creased diversion of water from the estuary followed by a severe drought (1986–1992), which suggests that fish populations are affected by a combination of natural and anthropogenic factors.

Three alien species in Suisun Marsh showed increases in yearly abundance. The shimofuri goby is a recent invader that quickly became one of the most abundant fishes in the marsh (Matern and Fleming 1995). The white catfish is not a recent invader, but its abundance increased dramatically when we added sampling sites in Denverton Slough late in the study. The yellowfin goby avoided a negative correlation with year by virtue of three very successful spawning events in the 1990s.

Our analyses support the conclusion of Meng et al. (1994) that, considered as a group, the resident native species are in serious decline, although there has been an apparent stabilization in overall abundance in the recent wet years. The decline is further supported by negative correlations with year for several abundant native species.

Species that use the marsh on a seasonal basis showed large fluctuations in catch, in part because of the predominance of short-lived species for which strong cohorts only affect the catch for 1 year (Meng et al. 1994). Our analyses show some seasonal species (delta and longfin smelt) to be in sharp decline.

The alien species index did not show a significant decline over time and included the only species with significant increases in abundance. Given the frequency with which new species invade the estuary (Cohen and Carlton 1998), it is certain that such invasions will continue for some time. Thus, while the pool of potential resident native species can only decline, the pool of potential resident alien species continues to grow. For example, the shimofuri goby is a new invader to North America (Matern and Fleming 1995) that did not occur in the estuary until 1985. By 1987, when it began to appear regularly in our catches, over one-half of the fish in our study had already been collected. Nevertheless, it became so abundant that it was the eighth most common species collected over the entire study. In 1999 we collected a closely related Asian species, the shokihaze goby, in Suisun Marsh for the first time. This goby appears to be rapidly increasing its population in the estuary (S. Slater, California Department of Fish and Game, personal communication).

Despite the contrast between increasing populations of some alien species and decreasing populations of many native species, we found no significant correlations between the species group indices. We were also unable to detect significant negative correlations between the abundances of alien gobies and those of the other abundant species. Because gobies were some of the most abundant species in the marsh, our findings support the conclusions of other studies (e.g., Weinstein 1979; Weinstein et al. 1980; Peterson and Ross 1991) suggesting that biological interactions among fish species usually play a relatively minor role in determining patterns of abundance in estuaries. Interactions are apparently overshadowed by the physiological demands of an estuarine lifestyle (Moyle and Cech 2000) and differences in the timing of reproduction or are undetectable in the San Francisco Estuary due to overall low population sizes. More important may be the interactions with ecosystem-altering invertebrates such as the overbite clam, which has decimated the zooplankton community (Alpine and Cloern 1992; Kimmerer and Orsi 1996; Orsi and Mecum 1996), shifting the food web from a pelagic toward a benthic base (Kimmerer et al. 1994) and forcing fish to find alternative prey. Herbold (1987) and Feyrer (1999) have shown that native species are more successful at switching to alternative prey when their preferred prey undergo periods of low abundance. On the other hand, analyses showed a decrease in the growth rate of splittail after the introduction of the overbite clam (Matern, unpublished data). Furthermore, the alien shimofuri goby (which was not present during Herbold's study) has been shown to utilize seasonally abundant prey and exploit novel food sources, including alien hydroids and barnacle cirri (Matern 1999). Additional interactions between fish and alien invertebrates may be revealed as the impacts of alien mysid shrimp (Modlin and Orsi 1997), copepods (Orsi et al. 1983), crabs (Cohen and Carlton 1997), and even cnidarians (Mills and Sommer 1995) are studied.

Effects of Environmental Variables on Patterns of Abundance and Co-occurrence

The CCAs indicated that species' responses to environmental variables were weak overall and changed little between years with high and low freshwater inflows. Although young of the year dominated our catches and spawning success for many species depends on freshwater inflow (Jassby et al. 1995), there was apparently enough survival between years to dampen annual inflow effects. The effect of freshwater inflow may have also been masked by the general downward trend in the abundance of most species with time (for reasons unrelated to inflow). Thus, while the relationships among temperature and the inflow variables changed, most species maintained the same general associations and positions relative to one another. Shimofuri goby, white catfish, yellowfin goby, and striped bass were associated with high temperature, delta smelt and threadfin shad were associated with cool water, and threespine stickleback and Pacific staghorn sculpin were associated with high variation in inflow. All of these associations can be related to species' spawning times. One species showing a distinctly different pattern was the longfin smelt, which was correlated with high salinity, transparency, and low 365-d inflow in high-inflow years but high 365-d inflow in low-inflow years. More than any other species, this species uses the entire estuary and the ocean off the estuary (the Gulf of the Farallones) to complete its life history. The factors regulating its abundance, however, are still poorly understood (Moyle 2002).

