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PREDICTING THE MAGNITUDE OF TEMPORAL VARIATION IN YOUNG-OF-YEAR CLASS STRENGTH OF SURFPERCH (TELEOSTEI: EMBIOTOCIDAE)

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ABSTRACT. **–** Members of the fish family Embiotocidae (surfperches) are viviparous and give birth to fully-developed, non-dispersing juveniles. We explored: a) whether fluctuations in recruitment of young-of-year surfperches were similar among a series of shallow rocky reefs off Southern California, USA and b) whether spatial variation in recruitment fluctuations mapped onto spatial differences in the fluctuations of the local forage base on the reef. For both surfperches examined (black surfperch, *Embiotoca jacksoni*; striped surfperch, *E. lateralis*), recruitment varied comparatively little through time on some reefs while it fluctuated substantially on others. These fishes harvest invertebrate prey from specific benthic foraging microhabitats (algal turf for black surfperch; the red alga, *Gelidium robustum* for striped surfperch) and these microhabitats showed a range in dynamics among the reefs examined over a 12 year period. Inter-annual fluctuations in foraging microhabitat were a strong predictor of the extent to which the abundance of young-of-year surfperches fluctuated. However, the foraging microhabitat for black surfperch (algal turf) on a reef fluctuated independently of that for striped surfperch (*G. robustum*). As a consequence, the extent to which the abundance of young of one species of surfperch varied on a given reef was unrelated to that of its congener. These data show that: 1) the magnitude of temporal variation in year-class strength of reef-associated fishes was related to the magnitude of variation in the forage base; 2) reefs in close proximity can show a range in resource dynamics that can affect reproductive output and 3) the reproductive output even of closely-related species can fluctuate independently of each other on the same reef.

KEY WORDS. **–** Reef fish, *Embiotoca*, recruitment, resource dynamics, year-class strength.

INTRODUCTION

Subtidal marine reefs are subjected to considerable variation in environmental conditions that can influence the abundance and dynamics of reef-associated organisms such as benthic fishes. Moreover, there is growing interest in understanding how fishes will respond to disturbances and climate forcing (Holbrook et al., 1997; Jenkins, 2005). Many studies have explored spatial co-variation between attributes of reefs and of the associated fish assemblages (e.g., Sale & Dybdahl, 1975; Gladfelter et al., 1980; Anderson et al., 1981; Ogden & Ebersole, 1981; Choat & Ayling, 1987; Choat et al., 1988; Tolimieri, 1995; Caley & St. John, 1996; Ault & Johnson, 1998; Holbrook et al., 1990, 1993, 1994, 2000, 2002; Schmitt & Holbrook, 2000; Holbrook & Schmitt, 2003). In contrast, there have been comparatively few explorations of whether or how the temporal dynamics of reef resources impinge on the structure or dynamics of associated fishes (e.g., Ault & Johnson, 1998; Schmitt & Holbrook, 1990a; Holbrook & Schmitt, 2003). When these reef resources were explored, they tended to involve structural attributes of the environment that might serve as refuge space from predators (e.g., Hixon & Beets, 1989, 1993; Holbrook & Schmitt, 2002). For example, in a factorial experimental design, Syms & Jones (2000) examined the effects of altered physical structure, habitat complexity of the reef and different levels of pulsed mortality of fish on resilience of the community.

A critical reef resource that can fluctuate on a relatively fast time scale is the food supply of benthic fishes (e.g., Schmitt & Holbrook, 1986). With one exception, we know comparatively little about the demographic or population-level consequences of variation in the food supply of reef fishes. The exception concerns body growth as numerous studies have shown that the individual growth rate of fishes is plastic and can absorb some variation in per capita availability of prey (e.g., Doherty, 1982, 1983; Jones, 1984, 1987a, 1987b, 1988; Forrester, 1990; Anderson & Sabado, 1995; Booth, 1995, 2004). Fluctuations in food should also influence fecundity of individuals directly and thus, their recruitment (e.g., McCauley et al., 1990). However, this aspect is difficult to assess in reef fishes because most species produce dispersing larvae. Further, larval dispersal can remove local effects of variation in reproduction on a reef (Shulman, 1985). Surfperches of the family Embiotocidae offer an unparalleled opportunity to explore the effect of fluctuations in the food supply on demographic and population-level attributes because these species are viviparous and give birth to fully-developed, non-dispersing juveniles (Baltz, 1984). Since adult surfperch convert food to young that are born into the parental population, it may be possible to determine the extent to which fluctuations in food affect reproductive output (here estimated as young-of-year class strength) and recruitment dynamics for this type of life history.

