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Abstract: Fisheries that target fish spawning aggregations can exhibit hyperstability, in which catch per unit effort (CPUE) remains elevated as stock abundance declines, but empirical support is limited. We compiled several fishery-dependent and fishery-independent data sets to assess stock trends in the barred sand bass (*Paralabrax nebulifer*) and the kelp bass (*Paralabrax clathratus*) in southern California, USA, evaluate the interaction between spawning aggregations and fishing activities, and test for hyperstability. Annual and seasonal trends from fisheries and population data indicate that regional stocks of both species have collapsed in response to overfishing of spawning aggregations and changes in environmental conditions. The aggregating behavior of fish and persistent targeting of spawning aggregations by recreational fisheries combined to produce a hyperstable relationship between CPUE and stock abundance in both species, which created the illusion that population levels were stable and masked fishery collapses. Differences in the rate of decline between the two species may be related to the size, duration, and spatial distribution of their spawning aggregations. Results of this study provide empirical evidence of hyperstability in aggregation-based fisheries and demonstrate that CPUE data be used with caution and given low weight when fishery-independent data are available.

Résumé : Les pêches commerciales qui ciblent les rassemblements de fraie des poissons peuvent présenter une hyperstabilité, dans laquelle la capture par unité d’effort (CPUE) reste élevée pendant que l’abondance du stock diminue; il n’existe cependant que peu de données empiriques pour prouver l’existence de ce phénomène. Nous avons compilé plusieurs ensembles de données reliées aux pêches et indépendantes de la pêche pour évaluer les tendances des stocks chez le serran farlot (*Paralabrax nebulifer*) et le serran des algues (*Paralabrax clathratus*) dans le sud de la Californie, É.-U., pour mesurer les interactions entre les rassemblements de fraie et les activités de pêche et pour tester l’hyperstabilité. Les tendances annuelles et saisonnières dans les données de pêche et les données démographiques indiquent que les stocks régionaux des deux espèces se sont effondrés à cause de la surpêche dans les rassemblements de fraie et à cause des changements dans les conditions du milieu. La combinaison du comportement de rassemblement des poissons et du ciblage persistant des rassemblements de fraie par les pêcheurs sportifs produit une relation hyperstable entre CPUE et l’abondance du stock chez les deux espèces; cela a créé l’illusion que les niveaux de population étaient stables et a masqué l’effondrement de la pêche. Les différences dans le taux de déclin entre les deux espèces peuvent être reliées à la taille, la durée et la répartition spatiale de leurs rassemblements de fraie. Les résultats de notre étude fournissent des données empiriques qui prouvent l’existence d’une hyperstabilité dans les pêches basées sur les rassemblements et démontrent que les données de CPUE doivent être utilisées avec prudence et qu’on doit leur donner une importance réduite lorsqu’il existe des données indépendantes de la pêche.

[Traduit par la Rédaction]

Introduction

Fishery-dependent proxies such as catch per unit effort (CPUE) are assumed to be proportional to population size and are regularly employed to diagnose stock condition (Quinn and Deriso 1999). However, CPUE may not accurately reflect changes in abundance, because the relationship between these two parameters is often disproportional and nonlinear (Bannerot and Austin 1983; Harley et al. 2001). One common form of disproportionality involves hyperstability (Hilborn and Walters 1992), in which CPUE remains

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stable while true abundance declines, leading to an overestimation of biomass and underestimation of fishing mortality (Crecco and Overholtz 1990). The relationship between CPUE data and stock abundance is dependent upon the spatial and temporal distribution of fish and the allocation and type of fishing effort, such that both fish and fisher behavior can lead to hyperstability (Harley et al. 2001; Post et al. 2002; Salthaug and Aanes 2003).

