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LARVAL STRIPED BASS CONDITION IN A DROUGHT-STRICKEN ESTUARY: EVALUATING PELAGIC FOOD-WEB LIMITATION[1]

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Abstract. Estuarine food webs are frequently altered by human interventions, including freshwater diversions, toxic compounds, and introduced species. From 1988 through 1991 we examined the external morphological and internal histopathologic condition of larval striped bass (*Morone saxatilis*) to evaluate the potential importance of starvation to fish recruitment in the San Francisco Bay estuary. During a recent drought (1987–1992), fish populations declined markedly, concurrent with dramatic reductions in phytoplankton and zooplankton food for larval fishes. Such patterns suggest pelagic food is limited during times of low freshwater input; therefore, larval starvation may limit recruitment. However, toxic compounds in agricultural runoff are also less diluted in low-outflow years, enhancing their potential impact. Histopathology enabled us to identify their possible effects. In the laboratory, indices of larval morphology and eye and liver tissue condition reflected starvation after 2 d of food deprivation. From 1988 through 1991 >90% of 980 field-caught specimens were classified morphologically as feeding larvae. Histopathological evaluation indicated that all field-caught specimens (N = 500) had food in their guts and lacked tissue alterations consistent with starvation. However, liver alterations consistent with toxic exposure were seen in 26–30% of the field-caught larvae from 1988 through 1990, dropping to 15% in 1991. While our findings implicate toxic exposure as a factor in the relationship between low freshwater input and poor year-class success of striped bass, reductions of toxic runoff and improvement in larval liver condition in 1991 did not improve larval survival. This suggests the potentially greater importance of interactions with food limitation and predation as well as the futility of pursuing single-factor explanations for recruitment failure. The potential obfuscation of food limitation by toxic exposure also indicates the need for interdisciplinary approaches to distinguishing anthropogenic intervention from estuarine food-web processes.

Key words: food limitation; food webs; histopathology; larval striped bass; morphometrics; recruitment processes; San Francisco Bay estuary; starvation; toxicity.

INTRODUCTION

Temporal variability of freshwater input often is associated with variation in year-class success of fish and invertebrates in estuaries and coastal oceans (Gunter 1967, Sutcliffe 1973, Birkeland 1982, Stevens et al. 1985, Skreslet 1986, Day et al. 1989, Livingston 1991). Such associations have been attributed to variation in food abundance for larvae, because starvation has long been considered an important regulator of larval survival (Hjort 1914, Thorson 1950). Freshwater flow transports nutrients that increase primary productivity, and tidal processes facilitate the transfer of productivity to consumers, amplifying biomass at higher trophic levels (Nixon 1982, Skreslet 1986, Day et al. 1989). This fertilization process, called the "agricultural model" (Nixon et al. 1986, Houde and Rutherford 1993), implies that food resources available to higher trophic levels are diminished when primary production is reduced during times of low freshwater input.

The existence and importance of food limitation to higher trophic levels has often been proposed in models (reviewed by Schoener 1989, Abrams 1993), and demonstrated in lakes (Carpenter and Kitchell 1993), often by extensive fertilization programs (Hyatt and Stockner 1985). However, in many estuaries and coastal oceans, evidence that food limits higher trophic levels has been elusive (May 1974, Huntley and Boyd 1984, Leggett 1986, Houde 1987, Sinclair 1988, Olson and Olson 1989). This suggests that the bases for associations between freshwater input and year-class success of fishes and invertebrates, i.e., the agricultural model, remain poorly understood for such systems (Stevens et al. 1985, Skreslet 1986, Olson 1987, Runge 1988, Sinclair 1988, Livingston 1991).

In estuaries the effects of various physical and anthropogenic processes can also covary with freshwater input, obscuring the importance of food limitation among trophic levels. Such couplings with biotic pro-

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cesses bypass the bottom-up route through the food chain, affecting recruitment directly (Sinclair 1988, Powell 1989, Rothschild 1991). River outflow, tidal currents, and wind may affect the size and cohesiveness of suitable larval habitat areas, rendering them patchy (Sinclair 1988, Cushing 1991). At much smaller scales turbulence may create or obliterate this patchiness, influencing the probability of encounter between larvae and their food organisms (Lasker 1975, Rothschild and Osborn 1988). Moreover, because estuaries are typically near urban and agricultural centers, cause-and-effect relationships in food webs can be obfuscated by anthropogenic interventions, including freshwater diversions and pollution (Stevens et al. 1985, Nichols et al. 1986, Hall 1991).

Here, we report on morphometric and histopathological studies evaluating the importance of food limitation for larval striped bass (*Morone saxatilis*) in the San Francisco Bay estuary, California. We compared the nutritional condition of field-caught larvae with that of larvae reared in the laboratory at different food concentrations. In addition, systemic histopathological analysis detected cell alterations that are consistent with a toxic etiology. During 1988–1992, drought, freshwater diversions, and filter-feeding by exotic bivalves dramatically reduced primary and secondary productivity, and produced record-low year classes of most pelagic fishes. Such patterns suggest that food limitation is an important source of mortality for larval fish. However, evidence for food limitation must be distinguished from exposure to toxic compounds that are less diluted during low outflow years. Our objective, therefore, was to determine whether food limitation and possibly anthropogenic intervention(s) produced poor year-classes during times of low outflow in this estuary.

Background of the study area

San Francisco Bay, the largest estuary in California, is formed by the confluence of the Sacramento and San Joaquin rivers and receives runoff from 40% of the state's surface area (Nichols et al. 1986). Striped bass, introduced from New Jersey in 1879, are the estuary's most important piscivore, and support a valuable sport fishery. Investigations by the California Interagency Ecological Study Program over the past 30 yr indicate that year-class success of many fishes and invertebrates, including striped bass, is positively correlated with the amount of freshwater outflow from the estuary (Turner and Chadwick 1972, Stevens and Miller 1983, Armor and Herrgesell 1985, Stevens et al. 1985, California Department of Fish and Game 1987, Moyle et al. 1992). Over time, freshwater diversions have increased, reducing outflow, while the abundance of striped bass has declined by ≈75% (Herbold et al. 1992). Similar patterns of declining abundance are exhibited by many species in the pelagic food web of the estuary, including most native zooplankters, delta smelt (*Hypomesus transpacificus*), longfin smelt (*Spirinchus thaleichthys*), American shad (*Alosa sapidissima*), and splittail (*Pogonichthys macrolepidotus*). The abundances of all but delta smelt have been shown to be positively correlated with freshwater outflow (Stevens and Miller 1983, Herbold et al. 1992, Kimmerer 1992).