We do not mean to imply that the environment plays a minor role in determining fish abundance. We believe that environmental variables act mainly on very young life stages and not on the larger juveniles and adults that we primarily capture in our trawls and seines. This hypothesis is supported by similar analyses of larval fish collected in Suisun Marsh in 1994–1999 (Meng and Matern 2001), which found that environmental variables (particularly freshwater inflow) played an important role in determining species abundance. Similarly, Kimmerer et al. (2001) found that the survival of striped bass in the San Francisco Estuary was strongly affected by freshwater inflow, but only during the first few weeks of life. Thus, we suggest that environmental variables determine which species spawn and recruit successfully and that subsequent minor fluctuations in those variables do not have a large enough effect on fish abundances to be detected in our sampling. The importance attributed to environmental variables in the literature varies, but most studies showing that such variables are highly important were conducted over areas encompassing much of the estuary (e.g., Weinstein et al. 1980; Allen 1982; Thiel and Potter 2001) and thus over a wide range of salinities and temperatures. Studies like ours that were conducted on a smaller portion of the estuary (e.g., Rozas and Hackney 1984; Loneragan et al. 1987) typically attribute less importance to these variables. However, the scale of our study is more likely to detect interaction effects among species than those at larger scales (Jackson et al. 2001).

Differences among Sloughs

After examining the first 13 years of catch data from this study, Meng et al. (1994) found that native fishes were more abundant in smaller sloughs and that seasonal species were more common in larger sloughs. They found alien species in both slough types but noticed that these species were becoming more abundant in the small sloughs over time, partly because of the increasing abundance of the shimofuri goby (Meng et al. 1994). Because the present analysis was based on a larger set of data, we were able to make comparisons among individual sloughs.

We found that sloughs differed from one another physically and chemically and that these differences helped to explain the differences in catch among sloughs. The biggest differences were related to overall slough size, with the largest sloughs having the lowest total catches and least diversity. This inverse relationship is partially due to decreased sampling efficiency in the larger sloughs. One anomaly was Boynton Slough, which had a high amount of flocculent substrate and in which catches were unusually low for a small slough. A difference between Boynton Slough and the others is that a local sewer district releases tertiary treated water into it.

Other small sloughs differed primarily in salinity and diversion density, but catches of most species were most likely related to local physical or chemical conditions that were not measured during our study. For example, on occasion we made large catches (>500) of threespine sticklebacks in a single otter trawl. These catches always occurred during January–May (usually February) in Goodyear Slough near duck pond drains. The habitat within duck ponds is likely conducive to threespine stickleback spawning, and our exceptionally large catches corresponded closely with the seasonal patterns of duck pond draining (S. Chappell, Suisun Resources Conservation District, personal communication). Denverton Slough was distinguished by large numbers of shimofuri goby, a species known to prefer hard substrates (Akihito and Sakamoto 1989; Matern 1999), which are absent from most sloughs. In contrast, yellowfin gobies are burrowers that require soft substrate (Dotu and Mito 1955); they were rare in the rocky habitat of Denverton Slough but abundant elsewhere in the marsh. We have no explanation for the high relative abundance of white catfish in Denverton Slough. They were abundant throughout the marsh at the beginning of our study (Moyle et al. 1986) but became rare during the extended drought (1985–1992). Although they were predicted to return to previous levels of abundance (Moyle et al. 1986), they have thus far failed to do so except in Denverton Slough.

Our seining data also showed differences in catch between the two sloughs sampled. Denverton Slough was distinguished by higher catches of chinook salmon. These fish were typically 30–50 mm SL and may have resulted from spawning upstream in Denverton Creek. Suisun Slough was subject to more marine influence and had high catches of seasonal species, including Pacific staghorn sculpin, starry flounder, and longfin smelt. At this location we also collected more yellowfin goby (probably because of the substrate differences mentioned above) and more Sacramento sucker (which spawn in upstream tributaries of the western marsh).

Synthesis: Factors Structuring Fish Assemblages in Suisun Marsh

The species composition in Suisun Marsh follows the model of Moyle and Light (1996), in which the potential species pool of over 200 marine, estuarine, and freshwater species is filtered by their ability to adapt to the local abiotic conditions, with biotic factors playing relatively minor roles. As in all estuaries, the pool of potential species contains not only "true" estuarine species but also those present in nearby freshwater and marine environments. In the San Francisco Estuary, this species pool is supplemented by frequent introductions, mainly from ballast water (Cohen and Carlton 1998). Which species colonize and become established in Suisun Marsh depends largely on the physiological tolerances of those species to the marsh environment, particularly its low salinity and fluctuating temperature. "Marine stragglers" (e.g., plainfin midshipman, white croaker, bay pipefish, speckled sanddab, Pacific sanddab, California halibut, surf smelt, and shiner perch; Loneragan et al. 1989) occasionally enter the marsh when salinity is high but do not establish persistent populations. Similarly, when freshwater conditions prevail, upstream colonists (e.g., centrarchids and bigscale logperch) temporarily move into the marsh. This pattern is similar to that of other altered estuaries (e.g., Thiel and Potter 2001).

