The nature of the cellular changes responsible for this loss is unclear. Possibly synaptic turnover (the coordinated production and removal of synapses) declines across the juvenile period, leaving the older rats with less ongoing growth to produce a sprouting response. However, there is no necessary reason to assume that sprouting represents an exaggeration of normal synaptogenesis; it may require the activation of novel or usually quiescent processes. The sudden onset of sprouting 5 or 6 days after the lesion would not be predicted from the continuous growth hypothesis, but can be accounted for by a modified version of that idea—factors are present that prevent the expression of growth until 5 days after the lesion.

Whatever the underlying mechanism may be, the sharp decline in growth responses provides a possible explanation for age-related changes in recovery from brain damage (*5, 25*). It will be of interest then to assess the rate and degree of behavioral recovery after commissural lesions in rats of the ages used in this study.

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13. Sprague-Dawley (ARS, Madison, Wis.) rats were reared in groups of three to five to a cage from 30 days after birth; food was available at all times. Rats in all groups were randomly selected from two or three different litters.
14. The number of multiple synaptic boutons increased by 25 to 30 percent between the control animals and the 15-day group (from approximately 1.6 to 2.1 per 100 μm^2). This increase after axonal sprouting has been reported elsewhere and its significance discussed (*6, 7, 15*).
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16. Approximately 40 photomicrographs were taken randomly throughout the outer 50 percent of the dendritic field containing the commissural projection for each animal at a magnification of ×10,000 (later enlarged twofold). Total area analyzed for each animal was generally 2500 μm^2. Two-tailed *t*-tests were used for statistical analysis. At 8 days, both the 35- and 60-day-old and the 60- and 90-day-old rats differed significantly ($P < 0.005$). At 15 days, the 35- and 60-day-old rats differed ($P < 0.005$).
17. Measurements of the height of the inner and entire molecular layer were calculated from tissue embedded in epoxy viewed in a light microscope (*6*). No significant changes in height were detected for either the inner or entire molecular layer at any of the ages tested.
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23. It is also possible that the astrocytes which phagocytize the degenerating axons and terminals show age-dependent changes in reactivity and may thus be partly responsible for the decreasing rates of degeneration removal observed with increasing age.
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27. Supported by a grant from the National Institute of Aging (AG00538-06). J.R.McW. is a National Institute of Communicative Disorders and Stroke postdoctoral fellow (5 F32 NS06821).

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Sex Change in a Coral-Reef Fish: Dependence of Stimulation and Inhibition on Relative Size

Abstract. *The removal of a single dominant individual has been shown to trigger a sex change in some coral-reef fish. In the saddleback wrasse (*Thalassoma duperrey*), however, female-to-male sex change requires visual stimulation from smaller conspecifics. This change is not dependent on the sex or color of the stimulus fish and can be inhibited by larger conspecifics. On the reef, a female probably changes sex when the relative numbers of larger and smaller conspecifics change within her home range.*

Social control of sex change in fishes has been demonstrated experimentally only among harem-living species or those with a rigid dominance hierarchy (*1–3*). In such cases sex change usually occurs as a simple one-to-one replacement: loss of the dominant male or female induces sex change in the dominant fish of the opposite sex. In nonharem species with less rigid social and mating systems, one would predict socially mediated sex change to be under the control of a more flexible mechanism. We report that such a mechanism does indeed control sex change in *Thalassoma duperrey*, a reef-dwelling wrasse abundant throughout the Hawaiian archipelago. This species exhibits protogynous (female to male) hermaphroditism, lives in sexually integrated, overlapping home ranges, and mates promiscuously rather than in a harem (*4*). Sex change in this species is not a function of paired replacement of dominant individuals. Rather, it is a function of the relative sizes of conspecifics in the social group. Their relative numbers on the reef may also be important. Experiments suggest that some threshold value of the proportion of larger or smaller fish within the home range probably triggers the initiation of sex change in individual females.

Fish were taken from coral reefs in Kaneohe Bay, Oahu, Hawaii, and brought immediately to the laboratory where they were held collectively in seawater tables for up to 2 days. During this period fish were sexed, weighed, measured, and placed individually in isolated seawater containers for 1 to 3 days before assignment and transfer to experimental pens. Pens, made of 12.7-mm (half-inch) wire mesh, measured 1 m on each side (*5*) and were submerged at fixed positions in a protected lagoon. There were no resident *T. duperrey* in the lagoon, which was an inappropriate habitat for these fish.

One to four adult wrasses were placed in each pen, with or without a barrier to separate individuals (Table 1). Small fish were 66 to 100 mm, standard length, and large fish, 101 to 135 mm. In the experiment with three fish, the entire size

range was divided into three parts. When two or more wrasses were placed in a single pen, a minimum size difference of 10 mm was initially established. Tactile barriers were 12.7-mm wire mesh screens, and tactile-visual barriers were double-louvered panels that faced in opposite directions, allowing water flow but obstructing vision.