Fisheries that target fish spawning aggregations (i.e., temporary gatherings of conspecific fish that form for the purpose of reproduction; Colin et al. 2003) are thought to exhibit hyperstability (Sadovy de Mitcheson and Erisman 2011). Aggregations tend to occur at predictable and specific sites and times, and the high concentration of fish contained in such gatherings serve as easy opportunities for fishers to harvest large amounts of fish quickly and with little effort (Sadovy de Mitcheson et al. 2008). Consequently, CPUE can remain high or even increase as true population abundance declines if fishers are capable of repeatedly locating aggregations and exploiting them (Rose and Kulka 1999; Walters 2003). The result is an “illusion of plenty”; the stock is presumed to be healthy, fishing activities continue unabated, and no management actions are taken until both the fishery and the population collapse (Post et al. 2002). Hyperstability has been demonstrated in only a few species that form spawning aggregations (e.g., *Gadus morhua*, *Hoplostethus antlanticus*), because coincident, long-term CPUE and fishery-independent data of stock abundance for the same aggregation fishery are rare (Clark 2001; Harley et al. 2001; Sadovy and Domeier 2005).

Barred sand bass (*Paralabrax nebulifer*) and kelp bass (*Paralabrax clathratus*) have comprised the two most important marine recreational fisheries of southern California, USA, for the last three decades (Dotson and Charter 2003; Jarvis et al. 2004; Love 2006), and both species form seasonal spawning aggregations that are heavily exploited by recreational fishers (Love et al. 1996*a*; Erisman and Allen 2006). Owing to their exclusion from commercial fishing, high annual catches from the 1970s through the mid-1990s, and the dominance of multiple age classes of adult fish in catch reports, both fisheries were long deemed as sustainable (Love et al. 1996*a*). However, catch and CPUE for both species have declined considerably since the late 1990s (Dotson and Charter 2003; Sweetnam 2010).

In this study, recreational fishery data and two sets of fishery-independent data were compiled to analyze seasonal and long-term fishery and population trends for barred sand bass and kelp bass in southern California. We evaluated the relationship between the timing of spawning aggregations and fishing activities for both species to assess the potential effects of fishing aggregations on stock condition. We then compared coincident time series of CPUE and fishery-independent estimates of population abundance to test for hyperstability, which we hypothesized to result from the aggregating behavior of fish and the targeting of aggregations by recreational fishers.

Materials and methods

Species information

In southern California, barred sand bass are most abundant in small groups over inshore, low-relief areas and ecotone habitats adjacent to reefs (Mason and Lowe 2010; Jarvis et al. 2011). Adults form large spawning aggregations of several thousand fish over offshore sand flats from June through August (Turner et al. 1969; Allen and Hovey 2001*a*). Kelp bass inhabit kelp beds, rocky reefs, and other nearshore habitats with high structural relief (Young 1963; Quast 1968). Adults spawn within aggregations of tens to several hundred fish on kelp beds and rocky reefs from May to September but also form aggregations of 50 or more fish during nonspawning periods (Quast 1968; Erisman and Allen 2006). Males and females of both species become sexually mature at 22–24 cm in total length (TL) and 2–4 years of age (Love et al. 1996*b*).

