfully aged by counting the marks on either the bones (opercula or cranial ridges) or the dorsal spines. However, the proximal portions of the bones tended to thicken and obscure the earlier marks on older California sheephead and only dorsal spine annuli could be used for age determination.

Dorsal spines were prepared as follows: the flesh was removed by means of a household enzyme product (Ossian 1970) and the spines were air dried. The classical methods of decalcification and/or thin sectioning (e.g., Cuerrier 1951) were not used. Instead, a high-speed grinding tool with a thin abrasive disc was used to cut cleanly through the spine at a point just distal to the swollen portion of the base. The spinous portion was then thrust through an opaque light shield so that only the cut base protruded. A strong microscope light was directed to the lower portion of the shield so that the only light visible on the other side then came through the projecting base of the spine. The hyaline layers of the spine transmit much more light and the illuminated pattern, resembling tree rings, is easily seen in a dissecting microscope.

The second dorsal spine was used for primary counts; the ring patterns on the other spines were identical, and were used to verify counts for individuals. Counts on each spine were made by two people and were used in the analysis of growth only when they agreed. False rings, probably caused by abnormal growth conditions, were identifiable in young individuals by their proximity to other annuli and their tendency to be incomplete.

Rarely, older fish showed a marked degeneration of the central portion of the spine, which became hollow and oil-filled, making age determination from spines impossible.

A series of measurements of 100 spines was made with an ocular micrometer at a magnification of 30 \times . At this magnification, one ocular micrometer unit equals 0.033 mm. The radius was measured at midspine on a line perpendicular to and beginning at the indentation axis. Distances from the center of the spine to each annulus were recorded for back calculation of length, along the radius line. Finally, the distance from the spine margin to the outermost annulus was measured for determination of the time of annulus formation.

Methods of Reproductive Biology

In the laboratory, each gonad was blotted dry, weighed, and a segment of one lobe was dehydrated in alcohol and embedded in paraffin. Slides were prepared of cross-sections of the lobe, cut at thicknesses of 5, 10, and 25 μm ; thicker sections have less tendency to collapse and were made to ensure that the overall configuration of the cross-section could be observed. Sections were stained with ehrlich's hematoxylin and eosin.

Each gonad was classified according to sex and state of development. Assignment of a developmental class depended on the predominate stage of gametogenesis seen in the gonad. The division of gametogenic stages is as follows:

Oogenesis was divided into five stages, following criteria detailed for a variety of species by Kraft and Peters (1963), Smith (1965), and Moe (1969).

Stage 1. Very small (15-30 μm in diameter) oocytes with a large nucleus, single nucleolus, and a relatively small amount of basophilic cytoplasm.

Stage 2. (30-50 μm) Previtellogenic oocytes with a strongly basophilic cytoplasm and multiple nucleoli around the nucleus margin.

Stage 3. (150-300 μm) Vitellogenesis begins with the deposition of yolk vesicles in the less darkly staining cytoplasm. A thin zona radiata can be seen in late stage 3.

Stage 4. (280-450 μm) Cytoplasm filled with yolk vesicles and globules; the zona radiata well developed and strongly acidophilic.

Stage 5. (450-1,050 μm) Mature or nearly mature oocytes, uniform in appearance due to the coalescence of the yolk globules. The nucleus is eccentric and the zona radiata is thin and non-striated. These oocytes are often extremely irregular in outline and Roede (1972), who noted

the same irregularity in mature eggs of other labrids, probably correctly attributed this to distortion during fixation and staining. This stage was seldom seen, but several specimens were seen with eggs in the ovarian lumen and stage 5 oocytes still within the follicle.

Spermatogenesis occurs in small crypts, in which all the cells are at the same stage. The development and appearance of the spermatogonia, primary spermatocytes, secondary spermatocytes, spermatids, and mature sperm follows very closely the descriptions given by Hyder (1969) for *Tilapia* and by Moe (1969) for *Epinephelus morio*, and will not be repeated here.

The gonadal development classes, intended to parallel those of Moe (1969) and Smith (1965), were designated as follows:

Class 1. Immature female. Stages 1 and 2 oocytes present, atretic or brown bodies (Chan et al. 1967) absent. The ovarian lamellae are pressed closely together and the lumen is small.

Class 2. Resting mature female. Oocyte stages 1, 2, and 3 present, with stage 2 predominating. Atretic bodies are usually present.

Class 3. Active mature female. Oocyte stages 3 and 4 predominate in the lamellae. In late class 3, stage 5 oocytes are also present.

Class 4. Postspawning female. Ovary is disrupted, with many empty follicles in the lamellae. Some degenerating stages 4 and 5 oocytes are usually found in the lamellae and lumen, respectively.

Class 5. Transitional. Seminiferous crypts begin to proliferate in the lamellae, but some stage 2 oocytes can be seen. These oocytes degenerate and decrease in number as spermatogenic activity begins to dominate the gonad.

Class 6. Inactive male. Crypts containing primary and secondary spermatocytes predominate; few spermatids and mature sperm are seen.

Class 7. Active male. Spermatids and tailed sperm increase in abundance until, in the ripe phase, sperm are densely packed in the collecting ducts and many crypts have coalesced.

Class 8. Postspawning male. Ducts are still expanded, but few sperm can be seen in them. Many new crypts containing spermatogonia are present. This apparently is a short-lived stage that rapidly gives way to the resting (class 6) testis.

Fecundity determinations were made by count-

ing yolky oocytes. A thick cross-section of the ovary was cut from near the middle of the lobe, weighed, and then agitated to dislodge as many oocytes as possible from the ovarian lamellae. Oocytes remaining in the lamellae were teased out so that a complete count could be made. An estimate of the number of yolky oocytes per gram of ovary could then be made directly from the sample. The total number of eggs in the ovary was then approximated by multiplying by the total weight of the ovary.

Relative abundance of coloration types was estimated directly from field observations. To eliminate the effects of any differential depth distribution, visual transects were either run perpendicular to depth contours or were compiled from a series of equal length runs parallel to successive contours. Transects were approximately 50 m in length. The number of California sheephead in each color phase was recorded. It was assumed that both coloration types are equally visible, and this is probably valid. California sheephead are not secretive when adults; only juveniles tend to remain close to cover. Larger males appear warier than other individuals, but still remain in sight. The problem in observing California sheephead is not in avoidance, but inquisitiveness. Occasionally transects had to be aborted because of the tendency of *Pimelometopon* to follow the diver.

RESULTS

Age and Growth

Van Oosten (1929) set forth criteria for the acceptance of annuli on scales or bones as yearly marks. These criteria apply equally well to spines, and are as follows: (1) The spine must remain constant in identity and grow proportionally with the fish. (2) Only one mark must be formed each year. (3) The body lengths calculated by using prior annuli on the spine (back-calculated lengths) should agree with the actual lengths of younger age groups.

The criteria will be discussed in order.

(1) Dorsal spines were certainly constantly identifiable in all individuals of *P. pulchrum* examined. The relationship of spine radius to standard length (Figure 1) is satisfactorily expressed in a linear fashion ($r = 0.787$) and there is no apparent indication of allometric growth of the spine, at least for fishes of lengths greater than 130 mm. Much of the scatter in the data is due

to variability in the location of the cut made across the tapering spine.

(2) The increment of distance from the last annulus to the outer edge of the spine should increase with the time since the formation of that mark. If one mark is formed each year at a particular time, the average marginal increment should drop to near zero at the time of annulus formation, then steadily increase for the rest of the year. This pattern is shown (Figure 2) for 77 California sheephead from Catalina taken throughout the year. Successive age groups did not differ in time of annulus formation, so the data are combined for all aged fish. The distinct hyaline bands appeared to be formed in June and July, at the beginning of the period of warming water in the Catalina area (Quast 1968). Formation of growth marks has been found to occur in other inshore California fishes at a similar time (Joseph 1962; Norris 1963; Clarke 1970). Ring formation also overlaps with the initiation of reproductive activity, although egg production and spawning continue well into September (see below).

(3) Lengths of *P. pulchrum* at previous ages were calculated by a modified direct-propor-

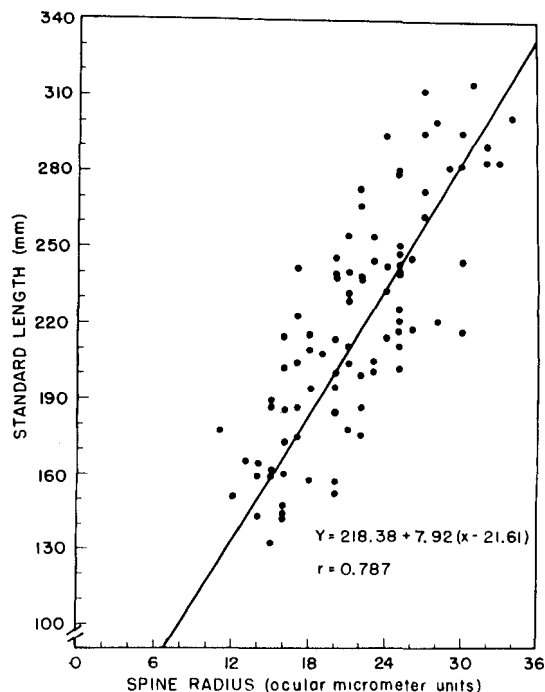


FIGURE 1.—The relationship of dorsal spine radius to standard length for 117 specimens of *Pimelometopon pulchrum* from Catalina Island. One ocular micrometer unit equals 0.033 mm at 30 \times .

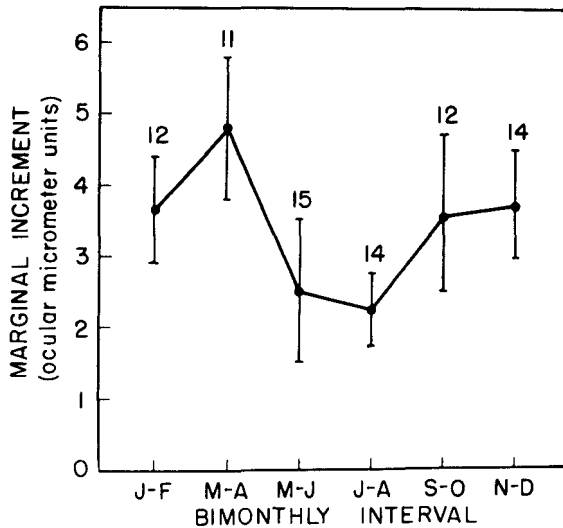


FIGURE 2.—Mean marginal increments for six bimonthly intervals from 78 specimens of *Pimelometopon pulchrum* from Catalina Island. Sample sizes are shown for each interval, and 95% confidence limits for the mean are drawn on either side of each point.

