LIFE HISTORY AND LARVAL DEVELOPMENT OF THE GIANT KELPFISH, *HETEROSTICHUS ROSTRATUS* GIRARD, 1854

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ABSTRACT

Life history data from about 1,200 giant kelpfish, including age, length, and weight relationships, are described and analyzed. Additionally, differences in habitats and behavior between larvae, juveniles, and adults are reported. Female giant kelpfish were found to be larger than males at given ages past sexual maturity. Age data indicate that females live longer and all individuals larger than 28 cm TL collected in this study were females. Males guard the algal nests until hatching, about 2 weeks after spawning. Giant kelpfish from nests collected in the field were reared in the laboratory, surviving for up to 9 months. Feeding and development of laboratory-reared larvae were compared with field-collected specimens. In situ, they school in the kelp canopy until 2 months old, gradually developing juvenile coloration and becoming increasingly thigmotactic and solitary. Giant kelpfish reach sexual maturity at 1-1.5 years, at which time they commence to defend territories in given plant habitats.

The cryptically colored giant kelpfish, *Heterostichus rostratus*, is abundant in southern California kelp forests and surrounding subtidal plant habitats. *Heterostichus* is one of the largest members of the clinid family, reaching a length of 41.2 cm and an age of 5 yr (J. E. Fitch in Feder et al. 1974). Although ranging from British Columbia, Canada, to Cape San Lucas, Baja California, Mexico, it is most commonly found from Point Conception to central Baja in depths of 35 m (Roedel 1953). Giant kelpfish occur in three different colormorphs—red, brown, and green—which closely match the color of their surrounding plant habitats (Hubbs 1952; Stepien 1985, 1986). They additionally exhibit four different dark melanin patterns, which appear superimposed on the basic color of the fish and, unlike colormorphs, can change rapidly (Stepien 1985, 1986).

Giant kelpfish spawn year-round, but most frequently during spring months (Limbaugh 1955; Feder et al. 1974). The eggs are attached to algal nests with entangling threads that extend from the egg membranes (Holder 1907; Feder et al. 1974). The males alone guard the nests from predators until hatching, averaging 2 wk after spawning (Coyer 1982). Giant kelpfish are relatively well-developed at hatching and are planktonic for several weeks. They school in the kelp canopy until they are about 6 cm long, then develop juvenile coloration and become solitary, living close to nearshore algae (Limbaugh 1955).

Although *Heterostichus* larvae are not uncommon in the nearshore ichthyoplankton, their development has not been previously described. *Heterostichus* egg morphology was described by Barnhart (1932), and the egg-laying process was described by Holder (1907). Matarese et al. (1984) published two drawings of kelpfish larvae. Although diet and some aspects of general life history have been described qualitatively by several investigators (Hubbs 1920, 1952; Roedell 1953; Limbaugh 1955; Quast 1968; Hobson 1971; Feder et al. 1974; Hobson et al. 1981; Coyer 1982) and one quantitative study was conducted on feeding and distribution of juveniles and adults in giant kelp (Coyer 1979), specific morphometric data for larval, juvenile, and adult stages have not previously been reported. This paper presents life history data, including the following: 1) Differences in larval, juvenile, and adult habitats and behavior; 2) size, weight, and age relationships, including differences between males and females; and 3) the sequence of larval development and metamorphosis.

MATERIALS AND METHODS

Collection and In Situ Observations

In situ observations were made during approximately 280 scuba dives from 1978 to 1983, the majority in the vicinity of the University of Southern California's Catalina Marine Science Center

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(CMSC) on Santa Catalina Island (Fig. 1). Most observations and collections were made in protected cove areas having well-developed kelpbeds of the giant kelp, *Macrocystis pyrifera*, and associated plant habitats, including surfgrass, *Phyllospadix torreyi*, and red and brown algae. Approximately 1,200 giant kelpfish were observed during the course of the study. The aging and sexing study material from Catalina was also supplemented by 42 specimens collected from subtidal sites off the southern California mainland, including Ventura, Lunada Bay on the Palos Verdes Peninsula, Huntington Beach, and La Jolla (Fig. 1).

Kelpfish were collected using a 0.5 × 0.8 m net, mounted on a 1 m long handle and constructed of 0.25 cm mesh dyed either brown or red to match the kelpfish algal habitats (it was found that white netting alarmed the fish, making them difficult to
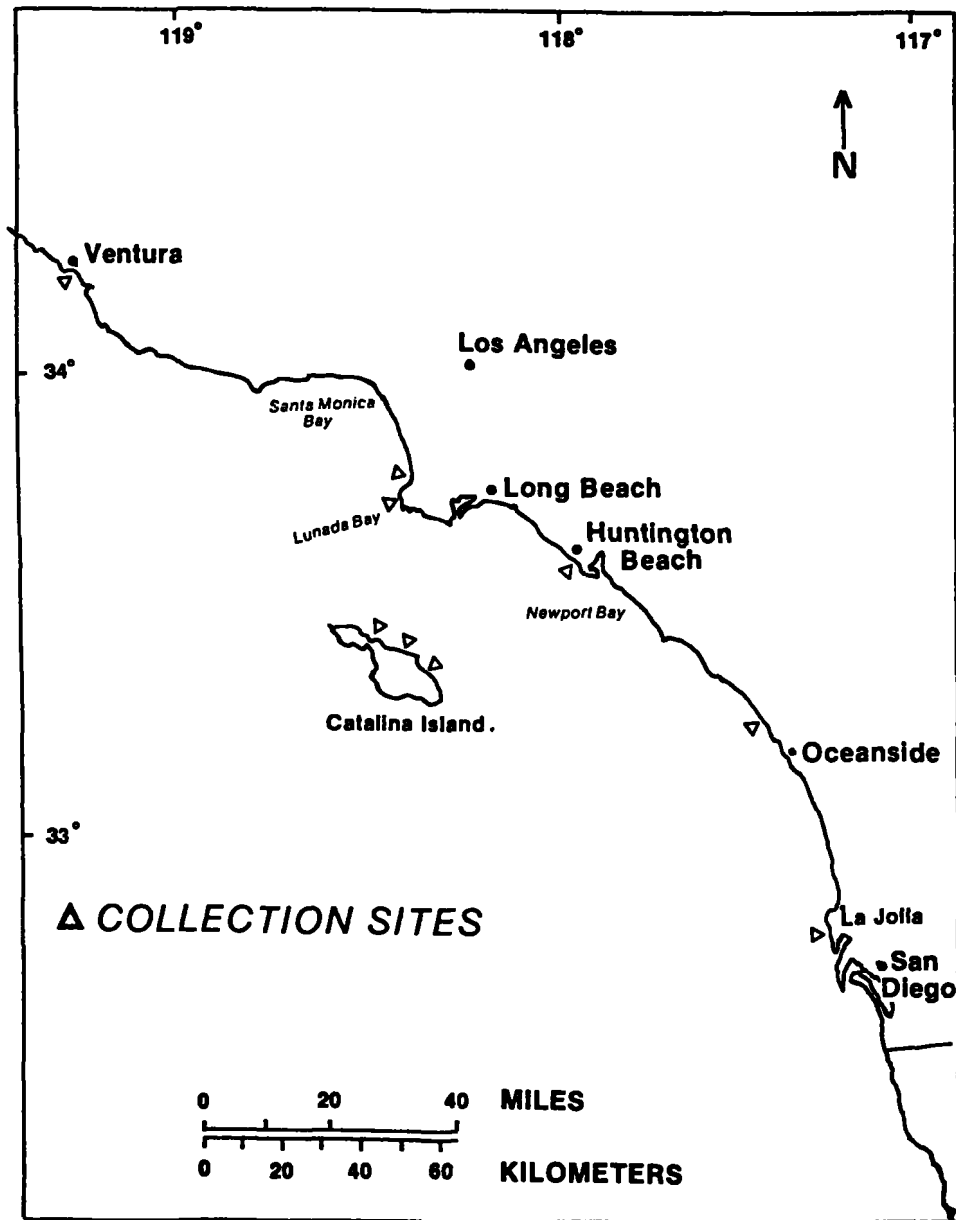

FIGURE 1.—Giant kelpfish collection sites (open triangles) off the southern California coast.

catch). Kelpfish were collected by sliding the net forward and downward over the fish. Collection of kelpfish was facilitated by their habit of hiding in algae when pursued rather than escaping by rapid swimming. Those that were actively swimming (usually through the kelp canopy) were less frequently captured. They were placed in a collecting bucket having mesh sides, a snap-on lid, and a funnel entryway, preventing escapes when the lid was opened for other fish. Care was taken to avoid putting the larger kelpfish in the same bucket as the smaller ones, because the smaller ones were occasionally eaten by the larger ones.