Here we explore the influence of temporal variation in the forage base of two species of surfperches, the black surfperch (*Embiotoca jacksoni*) and the striped surfperch (*E. lateralis*) that co-occur on shallow rocky reefs off the Pacific coast of North America. These species consume small invertebrates such as amphipods from the benthic substrata (Schmitt & Coyer, 1982; Schmitt & Holbrook, 1984). The two species concentrate their foraging activities on different reef substrata: black surfperch primarily feed on crustaceans harbored in turf, a low-dimensional mixture of debris, colonial animals and turf algae, whereas striped surfperch harvest crustaceans on foliose algae, primarily from the red alga, *Gelidium robustum* (Holbrook & Schmitt, 1989, 1996). While the densities of surfperch prey contained in these foraging microhabitats can fluctuate substantially (Schmitt & Holbrook, 1986), observational and experimental evidence has shown that the abundance of black surfperch or striped surfperch on a reef is positively and strongly related to the amount of turf or *G. robustum* present (Holbrook et al., 1990, 1994). These foraging microhabitats are biogenic in nature and therefore possess dynamics of their own (Schmitt & Holbrook, 1990a; Holbrook et al., 1994). Much of the dynamics are caused by disturbances that range from the local (e.g., sea urchin grazing, storm wave exposure; Schmitt & Holbrook, 1990a) to large scales (e.g., climatic regime; Holbrook et al., 1997). Since the crustaceans that reside on turf and *G. robustum* are the food of these surfperches, these particular substrata represent a major component of the forage base of black and striped surfperches, respectively. This suggests that fluctuations in turf and *G. robustum* can potentially have substantial influences on local reproductive output and recruitment of young, thereby driving dynamics of local surfperch populations. As surfperches do not consume their foraging substrata, there is likely no direct feedback between surfperches on the abundance of either turf or *G. robustum.*

The purposes of this study were: (1) to evaluate whether inter-annual variation in the abundance of young-of-year surfperch on a reef is correlated with fluctuation in the cover of turf and *G. robustum* and (2) to determine the extent to which the dynamics of the forage base and young-of-year class strength of black and striped surfperches co-vary among reefs. As all of the reefs examined occur within a 15 km stretch of shore, the study also indicated whether reef populations behave independently or coherently at this spatial scale.

MATERIALS AND METHODS

Field work was conducted on a series of reefs along a 15 km stretch of Santa Cruz Island (34°05'N 119°45'W), which is located in the Santa Barbara Channel of Southern California, USA. Reefs consisted of algae-covered bedrock that sloped from above the tide mark to sand at ~ 12 m depth. At each reef, permanent 40 × 2 m horizontal band transects were established at the 3, 6 and 9 m depth contours. The transects delineated a rectangular shaped study site on each reef that was similar in area among the reefs sampled. Study sites were established at 6 reefs in 1982 and 5 additional reef sites were established in 1986. The data reported here were collected annually for a 12 year period beginning in 1982 (except for 1984 and 1985). Only reefs where young-of-year surfperch were observed were included in these analyses, which reduced the number of reefs to 9 for black surfperch and 8 for striped surfperch.

The number of young-of-year surfperch at each study site was estimated from visual counts along the permanent transects from August to September each year after the annual breeding season. Young-of-year surfperches are easily distinguished from older conspecifics by their size, morphology and behaviour and the newborn cohort was up to 3 months old at the time they were counted. Fish on transects were counted repeatedly over multiple days and the number of counts ranged between 4 and 8 after each breeding season. For each survey, the number of young-of-year for each species was summed across the transects to yield a site-wide estimate of young-of-year abundance and the number of young seen per survey within a year was calculated.