Table 1 shows the back-calculated lengths for 100 California sheephead from Catalina over eight age groups, derived from spine radius measurements. The means from back calculation are also given in Figure 3 for comparison with empirical data. The mean standard lengths for each age (Figure 3) demonstrate good agreement with the back-calculated data.

There appears to be a slight slowing of growth after the fourth year in the Catalina California sheephead population. This may reflect the onset of a diversion of a significant amount of energy into egg production, since most 4-yr-old fish examined were mature females (see below). A second period of more rapid growth is suggested after the seventh year, at an age where many of the Catalina California sheephead are beginning to transform from female to male. There is no evidence for a decrease in the rate of growth up to age 13, where the average standard length is 470 mm. *Pimelometopon pulchrum* is quite capable of growing larger than this, and some individuals

TABLE 1.—Back-calculated lengths for age groups 1 through 8 of *Pimelometopon pulchrum* from Catalina Island.

Age group	N	Mean length of subsample (mm)	Mean length of total sample (mm)	Back-calculated lengths (mm) for ages									
				1	2	3	4	5	6	7	8		
1	8	100	116	97									
2	16	158	155	100	127								
3	22	198	197	106	139	168							
4	17	231	238	124	152	178	200						
5	11	246	245	130	164	185	203	225					
6	11	286	272	129	159	191	212	230	251				
7	7	289	294	128	163	190	225	247	274	295			
8	8	359	368	145	183	220	254	279	299	320	343		
Overall means of calculated lengths				117	150	184	214	242	272	308	343		
Number of individuals				100	92	76	54	37	26	15	8		

tionality method given by Rounsefell and Everhart (1953) as follows:

$$\frac{L' - C}{L - C} = \frac{S'}{S}$$

where L = length of the fish at the time the spine was obtained, L' = length at the time a particular annulus was formed, S = total length of the spine radius, and S' = length along the spine radius to the annulus in question. The term C is a factor used to correct for the length obtained before the spine was formed, and is estimated by the intercept of the length axis on a fish length versus spine radius plot (Figure 1). In the case of the Catalina California sheephead population, C was equal to 47.2 mm.

have very long lifespans. Fitch and Lavenberg (1971) mention a 32-inch (815-mm) male aged at 53 yr, and an 8.3-kg female, no length given, that was 30 yr old. Although exact age determination becomes difficult for large and old individuals, it is occasionally possible. The largest California sheephead encountered in this study were a 592 mm SL male, 20 yr of age, and a 538 mm SL male which had lived 18 yr. Size-age distributions can vary for different locations. In a sample taken by the California Department of Fish and Game at a spearfishing meet at San Pedro, Calif., on 28 March 1971, the mean standard length for males was 661 mm (range 545-745 mm) and for females was 450 mm (range 294-656 mm).

The pattern at Guadalupe Island is different from that at Catalina (Figure 4). While the sample

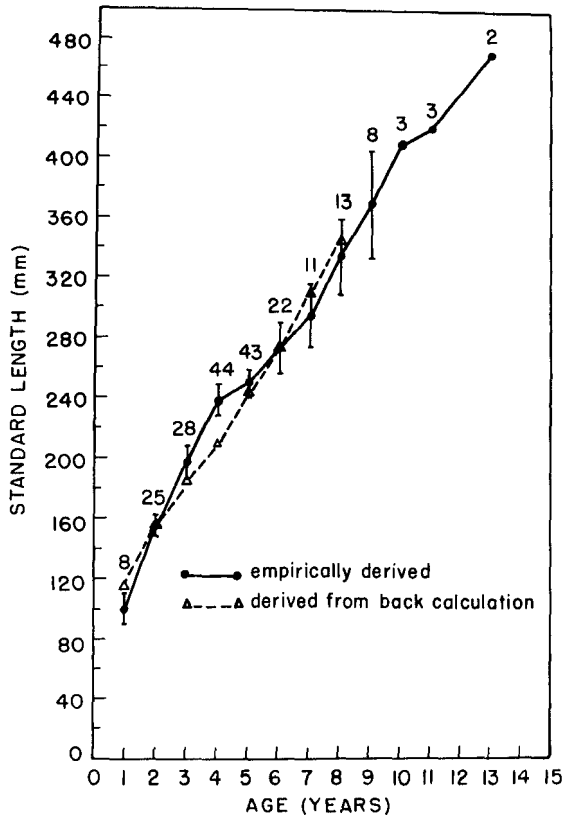


FIGURE 3.—Mean standard length versus age in the Catalina population of *Pimelometopon pulchrum*. Sample sizes are shown for each interval, and 95% confidence limits for the mean are drawn on either side of each point. Means for back-calculated lengths are shown for comparison.

is smaller and more variable than that from Catalina, a marked tendency towards dwarfing is clear. Judging from the mean lengths of each age class, the Guadalupe California sheephead complete their first year of growth at a standard length about 20 mm shorter than those at Catalina. For each of the next 3 yr they fall behind an additional 10 mm, after which relative growth slows even more. By the eighth year, the mean standard length of Guadalupe California sheephead is a full 100 mm less than that found at Catalina.

In spite of the dwarfing, the Guadalupe population shows some interesting parallels with Catalina. The slowing of the average rate of growth at the time of maturity (age four) is more striking here, and growth appears to pick up again after the sixth year, by which time at Guadalupe most individuals are males (see below). This suggests that an increase in the growth rate is associated with sex changes, a topic covered more fully in the

discussion. In the Catalina population, both the increase in growth rate and the maximum number of sex changes occur about a year later than in the Guadalupe population.

Anatomical Features of the Gonad and Sexual Transformation

The gonad of *P. pulchrum* consists of two hollow sacs in the extreme dorsal part of the body cavity. Genital arteries and veins run through the dorsal part of each lobe, giving off segmental branches. The wall of each lobe consists of connective tissue and smooth muscle.

The internal structure is made up of germinal epithelium in a series of folds or ridges, the gonadal lamellae. These are numerous in the female, but few in the male. There is a small

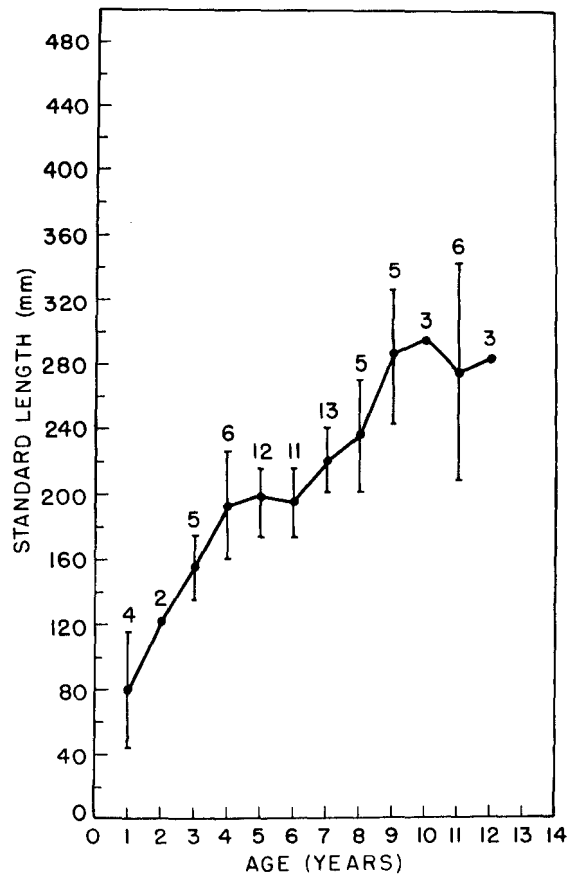


FIGURE 4.—Mean standard length versus age in the Guadalupe Island population of *Pimelometopon pulchrum*. Sample sizes are shown for each age, and 95% confidence limits are drawn on either side of each point.

alamellar portion in the most ventral section of the gonad, similar to that described by Smith (1965) for some serranids.

In the female, oogenesis takes place within the lamellae. When the egg ripens, it breaks into the central lumen, which leads to the common oviduct. Some oocytes are interrupted in their normal development and undergo a degeneration into various types of corpora atretica (Figure 5). These

During sexual transformation, crypts of developing spermatocytes appear, first at the base of the ovarian lamellae, and then throughout the gonad (Figure 7). Unshed eggs and nonvitellogenic (stage 2) oocytes are gradually reabsorbed and the number of lamellae visible in cross-section are reduced. The basic structure of the gonad remains ovarian, with a central lumen into which the lamellae protrude. The lumen

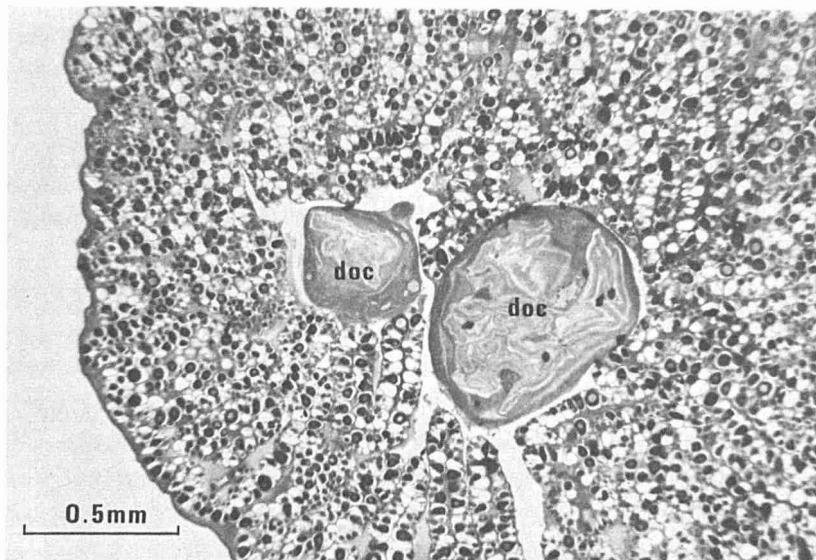


FIGURE 5.—Degenerating oocytes (doc) in the lumen of a resting ovary of *Pimelometopon pulchrum*. Specimen number PP411, 217 mm SL.

have been described briefly for serranids by Smith (1965) and in detail for *Monopterus albus* by Chan et al. (1967). Chan and his colleagues discuss the possible endocrine function of atretic structures, and state that all types of corpora atretica eventually end up as brown or yellowish bodies which are long lasting in the gonad. In *P. pulchrum*, brown bodies can usually be found near the gonad wall and in the central portion of the lamellae. Judging from the number of these terminal phase corpora atretica in resting (class 2) females compared with the usually greater number of earlier stage atretics (Chan et al. 1967) in postspawning females, the brown bodies are probably formed from more than one degenerating oocyte.