Experiments ran uninterrupted for 3 months, during which time fish were fed freely. Two replicates of each of the 12 experimental treatments (Table 1) were conducted simultaneously and repeated every 3 months until a sample size of five to nine individuals was reached for each treatment. At the end of each test, fish were killed and gonads examined histologically for evidence of sex change. Females were considered to have changed sex only if their gonads lacked intact oocytes and showed advanced stages of spermatogenesis. Treatment results were compared statistically by the Irwin-Fisher exact test, one-tailed (*6*).

Experimental treatments 1 to 4 were designed to test the effects of absolute and relative size as well as social environment on the sex-change process (Table 1). Sex change occurred only in the larger individuals of female pairs (the number of changes in treatments 3 and 4 was significantly greater than that in treatments 1 and 2, $P < 0.001$), regardless of absolute size (treatment 3 versus 4, $P = 0.73$). It did not occur interspecifically (treatments 3 and 4 versus 5, $P < 0.01$). These results show that sex change in one fish must be stimulated by the presence of at least one smaller conspecific.

The results of treatment 6 showed that the sex-change process is independent of the sex of the stimulus fish; smaller males were as effective as smaller females in inducing sex change (treatment 6 versus 3 and 4, $P = 0.73$). Adult wrasses normally undergo a color-phase conversion (initial phase to terminal phase) that is correlated with a change in spawning strategy (*4*). However, treatments 7 and 8 suggest that sex change is independent of the coloration of the stimulus fish ($P = 0.23$). Tactile cues were not needed for sex change to occur (treatment 9 versus 3 and 4, $P = 0.73$), but visual cues were crucial (treatment 10 versus 9, $P < 0.01$). Placing females in an enclosure 12 times larger than the standard size showed that, at least within this range, sex change was independent of the amount of space available to females (treatment 11 versus 3 and 4, $P = 0.37$).

Treatment 12 was designed to test whether sex change can be inhibited as well as stimulated. A female wrasse potentially capable of change when placed next to a larger female, did not change sex even though a smaller female was also present. This showed that inhibition indeed occurs (treatment 12 versus 9, $P < 0.001$).

Table 1. Results of sex-change experiments with *T. duperrey*. Vertical bars represent the placement of barriers by fish size and sex. Data on sample size and sex change refer to the largest female in each treatment (to the larger female of the pair of females opposite the male in treatments 7 and 8 and to the large and medium females in treatment 12).

Treatment	Fish/pen	Barrier	Fish size	Sex	Sample size	Sex change	
						N	Percent
1	1	None	Small	F	5	0	0
2	1	None	Large	F	6	0	0
3	2	None	Small	F F	7	6	86
4	2	None	Large	F F	6	5	83
5	2	None	Varied	F + *T. ballieui*	8	1	12
6	2	None	Varied	F M	7	6	86
7	4	Tactile	Varied|smaller	F F|M F*	6	6	100
8	4	Tactile	Varied|smaller	F F|M F*†	6	4	68
9	2	Tactile	Varied|smaller	F|F	7	6	86
10	2	Tactile-visual	Varied|smaller	F|F	9	1	11
11	2‡	None	Varied	F F	6	4	68
12	3	Tactiles	Large|medium|small	F|F|F	8|9	6|0	75|0

*The male fish was at least 10 mm smaller than the larger female across the barrier. †Differs from treatment 7 in that the male is terminal color phase. ‡Pen size was 12 times larger than in other treatments.

Sex change is socially controlled in *T. duperrey* and is initiated by visual stimuli. As long as the fish is reproductively mature, there is no apparent critical size at which sex change normally occurs. In our experiments, sex change in one individual was stimulated by some aspect of the presence of one or more smaller conspecifics. Though it did not require removal of a male or a larger individual, it apparently was inhibited by some aspect of the presence of one or more larger conspecifics. Relative size was critical to both stimulation and inhibition, while coloration and sex apparently were not.

Other hypotheses proposed to explain the proximate causes of sex change in various fishes are those dealing with suppression (*1*), priming (*2*), and a sex-ratio threshold (*2*). For *T. duperrey*, we suggest that size ratios, rather than sex ratios or loss of dominant individuals, may be important proximate cues to individual sex-change candidates. *Thalassoma duperrey* interact with relatively large numbers of conspecifics on a regular basis. The relative numbers of larger and smaller fish may be the best proximate indication of the chances for reproductive success. If, for example, there are many larger fish (usually male) and few smaller fish (usually female), there would be too few females with which a new male could mate. There would also be too many larger males competing for those mates. If, on the other hand, the proportion of larger fish is low, then sex change would be advantageous.

Thus in social systems such as that of *T. duperrey*, sex change in one-to-one correspondence with male loss would be too rigid a strategy to follow. The size-ratio mechanism provides maximum flexibility to individual sex-change candidates in socially variable environments. It would appear to operate efficiently only in fishes with large social units, however. Congeneric labrids and other labroids that live in overlapping home ranges at relatively high population densities may well exhibit such a mechanism. The precise role of behavior and the specific visual cues involved in this mechanism have yet to be determined.

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