Life History Data From Juveniles and Adults

In the present study, 140 juveniles and adults of representative sizes (ranging from 10 to 42 cm TL) were measured live to the nearest 0.1 cm. Total length (TL) was found to be more quickly measurable than standard length (SL). Both SL and TL were measured, in order to allow comparisons with other studies. Kelpfish were weighed to the nearest 0.1 g on a triple-beam balance while briefly contained in plastic bags, in which they were quiescent and unabraded. These data were graphed, and regression and F-test analyses were performed (Sokal and Rohlf 1981; Zimmerman and Kremer 1983).

The fish were sexed and aged. Females had clear or pink, rounded ovaries and most individuals over 14 cm TL had clearly visible developing eggs. Male gonads were cream-colored and had a characteristic ventral groove. In cases when sex of juveniles was questionable, the gonads were examined under a dissection microscope.

Otoliths (sagitta) were removed and stored dry in labeled glass. They were briefly submerged in water and examined against a black background with a dissecting microscope (25-50× magnification) for ring counting (Fig. 2). Ages were determined by counting alternating white (opaque) and translucent (hyaline) bands, each representing 6 mo of growth,

KELPFISH OTOLITH

A

B

NUCLEUS

1 YEAR OLD

2 YEARS OLD

3 YEARS OLD

4 YEARS OLD

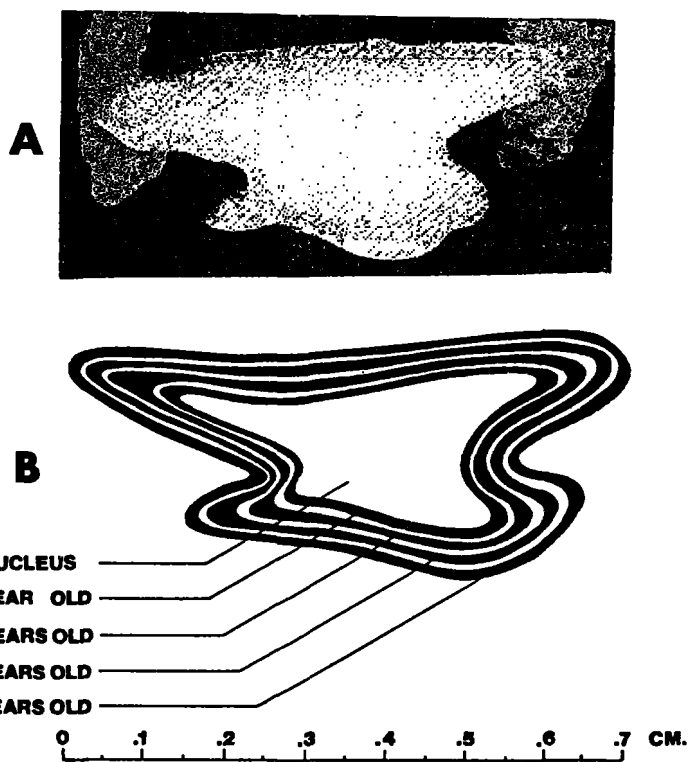0   .1   .2   .3   .4   .5   .6   .7 CM.

FIGURE 2.—(A) Photograph of otolith (actual length = 6.5 mm) of a 4 yr-old female giant kelpfish, 33 cm TL. (B) Drawing of otolith (sagitta) showing ring counts.

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using standard methods outlined by Fitch (1951), Jensen (1965), and Collins and Spratt (1969). Each pair of otoliths was read independently by me and another reader, neither knowing the identity of the fish. Our age estimates were in agreement in 80% of the examinations. When differences in ring count occurred, a joint reevaluation was made.

Total length versus age comparisons were graphed, and regression analysis and F-tests were performed on the log-log transformations. Mean sizes of male and female kelpfish in age classes where differences appeared to occur were tested for significance using t-tests and 2-way ANOVA. Separate regression equations were also calculated for males and females, and ANCOVA was performed to determine whether the distributions were significantly different (Sokal and Rohlf 1981).

Seasonal population structure was estimated from collection data taken from February 1981 through January 1983. Kelpfish were grouped in six size classes. Distribution of kelpfish in size classes was analyzed for significant seasonal variations using contingency tables and G-tests (Sokal and Rohlf 1981).

Larval Rearing

Nine giant kelpfish nests were collected, four in spring 1980 and five in spring 1982, off Santa Catalina Island. Both parents of the eggs were collected in three cases when spawning was observed. In six cases, only the male parents, which were guarding the nests, were collected. Eggs were also laid in the laboratory on five separate occasions, but did not hatch normally, apparently because of inadequate dispersion in the nests.

Algal nests containing eggs were suspended from a glass rod connected to an electric stirring device, simulating wave motion in shallow subtidal habitats (Fig. 3A). This method substantially decreased bacterial and fungal attacks. Parents were not kept with the eggs, as both males and females were sometimes found to eat eggs in the laboratory. Nests were placed in aerated 190 L plastic containers cooled in 1 m deep aquaria of running seawater. Filtered seawater in the containers was replaced every few days. Several eggs were removed daily for examination of development.

Newly hatched larvae were isolated in lightly aerated 76 L brown plastic containers bathed in large aquaria. Kelpfish larvae were fed laboratory-raised *Brachionus plicatilis* (marine rotifers) within 24 h after hatching. *Brachionus plicatilis* were cultured in high densities of the green flagellate,

Tetraselmis tetrahele, which was grown in a nutrient-rich medium under constant light, following methods developed for feeding northern anchovy larvae (Theilacker and McMaster 1971). *Brachionus plicatilis*, ranging from 0.01 × 0.02 mm to 0.07 × 0.20 mm in size, were maintained in the larval kelpfish containers at concentrations of 10-40/mL. At age 1 wk, kelpfish larvae were changed from closed to open containers of filtered and aerated running seawater, having two 20 × 30 cm panels of 100 μm mesh.

After age 2 wk, kelpfish larvae were also fed wild plankton, which primarily contained various developmental stages of the copepod *Acartia* sp. (92% wet weight) and some barnacle nauplii and cyprid larvae (7% wet weight). Wild plankton were collected using a submersible pump attached to a float off the laboratory pier. A light was suspended over the pump and the system connected to an electrical timer. Plankton were filtered through a 335 μm mesh bag into a 190 L plastic container. The container had a removable inner 100 μm mesh lining and a spillover pipe, retaining only appropriate-sized plankton between the two filter bags (Fig. 4). Best copepod catches were obtained from dusk to 2 h after sunset. Running filtered seawater and an aerator were used to maintain temperature and oxygen levels in the collecting container until the fish larvae were fed the following morning. Densities averaged 1-3/mL, which have been shown to support high survival rates in laboratory rearing of other fish larvae (Houde 1973; Hunter 1981).

When plankton catches were low, giant kelpfish diet was supplemented with cultured *Artemia salina* (brine shrimp) nauplii. *Brachionus plicatilis* were discontinued after age 3 wk and plankton continued until age 3 mo. After age 2 mo, diet was supplemented with frozen adult brine shrimp, Tetramin[2] commercial flake food, and live mysids captured from net tows in kelpbeds.

Ten larvae were removed every 2 d during the first 2 wk of development for measurement and description. After this period, 10 larvae were examined weekly until 2 mo had elapsed. All measurements were made on fresh material. Drawings of several stages of larval development were made using a camera lucida and a dissecting microscope.