Brown bodies are also found in male gonads; some of these are almost certainly the result of oocyte degeneration in the previous female phase (Figure 6), while others may be the result of degeneration and coalescence of unshed sperm.

however no longer functions in gamete transport and sperm are collected in a series of sinuses on the periphery of the gonad, reaching the outside by means of ducts in the wall of the now unused oviduct. This is very similar to the anatomy described by Reinboth (1962, 1970) for other labrid secondary (sex-reversed) males. No testes of the primary type were seen.

Transformation Schedule

To illuminate the life history patterns of the California sheephead populations, the gonad development classes were grouped in the following way:

- Immature: Class 1 only.
- Female: Classes 2, 3, and 4.
- Transitional: Class 5 only.
- Male: Classes 6, 7, and 8.

The distribution of sexual types by standard

length for *P. pulchrum* from Catalina Island (Table 2) and Guadalupe Island (Table 3), as well as the relative frequencies for each size grouping (Figure 8), are similar in both localities in that the

small size classes are made up exclusively of immature females. Mature females are most abundant in the next size classes, and then become less numerous as males begin to predominate in the

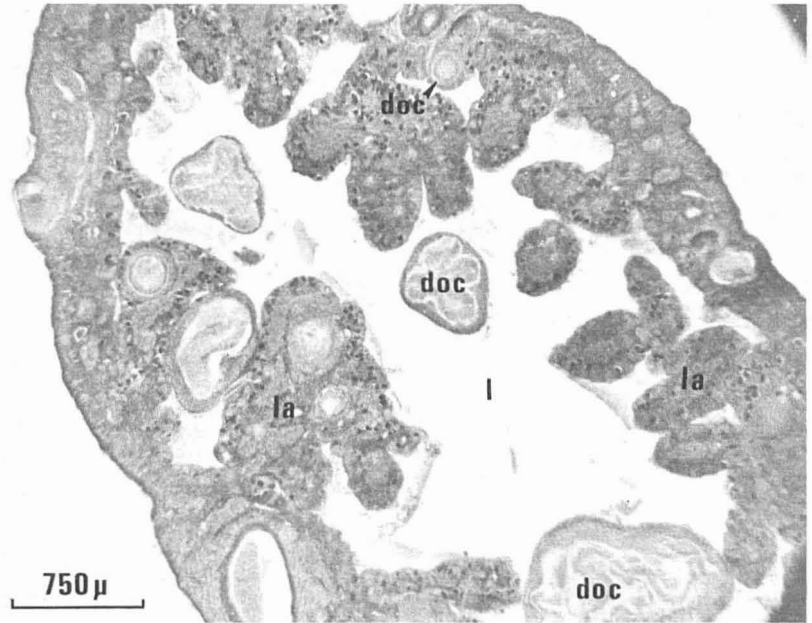


FIGURE 6.—Degenerating oocytes (doc) in the lumen (l) and lamellae (la) of the gonad of a transitional individual of *Pimelometopon pulchrum*. Specimen number PP405, 317 mm SL.

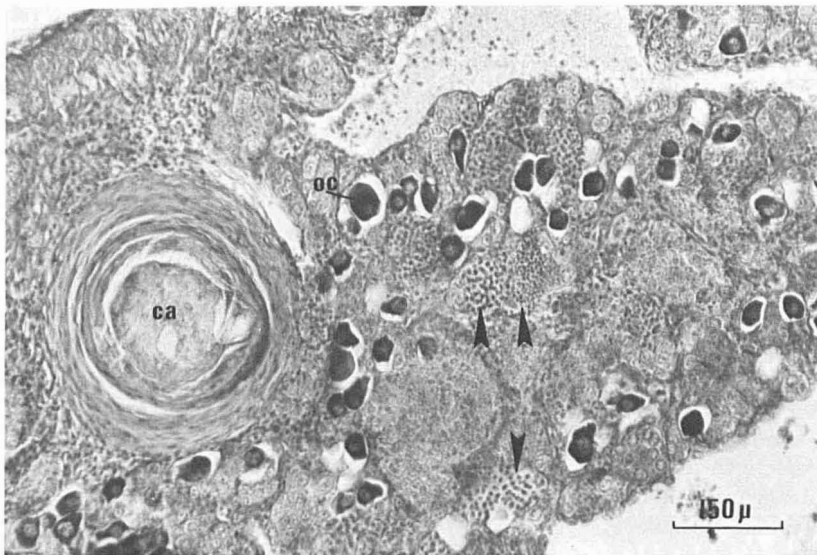


FIGURE 7.—Spermatogenic crypts (shown by arrows) developing in a gonadal lamella of a transforming *Pimelometopon pulchrum*. Stage 2 oocytes (oc) and a corpus atreticum (ca) can also be seen. Specimen number PP405, 317 mm SL.

TABLE 2.—Frequency of sexual types in each 20-mm size class for the Catalina Island population of *Pimelometopon pulchrum*.

Standard length (mm)	Number of fish	Immature	Mature female	Transitional	Mature Male
<100	7	7	0	0	0
100-119	5	5	0	0	0
120-139	6	6	0	0	0
140-159	28	28	0	0	0
160-179	18	18	0	0	0
180-199	25	24	1	0	0
200-219	34	15	19	0	0
220-239	40	6	33	0	1
240-259	49	2	39	5	3
260-279	33	0	25	4	4
280-299	23	0	15	2	6
300-319	14	0	9	1	4
320-339	10	0	3	0	7
340-359	16	0	5	0	11
360-379	9	0	1	0	8
380-399	7	0	2	0	5
> 400	17	0	1	0	16
Totals	341	111	153	12	65

TABLE 3.—Frequency of sexual types in each 20-mm size class for the Guadalupe Island population of *Pimelometopon pulchrum*.

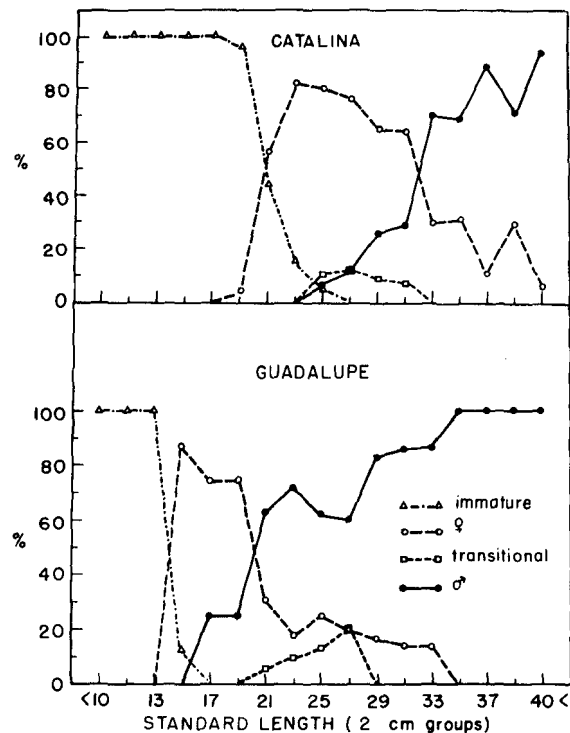
Standard length (mm)	Number of fish	Immature	Mature female	Transitional	Mature Male
< 100	5	5	0	0	0
100-119	5	5	0	0	0
120-139	3	3	0	0	0
140-159	8	1	7	0	0
160-179	12	0	9	0	3
180-199	15	0	10	0	5
200-219	16	0	5	1	10
220-239	11	0	2	1	8
240-259	16	0	4	2	10
260-279	10	0	2	2	6
280-299	6	0	1	0	5
300-319	7	0	1	0	6
320-339	7	0	1	0	6
340-359	2	0	0	0	2
360-379	3	0	0	0	3
380-399	1	0	0	0	1
> 400	3	0	0	0	3
Totals	130	14	42	6	68

largest sizes. Transitionals were found in intermediate sizes, in numbers which varied seasonally (see below).

At Catalina, most California sheephead mature at standard lengths between 190 and 230 mm. Sexual transformation occurs over a broader size range beginning at 250 mm, with a peak of activity apparently occurring at standard lengths between 310 and 330 mm.

The dwarfing phenomenon found in the Guadalupe population is again evident (Table 3, Figure 8). Maturity begins at a length near 140 mm, and the majority of individuals are male by a length of 210 mm. Peak transformation activity appears to occur in the population in fishes ranging from 190 to 230 mm in standard length.

The actual time courses for all these events become evident when the relative frequencies of

FIGURE 8.—Proportions of each sexual type in successive 2 cm standard length groupings for the Catalina Island (top) and Guadalupe Island (bottom) populations of *Pimelometopon pulchrum*.TABLE 4.—Frequency of sexual types in each year class of *Pimelometopon pulchrum*.

	Age class	Number of fish	Immature	Mature female	Transitional	Mature male
Catalina population	1	7	7	0	0	0
	2	33	33	0	0	0
	3	34	34	0	0	0
	4	42	5	35	1	1
	5	40	0	33	2	5
	6	27	0	16	3	8
	7	15	0	9	1	5
	8	14	0	4	0	10
	9	8	0	2	0	6
	10+	8	0	1	0	7
Totals		228	79	100	7	42
Guadalupe population	1	4	4	0	0	0
	2	2	2	0	0	0
	3	5	5	0	0	0
	4	4	0	4	0	0
	5	10	0	5	1	4
	6	13	0	7	0	6
	7	14	0	2	3	9
	8	9	0	2	0	7
	9	6	0	0	1	5
	10+	13	0	3	0	10
Totals		80	11	23	5	41

the sexual types in each age class are graphed (Figure 9). The curves are based on the frequency distributions listed in Table 4.

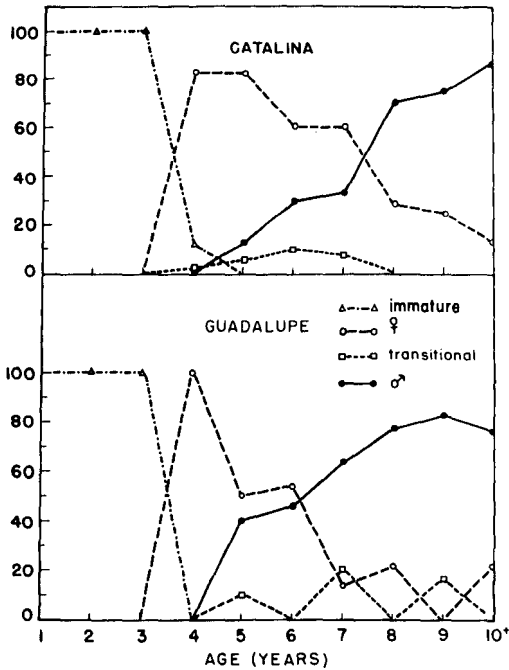


FIGURE 9.—Proportions of sexual types in each year class of *Pimelometopon pulchrum* from Catalina Island (top) and Guadalupe Island (bottom). The last age grouping consists of all fishes 10 or more years old.