We did not find convincing evidence of important interactions among fish species, possibly because most population sizes were relatively low. It is likely that biotic interactions among fishes and invertebrates play a secondary role in structuring the assemblage even during times of abundance. The recent invasion of the overbite clam has resulted in the depletion of zooplankton and increased the potential for competitive interactions among fishes (Feyrer 1999). This deserves further investigation.

While species' presence in the marsh reflects both opportunity and physiology, their abundance and distribution are a result of several other interacting factors. Clearly, the most important of these is the timing of reproduction of the abundant resident species. In probable order of importance, the abundance and distribution of most species can be related to (1) spawning habits within the marsh (e.g., yellowfin goby, shimofuri goby, and occasionally splittail), (2) the recruitment of young of the year to the marsh from upstream (e.g., striped bass, Sacramento sucker, and splittail), (3) the recruitment of young of the year to the marsh from downstream (e.g., starry flounder and Pacific staghorn sculpin), (4) the passage of young of the year through the marsh during their downstream migrations (e.g., chinook salmon and Pacific lamprey), and (5) the passage of adults through the marsh to spawn upstream (e.g., longfin smelt).

After seasonal patterns of reproduction, the most useful predictor of species abundance is past reproductive success, which may be determined by environmental conditions (Meng and Matern 2001). Because the young of the year of many species recruit to the marsh, it is often possible to follow a particular successful cohort over many consecutive months. With apparent disregard for changing environmental conditions in the marsh, abundant cohorts of splittail, striped bass, and yellowfin goby continued to appear in our trawls for many months.

Catches also vary by location within the marsh. We have documented differences due to slough size (small versus large) and substrate (rocky versus muddy). It is also apparent that proximity to sources of freshwater, saline water, and even duck pond drainage water affects catch in certain sloughs.

All of the major trends in abundance were explained by the above factors. Only after they are taken into account do the minor fluctuations in the environmental variables that we measured play a role in structuring the juvenile and adult fish assemblages. While we found no evidence of important interactions among species, such interactions may become more important as the assemblage continues to change as a result of alien invasions or environmental conditions stabilize in ways that cause dramatic increases in fish populations.

Conclusions

The fishes of Suisun Marsh consist of groups of co-occurring species, but the composition and relative abundance of species within these groups shift in major ways through time and space, suggesting a lack of real structure (the result of species interactions). The longer the fishes are studied, the less apparent fish assemblages become. Differences among species within groups in feeding habits and habitat use are presumably more attributable to intrinsic differences in morphology and physiology than to interspecific interactions. Indeed, it appears that the major driving force for the relative abundances of species is reproductive success both inside and outside the marsh; species that regularly co-occur have similar spawning times and requirements for larvae and juveniles.

The lack of assemblage structure is not surprising considering (1) the natural fluctuating conditions of estuaries in general, especially in the brackish regions where species come and go according to changes in temperature and salinity; (2) the general decline in fish abundance in the brackish and freshwater portions of the estuary, which suggests a high level of anthropogenic disturbance; and (3) the frequent invasions of alien species of both fish and invertebrates.

The environment of the marsh nevertheless selects for a distinct subset of the species available. Even given the biases in our sampling, only about one-third of the species we have collected over the years have been abundant enough to be important players in the ecosystem. Furthermore, the total species list for the marsh is less than one-third of that for the entire estuary when stenohaline marine and freshwater species are counted. Thus, it seems possible to create predictable, persistent, interacting subsets of species (fish communities) in the marsh if the stochastic factors of human disturbance and alien invasions are reduced.

We think that these conclusions apply not just to Suisun Marsh but to the San Francisco Estuary as a whole and, in general, to temperate estuaries with a high degree of human-caused disturbance and frequent invasions by alien species. They suggest that there will be a high degree of unpredictability in fish abundances and assemblage composition until estuarine processes return to some semblance of their historic variability and invasions by alien species are halted. In the short run, management strategies for desirable fish species (especially threatened native species) should focus on the reproductive requirements of those species because returning the estuary to a more predictable condition (as much as estuaries are ever predictable) is unlikely in the immediate future. Fortunately, the tendency of native fishes to exhibit some degree of concordance in their abundances suggests that actions that benefit one species are likely to benefit others as well.

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