Stevens et al. (1985) suggested food limitation to be among the factors underlying the correlation of striped bass decline with low freshwater outflow. During the spring, adult striped bass migrate into the lower Sacramento and San Joaquin rivers (Fig. 1) to spawn. River flow subsequently transports eggs and larvae downstream to the upper portion of the mixing zone between fresh and salt water (entrapment zone or turbidity maximum) where food organisms (copepods and cladocerans) and phytoplankton also accumulate (Herbold et al. 1992, Kimmerer 1992). Low freshwater outflow results in the intrusion of salt water into the estuary, forcing the entrapment zone inland from Suisun Bay to the narrow river channels (Fig. 1), shrinking the surface area of the photic zone, and decreasing primary productivity (Arthur and Ball 1980, Cloern et al. 1983, Alpine and Cloern 1992). Saltwater intrusion also facilitates the colonization of upstream areas by benthic filter-feeders, transferring primary productivity to the benthos, thereby limiting the pelagic component of the estuarine food web (Nichols 1985). Such conditions also facilitate benthic grazing because low outflow reduces vertical stratification, and this may render the photic zone more susceptible to filtration by bivalve mollusks (Cloern et al. 1983).

During the recent drought (1988–1992), an upstream position of the entrapment zone was associated with the lowest recorded year-classes of striped bass (Herbold et al. 1992), and also raised concerns that delta smelt may be close to extinction (Moyle et al. 1992). In 1988 an exotic bivalve, *Potamocorbula amurensis,* experienced a population explosion (Nichols et al. 1990). The clam has been shown to effectively filter phytoplankton and copepod nauplii, and has maintained extremely high (1000–10 000 clams/m^2) densities throughout the system. The combined effects of drought and benthic grazing appear to have reduced primary productivity by an order of magnitude, and the densities of preferred food organisms of larval striped bass by 1–2 orders of magnitude (Alpine and Cloern 1992, Obrebski et al. 1992). Moreover, an exotic calanoid, *Sinocalanus dorreii,* has recently become established in the larval fish habitat, but is apparently difficult for first-feeding larval striped bass to capture (Meng and Orsi 1991). Therefore, the growing amount of circumstantial evidence suggests that food limitation may be a direct (i.e., by starvation) and/or interactive (i.e., by increased predation on malnourished individuals) source of larval mortality.

In addition to food limitation, Stevens et al. (1985) suggested that toxic exposure from agricultural and urban runoff also may affect survival. In low-outflow

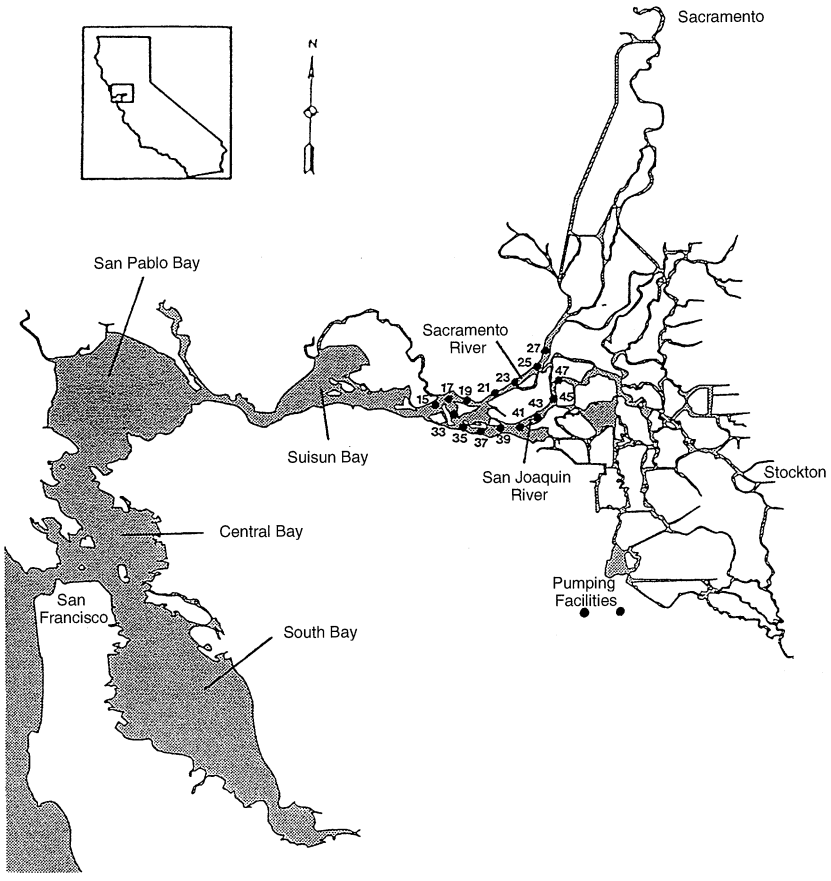

FIG. 1. The San Francisco Bay estuary (California, USA), showing four sub-enbayments, the Delta (area between Sacramento, Stockton, pumping facilities, and Suisun Bay), major river inputs, and principal water diversion facilities. Numbers indicate Interagency Ecological Study Program stations sampled for striped bass larvae from late April to July, 1988–1991.

years toxic runoff is more concentrated and larval fish are retained longer near sites of runoff to the Delta portion of the estuary (Stevens et al. 1985, Nichols et al. 1986). For example, most of the area surrounding the striped bass spawning habitat in the Sacramento River is irrigated for rice cultivation (Rutger and Brandon 1981). During the spawning season, water discharged from irrigated fields can exceed 30% of the river flow (Cornacchia et al. 1984). Discharge water contains several compounds shown to be toxic to larval striped bass and invertebrates, primarily the insecticides methyl parathion and carbofuran, and the herbicide molinate (Foe and Connor 1989, Norberg-King et al. 1991, Bailey et al. 1994). While concentrations of each compound in the rice field runoff are typically 1–2 orders of magnitude lower than acute (LC50, lethal concentration that kills 50% of a sample) levels for larval striped bass (Fujimura et al. 1991), larvae exposed to rice field runoff in 1988–1989 experienced 60–80% mortality in laboratory bioassays (Foe and Connor 1989, Bailey et al. 1994), suggesting an additive or synergistic interaction among the individual pesticides and/or their degradation compounds. In addition, exposure to rice pesticides also produces sublethal effects in larvae (Heath et al. 1993), including altered growth and swimming behavior that can affect prey capture and/or predator avoidance ability. However, while runoff from rice cultivation and other agricultural activities (Saiki et al. 1992) have been shown to be toxic to young striped bass and invertebrates in laboratory bioassays, their effects have not been quantified in the field or shown to regulate year-class success.