In both populations, sexual maturity begins in the fourth year of life for virtually all members. By using age groupings, the skewness introduced by the dwarfing at Guadalupe is removed, and differences in the transformation activity time schedule in the two populations are revealed. At Guadalupe, males are present in essentially the same abundance as females in age classes 5 and 6, and strongly predominate at age 7 and thereafter. Therefore the majority of California sheephead at Guadalupe Island spend no more than 2 or 3 yr as functional females.

Transformation generally occurs later in the Catalina population. Most individuals are functional females for at least 4 yr, and males predominate only after age 8.

Distribution of Gonad Development Classes with Time

The active state of gonads may be determined directly through histological examination or inferred from the appearance and the size of gonad (gonad indices).

The seasonal distribution of mature gonad

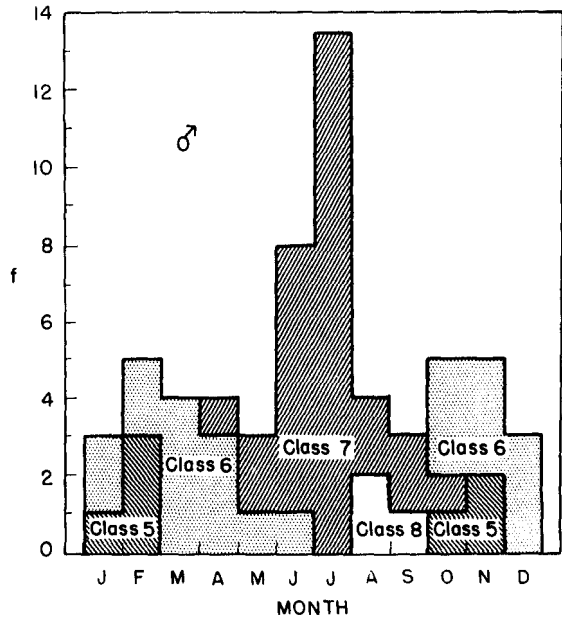
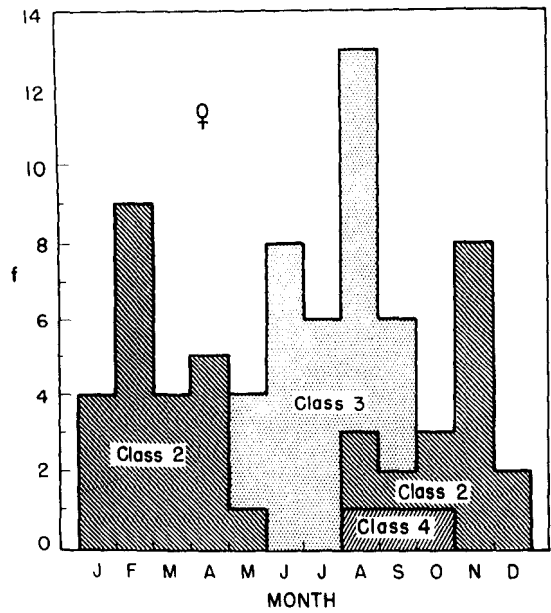


FIGURE 10.—Number of individuals of *Pimelometopon pulchrum* in each mature gonadal development class from monthly samples taken at Catalina Island.

development classes for 166 California sheephead from Catalina is shown in Figure 10. As expected, immature fishes, which are not shown in the Figure, occur throughout the year. Resting stage females (class 2) were encountered from August through May, and predominated from October to April. Active females (class 3) were present May

through September. Late class 3 gonads were seen in July, August, and September, and most spawning activity probably takes place in these months. Females with postspawning ovaries (class 4) were captured in low numbers from August to early October. Class 4 appears short-lived, quickly receding into a resting class (class 2) or transitional (class 5) phase.

Transitional individuals were found only from October to March at Catalina. Those taken in October and November were all in the early stages of transformation, with many stage 2 oocytes and a few scattered spermatogenic crypts in evidence. Transitionals captured in February at Catalina or in May at Guadalupe were more advanced, with few stage 2 oocytes and spermatogenic crypts dominating the gonad.

Most males at Catalina were inactive (class 6) from October through April, closely paralleling the period seen for females. Active gonads predominated in samples from fish taken in May through September. Again the pattern suggests that spawning activity takes place from August through early October.

Further support for designating this period as the spawning season comes from the gonad indices (Figure 11) of Catalina females caught in different months. These reflect a similar pattern seen in the analysis of gonad development states. After a quiescent period from October through April, the ovaries begin to increase in size until a maximum is reached in June and July. Spawning reduces the average index steadily from then until

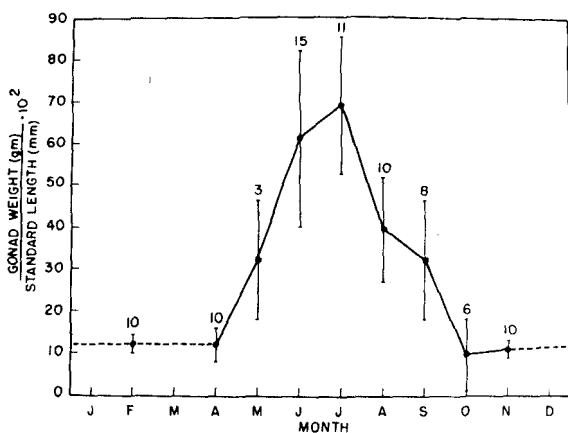


FIGURE 11.—Average gonad indices for monthly samples of mature female *Pimelometopon pulchrum*, all of standard lengths less than 300 mm. Sample sizes are shown above the bracketed lines, which are the 95% confidence limits of the mean.

September. The resting value is then seen again, remaining constant through the winter.

The index used was gonad weight scaled to compensate for different lengths of individuals. When only the mature females less than 310 mm in standard length are included in the analysis, the relationship between gonad weight and standard weight is sufficiently linear (Pearson correlation coefficient = 0.845 [$P < 0.001$] on 24 individuals caught in June) that the use of the following formula is justified:

$$\text{Gonad index} = \frac{(\text{gonad weight in grams}) (100)}{(\text{standard length in mm})}$$

The size range used includes the great majority of reproductive females at Catalina.

An analysis of the spawning season of *P. pulchrum* at Guadalupe Island was not possible due to the lack of year-round sampling.

Multiple Spawning and Fecundity

Two or more distinct groups of ripening oocytes were usually apparent in the ovaries of *P. pulchrum* examined in June and July. The size distribution of yolky oocytes in an ovarian cross-section (Figure 12) from a female, 244 mm SL, captured at Catalina in mid-July, shows that there is one group of eggs ready to be spawned, and that two other distinct groups are undergoing vitellogenesis. This type of successive maturation of several groups of oocytes is termed asynchrony, and is characteristic of species that have comparatively long breeding seasons and multiple spawnings by individuals within each season (Yamamoto and Yamazaki 1961).

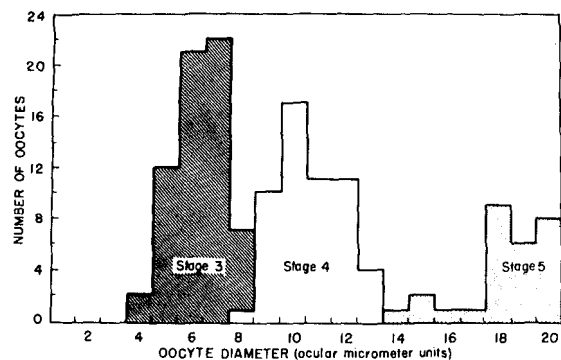


FIGURE 12.—Size distribution of yolky oocytes in an ovarian cross-section of a 244 mm SL female of *Pimelometopon pulchrum* captured 22 July at Catalina Island. The oocytes are also classified according to their degree of development.

Further evidence for multiple spawning is seen in the ovaries from some females captured in August and early September. There were a few mature eggs free in the lumen and numerous empty follicles in the lamellae, both indications of recent spawning. At the same time, another group of vitellogenic oocytes were observed developing in the lamellae and these would presumably have been spawned at a later time.

As Yamamoto and Yamazaki (1961) point out, the presence of multiple spawning complicates any determination of the number of eggs produced each year by an individual fish. Estimates can be made from an analysis over time of frequencies of egg diameters, such as that done by Clark (1934) for *Sardinops caerulea*. Such analyses require a large sample over the mature size range and this was not available for *P. pulchrum*.

Counts of the yolky oocytes in subsamples of ovaries made for California sheephead females captured in July (Table 5) are probably overestimates of the number of eggs spawned during the

TABLE 5.—Estimates of the total number of vitellogenic oocytes and density of those oocytes in the ovaries of *Pimelometopon pulchrum* captured at Catalina Island in July 1970.

Standard length (mm)	Date of capture	Weight of ovary (g)	Estimated number of yolky oocytes, total	Estimated number of yolky oocytes per gram of ovary
209	7/24	6.87	36,068	5,250
235	7/22	16.69	74,270	4,450
238	7/22	16.53	76,870	4,650
254	7/19	28.00	171,500	6,125
280	7/22	17.23	88,300	5,125
311	7/19	50.02	296,600	5,930
314	7/19	19.80	113,850	5,750
330	7/19	34.07	167,600	4,920
359	7/19	41.63	258,100	6,200

Mean and 95% confidence limits of oocyte density, oocytes per gram = $5,377 \pm 499$.

season. This is because, as pointed out above, the relationship between the number of these oocytes and the number actually spawned depends on the survival rate of the oocytes to maturity and the proportion that are actually ejected from the body. The smaller numbers of stage 5 oocytes relative to stages 3 and 4 (Figure 12) indicates a loss during development. There are certainly some eggs left in the lumen of postspawning females. These degenerate and are presumably absorbed during the resting phase.

For an analysis of the functional significance of sequential hermaphroditism, actual egg numbers are less important than data on the relative values for age- or size-specific fecundities (Williams 1966;

Warner in press). As long as the number of eggs per unit weight of ovary does not vary appreciably with size or age, weights of active prespawning ovaries can be used to represent relative fecundities. The last column of Table 5 shows there is no apparent effect of fish length on egg density within the ovary.