Gut contents of three specimens from each weekly sample through age 4 wk were analyzed. While viewing with a dissecting microscope, guts were dissected away from the body and food particles
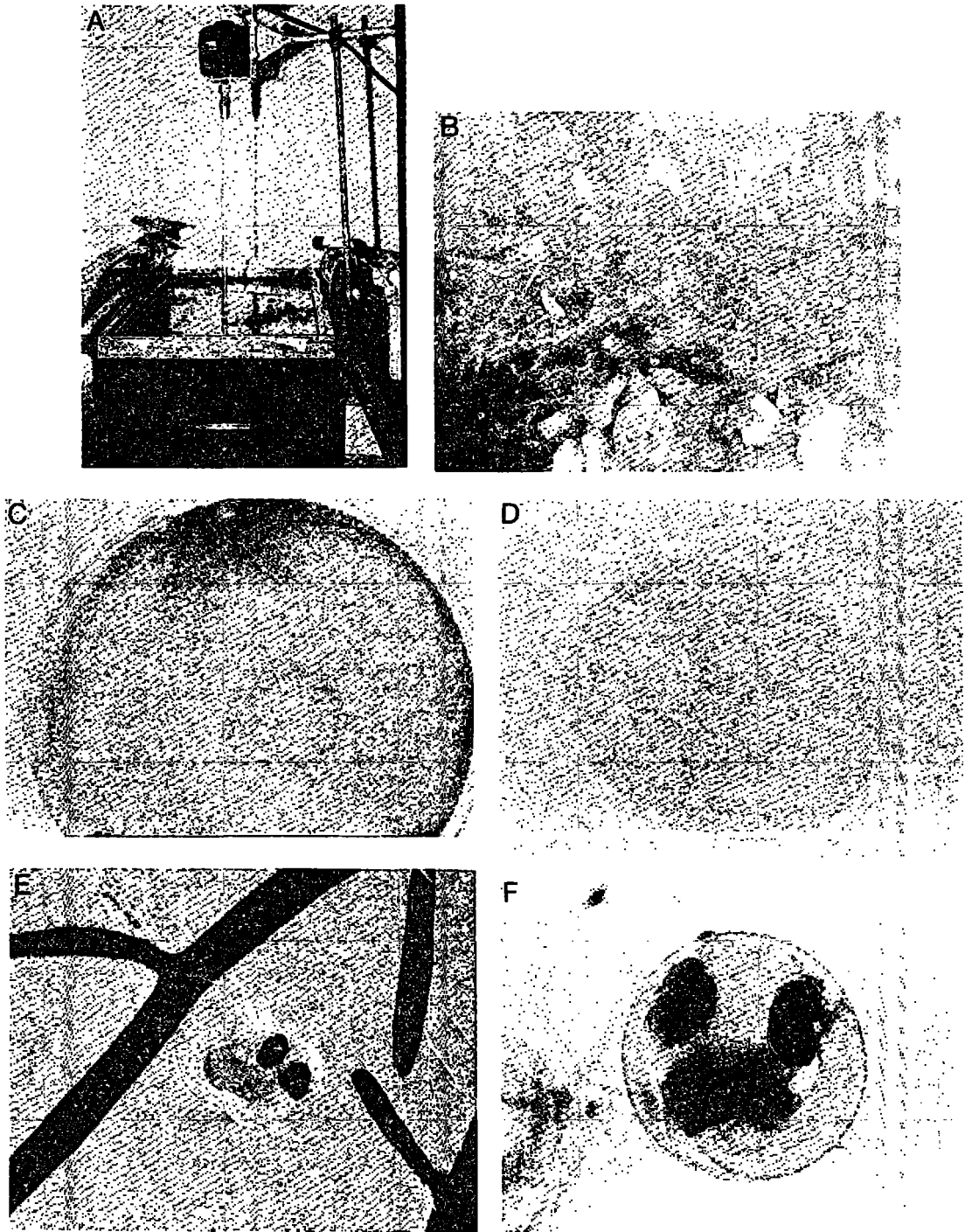

FIGURE 3.—(A) Giant kelpfish nest in aquarium, attached to an electric stirrer, which simulated wave motion. (B) Photograph of nest with eggs in brown algae, taken with 70 mm macrolens. (C) Photograph under compound scope of 24-h kelpfish egg showing blastodisc, egg diameter = 1.4 mm. (D-F) Developing kelpfish eggs photographed under dissection microscope (diameters = 1.4 mm). (D) 72 h after spawning. (E) 10 d after spawning. Note adhesive threads attaching egg to red alga. (F) 12 d after spawning.
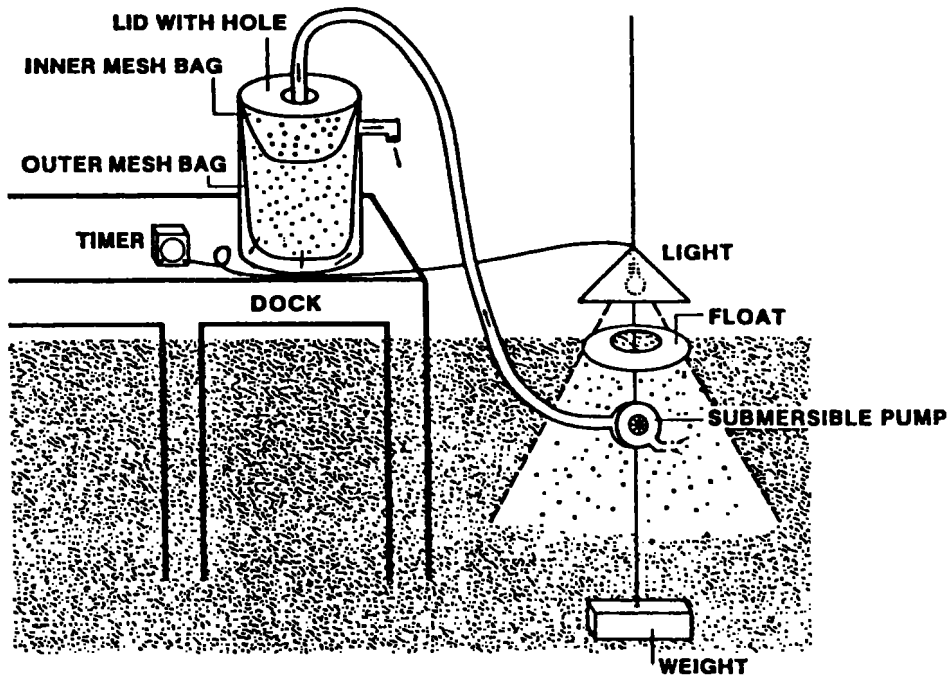
PLANKTON COLLECTOR DESIGN

FIGURE 4.—"Automatic" plankton collector design for feeding giant kelpfish larvae. Plankton were attracted to light on timer after dark. Submersible pump, suspended beneath the float, pumped plankton into large plastic container on dock. Plankton ranging from 100 to 325 μm were filtered between two mesh bags. Aeration and running seawater kept the plankton alive.

teased out using either a single human hair or a modified paint brush from which only a few long strands protruded. Gut contents were viewed under a compound microscope and identified, and average lengths and widths of prey items were recorded.

At age 2 mo, the kelpfish larvae were moved to containers having 0.3 cm mesh panels and containing artificial plant habitats (see Stepien 1985 and 1986). They were subsequently measured bimonthly and their development described. Development and feeding of laboratory-reared kelpfish larvae were also compared with 20 field-collected individuals. Kelpfish larvae of various ages and sizes were collected in hand nets while night-lighting from a dock and while scuba diving in kelpbed canopies using a 1 mm mesh handnet. Other kelpfish larvae were examined from bongo net collections made in Santa Monica Bay in 1982. Their development was compared with similar-sized laboratory-reared larvae. Gut contents of four early-stage larvae (estimated 0-9 d old) were analyzed for food types and sizes, in comparison with laboratory-reared kelpfish.

RESULTS

Spawning

Giant kelpfish nests were guarded by the male parent, the eggs being interspersed and held by adhesive threads in either red or brown algae (Fig. 3B). Seven of the nine nests collected were located in isolated clumps of algae, and all were found between 6 and 12 m deep. Kelpfish nests were most common in the red alga *Gelidium nudifrons* (6 of 9 nests collected) in areas where clumps of taller brown algae covered patches of red algae. Three of the nests were located in brown algae, two in *Cystoseira neglecta*, and one in *Sargassum muticum*.

The male parent hid in the overlying clump of brown algae, emerging to chase away intruding fishes. Male kelpfish were observed to defend their nests against other kelpfish, sheephead, and rock wrasse. Female kelpfish may spawn several times a year since a female kept in the laboratory laid eggs twice within 3 mo. Gonads of all females examined after spawning were almost entirely spent. Since

all eggs in the nests examined were in similar stages of development, it is likely that each nest contains the eggs of a single female. After spawning (the behavior sequence of which is described in Coyer 1982), the male kelpfish chases away the female parent, as was observed in the laboratory on three separate occasions. In one case, the male's repeated pursuits resulted in the female jumping out of the aquarium.