For the years when surfperch were counted, the percent cover of benthic substrata was also estimated within the study site of each reef using four 50 m lines per depth zone that were centered around the 3, 6 and 9 m fish transects. The substratum under 100 randomly selected points per line was identified (yielding N = 400 points per depth zone, per reef, per year). Previous work indicated that turf was the critical foraging microhabitat for black surfperch and the red alga *Gelidium robustum* was that for striped surfperch (Schmitt & Holbrook, 1986; Holbrook & Schmitt, 1989). To explore patterns of co-variation in the amount of variation in foraging habitats and young-of-year abundance, we calculated the temporal (inter-annual) variability in percent cover of these microhabitats separately for each reef sampled. Our main goal was to see if differences among reefs in the extent to which the forage microhabitat fluctuated were a good predictor of the spatial differences in the extent to which surfperch year-class strength varied among years. A secondary goal was to explore whether the two species of surfperches showed spatial coherence (i.e., same patterns among reefs) in the amount of temporal variation in the abundance of young-of-year. The measure of temporal variability used was the coefficient of variation (CV), which is the (standard deviation × 100) / mean. Similarly, temporal variability in the number of young-of-year of each surfperch was estimated, again using the CV, for each reef. To determine how well temporal variation in the forage base (turf or *G. robustum*) predicted the pattern of temporal variation in abundance of young-of-year, we regressed the CV for black surfperch or striped surfperch young for each site against the CV for turf or *G. robustum* at that reef. We also calculated the correlation between the CV for turf against the CV for *G. robustum* to explore spatial co-variation in the dynamic pattern of the foraging microhabitats. Finally, we calculated the correlation between CV in black surfperch young against that for striped surfperch young to explore whether there was spatial co-variation in the dynamic pattern of abundance of (locally produced) young-of-year among the reefs sampled.

RESULTS

Turf and *Gelidium robustum*, the foraging microhabitats for black surfperch and striped surfperch respectively, did not remain constant over the 12 years of the study. The difference between the maximum and minimum availability of these microhabitats, averaged across the reefs examined, was ~ two-fold for turf and ~ four-fold for *G. robustum*. The amount of temporal variability in these foraging microhabitats differed among the reefs, with some showing relatively little variability in the cover of turf or *G. robustum* while other reefs showed substantially greater fluctuation (Fig. 1). However, the degree to which turf fluctuated at a given site was independent of the magnitude of the temporal variability in *G. robustum* on that reef (r = - 0.09; P > 0.80).

For both surfperches, there was considerable variation among reefs in the magnitude of inter-annual variation in recruitment of young-of-year (Fig. 2a & 2b). The extent to which the abundance of young-of-year varied from year to year on a reef was positively related to the dynamics of their foraging microhabitat (Fig. 2a & 2b). The degree of fluctuation in turf predicted almost two-thirds of the among-reef variance in the amount of temporal variability in the abundance of young-of-year black surfperch (Fig. 2a) (r^2 = 0.64; P < 0.01). The amount of temporal variability in *G. robustum* predicted even more of the between-reef difference in temporal variability in abundance of young-of-year striped surfperch (Fig. 2b) (r^2 = 0.72; P < 0.01). However, there was no relationship between the two species in the degree of temporal variation in the abundance of their young on a reef (Fig. 3) (r = + 0.30; P > 0.40). Thus, while microhabitat and young-of-year dynamics were tightly coupled for each surfperch species, there was no spatial co-variation between the species.

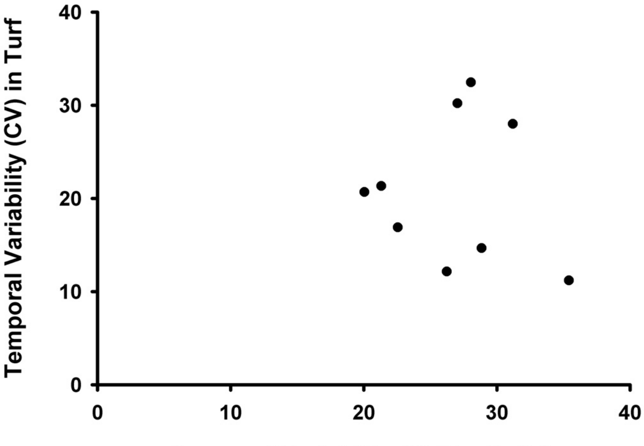

Fig. 1. The pattern of co-variation in magnitudes of temporal variability (measured by the coefficient of variation, CV), between turf and *Gelidium robustum*, the foraging microhabitats for black surfperch and striped surfperch respectively (correlation coefficient, r = - 0.09; P > 0.80). Each point represents a reef followed for either 8 or 12 years.