Comparison of ovary weights and standard lengths for mature females captured at Catalina in June and July (Figure 13) shows that fecundity increases exponentially with the length. The exponential equation:

$$W = 1.31 \times 10^{-3} L^{2.95}$$

(W = gonad weight, L = standard length) indicates that the increase of gonad weight with

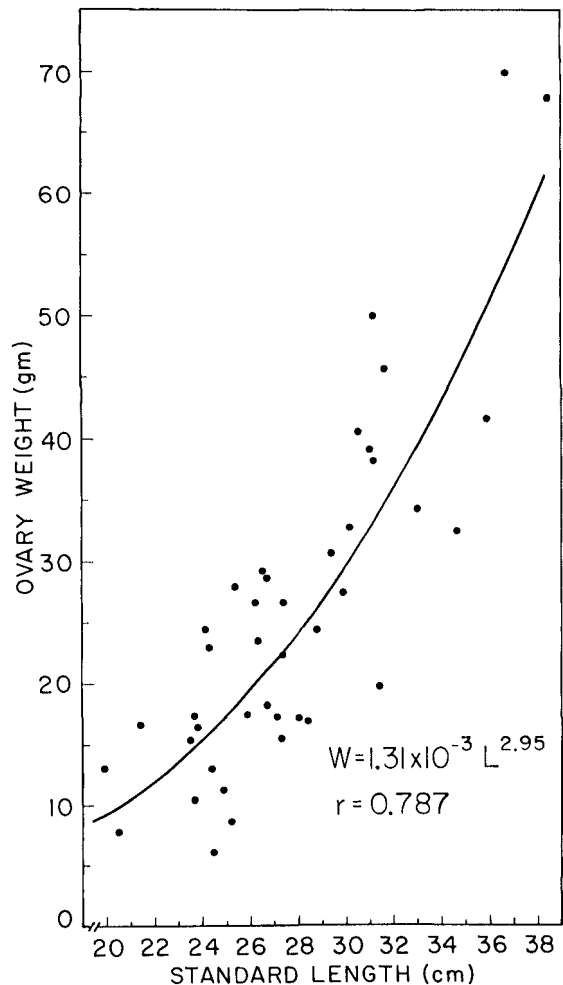


FIGURE 13.—Ovary weight versus standard length for females of *Pimelometopon pulchrum* captured in June and July at Catalina Island.

length conforms to a simple cube law relationship, which would be expected if gonad weight remains some constant proportion of the total weight. The exponent 2.95 was determined by a least-squares regression fit to a logarithmic transformation of the data. The confidence limits around the regression line become increasingly large with higher values of W and L , and the curve should not be used for extrapolations beyond the range of the data. Ovary weights in relation to age are shown in Figure 14. There are few data for the older age classes, but there is a definite positive correlation of the fecundity and the age of the individual.

Coloration, Sex, and Field Distribution of Coloration Types

The California sheephead is found in three main color phases (Crozier 1966), all of which are closely correlated with sexual state.

For the first year, *P. pulchrum* has juvenile coloration, a gold or salmon body color with black spots on the anal fin, the anterior and posterior portions of the dorsal fins, and on the caudal peduncle, and with a silver lateral stripe extending from the eye to the caudal fin. Crozier (1966) stated that the initial body color was gold, and this was gradually replaced by the reddish adult shade. The juvenile coloration was seldom seen in individuals over 100 mm SL, and has never been found in sexually mature individuals.

The most common color pattern of *P. pulchrum* is a uniform rose or salmon color, covering the entire body with the exception of the chin, which is usually white in mature individuals. The median and pelvic fins are darker than the body, ranging from dusky red to black. The pectoral fins usually match body color. Uniform coloration may be obscured by a melanistic condition which causes the entire body to appear brown. This occurs in varying degrees, making the fish appear almost black in extreme cases. Eleven percent of the uniformly colored fish captured at Catalina were designated melanistic, as were one-third of all uniform types at Guadalupe.

A uniform coloration is characteristic of immature fish as well as mature females. Histological analysis indicated, however, that the relationship was not perfect. At Catalina, 3.5% of the individuals designated uniform in color were discovered to have male gonads. When only sexually mature uniformly colored California sheephead were tallied, 5.1% were male. These males ranged

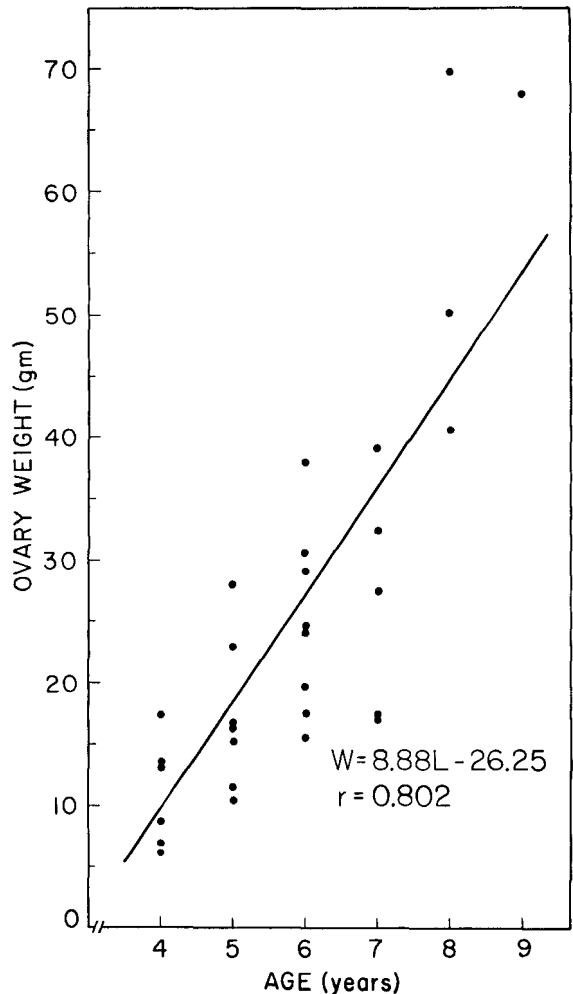


FIGURE 14.—Ovary weight versus age for females of *Pimelotomon pulchrum* captured in June and July at Catalina Island.

in length from 245 to 315 mm. and were captured in June, July, and December. Examination of a large series of gonad cross-sections from these individuals revealed a few stage 2 oocytes within the lamellae from two captured in July. This can be taken as evidence for a recent sex change. All the others had gonads of completely normal male appearance.

Field notes revealed that all of these individuals were melanistic, and 70% were recorded as having some male external characteristics, such as a small nuchal hump or slight differential darkenings of either the head or tail regions (see below). This suggests the possibility that some of these individuals may have been incorrectly typed due to the ground color being obscured by melanin.

Males in uniform coloration are more frequent in the Guadalupe population. A total of 6 out of 57 (10.5%) uniformly colored individuals were males. Elimination of immature fish from the count raises the figure to 12.3% males. Four of the six were melanistic, one of these with slight male characteristics. The other two individuals possessed normal uniform coloration with no darkening.

In the third color phase the head region, including the opercle, is dark brown or black. The chin remains white, and the midsection retains the reddish hue of the uniform type. The caudal portion, beginning approximately on a line connecting the initial soft rays of the dorsal fin with the anterior limit of the anal fin, is also dark brown or black. The median fins and pelvics remain generally dark in color, and the pectorals may acquire a dark band at their tips.

This coloration is found exclusively in males and some transitionals (see below). It is usually accompanied by two other male secondary sexual features common in the Bodianinae, the nuchal hump and filamentous extensions of the median fins. The hump appears to increase in relative size as the male gets larger, making the head appear increasingly angular in profile. No individual with this bicolored pattern was found to have functional ovaries. During the breeding season, the pattern serves as an excellent indicator of a functional male.

Individuals classified as transitional varied in coloration. Of 11 transforming California sheephead for which coloration records exist, 3 were scored uniform in color and 2 as bicolored. The remaining 6 were recorded as intermediate in coloration, usually involving a slight darkening of the head, caudal region, or both. The three uniform individuals were classed as early transitionals (large amounts of stage 2 oocytes still in the gonad); the two bicolored fishes were classed as late transitionals (only a few degenerating oocytes in the gonad cross-sections).

The distribution of uniform and bicolored types in field populations, determined by visual transects (Table 6) shows that bicolored males are present in remarkably similar proportions in both localities, occurring in a ratio of about 5.5 uniform individuals to every bicolored individual. Confidence limits for estimating the proportion of bicolored individuals were calculated from a binomial distribution, $n = 216$ and 407 for Catalina Island and Guadalupe Island, respectively (Dixon and Massey 1969).

TABLE 6.—Numbers of coloration types in two populations of *Pimelometopon pulchrum*, determined by a series of visual transects.

Locality	No. of transects	No. of uniform type	No. of bicolored type	Proportion p of bicolored types and 95% conf. limit
Catalina Island	70	183	33	0.153 ± 0.048
Guadalupe Island	93	343	64	0.157 ± 0.035

DISCUSSION

Anatomical Features of the Gonad and Sexual Transformation

The ovary of *P. pulchrum* is essentially identical with that of the labrid *Coris julis*, which was studied in detail by Reinboth (1962). Reinboth, however, did distinguish between the testes of those *C. julis* born as males (primary males) and those that become males through sex reversal (secondary males). In the former, the testis appears rather solid and flattened, and sperm are transported by means of a single vas deferens in each lobe. The secondary male has a testis like that described here for *P. pulchrum*. The two types differ in the structure of the vas deferens posterior to the gonadal lobes, which surrounds the old oviduct in secondary males, but is a simple tube in primary males (Reinboth 1970).

When primary and secondary males are present in a single species, Reinboth (1970) termed the species diandric. When only secondary males are present, the species is termed monandric. To Reinboth's (1970) list of monandric species (*Labrus turdus*, *L. merula*, *L. bergyitta*, *Hemipteronotus novacula*, and possibly *L. bimaculatus*) we may add *P. pulchrum*. Other labrid species have been studied without regard for the primary-secondary male phenomenon (Atz 1964; Reinboth 1970), and cannot be categorized with certainty as monandric or diandric.