Eggs occurred in two different colors, red and brown, which microscopic examination showed was due to color of the yolk. All eggs in a given nest were either red or brown and remained that color throughout development. Nest and egg color did not always match. Brown eggs were found in four nests of red algae and two nests of brown algae, while red eggs were found in two nests of red algae and one nest of brown algae.

Fertilized eggs laid in the laboratory developed poorly and few of them hatched, apparently due to abnormal dispersal in the algal nests by the females. In all three cases of laboratory spawnings, eggs were laid in clumps rather than being well-spaced throughout the algae, as observed in field-collected nests. Freshly laid nests were collected in the field on three occasions from pairs that had just completed spawning. Two of the three spawning females were brown colormorphs and one was a red morph, but all three showed the barred melanin pattern. All nine field-collected male parents were brown colormorphs exhibiting the characteristic male nuptial striped melanin pattern (Coyer 1982; Stepien 1985, 1986).

Egg Development and Hatching

Eggs from freshly laid nests hatched in 12-17 d at 18°C, the largest number hatching in 13 d. Eggs averaged 1.4 mm in diameter and nests contained an average of 700 eggs, ranging from 400 to 1,200 eggs. An estimated 800 of the 1,200 eggs hatched from the most successful laboratory incubation. Nests that were rotated vigorously and kept well-aerated produced the most successful hatchings.

The sequence of egg development is summarized in Table 1 and photographs of the developing eggs are shown in Figure 3. Hatching occurred from day 14 through day 15. Hatching took about 20 min, the larvae emerging head-first from the egg membrane.

Early Larval Development
(Prenotochord Flexion)

Giant kelpfish larvae can be distinguished from other southern California clinid larvae by their large numbers of myomeres, averaging 55-59. Newly hatched larvae had large yolk sacs and well-developed mouths, guts, melanophores, and fin folds and averaged 6.2 mm TL (Fig. 5A). Larvae floated upside-down, yolk up, for the first 24-36 h after hatching. They swam with wriggling movements, lasting about 30 s, interspersed with longer periods of inactivity, lasting up to several minutes.

Yolk sacs were present 36-48 h after hatching. Two-day-old larvae averaged 7.0 mm TL and swam strongly upright, showing positive attraction to light and concentrating near the white mesh areas of the containers. After 4 d, the larvae were less positively phototactic, concentrating towards the bottom of the containers. Mean sizes and a summary of the sequence of larval development are listed in Table 2. Illustrations of larvae are found in Figure 5.

Later Larval Development
(Postnotochord Flexion)

Flexion of the notochord had begun by 7-9 d and an average size of 8.5 mm (ranging from 7.6 to 8.9 mm, $N = 12$). Field-collected giant kelpfish larvae also showed the beginnings of notochord flexion at a similar size (7.4-9.3 mm, $N = 5$). Size at notochord flexion is smaller than that reported by Matarese et al. (1984) for other clinid larvae.

Two-week-old giant kelpfish larvae began swimming in organized schools, which also were observed in situ in giant kelp canopies. Other researchers have also noted this phenomenon (Feder et al. 1974), which was not observed in giant kelpfish past the age of 2 mo in both the laboratory and the field. By 3 wk, the schooling larvae became progressively more difficult to catch with dip nets, exhibiting well-

TABLE 1.—Summary of kelpfish egg developmental stages.

| Time after spawning	Developmental features
24 h	well-developed blastodisc, beginnings of epiboly
36 h	head fold apparent, neural tube forming
72 h	embryo wrapped 180° around egg's circumference; notochord, somites, eyes, and lenses visible
6 d	embryo wrapped 240° around egg's circumference, myomeres well-developed, lenses of eyes pigmented, heart beating 95 times per minute
10 d	yolk shrunk to 1/2 size of egg; embryo curled 1.5 times around egg; mouth differentiated; gut, liver, and inner ear developing
12 d	otoliths and pectoral and dorsal fin folds visible, vigorous tail movements, heart beats 90 to 100 times per minute
14 d	hatching at 18°C., larva exits head-first, hatching takes about 20 min
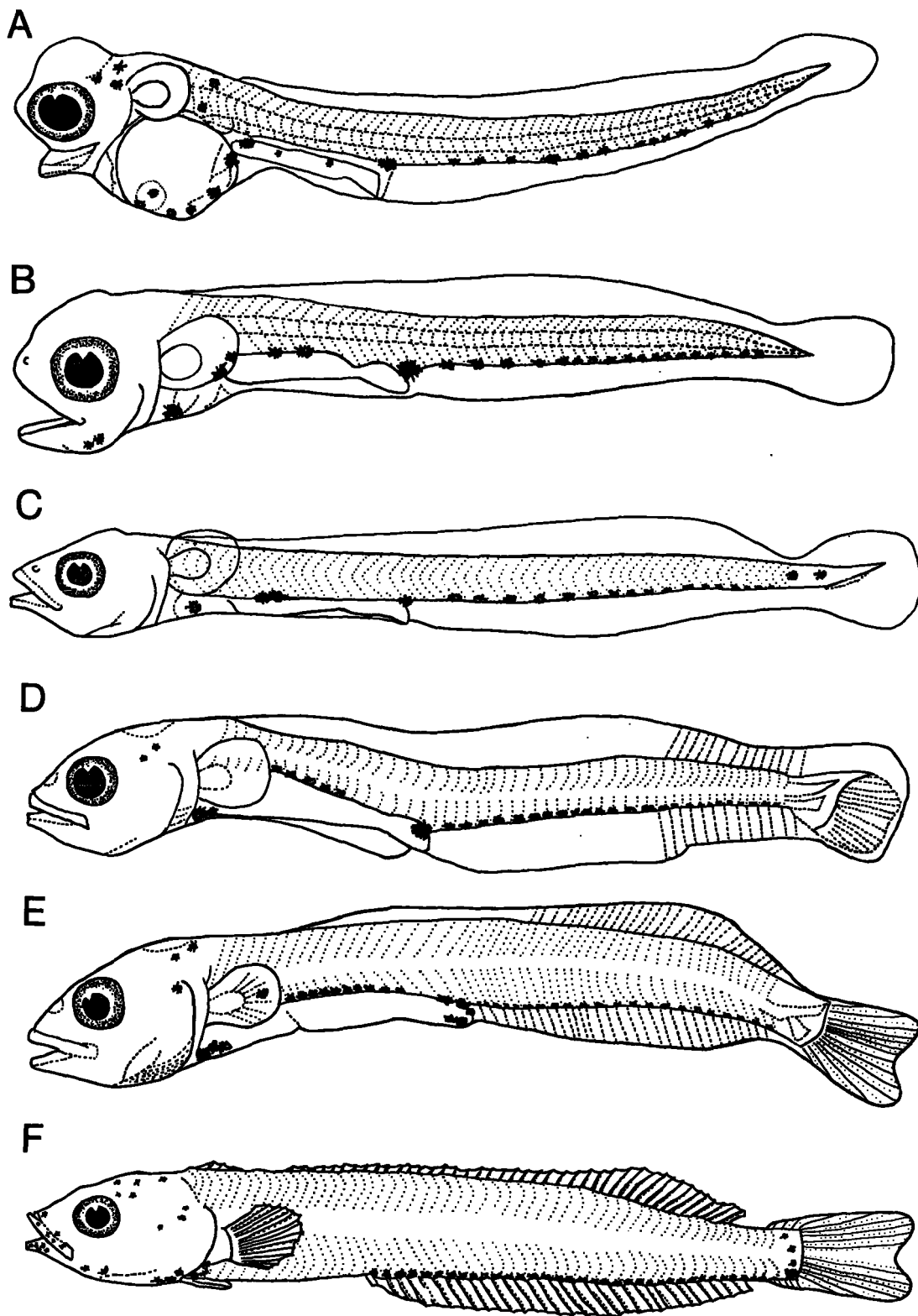
TABLE 2.—Mean sizes (TL, mm) and developmental stages of laboratory-reared giant kelpfish larvae 0-60 d.