Finally, many larvae become entrained in freshwater diversions en route to the entrapment zone, especially in large-scale state and federal water-pumping projects located in the southern Delta and in hundreds of smaller diversions throughout the Delta (Fig. 1). While entrainment may be an important factor causing mortality of young striped bass (Stevens et al. 1985), it has been the only factor evaluated quantitatively (Turner and Chadwick 1972, Stevens et al. 1985, California Department of Fish and Game 1987) and does not adequately account for declines in abundances of other species less susceptible to this process (Herbold et al. 1992).

Methods and Materials

Field collections

In 1988, striped bass larvae were collected from two stations (25 and 47) in the Sacramento and San Joaquin rivers (Fig. 1). In 1989–1991 an additional 13 stations were added to provide improved coverage of the larval fish habitat (Fig. 1). These stations were chosen because they encompassed the upstream end of the entrapment zone where higher concentrations of first-feeding larval striped bass were consistently present during the spawning season. Sampling consisted of 2–5 min oblique tows with a 1-m plankton net (mesh size: 0.505 mm) (Stevens et al. 1985). In all years, samples were taken every other week (sometimes weekly) from late April to early July.

To reduce capture stress effects (G. H. Theilacker 1986 and *personal communication*) on larvae, we minimized the time each larva spent in the net before preservation. The unwashed contents of the collection jar were immediately placed on a Nitex screen (mesh size: 0.505 mm) and allowed to drain briefly. Retained material was rapidly immersed in Bouin's fixative solution (10× sample volume). The average time between retrieval of cod-end and fixation was 1 min. After 24-h fixation, the material was removed from the fixative, rinsed, and stored in 70% ethanol. Larvae then were separated from the other fixed material, identified, sorted, and stored until time of processing.

Laboratory nutrition experiments

In June 1989, 4-d post-hatch (4 dph) striped bass larvae were obtained from the Central Valley Hatchery, Elk Grove, California. Following transport to our laboratory, 100–150 larvae were stocked into each of nine 20-L cylindrical tanks supplied with fresh well water (17–18°C) under slow continuous flow. Beginning on the night of day 5, larvae in five randomly selected tanks were fed live *Artemia* nauplii (0.8–1.0 animals/mL) twice daily. Larvae in the four remaining tanks were not fed. On alternate days, through day 19, 12–15 larvae were removed from each treatment and fixed as above. In this way, a total of 89 fed and 79 starved larvae were used to establish morphometric and histopathologic indices of starved and fed larvae.

In May 1992 another "starved/fed" experiment included larvae maintained in recirculated well water with sea water added to maintain 1–1.5 mL/L salinity in 60-L cylindrical tanks ($N = 12$). All other conditions (e.g., larval density) were identical to the initial experiment. Actual comparisons with field-caught larvae were made using freshwater (electrical conductivity = 0.410 mS/cm). This more closely matched environmental conditions, because 83% of larvae were caught in <1.0 mS/cm.

Morphometry

All external measurements on larvae were facilitated by a computerized Cue II Image Analysis System (Olympus Corporation, Lake Success, New York, USA) with input from magnified images using a Wild dissecting microscope. Providing precision to 0.01 mm, this system was used to collect linear and surface (area) measurements. Each larva was measured individually for 15 morphological parameters. After inspection of correlation matrices revealed redundancies among several variables, a total of seven variables were used in statistical analyses. Orientation, magnification, and definition of the seven variables were as follows:

Lateral view (15×): Standard length (SL), Head length (HL), and Eye diameter (ED);

Lateral view (60×): Body depth at pectorals (BDP) and Body depth at anus (BDA);

Dorsal view (15×): Inter-orbital distance (IO) and Dorsal surface area (DSA).

After measuring, each larva was returned to a separate coded vial and stored in 70% ethanol until histologic processing.

To determine whether age differences existed between laboratory and field-caught specimens, results of otolith aging analyses on our 1989 field specimens were compared between groups. Analyses were performed by California Department of Fish and Game personnel (L. Miller, *unpublished data*) using light microscopy. Validation of otolith ring count with known-age larvae <30 dph was obtained by the following regression equation: estimated age = 1.036(actual age) − 0.165; ($R^2 = 0.971$). This information confirmed that the majority of field-caught larvae without yolk-sacs and <8 mm SL were also <19 dph. Therefore, size characteristics of 1989 larvae reflected little age-related bias.

Bivariate and multivariate indices of size and shape variation were constructed using the conventional ratio method and principal components analysis (PCA), respectively. For each larva, ratio indices were obtained by dividing each measurement by SL. Prior to PCA, data for all seven morphometric parameters were transformed with natural logarithms and standardized to mean = 0 with z scores. Since the potential exists for different patterns of variation between surface area and linear measurements (Pimentel 1979, McGurk 1985), PCA was performed using a correlation matrix rather than a covariance matrix. Once ratio indices and the matrix of factor scores from the PCA were obtained, they were subjected to multivariate analysis of variance (MANOVA) to determine whether laboratory treatments (starved vs. fed larvae) were significantly different in multivariate space. Finally, a discriminant function was calculated, and each individual (laboratory and field specimens) was classified as either starved or fed. All statistical analyses were performed using SYSTAT (Wilkinson 1987).

Histopathology

All larvae for histologic analysis were fixed as above, rinsed in 70% ethanol, dehydrated in a graded series of ethanols, infiltrated, and embedded (3–5 an-

TABLE 1. Criteria used to score larval striped bass tissues.