The transition from a functional ovary to a testis has been described in detail for labrid fishes in both naturally occurring situations (Reinboth 1962; Sordi 1962; Okada 1962; Roede 1972) and under the influence of hormone administration (Reinboth 1962, 1963; Roede 1972). These reports are essentially in agreement with the present observations on *P. pulchrum*. There is no evidence of synchronous hermaphroditism (Atz 1964:147) in the Labridae, but Robertson (1972) found spermatogenic cysts in the ovaries of 28 of 29 females of

Labroides dimidiatus, and 15 of these had crypts with sperm or spermatids. Thus, the possibility of encountering a synchronously hermaphroditic labrid species should not be ruled out.

Transformation Schedule

Pimelometopon pulchrum fits the general labrid pattern of size and sex distribution. No males were found smaller than 230 mm SL at Catalina Island, and none smaller than 150 mm at Guadalupe. The longer size classes (above 350 mm and 230 mm at Catalina and Guadalupe, respectively) contain mostly males.

Data for labrid sexuality are usually in the form of size frequency distributions of males and females within a species (Atz 1964; Remacle 1970; Roede 1972). Some of these studies have been confounded by the presence of two distinct color patterns, the investigators wrongly assuming strict sexual dichromatism (see below). An additional complication is the possibility of two different types of males being present in some species, usually with different life histories and behavior (Reinboth 1970). Both of these problems are eliminated by histological examinations of the gonad, which also reveals the presence of intersexual or transitional individuals.

The absence of males from the smaller size classes at least suggests protogyny. However, similar patterns can also result from samples of a species exhibiting differential growth rates for the sexes (e.g., see Strasburg 1970, for weight and sex distributions of blue marlin, *Makaira nigricans*), and this should be taken into consideration.

Fourteen of the fifteen labrid species either reviewed or dealt with originally by Roede (1972) had similar patterns of length-sex distribution. Females predominated in the smaller size classes, males in the larger. The proportion of males in the smaller sizes (usually associated with a particular color pattern; see below) varied from practically none in some species of *Halichoeres* and *Hemipteronotus* up to nearly 30% for *Stethojulis strigiventer* (Randall 1955). Males became increasingly common as length increased and the longest size classes consisted almost exclusively of males.

Species of the genus *Symphodus* (*Crenilabrus*) appeared to exhibit a different pattern, with nearly equal numbers of males and females in the small size classes (Söljan 1930a, b). Remacle (1970)

believed that sex reversal is a rare phenomenon in this genus.

Age determinations allow several more inferences about the sexual life history of a species. When few or no young males can be found, there is strong evidence for protogyny since the possibility of differential growth is eliminated. The rate of transformation in different age classes can be estimated, and this provides an idea of how long the average individual spends in different sexual phases. Finally, by comparing the distribution of sex versus length with sex versus the age of the individual, it may be possible to assign a more critical role to one or the other as a causative factor for sex reversal.

The age at first maturity (4 yr) does not differ for *P. pulchrum* at Catalina and Guadalupe Islands, but the distribution of sexual transformation with age differs markedly. Most individuals in both populations function at least 1 yr as females. At Guadalupe, many change sex after 1 yr, and most are males within 3 yr after maturing. Most sex reversals occur at Catalina between the seventh and eighth year, 4 yr after maturing as a female. Some individuals remain female for shorter or longer periods of time. The oldest female encountered in this study was 17 yr old.

The dwarfing phenomenon at Guadalupe, which should bring about a slower rate of increase of fecundity with age, would have enough effect to decrease the optimum age of transformation in that population when compared to the Catalina population. This will be discussed in detail elsewhere (Warner in press).

Lonnberg and Gustafson (1937) determined the ages of a series of specimens of *Labrus bimaculatus* (as *L. ossifagus*) which they correlated with sexual state. They found that sex reversal occurred in individuals from age seven onward, and was associated with a color change from red to blue-striped. Females were found in diminishing numbers up to age 18, mostly confined to the red phase. Males in the red phase ranged from around 3 to 7 yr old; blue-striped males got as old as 25.

Other protogynous teleosts which have been investigated regarding age of transformation show a variety of patterns in the distribution of sex reversal over their life-span. Liem (1963) demonstrated that sex transformation in the synbranchid rice eel *Monopterus albus* occurs mainly when individuals reach about 30 mo of age (about 35 cm in length). Few fishes in nature deviated from this pattern. Liem (1963) was able

to induce earlier transformations by starving the individuals. Moe (1969) has carefully worked out the age distribution of sex reversal in the serranid *Epinephelus morio*, and found a rather smooth period of transition from female to male over at least 5 yr (ages 5 to 10), at a rate of about 15% of the individuals in a year class reversing per year. In a less comprehensive survey, McErlean and Smith (1964) estimated that transformation occurred at age 10 or 11 in *Mycteroperca microlepis* (Serranidae), and speculated that the age of the fish had more effect on sex reversal than the length.

To determine the effect of individual size on sex transformation in *P. pulchrum*, mean lengths of males and females in each age class were compared (Figure 15). If length is closely related to sex reversal, one would expect males to be larger than females of the same age, and this was found in both the Catalina and Guadalupe populations. In every age grouping where sample size permitted statistical analysis, males tended to be larger than females. Five of the seven groups tested (one-sid-

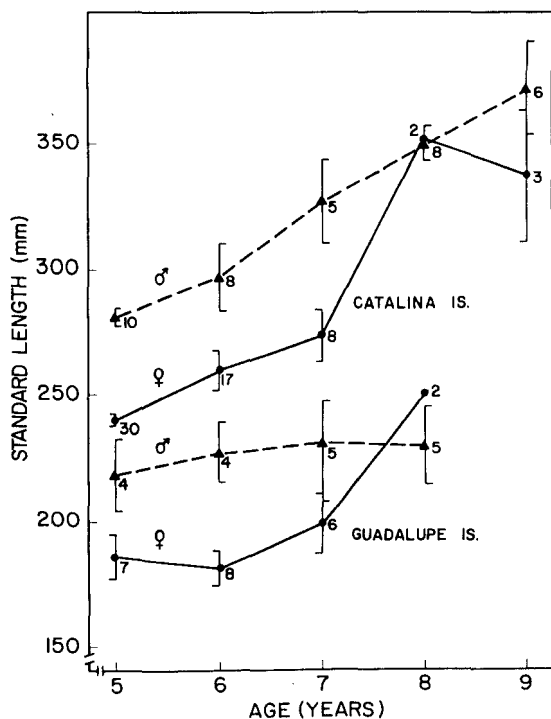


FIGURE 15.—Mean lengths for successive age classes of males and females of *Pimelometopon pulchrum*. Sample sizes are shown for each point, and standard error brackets are given when samples are large enough. For clarity, standard error brackets for males point to the right, and brackets for females point to the left.

ed *t*-test for difference in means) were significantly different at the 5% level or less, and the remaining two were significant at the 10% level.

An assessment of the effect of age on sex reversal was made in similar fashion, comparing the mean ages of males and females in successive size groupings (Figure 16). If sex reversal were closely related to the age of an individual, then males would tend to be older than females in a given length group. The relationship between age and sex is less strong (Figure 16). Sample sizes are not large, and the range of ages encountered in a sample is small relative to measured length values, so fewer significant results might be expected. Only one size group was found where males were significantly older than the females. However, the existence of several large negative *t* values in groups where the age of females is greater than that of males supports the idea that size is more important than age in effecting sex change.

The high average age of females in the larger size groupings of both populations (Figure 16) was not expected, and suggests that the individual growth rate may also be involved in sex reversal. The large separation between male and female mean ages begins with the 300-mm size grouping at Catalina, and the 200-mm group at Guadalupe. Inspection of Figure 8 reveals that at about these lengths, the proportions of males and females undergo an abrupt shift. A large percentage of the individuals in the populations apparently reverse sex at these sizes. Furthermore, the difference in ages between males and females of lengths above these "critical" sizes appears to be significant. The mean age of females larger than 300 mm at Catalina is 7.9, a full year older than males in the same size range ($t_{31} = 1.51, P < 0.10$). Similarly, females larger than 200 mm at Guadalupe have a mean age of 9.5 yr, and males at that size range average 7.0 yr ($t_{32} = 2.80, P < 0.001$). Thus the females that pass through the "critical" lengths without changing sex appear to be those individuals with relatively low rates of growth, suggesting both that slow growing individuals tend to be refractory to sex change, and that fishes with high rates of growth change sex more readily. The data of Figure 15 support this idea, as males are faster growing (larger) members of each age class. A check of the back-calculation information revealed that the growth rates of the large females were consistently low throughout their lifetime, and those of the small males had been high relative to other members of the age class.

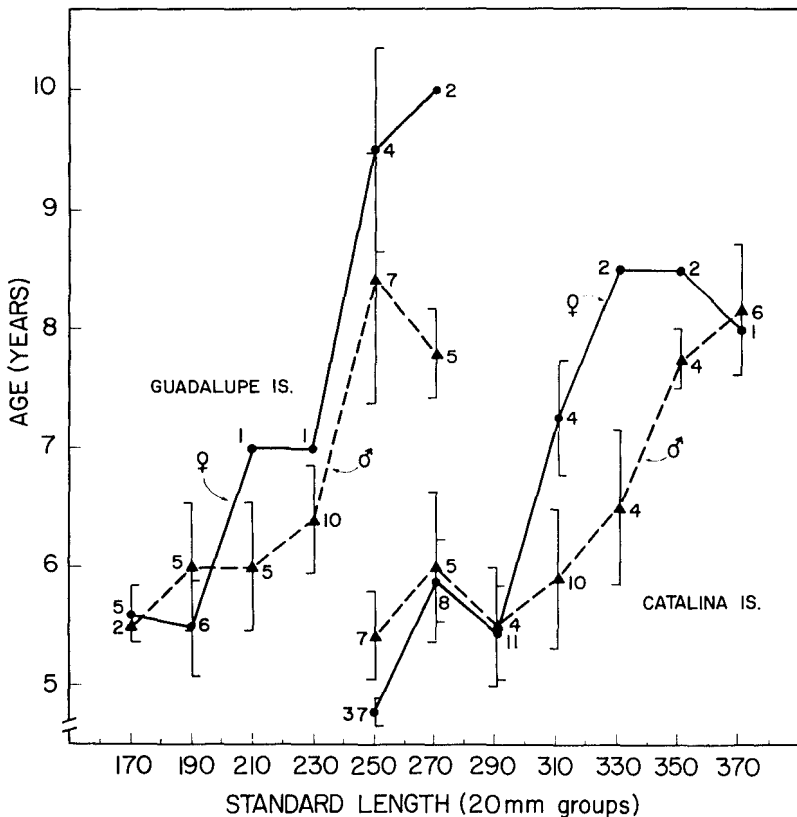


FIGURE 16.—Mean ages for successive 20 mm standard length groupings of male and female *Pimelometopon pulchrum*. Sample sizes and standard errors are shown as in Figure 15.