Age[1] (d)	Mean length	Range (TL, mm)	No.	Developmental features
0	6.2	6.0-6.5	10	well-developed mouth, gut, and fin folds; 12 postanal serial melanophores
2	7.0	6.7-7.5	10	12-19 postanal melanophores, first feeding, yolk sac 1/3 original size
4	7.7	7.0-8.0	5	20 postanal melanophores, 2 melanophore spots on liver, melanophores dorsal to anus, yolk sac disappeared
6	7.9	7.4-8.4	10	some ventral caudal fin rays visible, gill rakers formed, operculum visible
7	8.3	7.5-9.0	5	notochord flexion begun in some
9	8.8	7.9-9.4	10	notochord flexion completed, swim bladder formed
11	9.7	7.9-10.7	10	caudal fin rays well-developed
13	10.3	8.2-11.2	5	schooling behavior is pronounced
15	10.9	9.5-11.7	10	fin rays in rear of dorsal and anal fin folds
17	11.4	10.0-12.3	10	scattered melanophores on top of head and lower jaw, melanophores over gut
19	11.5	10.1-12.5	5	well-developed schooling and avoidance behavior
21	11.7	10.6-13.6	10	pectoral, dorsal, and anal fin rays formed
23	12.0	11.4-14.3	10	continuous line of stellate melanophores above the gut
25	12.2	10.3-16.8	10	pelvic fins beginning to develop, melanin pigmentation in pelvic region
30	16.8	13.0-19.0	10	orange xanthophore pigmentation on top of the head, over the gut and at the base of the caudal fin; teeth visible
39	23.8	18.0-28.0	5	pelvic fins formed, 32 postanal ventral melanophores
46	25.6	22.0-27.0	10	larvae are pale gold in color
53	25.7	18.0-35.0	10	schooling no longer pronounced
60	30.6	25.0-37.0	10	most have settled onto algae

[1]Age (d) after hatching.

developed avoidance patterns and fright responses. By 5 wk, schooling was no longer as pronounced and the larvae were observed to stalk their copepod prey very efficiently.

Larval Feeding

Unless giant kelpfish larvae were given food within the first 48 h, a point of no-return was reached, after which they starved to death even if given food. Best results were obtained if larvae were fed within 24 h of hatching. *Brachionus* (rotifers) and *Tetraselmis* (algae) were found in the guts of 2-d-old larvae in the laboratory. Three-day-old larvae, even those still having yolk sacs, contained an average of 5.6 *Brachionus* and 2.9 *Tetraselmis* (Table 3). High mortality (nearly 60% of those hatched) occurred after hatching and through day 5. Dead larvae examined had apparently never eaten, despite relatively high levels of appropriately sized food items.

Gut contents of field-collected kelpfish larvae (estimated to range from 0 to 9 d old) showed that they fed on a wide variety of food items, including single-celled algae, rotifers, mollusk larvae, and barnacle and copepod larvae (Table 4). Similar sizes and quantities of food items were consumed by both the laboratory-reared and field-collected larvae (Tables 3, 4).

Significantly larger food items were consumed by 2-wk-old laboratory-reared larvae, the largest widths being 52% of the mouth size (Fig. 6). Larger copepods were eaten more frequently than rotifers, although both food items were present in guts (Table 3). High mortality (ranging from 20 to 40%) also occurred at about 2.5 wk of age in both the 1980 and 1982 rearing experiments. At this age, gut examinations indicated that the larvae were switching from the smaller prey (rotifers and algae) to the larger copepods. Older larvae progressively consumed larger copepods whose size reached 70% of the mouth width by week 3 (Fig. 6, Table 3).

FIGURE 5.—Drawings of laboratory-reared giant kelpfish larvae, made with camera lucida and dissection microscope. (A) Day 0 (after hatching), 6.1 mm TL. (B) Day 4 after hatching, 7.0 mm TL. (C) Day 7 after hatching, 8.4 mm TL. (D) 2 wk, 10.9 mm TL. (E) 3 wk, 11.6 mm TL. (F) 5 wk, 22.2 mm TL.

Settlement and Metamorphosis

After 8 wk and at a mean length of 30.6 mm, giant kelpfish larvae had well-developed, pale gold-brown pigmentation. They became increasingly thigmotac-

TABLE 3.—Gut contents of laboratory-reared giant kelpfish larvae, 3 d to 5 wk, indicating mean numbers and sizes of prey items. *N* = 18 (*N* = 3/sample). Laboratory diets 0-3 wk consisted of *Tetraselmis* and *Brachionus. Acartia* copepods were added to the diet at 2 wk. Sizes of kelpfish (TL, mm) and mean sizes of prey items (width × length) given.

| Kelpfish larvae | | Prey items | | | | | |
| | | *Tetraselmis* algae | | *Brachionus* rotifers | | *Acartia* copepods | |
Age	Size (mm)	Mean No.	Size (mm)	Mean No.	Size (mm)	Mean No.	Size (mm)
3 d	6.8 7.1 7.4	2.9	0.039 × 0.120	5.6	0.10 × 0.149	—	—
1 wk	8.0 8.2 8.2	3.3	0.050 × 0.120	14.7	0.103 × 0.157	—	—
2 wk	9.4 9.7 10.8	10.0	0.078 × 0.130	10.2	0.160 × 0.220	1.2	0.100 × 0.390
3 wk	10.7 11.5 13.6	—	—	6.8	0.130 × 0.195	2.4	0.221 × 0.520
4 wk	11.9 13.3 16.4	—	—	—	—	3.3	0.221 × 0.520
5 wk	19.7 22.0 23.0	—	—	—	—	7.9	0.220 × 0.850

TABLE 4.—Gut contents of field-collected giant kelpfish larvae 6.24-8.2 mm TL. *N* = 4. Mean TL of kelpfish = 6.93 mm (range 6.24-8.82 mm). Mean mouth width = 0.42 mm (0.40-0.44 mm).

Food item	Mean no./ larva	Mean width and range (mm)	Mean length and range (mm)
Diatoms	3.00	0.03 (0.01-0.07)	0.06 (0.04-0.08)
Dinoflagellates	2.00	0.03 (0.01-0.07)	0.04 (0.02-0.20)
Tintinnid protozoans	0.75	0.04 (0.03-0.07)	0.13 (0.10-0.16)
Rotifers	0.75	0.08 (0.03-0.13)	0.19 (0.08-0.35)
Barnacle nauplii and cyprids	0.75	0.10 (0.07-0.13)	0.16 (0.12-0.23)
Copepod nauplii and copepodites	3.50	0.12 (0.07-0.21)	0.40 (0.14-0.46)
Mollusk larvae	1.00	0.11 (0.09-0.12)	0.25 (0.22-0.29)
Nemertean worms	0.25	0.10	0.34
Siphonophores	0.25	0.29	0.30

tic during the next few weeks, darting amongst the artificial plants placed in their containers. Similarly, kelpfish individuals observed in situ had "settled" onto juvenile habitats by 30-50 mm TL. Juvenile habitats included the fronds of giant kelp; the brown alga, *Sargassum muticum*; and green surfgrass. Juveniles were usually in loose aggregations of three to seven similar-sized individuals until reaching a size of 7-9 cm TL.

At 5-7 cm (between 2 and 4 mo), laboratory-reared and field-collected giant kelpfish lost their transparent light gold-colored appearance, developing either green, gold, or brown pigmentation depending on their juvenile habitat, whether surfgrass, kelp, or *Sargassum*. The majority of juveniles found in surfgrass were green with striped or mottled

melanin patterns and had silvery horizontal patches. Those in kelp were usually plain or mottled gold-brown with gold bellies while those in *Sargassum* developed brown pigmentation and barred or mottled melanin patterns (see Stepien 1985 and 1986 for detailed descriptions of color patterns).