Tissue source	Score		
	1–1.5 (poor condition)	2–2.5 (average condition)	3 (healthy condition)
Eye	Over 70% separation of the pigmented cell layer (visual cell layer) in the retina	About 25–50% separation of the pigmented cell layer in the retina	Little (<15%) separation of pigmented layer
Liver	Shrunken overall, atrophy and indistinct cells, no glycogen or mitotic features, nuclei bunched and cytoplasm granular	Slightly shrunken, some atrophy, some glycogen but no mitotic features, cytoplasm granular	Large, cells and nuclei distinct, glycogen laden, some mitotic features
Gut contents	Lumen empty	Lumen about half full	Lumen over half full
Midgut cells and brush border	Sloughing of epithelial cells, vacuolization and atrophy of cells, loss of villi and broken brush border, no mitotic figures	Slight vacuolization and separation of epithelium, brush border intact, few mitotic features	Little separation of epithelium, brush border distinct, mitotic features common
Brain	Many intercellular spaces, vacuolization	Limited intercellular space formation	No intercellular spaces
Cartilage	Necrotic appearance, large pericellular spaces, high vacuolization of intercellular matrix	Some pericellular spaces, slight vacuolization	Intercellular matrix uniform
Skeletal muscle	Fiber bundles indistinct, interfibrillar spaces, cross striations absent, muscle mass small, no mitotic figures	Some interfibrillar spaces, fiber bundles evident, erratic cross striations, few mitotic figures	Interfibrilla intact, fiber bundles and cross striations distinct, mitotic features common

imals per block) in glycol methacrylate (GMA). The orientation of individual larvae was consistent so each could be separately identified. Sections (2–3 μm thick; in series) were cut with glass knives and mounted on one of two separate histologic glass slides. One slide from each pair was stained by toluidine blue or hematoxylin and eosin (H&E) and examined. The small block size, the tiny larvae, the added resolution of the semi-thin sections, and the use of multiple sections ensured adequate coverage of major visceral organs, their tissues, and cells. Labeled slides were blindly coded prior to reading to ensure that the reader was unaware of the history of each specimen.

A three-level semi-quantitative grading system (O'Connell 1976, 1980, Theilacker 1978, 1986) was used to evaluate larval condition. The histologic condition of the eye (retina), gut lumen and contents, intestinal mucosal epithelium and associated brush border, brain, cartilage, liver, and skeletal muscle were determined. Each tissue was given a score of 1 or 1.5 (poor condition); 2 or 2.5 (intermediate condition); or 3 (good condition). Criteria for each structure are given in Table 1. In this manner, a total histologic score could range from 8 to 24. A total of 168 laboratory-reared and 500 field-caught specimens were ranked as above.

After altered hepatocytes, some depleted of glycogen, had been found in 1988 and 1989, selected specimens from additional tows at stations 17, 19, and 21 (Fig. 1) during May 1990 were processed for transmission electron microscopy (TEM). Whole specimens were immersed in one-half-strength Karnovsky's fixative, post-fixed in osmium tetroxide, and stained en bloc with uranyl acetate following standard methods. Specimens were dehydrated in a graded series, passed through three changes of propylene oxide, infiltrated in the polymer Eponate-12 and mounted in polyethylene embedding (Beem) capsules. After polymerization, blocks were trimmed and sections (silver to gold interference) were cut with a diamond knife and floated onto copper grids. After drying, sections were stained with lead citrate and viewed in a Phillips 401 electron microscope with accelerating voltage of 80 kV.

RESULTS

Laboratory nutrition experiments

After 1 wk, larval mortality was ≈50% in freshwater and ≈25% in brackish water. In addition, some starved larvae in freshwater lived until day 19 after hatch, whereas some larvae in brackish water lasted until day 26 (Fig. 2). Plots of changes in the standard length measurement over time show that larvae in the freshwater study did not grow appreciably until after day 14, while larvae grown in brackish water increased in standard length (SL) continuously after day 8 (Fig. 2). By day 19, fed larvae in freshwater attained a mean SL of 6.20 ± 0.41 mm (mean ± 1 SD, $N = 12$), and the two starved larvae remaining had shrunken to standard lengths of 4.75 mm and 4.51 mm (Fig. 2). In brackish water, fed larvae on day 18 had a mean SL of 6.32 ± 0.43; starved larvae were 5.31 ± 0.21. Therefore, overall survival was higher in brackish water, but mean SL of larvae surviving the first 2 wk was not significantly different between the fresh and brackish water experiments.

Morphometry

The magnitudes of the factor loadings for the first component (PC1) from the PCA (principal components analysis) ranged from 0.773 to 0.958, indicating that

PC1 reflected primarily variation due to size (Pimentel 1979, Humphries et al. 1981). Loadings of subsequent components (PC2–PC7) were positive and negative, reflecting primarily changes in larva shape among the seven morphometric parameters, although some size variation may also be represented (Humphries et al. 1981). A plot of PC1 on PC5 (Fig. 3A), where the points are the factor scores of larvae from the starved/fed experiment, illustrates the separation of the nutritional treatments in morphological space. A similar plot (Fig. 3B) with the fed treatment replaced by a random subsample of field-caught larvae from 1988–1991 (N = 186), indicates the similarity between the field and fed specimens. Fed and field-caught larvae were larger overall, and proportionally expanded in their body depth dimensions relative to other body dimensions than starved larvae (Fig. 3, Table 2).

Discriminant analysis using PCA indices supports the above observations. Results from MANOVA were significant (F = 20.84, df = 8, 159, $P < 0.0001$), indicating that starved and fed larvae were distinct morphometrically. The discriminant function:

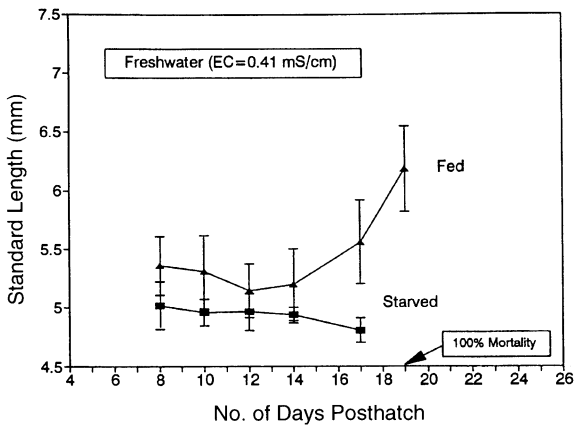

FIG. 2. Change in standard length (mean ± 1 SD) of larval striped bass under two food treatments in freshwater and brackish water, during the first 3 wk after hatch. EC = electrical conductivity of the water.