The best picture, then, that can be drawn from the present information is that rapidly growing individuals may transform sooner than other fishes of the same age. The bulk of the population, growing at the average rate, eventually reaches a "critical" size where most of them change sex. Fishes that grow slowly may not change sex at all.

The Breeding Season, Multiple Spawning, and Fecundity

Breder and Rosen (1966) have summarized the information available on the spawning seasons of labrids. In temperate species, most activity occurs over a period of approximately 3 mo, most commonly in April, May, and June. The Catalina population of *P. pulchrum* is exceptional in this case, since spawning occurs from August to October. The two other wrasses commonly found at Catalina Island also spawn later in the year than other labrids. *Oxyjulis californica* spawns from May until October (Bolin 1930), and *Halichoeres semicinctus* probably spawns in late June, July, and August (D. R. Diener, pers. commun.). The

relatively late spawning seasons of these species may be caused by upwelling along the southern California coast which usually persists well into June or July, resulting in a delay of inshore water warming until that time (Quast 1968).

Multiple spawning has not often been considered in studies of labrid breeding seasons. Roede (1972) stated that labrids have "continuous, successive spawning cycles," and based this view upon the presence of many vitellogenic oocyte stages in mature ovaries of the seven species she investigated. She contended there is no resting stage of the ovary, but a series of year-round spawnings. At all times of the year she was able to find ovaries with several stages of developing oocytes as well as the stage 2 recruitment stock. This clearly is not the case in *P. pulchrum*, where the winter-resting ovary contains virtually no signs of vitellogenesis. Active ovaries of the California sheephead strongly resemble those pictured by Roede (1972, plates II and III) for *Halichoeres* and *Hemipteronotus*. The successive spawnings within a restricted season indicated for *P. pulchrum* may then be a curtailed version of a

year-round condition in its presumably tropical ancestor, representing an adaptation to the fluctuations of food availability characteristic of temperate regions.

The size-specific increases in fecundity seen in Catalina *P. pulchrum* are, of course, common in most long-lived fishes. Many of the Guadalupe females were not sexually active when the sample was taken and no fecundity data are available. However, it can be predicted that the average fecundity of Guadalupe Island individuals will increase much more slowly with age than that of individuals from Catalina, due to the low growth rate of the Guadalupe individuals discussed in an earlier section. If the active ovary weight increases with size in a fashion similar to that seen at Catalina (Figure 13), the average ovary weight for a 4-yr-old fish at Guadalupe would be approximately 8 g. Age class 4 California sheephead at Catalina had ovaries with an average weight of 13.13 g. The difference increases with age. Six- and eight-year-old individuals at Guadalupe should have ovaries weighing 9 and 15 g respectively. Weights for the same ages at Catalina were 23.1 g and 53.5 g.

In the Catalina population, there may be an abrupt increase in the fecundity of fishes remaining female after age seven; this is the age where most sexual transformations occur (compare Figures 9 and 14). If such an increase does exist, it may be an indication of compensation by those remaining females for the relative gain in age-specific reproductive potential experienced by individuals that do change sex. A more complete discussion of relative male and female age-specific fecundities can be found elsewhere (Warner in press).

The Relationship of Color and Sex

Pimelometopon pulchrum appears to follow the general labrid coloration pattern quite closely, with a preponderance of females and immatures in the initial uniform color phase, and the terminal bicolored phase containing only males. Thus the designation of the uniform phase as the "female" coloration and the bicolored phase as the "male" coloration (Jordan and Evermann 1898; Fitch and Lavenberg 1971; Miller and Lea 1972) is more or less correct, especially when immatures are included under the uniform designation (Barnhart 1936; Roedel 1948). Dichromatism, however, is not necessarily an indication of sexual dimorphism in

the Labridae, and extensive sampling is usually needed before the relationship between sex and coloration can be accurately described.

Many labrid species exhibit a number of color phases, and these have often been attributed to sexual dimorphism or to differences between immatures and adults. Roede (1972) has reviewed a number of cases where such an interpretation was incorrect, being based on casual observation or small samples. Apparently there is no strict distribution of sex with color in the Labridae and the only generalization possible is that females tend to strongly predominate in the "first adult" (Roede 1972) colors, and the terminal-phase coloration is made up almost exclusively of males.

In most species investigated, males make up 10 to 35% of the first adult-colored individuals (Roede 1972). In *Gomphosus varius* (Strasburg and Hiatt 1957), *Halichoeres maculipinna*, *H. garnoti*, and *Hemipteronotus martinicensis* (Roede 1972), no males are found in the initial color phase. In contrast, Söljan (1930a, b) found that 48% of the *Symphodus (Crenilabrus) ocellatus* examined in the first adult phase were males.

The terminal-phase coloration appears to be much more closely restricted as to sex. Of 14 labrid species exhibiting color phases mentioned by Roede (1972), the terminal phase consisted exclusively of males in all but two (*Halichoeres garnoti* and *H. bivittatus*). When other coloration classes are described, intermediate between the initial and terminal phases, the proportions of males and females in them are also intermediate. Roede (1972) notes that where color changes are more gradual, as in *H. garnoti* and *H. bivittatus*, the relationship between size and sex is the least exact.

Sex Ratio and an Estimate of Survival

Roede (1972) believed that her collections were true random samples of populations and was able to estimate the sex ratio in the seven labrid species she investigated. There were two to four times as many females as males in all but one species (*Hemipteronotus splendens*), which had an equal sex ratio.

The samples of *P. pulchrum* were not considered random and direct sex ratio estimates could not be made. Field transects at Catalina and Guadalupe islands yielded a ratio of about 5.5 uniformly colored individuals to every bicolored male. To estimate the sex ratios of mature individuals, the

proportion of immatures and males in the uniform group must be known, and this requires some knowledge of mortality rates.

A rough estimate of mortality can be made from the transect data and the known color composition of each age. The yearly survival rate is calculated using a modification of a simple fisheries estimate (Ricker 1958). The rate is assumed to be constant, and can be estimated as:

$$\hat{s} = \frac{N_{t+1}}{N_t}$$

where N is the number of individuals in a particular age class in a sample. Where a large number of age classes are available, one can weight the classes according to their abundance and separate two or more ages from the numerator and denominator, giving, for example:

$$\hat{s}^2 = \frac{N_3 + N_4 + \dots + N_r}{N_1 + N_2 + \dots + N_{r-2}}$$

For the Catalina population of *P. pulchrum*, the formula used was:

$$\hat{s}^6 = \frac{N_8 + N_9 + \dots + N_{13}}{N_2 + N_3 + \dots + N_7}$$

In this first approximation we assume that bicolored fishes are all 8 or more years old, and younger fish (ages 2 through 7) are uniform. The decision to use age 7 as the dividing point comes from Figure 9, where between ages 7 and 8 the proportion of females drops to a low level and the males become predominant.

From Catalina transect data, \hat{s} is estimated by:

$$\hat{s}^6 = \frac{33}{183} \text{ and } \hat{s} = 0.735.$$

The transect ratio can then be adjusted to compensate for bicolored individuals younger than age 8 and uniform individuals older than age 7 by using proportions derived from Table 4, and each age's contribution to the numerator or denominator can be weighted according to the first estimate of survival derived above. The new estimate of survival from the adjusted transect ratio is not very different from the original, $\hat{s} = 0.71$.

A similar estimate for the Guadalupe Island population, assuming in this case that the uniform individuals are ages 2 through 7 (see Figure 9) and adjusting as before, is $\hat{s} = 0.69$.

Mature sex ratios can now be estimated. Using 0.7 as the yearly survival rate, about 36% of the uniform individuals seen at Catalina should be

mature, and approximately 5% of those individuals would be male. The ratio of mature males to mature females from field transects would then be derived as:

$$\frac{33 + (183 \times 0.36 \times 0.05)}{183 \times 0.36 \times 0.95} = \frac{36}{63} = 0.57$$

or about two females for every mature male.

For Guadalupe, about a third (34%) of the uniform individuals should be mature, and 90% of these would be female. The sex ratio at Guadalupe would then best estimated as:

$$\frac{64 + (343 \times 0.34 \times 0.1)}{343 \times 0.34 \times 0.9} = \frac{76}{105} = 0.72$$

or approximately three females for every two males.

An artifact of protogynous hermaphroditism is the concentration of females in the younger ages. Thus, the observed sex ratio depends on when the animals change sex, and upon the mortality occurring from year to year. Mortality causes sex ratios to be biased towards females and these become even more biased the greater the average age of transformation is in the population. This effect can be seen by comparing the estimated sex ratio of the Guadalupe population (0.72), where most females change sex within 3 yr after maturity, with that of Catalina (0.57), where transformation is relatively delayed.

The deviations of sex ratio from unity seen here should not be taken as contradictions of the theories put forth on the adaptiveness of the 1:1 ratio (Fisher 1930; Bodmer and Edwards 1960; Kalmus and Smith 1960), as these were developed for nonhermaphroditic species, and sought to equalize the lifetime reproductive potentials for males and females. In sequential hermaphrodites, the same individual functions as both male and female at sometime in its life, and the question becomes one of changing sex at the proper time to maximize the individual's reproductive potential (Warner in press).

SUMMARY

Year-round sampling of a population of the California sheephead, *Pimelometopon pulchrum*, was carried out at Catalina Island, Calif., and comparative material was collected from a population at Guadalupe Island, Mexico.

Age determinations indicate individuals in the Guadalupe population are dwarfed relative to

those at Catalina. The growth rate is lower for Guadalupe fishes and in both populations there may be a slowing of growth at the onset of maturity, as well as an increase in the growth rate after sexual transformation.

Pimelometopon pulchrum is a protogynous hermaphrodite. During the sex change from female to male, the ovary degenerates and spermatogenic crypts dominate the gonad. The basic structure of the gonad remains ovarian however, with lamellae protruding into a central lumen. Sperm transport is through a series of ducts on the periphery of the gonad and oviduct.

Catalina California sheephead attain sexual maturity at age 4, at a standard length of about 200 mm. Most function as females for 4 yr and then change sex, at a length of about 310 mm. Some individuals may transform earlier or later, or not at all. The Guadalupe population also matures at age 4, at a length of about 140 mm. But transformation occurs at an earlier age, with most individuals becoming males by age 7. Peak transformation activity occurs in fishes between 190 and 230 mm SL at Guadalupe.

Gonad development states and gonad indices of Catalina California sheephead suggest that spawning occurs in July, August, and September and that sexual transformation occurs in the winter months between breeding seasons.