Morphometrics of Larvae, Juveniles, and Adults

The SL and TL of giant kelpfish larvae were linearly related (Fig. 7). Early growth (to 40 d) of laboratory-reared larvae was logarithmic (Fig. 8A) while length and age were linearly related between 1 and 9 mo of age (Fig. 8B). Otoliths of laboratory-reared kelpfish showed abnormal ring patterns,
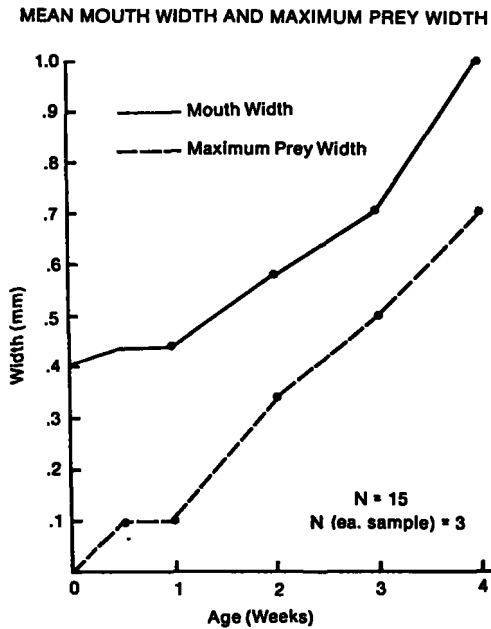
MEAN MOUTH WIDTH AND MAXIMUM PREY WIDTH

FIGURE 6.—Mean mouth width and maximum prey width consumed by laboratory-reared giant kelpfish larvae 0-4 wk old. N = 15 (N each sample = 3).

having several "checks" (false rings). Maximum age reached by laboratory-reared kelpfish in these experiments was 9 mo, at which time they succumbed to a bacterial infection.

Weight versus length of juvenile and adult kelpfish was exponentially related (Fig. 9), and SL and TL were directly linearly related (Fig. 10). Length versus age determinations also followed an exponential curve (Fig. 11). Sexual maturity occurred at a mean size of 18.6 cm TL and an age of 1-1.5 yr.

Regressions of sizes of adult males and adult females on age class were found to be significantly different using ANCOVA (see Fig. 11 legend). When sizes at given ages were compared using t-tests, females were found to be significantly larger than males at given ages past 2 yr (Fig. 12). The largest males sampled in this study were not older than 3 yr or larger than 28 cm TL. In contrast, large females, reaching ages of 4.5 yr and sizes of 42 cm (TL) were collected. Larger individuals collected throughout the 5-yr sampling regime were consistently females.

Population Structure

Seasonal size class structure of the giant kelpfish population was consistent over 2 yr of regular sam-

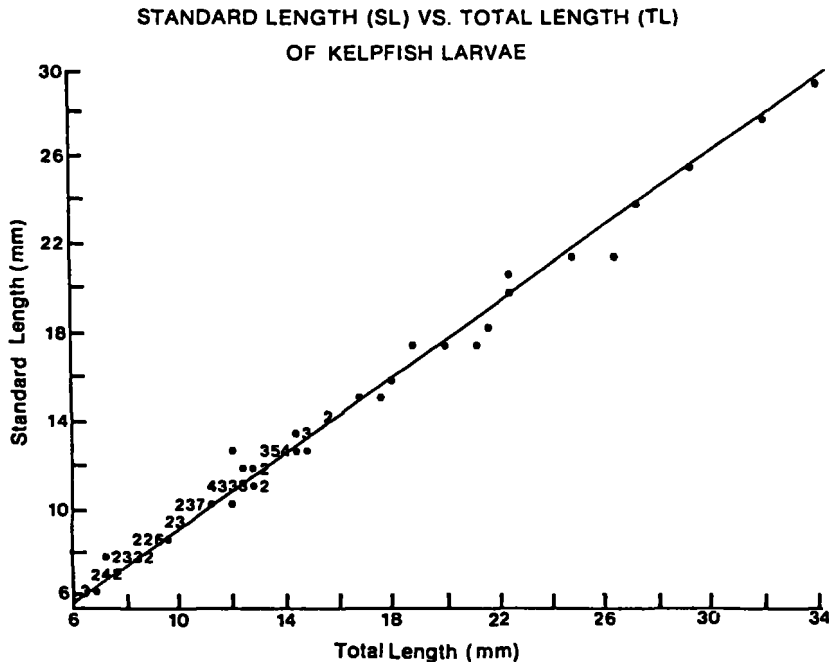## STANDARD LENGTH (SL) VS. TOTAL LENGTH (TL) OF KELPFISH LARVAE

FIGURE 7.—SL (mm) versus TL (mm) of laboratory-reared giant kelpfish larvae 0-30 d old. * = one fish. N = 108. Regression equation: SL = 0.598 + 0.819 (TL). F = 11,588.62, P < 0.00001.
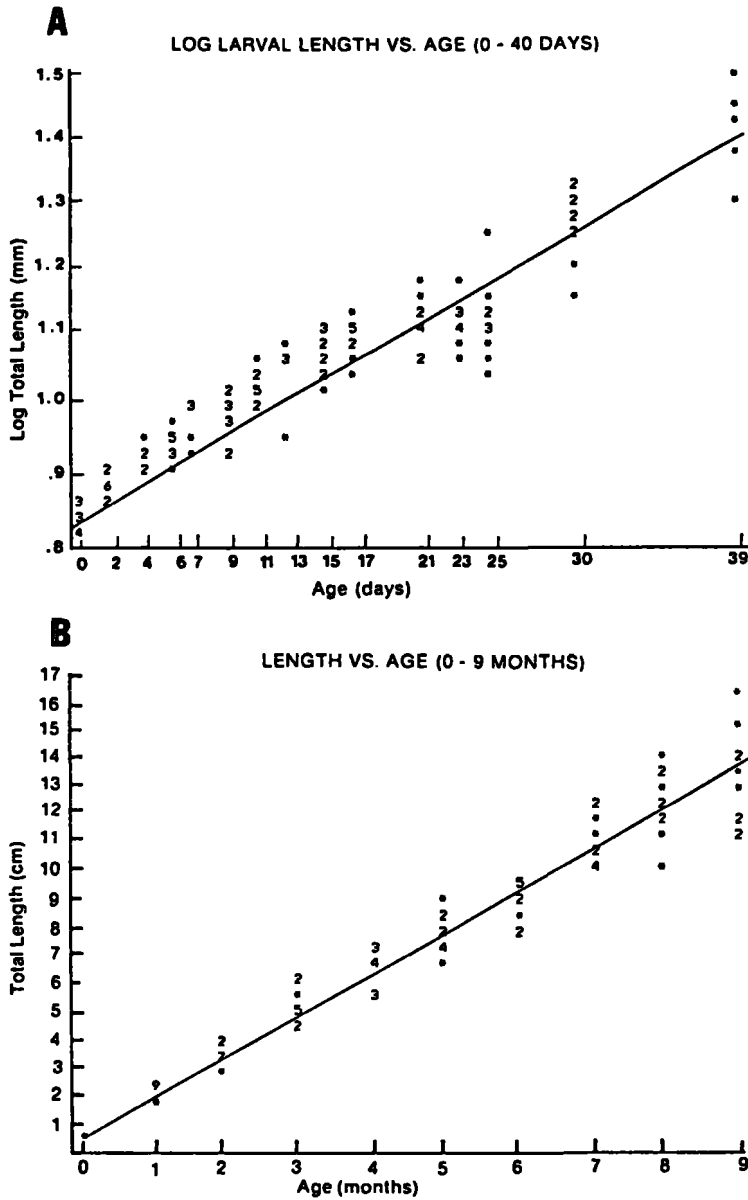
A

LOG LARVAL LENGTH VS. AGE (0 - 40 DAYS)

B

LENGTH VS. AGE (0 - 9 MONTHS)

FIGURE 8.—(A) Log length (TL, mm) versus age (0-40 d) of laboratory-reared giant kelpfish larvae. * = one fish. N = 130. Regression equation: Log TL = 0.814 + 0.013 (days). F = 1,211.9, $P < 0.0001$. (B) Growth of laboratory-reared giant kelpfish (0-9 mo), length (cm) versus age (months). * = one fish. N = 100. Regression equation: TL = 0.379 + 1.482 (months). F = 2,230.8, $P < 0.0001$.

pling (Fig. 13). Contingency tests of independence showed that numbers of individuals in various size classes differed significantly with season in 1981-82 and 1982-83. Juveniles appeared in significant numbers during the spring and summer months. These data agreed with observations on spawning and

appearance of larvae in the water column, indicating that most Catalina Island kelpfish in these years spawned from January through May. During spring and summer, a large portion of the population was estimated to be 1 and 2 yr old, composed of individuals of reproductive age. During the fall