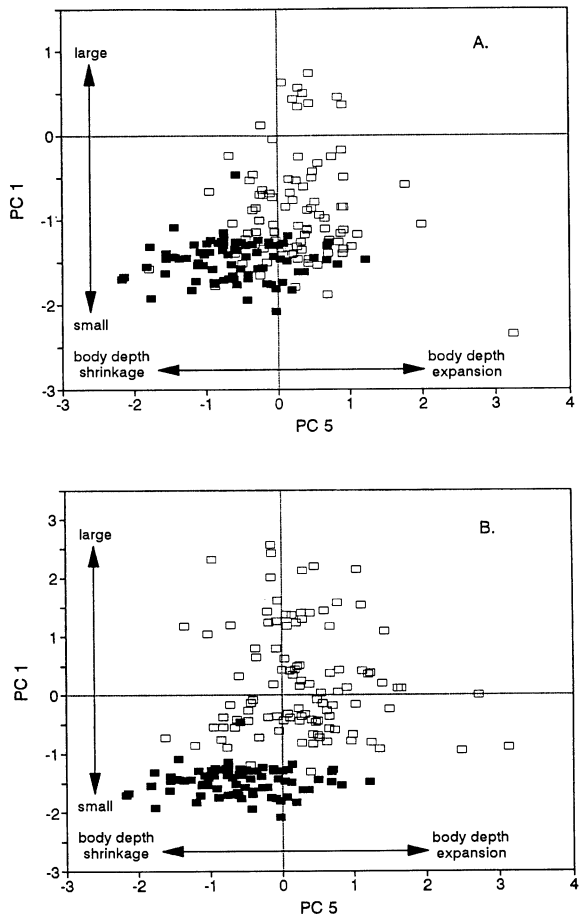

FIG. 3. Comparison of larval morphometry of (A) starved (solid boxes) with fed (open boxes) striped bass and (B) starved (solid boxes) with field-caught (open boxes) striped bass as described by components 1 and 5 from principal components analysis using seven morphometric parameters.

Canonical score
= (0.688)PC1 score + (0.328)PC2 score
+ (−0.011)PC3 score + (0.525)PC4 score
+ (0.719)PC5 score + (−0.098)PC6 score
+ (−0.090)PC7 score

indicates that PC5 contributed most (had the largest coefficient) to the discrimination between starved and fed larvae, followed by PC1. This suggests larval starvation may be characterized by the proportional shrinkage in the two body-depth dimensions relative to other body dimensions and, secondarily, by a lack of growth in all dimensions as indicated in Fig. 3. This discriminant function classified 89.9% of the fed larvae as fed and 85.0% of the starved larvae as starved (Table 3). With all years pooled, 81.4–92.7% of the field-caught specimens in each year were classified as fed. Slightly higher proportions were similarly classified when each year was analyzed separately with the laboratory specimens. In comparison, the ratio indices, overall, clas-

TABLE 2. Morphological variables for striped bass larvae (mean ± 1 SD) from laboratory growth experiment in freshwater and the San Francisco Bay estuary. N = number of larval fish.

Morphological variable*	Group					
	Fed treatment (N = 89)	Starved treatment (N = 79)	1988 (N = 322)	1989 (N = 259)	1990 (N = 196)	1991 (N = 171)
SL	5.398 ± 0.437	4.928 ± 0.156	5.729 ± 0.693	5.894 ± 0.650	6.129 ± 0.751	6.929 ± 0.710
BDA	0.287 ± 0.071	0.253 ± 0.137	0.404 ± 0.138	0.403 ± 0.111	0.448 ± 0.146	0.564 ± 0.149
BDP	0.650 ± 0.071	0.603 ± 0.039	0.747 ± 0.172	0.815 ± 0.148	0.879 ± 0.172	1.030 ± 0.175
HL	1.143 ± 0.182	1.048 ± 0.059	1.224 ± 0.185	0.959 ± 0.180	1.024 ± 0.202	1.412 ± 0.181
IO	0.260 ± 0.047	0.216 ± 0.030	0.348 ± 0.047	0.332 ± 0.059	0.367 ± 0.099	0.447 ± 0.062
DSA	1.661 ± 0.331	1.368 ± 0.144	2.281 ± 0.642	2.081 ± 0.577	2.293 ± 0.699	2.860 ± 0.706
ED	0.074 ± 0.017	0.057 ± 0.005	0.087 ± 0.026	0.111 ± 0.033	0.125 ± 0.036	0.154 ± 0.038

* SL = standard length, BDA = body depth at anus, BDP = body depth at pectorals, HL = head length, IO = inter-orbital distance, DSA = dorsal surface area, and ED = eye area.

sified fewer larvae as fed, except for 1988 in the pooled analysis (Table 3).

Histopathology

Histologic scoring indicated almost complete separation of the starved and fed laboratory treatments (Fig. 4). All but one of the fed larvae scored higher than 18, whereas all but three starved larvae scored <17. All field-caught larvae from 1988–1991 scored higher than 18 (Fig. 5). The histological results clearly indicate that all field-caught larvae scored similarly to the fed laboratory specimens.

The eye and liver (Fig. 6) tissues appeared most sensitive to starvation, exhibiting obvious deterioration. After 2 d without food (day 8 after hatch), 8 of 10 larvae sampled had livers in "poor" condition, and 9 out of 10 larvae received similar scores for eye condition. The remaining larvae sampled on day 8 were in "average" condition for each tissue. During starvation the eye experienced marked deterioration of the pigmented/visual layer of the retina, such that "poor" eye tissue exhibited almost complete separation, "average" eye tissue ≈50% separation; and "healthy" tissue was almost, or completely intact (Fig. 6). Changes in the liver were similarly dramatic (Fig. 6). "Healthy" liver tissue contained hepatocytes laden with glycogen (clear spaces), had very distinct cellular architecture, and was comparatively large (Fig. 6). "Average" liver tissue contained considerably less glycogen, exhibited less discernable cell architecture, somewhat granular cytoplasm, and was smaller overall (Fig. 6). "Poor" liver tissue completely lacked glycogen, exhibited significant deterioration of cellular architecture, vacuolation, and appeared shrunken (Fig. 6).