Spawning probably takes place a number of times in a single breeding season, which complicates the determination of the actual number of eggs produced by a female each year. Ovary weight, however, can give a good indication of relative age and size-specific fecundities, since egg density does not appear to vary with fish length. The ovary weight of *P. pulchrum* increases exponentially with length and linearly with the age of the individual in the Catalina population.

At Guadalupe, the average fecundity probably increases more slowly with age when compared to Catalina, due to the low average rate of growth.

Pimelometopon pulchrum has three color phases. Juvenile coloration occurs in individuals usually less than a year old and smaller than 100 mm in length, and never in sexually mature individuals.

The uniform coloration is found in immatures and mature females. Melanization may obscure the ground coloration, but it appears that about 5% of the mature uniform individuals were males at Catalina, and 12% at Guadalupe.

Bicolored fishes are exclusively males or late

transitionals and usually have a nuchal hump and filamentous extensions of the median fins.

Field observations indicate that there are about 5.5 uniformly colored individuals to every bicolored male at both Catalina and Guadalupe.

Individual size appears to have a greater effect on the sex change than does age, and rapidly growing fishes may change sex sooner than slow growing individuals of the same age, which may not change sex at all.

With the assumption of constant, age-independent mortality, the annual survival rate at both Catalina and Guadalupe was estimated as about 0.7, as judged from the field transect data.

The mature sex ratio at Catalina was approximately two females for every male. At Guadalupe the ratio was closer to three females for every two males, due in part to the earlier sexual transformation seen there.

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LITERATURE CITED

- ATZ, J. W.
1964. Intersexuality in fishes. In C. N. Armstrong and A. J. Marshall (editors), *Intersexuality in vertebrates including man*, p. 145-232. Academic Press., Lond.
- BARNHART, P. S.
1936. *Marine fishes of southern California*. Univ. Calif. Press, Berkeley, 209 p.
- BODMER, W. F., AND A. W. F. EDWARDS.
1960. Natural selection and the sex ratio. *Ann. Hum. Genet.* 24:239-244.
- BOLIN, R. L.
1930. Embryonic development of the labrid fish *Oxyjulis californicus* Günther. *Copeia* 1930(4):122-128.
- BREDER, C. M., JR., AND D. E. ROSEN.
1966. *Modes of reproduction in fishes*. Natural History Press, Garden City, N.Y., 941 p.
- CHAN, S. T. H.
1971. Natural sex reversal in vertebrates. *Philos. Trans. R. Soc. Lond., Ser. B, Biol. Sci.* 259:59-71.
- CHAN, S. T. H., A. WRIGHT, AND J. G. PHILLIPS.
1967. The atretic structures in the gonads of the rice-field

- eel (*Monopterus albus*) during natural sex-reversal. J. Zool. (Lond.) 153:527-539.
- CLARK, F. N.
1934. Maturity of the California sardine (*Sardina caerulea*), determined by ova diameter measurements. Calif. Dep. Fish Game, Fish Bull. 42, 49 p.
- CLARKE, T. A.
1970. Territorial behavior and population dynamics of a pomacentrid fish, the garibaldi, *Hypsypops rubicunda*. Ecol. Monogr. 40:189-212.
- CROZIER, G. F., JR.
1966. Features of carotenoid metabolism in growth and sexual maturation of the labrid fish, *Pimelometopon pulchrum* (Ayres). Ph.D. Thesis, Univ. California, San Diego, 93 p.
- CUERRIER, J. P.
1951. The use of pectoral fin rays for determining age of sturgeon and other species of fish. Can. Fish Cult. 11:10-18.
- DIXON, W. J., AND F. J. MASSEY, JR.
1969. Introduction to statistical analysis. 3rd ed. McGraw-Hill, N.Y., 638 p.
- FISHER, R. A.
1930. The genetical theory of natural selection. The Clarendon Press, Oxford, 272 p.
- FITCH, J. E., AND R. J. LAVENBERG.
1971. Marine food and game fishes of California. Univ. Calif. Press, Berkeley, 179 p.
- HYDER, M.
1969. Histological studies on the testis of *Tilapia leucosticta* and other species of the genus *Tilapia* (Pisces: Teleostei). Trans. Am. Microsc. Soc. 88:211-231.
- JORDAN, D. S., AND B. W. EVERMANN.
1898. The fishes of North and Middle America. Bull. U.S. Natl. Mus. 47, Part 2:1241-2183.
- JOSEPH, D. C.
1962. Growth characteristics of two southern California surfishes, the California corbina and spotfin croaker, family Sciaenidae. Calif. Fish Game, Fish Bull. 119, 54 p.
- KALMUS H., AND C. A. B. SMITH.
1960. Evolutionary origin of sexual differentiation and the sex-ratio. Nature (Lond.) 186:1004-1006.
- KRAFT, A. N., AND H. M. PETERS.
1963. Vergleichende Studien über die Oogenese in der Gattung *Tilapia* (Cichlidae, Teleostei). Z. Zellforsch. Mikrosk. Anat. 61:434-485.
- LIEM, K. F.
1963. Sex reversal as a natural process in the synbranchiform fish, *Monopterus albus*. Copeia 1963:303-312.
1968. Geographical and taxonomic variation in the pattern of natural sex reversal in the teleost fish order Synbranchiformes. J. Zool. (Lond.) 156:225-238.
- LONNEBERG, E., AND G. GUSTAFSON.
1937. Contributions to the life history of the striped wrasse, *Labrus ossifagus* Lin. Ark. Zool. 29A(7):1-16.
- MCEERLEAN, A. J., AND C. L. SMITH.
1964. The age of sexual succession in the protogynous hermaphrodite *Mycteroperca microlepis*. Trans. Am. Fish. Soc. 93:301-302.
- MILLER, D. J., AND R. N. LEA.
1972. Guide to the coastal marine fishes of California. Calif. Dep. Fish Game, Bull. 157, 235 p.
- MOE, M. A., JR.
1969. Biology of the red grouper, *Epinephelus morio* (Valenciennes), from the eastern Gulf of Mexico. Fla. Dep. Nat. Resour. Mar. Res. Lab., Prof. Pap. 10, 95 p.
- NORRIS, K. S.
1963. The functions of temperature in the ecology of the percoid fish *Girella nigricans* (Ayres). Ecol. Monogr. 33:23-62.
- OKADA, Y. K.
1962. Sex reversal in the Japanese wrasse, *Halichoeres poecilopterus*. Proc. Jap. Acad. Sci. 38:508-513.
- OSSIAN, C. R.
1970. Preparation of disarticulated skeletons using enzyme-based laundry "pre-soakers." Copeia 1970:199-200.
- QUAST, J. C.
1968. 4. Some physical aspects of the inshore environment, particularly as it affects kelp-bed fishes. In W. J. North and C. L. Hubbs (editors), Utilization of kelp-bed resources in southern California. Calif. Dep. Fish Game, Bull. 139:25-34.
- RANDALL, J. E.
1955. *Stethojulis renardi*, the adult male of the labrid fish *Stethojulis strigiventer*. Copeia 1955:237.
- REINBOTH, R.
1957. Sur la sexualité' du téléostéen *Coris julis* (L.). C. R. Acad. Sci. Paris 245:1662-1665.
1962. Morphologische und funktionelle Zweigeschlechtlichkeit bei marinen Teleostiern (Serranidae, Sparidae, Centracanthidae, Labridae). Zool. Jahrb. Abt. Zool. Physiol. Tiere 69:405-480.
1963. Experimentell induzierter Geschlechtswechsel bei Fischen. Verh. Deutsch. Zool. Ges. München 27:67-73.
1970. Intersexuality in fishes. Mem. Soc. Endocrinol. (Hormones and the Environment) 18:515-543.
- REMACLE, C.
1970. Contribution à l'étude de la sexualité chez certain Labridae et Sparidae. Bull. Inst. R. Sci. Belg. 46(35):1-13.
- RICKER, W. E.
1958. Handbook of computations for biological statistics of fish populations. Fish Res. Board Can., Bull. 119, 300 p.
- ROBERTSON, D. R.
1972. Social control of sex reversal in a coral-reef fish. Science (Wash., D.C.) 177:1007-1009.
- ROEDE, M. J.
1966. Notes on the labrid fish *Coris julis* (Linnaeus, 1758) with emphasis on dichromatism and sex. Vie Milieu A 17:1317-1333.
1972. Color as related to size, sex, and behavior in seven Caribbean labrid fish species (Genera *Thalassoma*, *Halichoeres*, and *Hemipterinothus*). Studies on the Fauna of Curaçao and other Caribbean Islands 138:1-264.
- ROEDEL, P. M.
1948. Common marine fishes of California. Calif. Dep. Fish Game, Fish Bull. 68, 150 p.
- ROUNSEFELL, G. A., AND W. H. EVERHART.
1953. Fisheries science, its methods and applications. John Wiley and Sons, N.Y., 444 p.
- SMITH, C. L.
1965. The patterns of sexuality and the classification of serranid fishes. Am. Mus. Novit. 2207, 20 p.
- SÖLJAN, T.
1930a. Nestbau eines adriatischen Lippfisches—*Crenilabrus ocellatus* Forsk. Z. Morphol. Oekol. Tiere 17:145-153.
1930b. Die Fortpflanzung und das Wachstum von *Crenilabrus ocellatus* Forsk., einem Lippfisch des Mittelmeeres. Z. Wiss. Zool. 137:150-174.

- SORDI, M.
1962. Ermafroditismo proteroginoco in *Labrus turdus* L. e in *L. merula* L. *Monitore Zool. Ital.* 69(3-4):69-89.
- STRASBURG, D. W.
1970. A report on the billfishes of the central Pacific Ocean. *Bull. Mar. Sci.* 20:575-604.
- STRASBURG, D. W., AND R. W. HIATT.
1957. Sexual dimorphism in the labrid fish genus *Gomphosus*. *Pac. Sci.* 11:133-134.
- VAN OOSTEN, J.
1929. Life history of the lake herring (*Leucichtys artedi* Le Seuer) of Lake Huron as revealed by its scales, with a critique of the scale method. *Bull. U.S. Bur. Fish.* 44:265-428.
- WARNER, R. R.
In press. The adaptive significance of sequential hermaphroditism in animals. *Am. Nat.* 109(965).
- WILLIAMS, G. C.
1966. Adaptation and natural selection: A critique of some current evolutionary thought. *Princeton Univ. Press*, Princeton, 307 p.
- YAMAMOTO, K., AND F. YAMAZAKI.
1961. Rhythm of development in the oocyte of the gold-fish, *Carassius auratus*. *Bull. Fac. Fish., Hokkaido Univ.* 12:93-110.