LOG WEIGHT VS. LOG LENGTH OF JUVENILES AND ADULTS
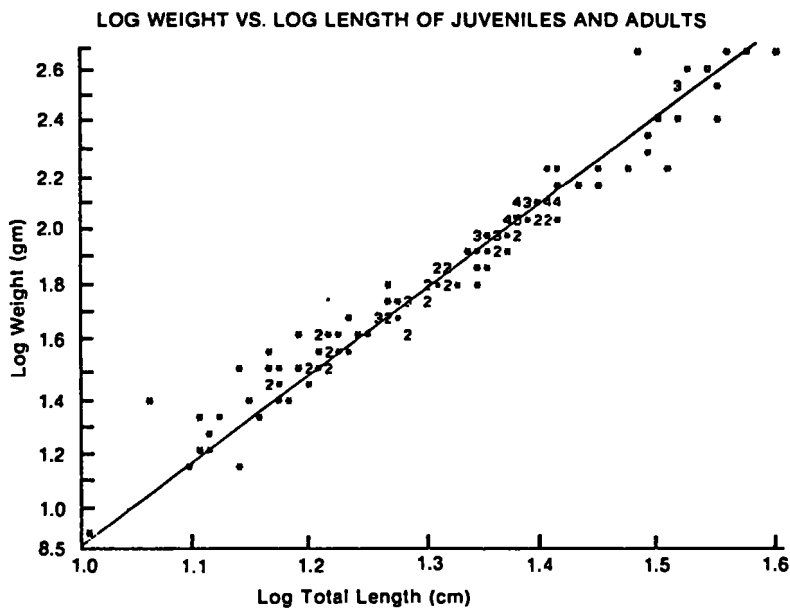
FIGURE 9.—Log weight (g) versus log TL (cm) of juvenile and adult giant kelpfish. * = one fish. N = 140. Regression equation: Log weight = −2.508 + 3.243 (log TL). F = 3,622.7, P < 0.0001.
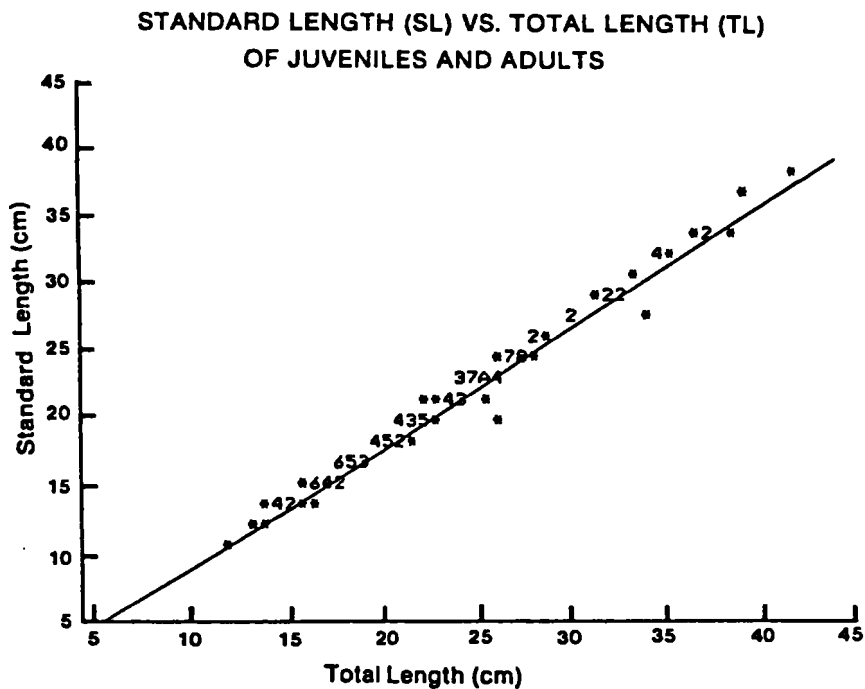
STANDARD LENGTH (SL) VS. TOTAL LENGTH (TL) OF JUVENILES AND ADULTS

FIGURE 10.—SL (cm) versus TL (cm) of juvenile and adult giant kelpfish. * = one fish. A = 11 fish. N = 140. Regression equation: SL = −0.580 + 0.906 (TL). F = 15,993.0, P < 0.0001.

LOG LENGTH VS. LOG AGE
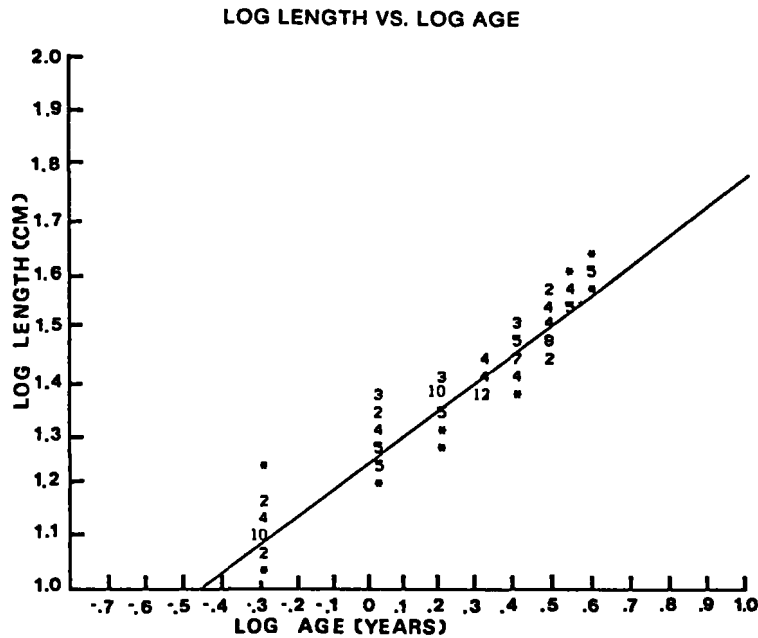
FIGURE 11.—Log TL (cm) versus log age class (years) of juvenile and adult giant kelpfish (males and females). * = one fish. N = 137. Regression equation: Log TL = 1.234 + 0.528 (log age). F = 1,589.28, P < 0.0001. Regression equation for females only (N = 77): Log TL = 1.234 + 0.561 (log age); F = 1,460.7, P < 0.0001. Regression equation for males only (N = 60): Log TL = 1.235 + 0.453 (log age); F = 535.0, P < 0.001. ANCOVA regression analysis of log TL for males and females (two different groups versus log age class (years): F = 5.82 (P < 0.05).