The presence of food in the gut and healthy eye tissue were the two most obvious indications that all field-caught specimens had been feeding. Also evident was the appearance of glycogen-containing hepatocytes in many of the livers. However, from 1988 through 1990, 25–30% of the larval livers were in "poor" condition (Table 4), exhibiting less glycogen, more cytoplasmic basophilia, vacuolation, and a loss of cellular architecture. In 1991 this proportion dropped to 15%. Whereas the livers of starved laboratory specimens exhibit a loss of glycogen and increased cytoplasmic basophilia (Fig. 6), they rarely contained vacuolated hepatocytes. In addition, while the starved laboratory specimens showed marked and consistent deterioration of several tissues/organs, those field-caught larvae that exhibited abnormal livers showed very little (or no) deterioration of tissues other than the liver. Thus, the histologic appearance of the livers of many field-caught

TABLE 3. Percentages of larval striped bass from the San Francisco Bay estuary classified as the "fed" treatment. Results are from discriminant analysis of their nutritional condition, using morphometric indices derived from ratios and principal components analyses (PCA). N = no. of larvae. Station numbers refer to the collection stations shown in Fig. 1.

Group	1988			1989			1990			1991		
	N	Ratio (%)	PCA (%)	N	Ratio (%)	PCA (%)	N	Ratio (%)	PCA (%)	N	Ratio (%)	PCA (%)
Laboratory study												
Fed treatment				89	86.5	89.9						
Starved treatment				79	15.2	15.0						
Field collections												
Stations 21–27	114	85.1	84.2	76	71.1	80.3	73	82.0	97.3	98	65.3	89.8
Stations 15–19	...	...	...	61	82.0	88.5	19	68.4	89.5	21	90.5	95.2
Stations 41–47	208	85.6	79.8	63	90.5	96.8	85	69.4	90.6	50	86.0	96.0
Stations 33–39	...	...	...	59	84.7	96.6	14	64.3	85.7	2	100	100
Total field-caught larvae	322	85.4	81.4	259	81.5	90.0	191	71.2	92.7	171	74.9	92.4

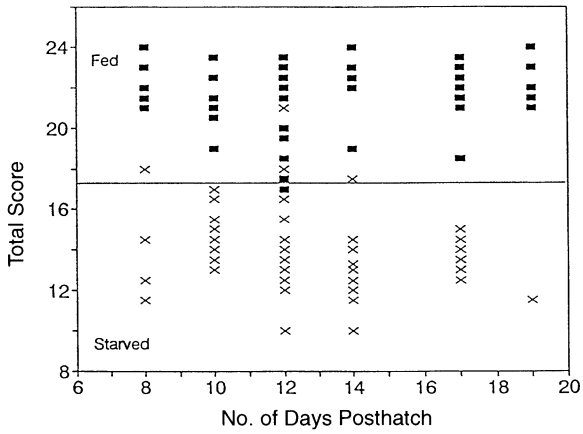

FIG. 4. Distribution of total histopathological scores for starved (Xs, $N = 79$) and fed (solid boxes, $N = 89$) striped bass larvae from laboratory study in freshwater. Each larva received a score of 1 (poor), 2 (average), or 3 (healthy) for each of seven tissues/organs and gut fullness.

specimens was "poor," exhibiting abnormalities unlike our starved laboratory specimens. Comparison of liver scores between the Sacramento (Fig. 1: stations 15–27) and San Joaquin (Fig. 1: stations 33–47) rivers (Table 4) indicates that the proportion of larvae with "poor" liver condition was significantly greater in the Sacramento river ($\chi^2 = 5.74$, df = 1, $P < 0.02$) in 1988, although no statistical difference was detected in 1989–1991.

Transmission electron microscopy of larval striped bass livers in 1990 indicated that 33% ($N = 10$) contained alterations. Transmission electron micrographs (Fig. 7) of normal liver tissue (Fig. 7A) include hepatocytes with large and abundant mitochondria and rough endoplasmic reticulum. The hepatocytes are uniform and show no vacuolation. The altered hepatocytes (Fig. 7B) are enlarged, showing swollen mitochondria and swollen, apparently fluid-filled, cisternae of the endoplasmic reticulum. These hallmarks of cellular injury follow ion shifts and membrane alteration, and are the ultrastructural equivalent of vacuolated hepatocytes seen at the light-microscope level (Cotran et al. 1989). Because a variety of pesticides can produce similar hepatic injury, it is difficult to attribute these alterations to specific compounds or mixtures of compounds (Murty 1986). However, vacuolated hepatocytes are typical in adult fish exposed to various pollutants, including pesticides (Murty 1986, Moore et al. 1989, Myers et