DISCUSSION

Understanding processes that influence abundance and dynamics of marine reef fishes has been a central focus in marine ecological research. Much effort has been devoted to understanding whether and if so, how local dynamics of reef fish are coupled to processes that occur in other locations, which reflect the fact that most species have dispersing larvae (Doherty, 1991). To the extent that the influence of variation in abundance of a reef resource on local dynamics of reef fishes has been explored, the main thrust has been to

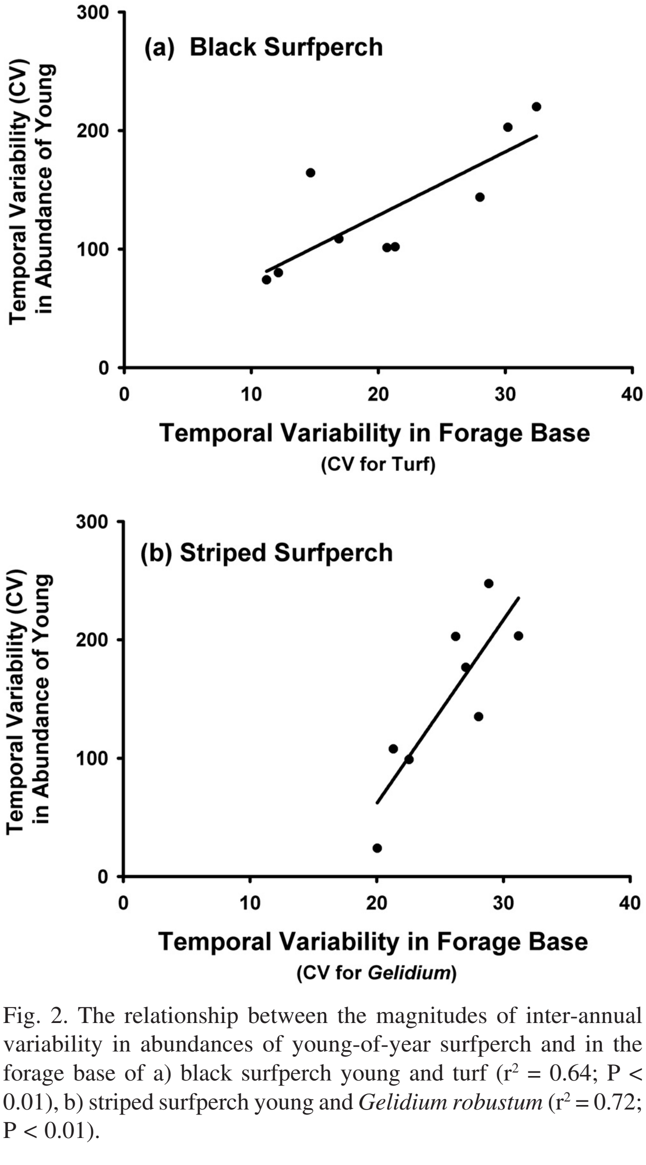

Fig. 2. The relationship between the magnitudes of inter-annual variability in abundances of young-of-year surfperch and in the forage base of a) black surfperch young and turf (r^2 = 0.64; P < 0.01), b) striped surfperch young and *Gelidium robustum* (r^2 = 0.72; P < 0.01).