MEAN LENGTH VS. AGE OF FEMALES AND MALES
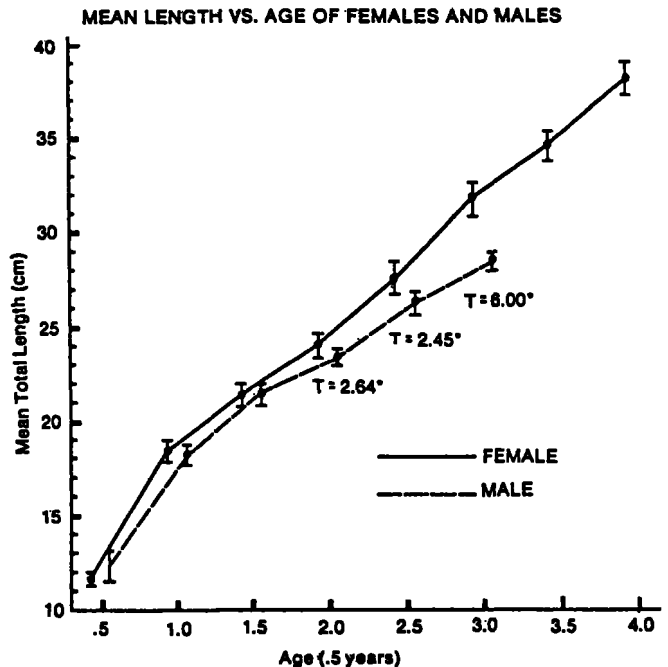
FIGURE 12.—Mean TL (cm) versus age class (years) of female and male giant kelpfish. Significant differences between male and female mean sizes indicated. * = Significant difference in t-test results (0.05 level). Standard error bars shown. N = 137. Two-way ANOVA with replication for mean lengths of male and female kelpfish at three ages (2.0, 2.5, and 3.0 yr) showed significant differences between the sexes (F = 38.52, P < 0.001) and the age classes (F = 78.01, P < 0.001), but no interaction (sex x ages; F = 3.37).
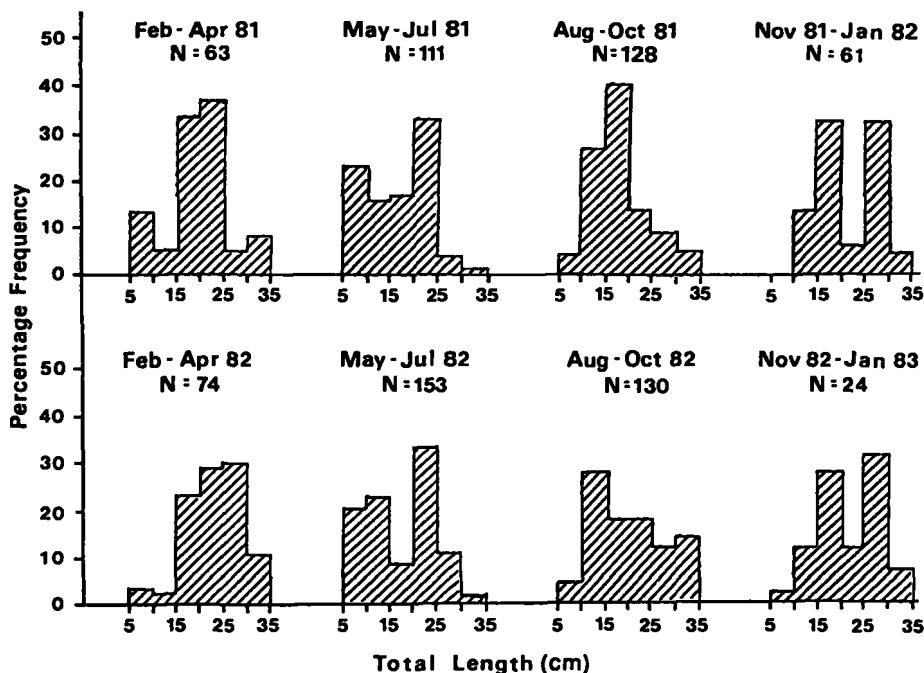
SIZE FREQUENCIES OF KELPFISH

FIGURE 13.—Percentage frequencies of giant kelpfish size classes collected seasonally from February 1981 to January 1983. N = 744. Contingency table R × C G tests of independence showed significant seasonal variations in frequencies of kelpfish size classes in 1981-82 (N = 363; χ^2 = 167.73, 15 df, P < 0.001) and 1982-83 (N = 381; χ^2 = 86.07, 15 df; P < 0.001). (Sokal and Rohlf 1981.)

months, the most abundant size classes were estimated as 0.5 and 1.5 yr of age. These size frequencies also indicate that a relatively low percentage of the population is composed of individuals 3 yr and older.

DISCUSSION

Reproduction and Development

Unlike *Heterostichus*, whose nests contain eggs in similar stages of development, those of the fringehead *Neoclinus bryope* (family Clinidae; subfamily Chaenopsidae) contain various developmental stages, apparently from several spawnings (Shiogaki and Dotsu 1972). *Heterostichus* eggs have a single large oil globule (see Barnhart 1932 and Figure 3C), while other described clinid eggs have several (Sparta 1948; Shiogaki and Dotsu 1972; Matarese et al. 1984). Unfertilized eggs of *Gibbonsia elegans* contain a mass of 6-16 small oil globules (Stepien[3]). Like

Heterostichus (see Figure 3D), *Clinus argentatus* eggs develop large black melanophores over the surface (Sparta 1948).

Early larval development in other clinids resembles that of *Heterostichus*, although few species have been studied and none have been reared past the yolk-sac stage. Other clinids are reported to hatch at similar sizes and at comparable development (Sparta 1948; Shiogaki and Dotsu 1972; Matarese et al. 1984). As in *Heterostichus*, the yolk-sac stage persists for 2-3 d (Shiogaki and Dotsu 1972), caudal fin rays develop first (Matarese et al. 1984), and dorsal and anal fin rays form posteriorly to anteriorly (Risso 1948; Shiogaki and Dotsu 1972; Matarese et al. 1984). Flexion of the notochord appears to occur at a smaller size in *Heterostichus* (mean 8.5 mm TL) than in some other clinids (by 11.1 mm TL in *Neoclinus* and 11.52 mm TL in *Clinus argentatus*) (Sparta 1948; Shiogaki and Dotsu 1972).

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[3]Stepien, C. A. 1986b. Life history of the spotted kelpfish, *Gib-*

bonsia elegans Cooper. Unpubl. manuscr. Marine Biology Research Division A-002, Scripps Institution of Oceanography, University of California at San Diego, La Jolla, CA 92093.

Swimming behavior of newly hatched kelpfish larvae, characterized by short periods of swimming interspersed with longer periods of inactivity, is common in many small marine yolk-sac larvae (Hunter 1972; Ellertsen et al. 1980; Weihs 1980). Like kelpfish, some other newly hatched larvae including cod, *Gadus morhua*, (Ellertsen et al. 1980) and white seabass, *Atractoscion (Cynoscion) nobilis*, (Orhun[4]) swim upside-down for the first 24 h after hatching. This behavior is due to positive buoyancy of the yolk (Hunter[5]). Kelpfish larvae, in situ as well as in the laboratory, schooled between 2 wk and 2 mo of age. Larval schooling is common in species of nearshore fishes which also school as adults (Smith 1981; Hunter 1981) and may serve to increase the probability of locating patches of food and/or may help them avoid predation. No reference to larval schooling in fishes that do not school as adults was found in the literature.

Larval Feeding

A point of no-return at which starvation occurs even if larvae are fed appears to occur earlier in giant kelpfish (after 36 h) than in fish larvae hatching from pelagic eggs (Hunter 1981) and is probably due to their greater degree of development at hatching (i.e., smaller yolks and well-developed mouths and digestive tracts). Only a small number of species are sufficiently developed to consume exogenous food shortly after hatching (Balon 1984a, b). Early feeding during the yolk-sac stage may be critical for the larvae to develop a "search" image and capture skills (Hunter 1981).

In this study, high mortality following the yolk-sac stage was apparently due to starvation, despite relatively high levels of appropriate-sized food items. In many marine fishes, relatively low feeding success is apparently common in field-collected, as well as laboratory-reared, larvae (Hunter 1981). During the first week, field-collected, as well as the laboratory-reared, larvae consume a wide variety of food items, primarily smaller ones such as unicellular algae. Like *Heterostichus*, most species of larval fishes have been found to eat many more small prey items than larger ones (Hunter and Kimbrell 1980; Hunter 1981).

High mortality also occurred in the laboratory at about 2.5 wk, when larvae were apparently switching from smaller to larger prey. This may be a critical period when the larvae have to learn to capture larger, faster swimming crustaceans as the primary dietary component in order to obtain sufficient caloric intake. Studies on other fish larvae have demonstrated the necessity of increasing prey size with growth (Hunter 1977; Hunter and Kimbrell 1980).

Juvenile and Adult Life History

Ages of juveniles and adults calculated in the present study agree with estimates for giant kelpfish determined by J. E. Fitch (in Feder et al. 1974) and by R. Collins[6]. Ages by Coyer (1982), based on 42 kelpfish samples, do not agree with those in the present study. Coyer appeared to have overestimated the oldest kelpfish by 3 yr. This may have been due to the prevalence of "checks" or partially completed false rings on the otoliths which are commonly formed during spawning (Collins and Spratt 1969) and were frequently observed in the present study. Estimated size at sexual maturity (mean 18.6 cm TL) agrees with that reported by Coyer (1982).

Past the age of sexual maturity, female giant kelpfish are significantly larger than males and also live several years longer. Size discrepancy between adult males and females may have evolved from the females' behavior of venturing away from their territories during the spring spawning season into those occupied by males (Stepien 1985, 1986). They are often readily visible at this time while away from plants of matching colors. Large size may help females to avoid predation or, alternatively, may be the result of selection for increased fecundity.

ACKNOWLEDGMENTS

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[5]John Hunter, Southwest Fisheries Center La Jolla Laboratory, National Marine Fisheries Service, NOAA, 8604 La Jolla Shores Drive, La Jolla, CA 92038, pers. commun. January 1986.

[6]Robson Collins, California State Department of Fish and Game, Long Beach, CA 90813, pers. commun. March 1982.

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