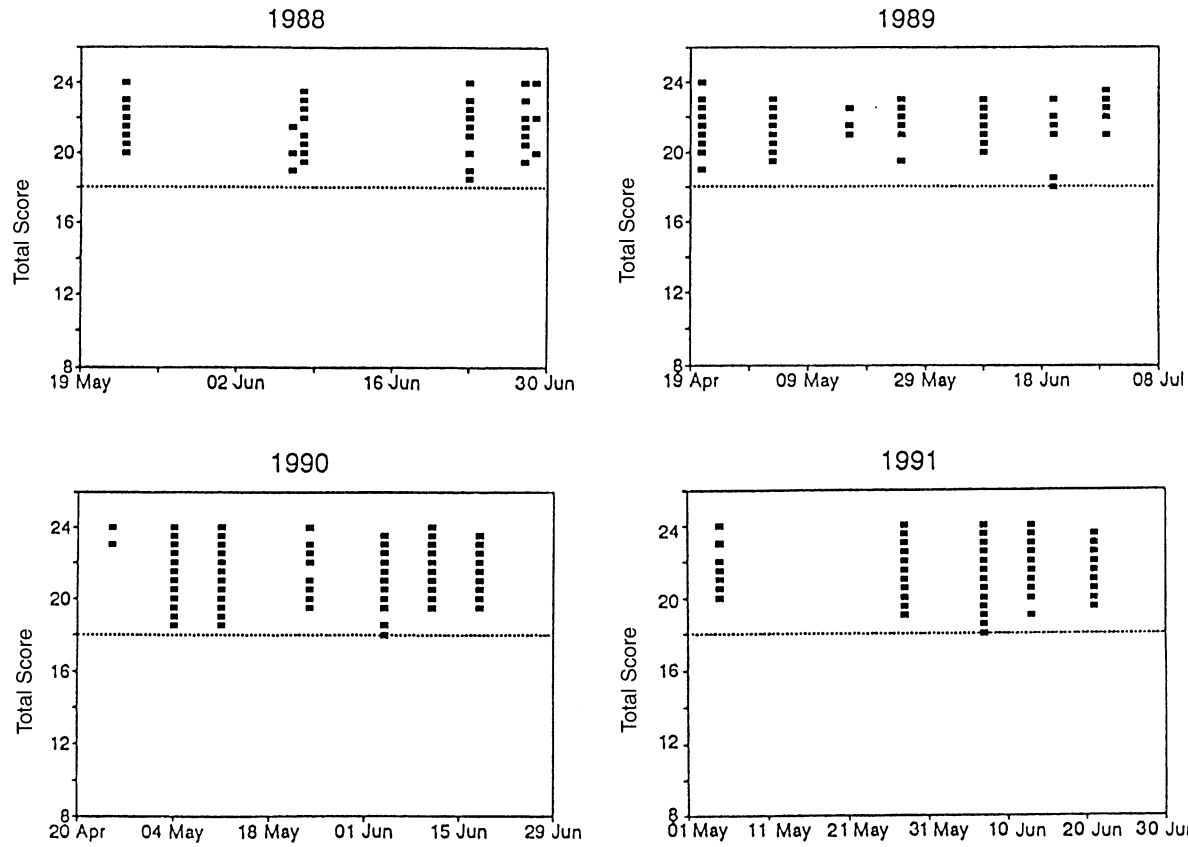

FIG. 5. Distribution of total histopathological scores for striped bass larvae collected from the San Francisco Bay estuary in 1988 ($N = 100$), 1989 ($N = 100$), 1990 ($N = 200$), and 1991 ($N = 100$). Each larva received a score of 1 (poor), 2 (average), or 3 (healthy) for each of seven tissues/organs and gut fullness.

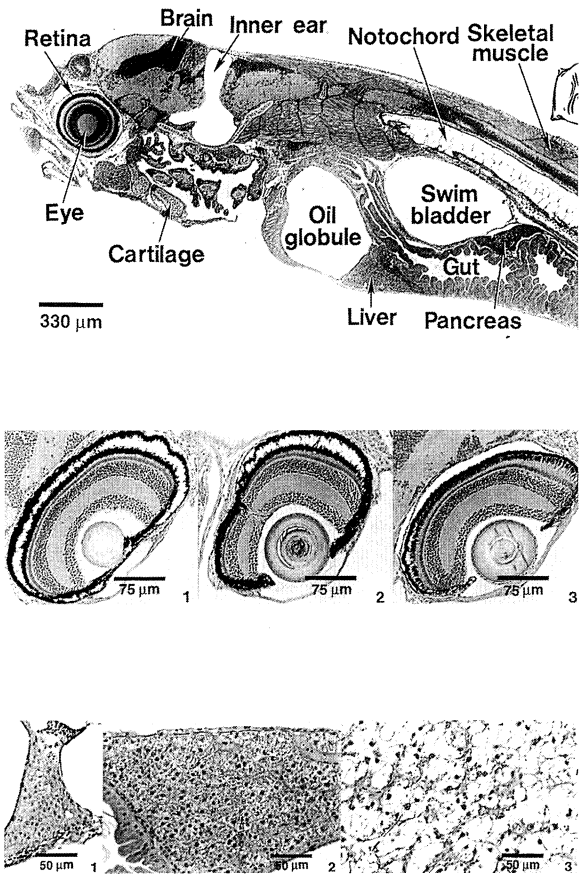

FIG. 6. Histopathology of striped bass larvae. Top panel: longitudinal section showing tissues used in scoring of nutritional condition. Examples of eye (middle panel) and liver (bottom panel) condition: (1) poor, (2) average, (3) healthy. Scoring criteria for each condition are described in Table 1.

al. 1992, Hinton 1993). In addition, similar liver alterations have been produced by rice pesticides (methyl parathion, carbofuran, molinate) in recent laboratory bioassays (D. J. Ostrach, W. A. Bennett, and D. E. Hinton, *unpublished manuscript*).

DISCUSSION

Contrary to our expectations, morphological and histological evaluation of field-caught striped bass larvae provided no evidence of starvation during 1988–1991 in the San Francisco Bay estuary. The overall healthy appearance of seven organs/tissues is a clear indication that all field-caught larvae evaluated by histopathology (N = 500) had been successfully feeding within 2 d of capture. Moreover, the presence of food in the gut suggests recent feeding had occurred prior to capture. In addition, because >90% of all field specimens (N = 980) also were classified as "fed" by morphometry, starvation appears to have been uncommon in the larval striped bass population. These findings suggest other factors may regulate larval survival in low-outflow years.

Larvae may be food limited without being starved. Our laboratory investigations and others (see Martin and Mallory 1980, Eldridge et al. 1981, Rogers and Westin 1981) indicate that striped bass larvae are starvation resistant and can survive for at least 14 d without food (see also Fig. 2). While starving striped bass larvae have been detected in parts of Chesapeake Bay where food typically is 10–100 times more abundant than in our study area (Martin et al. 1985, Setzler-Hamilton et al. 1987), larval densities in the Chesapeake also are higher, which may result in local food depletions (Cowan et al. 1993). In the San Francisco Bay estuary we believe food-limited larvae may simply grow more slowly, lacking external or internal indicators detectable by our indices. Slow growth extends the duration of the larval stage and can increase the cumulative impact of predation (Ricker and Forester 1948, Shepard and Cushing 1970, Houde 1987). This subtle form of food limitation is not detectable by our analyses; however, additional studies (see Bennett 1993, K. A. Rose, J. H. Cowan, Jr., L. W. Miller, and D. E. Stevens, *unpubished manuscript*) suggest that the interactive effects of slow growth and increased susceptibility to predators may be an important source of larval mortality in the estuary.

The ultrastructural evidence of hepatocellular injury, coupled with light-microscope observations showing the high proportion of liver volume involved, suggests that toxic exposure may be an important source of mortality through impaired liver function. Field-caught larvae showed evidence of liver injury consistent with exposure to rice pesticides that are discharged into the

TABLE 4. Number and percentage of striped bass larvae with liver alterations consistent with toxic exposure (poor condition = scores of 1 or 1.5) from histopathological analyses of specimens from the San Francisco Bay estuary. N = total no. of larvae caught. Station numbers refer to collection stations shown in Fig. 1.