understand the nature of loss rates after larval recruitment (see reviews by Hixon & Webster, 2002; Osenberg et al., 2002). Again, this reflects the notion that variation in mortality is expressed locally while that for fecundity probably is not (Shulman, 1985). As local populations typically are connected via exchange of reproductive output, local events that affect fecundity surely will be expressed 'downstream', giving rise to the need to consider metapopulation dynamics and connectivity (e.g., Armsworth, 2002). However, there is growing evidence of relatively localized retention of larval fishes (e.g., Jones et al., 1999), suggesting that local fecundity and local recruitment may not be as decoupled as once believed. Despite this relevance, little attention has been paid to whether and if so, how fluctuations of reef resources affect reproductive output and recruitment of marine reef fish. Further, there have been extremely few long-term studies that have simultaneously estimated demographic rates and resources in assemblages of marine reef fish, adding to the difficulties in evaluating this important but under-studied issue (Holbrook & Schmitt, 1996).

The surfperch system provides an excellent model to explore the link between the variability of reef resources and demographic and population-level responses since fecundity is expressed locally and newborn fish do not disperse from the parental population (Baltz, 1984). Our long-term study revealed that the degree to which the forage base on a reef fluctuated predicted around two-thirds of the inter-annual variation in recruitment of young-of-year surfperch (i.e., the greater the variation in the forage base of a reef, the more the abundance of young varied from year to year). While previously published experiments confirmed the importance of turf and *Gelidium robustum* to the local abundance of adult black and striped surfperches respectively (Holbrook et al., 1990, 1994), the present findings strongly suggest that the availability of these foraging microhabitats influences the production of young-of-year surfperches on a reef. Furthermore, there was considerable variation among the study sites in the dynamics of the forage base and hence, the production/recruitment of young surfperches. The spatial scale of this heterogeneity was highly localized as all reefs were situated along a 15 km stretch of the same shore.

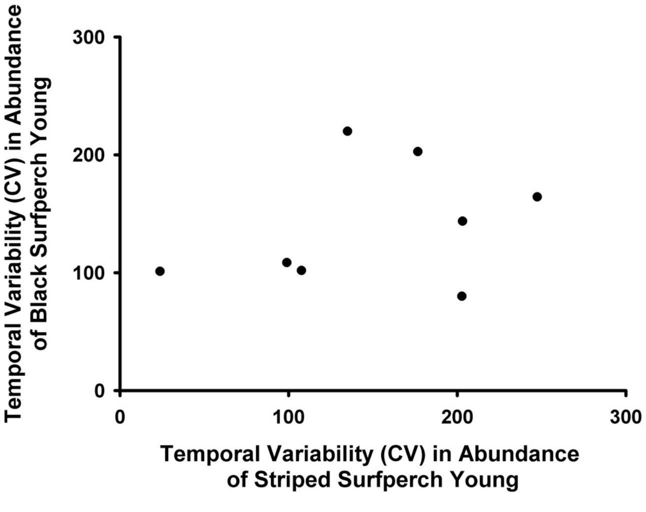

Fig. 3. The pattern of co-variation in magnitudes of inter-annual variability in abundances of black surfperch and striped surfperch young-of-year (correlation coefficient, r = 0.30; P > 0.40).

The current study further revealed that the different forage bases of the two surfperch species varied independently among the sites. As a result, recruitment dynamics of the co-occurring surfperches were also independent. Given that these species of fish compete with one another (Hixon, 1980; Schmitt & Holbrook, 1986, 1990b), the independent responses to environmental fluctuations may be a mechanism that helps promote their coexistence (Chesson, 1994, 2000a, 2000b). At the very least, the results imply that the local dynamics of these surfperch species need not be similar.

The results reported here may provide insights into the species of reef fishes that have a more typical life history where dispersing larvae are produced. In these cases, the demographic or population-level consequences of a fluctuating food supply may not be easily discerned. Since mature fish convert food to reproductive products, fluctuations in the supply of food over an appropriate time scale should not only affect individual growth rates (Anderson & Sabado, 1995), but should also produce temporally-varying, size-specific fecundity relationships. Furthermore, the surfperch system revealed considerable asynchrony in resource dynamics over relatively short distances. While connectivity and retention are now being included as potentially important aspects in metapopulation models of reef fishes (e.g., Armsworth, 2002), resource dynamics and its effect on fecundity also need to be incorporated, if we are to fully understand effects of environmental fluctuations on reef fishes.

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