	1988			1989			1990			1991		
		Poor condition			Poor condition			Poor condition			Poor condition	
Group	N	No.	%	N	No.	%	N	No.	%	N	No.	%
Stations 21–27	45	16	35.5	46	14	28.8	78	28	35.9	99	17	17.2
Stations 15–19	...	...	...	28	6	21.4	14	6	42.8	22	5	22.7
Stations 41–47	42	6	14.3	19	4	21.0	87	21	24.1	49	3	6.1
Stations 33–39	...	...	...	7	3	42.8	21	5	23.8	2	1	50.0
Total	87	22	25.3	100	27	27.0	200	60	30.0	172	26	15.1

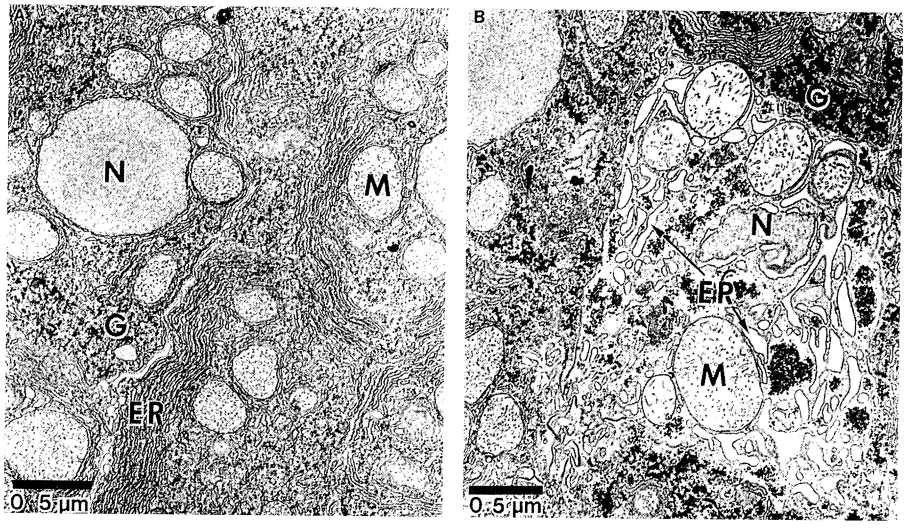

FIG. 7. Transmission electron micrographs of (A) normal and (B) altered liver hepatocytes, indicating nuclei (N), mitochondria (M), rough endoplasmic reticulum (ER), and glycogen (G).

spawning habitat (Table 4). In addition, affected larvae lacked alterations in other tissues previously associated with food limitation. Besides organelle swelling, transmission electron micrographs also show that the altered livers contain glycogen (Fig. 7: dark areas), indicating the larvae had recently been feeding. Moreover, the incidence of poor liver scores dropped from 26–30% (in 1988–1990) to 15% in 1991 (Table 4) concurrent with changes in pesticide use by rice growers. These policy changes increased substantially the on-field holding times of contaminated irrigation water before release, reducing the concentration of molinate (and presumably other compounds) by ≈60% (Bailey et al. 1994), so that about a 50% reduction was detected in the frequency and magnitude of rice runoff toxicity to striped bass larvae during 1991 (Bailey et al. 1994). Residual toxicity may reflect accumulated pesticides in the soil, or applications of less commonly used pesticides. Therefore, we hypothesize that the liver alterations seen in field-caught larvae are due to the effects of rice pesticide effluent in the striped bass spawning habitat.

While we can only speculate about the magnitude of direct mortality due to toxic exposure, sublethal hepatic injury may prolong the larval stage of affected individuals (Eldridge et al. 1977, von Westernhagen 1988). Alterations such as those seen here (Fig. 6, Table 4) encompass a large volume of the liver and thus potentially impair the conversion of food to energy, reducing the growth and survival of affected larvae. Without histopathologic diagnosis, such larvae would have appeared food limited. Recent individual-based modeling of larval striped bass (Rose et al. 1993) indicates that reduced growth rate or prey-capture success due to sublethal toxic exposure could reduce larval survival by ≈40–45%. In addition, sice many zooplankters (copepods and cladocerans) also are highly sensitive to pesticides and other toxic compounds (Evans et al. 1988, Norberg-King et al. 1991, Moore and Folt 1993), depression of larval food abundance may occur in the proximity of exposed larvae. Local food depletion would exacerbate the effects of sublethal exposure as well as further confuse attempts to distinguish among causative factors affecting recruitment.

Anthropogenic intervention and the agricultural model

Our results show how anthropogenic processes could affect striped bass year-class success, complicating predictions of the agricultural model (see *Introduction*). Although food limitation may occur, it probably acts in an interactive fashion with predation and sublethal exposure to toxics. If toxic exposure was the single most important factor affecting larval survival, improvement in young-of-the-year abundance would have been expected in 1991 because of the 50% reduction in toxic runoff. However, while liver condition in the larval population improved by ≈50%, the abundance of young-of-the-year striped bass remained among the lowest on record. Therefore, toxic-load reductions alone were not sufficient to improve survival of larval striped bass during the recent drought. Larvae spared by cleaner runoff apparently succumbed to other factors (e.g., food limitation, predation, entrainment). This suggests interactions among factors may be more important than each factor acting alone. Cowan et al. (1993) used individual-based modeling to simulate larval striped bass survival in the Potomac River. They showed that single factors alone (e.g., prey density, temperature) produced 10-fold variation in year-class success, whereas combinations of factors produced 145-fold variation similar to that observed in the field. Therefore, the high potential for interactive effects among various regulatory factors indicates the futility

of pursuing single-factor explanations for recruitment problems.

The regulation of year-class success in low-outflow years has a complex basis, depending on the dynamic interaction of physical, biotic, and anthropogenic processes. While we can only speculate why high outflows provide the potential for good year-classes (e.g., toxic runoff may be diluted and/or flushed downstream, food levels may be higher, or larvae are less susceptible to entrainment), this study has shown how various factors can interact to affect fish larvae during times of low freshwater outflow in estuaries. Within and among years, the interactive bases for relationships between freshwater outflow and year-class success may change in relative importance and thus be more complex than predicted by the agricultural model. Therefore, future interpretations of food web processes (Schoener 1989, Abrams 1993) may become distorted without understanding the interactive contribution of human impacts on them. Interdisciplinary investigations will be necessary to unravel such complexities.

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