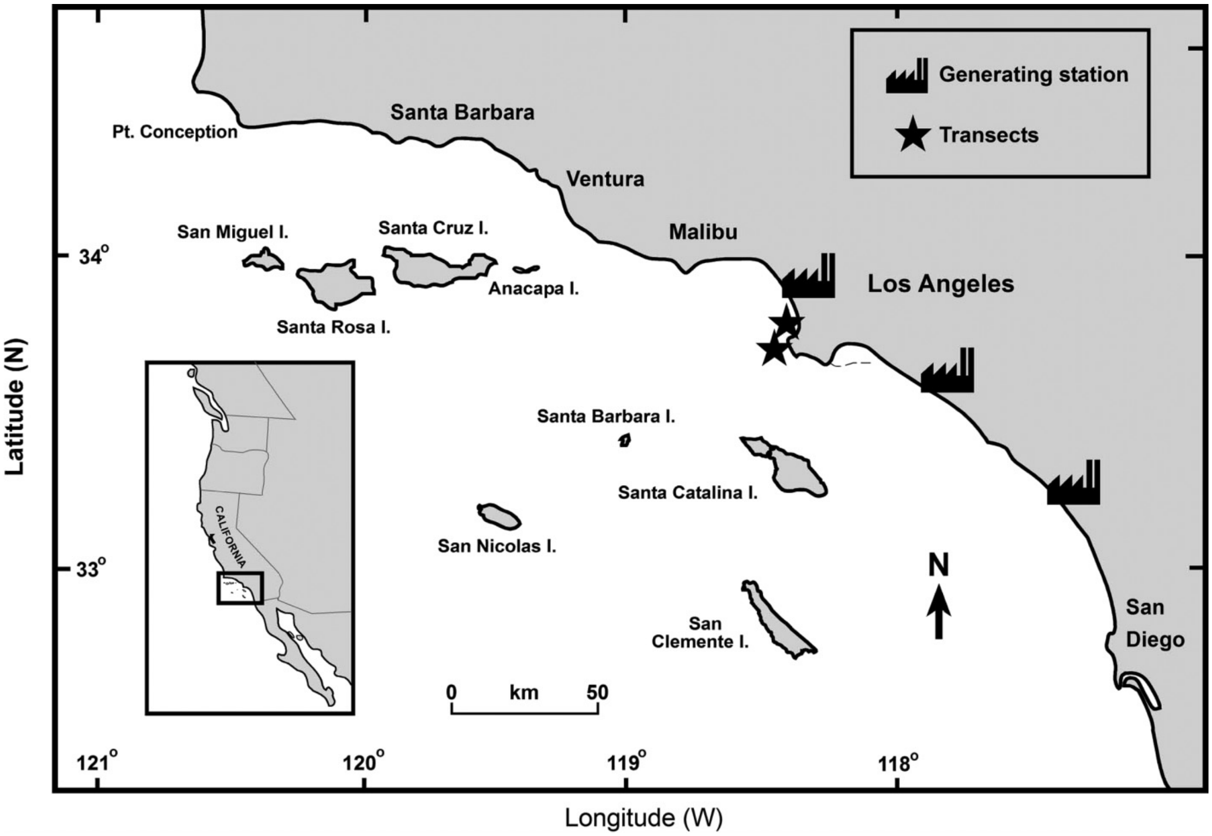
Barred sand bass and kelp bass are exploited exclusively by recreational fisheries in southern California, as commercial harvest bans were enacted in 1953 because of concerns about population and fishery declines (Young 1963). There are three species of *Paralabrax* (*P. nebulifer*, *P. clathratus*, and *P. maculatofasciatus*) in the region, which have been managed collectively by a 10-fish daily bag limit and a 12 inch (1 inch = 2.5 cm) minimum size limit since 1959 (Allen and Hovey 2001*a*, 2001*b*). Together, barred sand bass and kelp bass rank as the most important recreational fishery in southern California in terms of the number of fish taken by commercial passenger fishing vessel (CPFV) fisheries since 1959 (Dotson and Charter 2003). Individually, they rank as the second (kelp bass) and fourth (barred sand bass) most important species in terms of total catch of all recreational marine fisheries in the region since 1980 (Jarvis et al. 2004), and both have tallied the highest catch of any species taken by the CPFV fleet on numerous years during that period (Allen and Hovey 2001*a*, 2001*b*; Love 2006).

Fisheries data

We used monthly catch and effort data of the CPFV fleet from two databases to assess temporal trends in the recreational fishery of both species from 1963 to 2008 in southern California. Data from 1963 to 2003 were from an electronic database of the Los Angeles Times (http://swfscdata.nmfs.noaa.gov/Latimes/), and data from 2004 to 2008 were from the California Recreational Fisheries Survey (CRFS) database (http://data.recfin.org/forms/est2004.html). The databases were deemed compatible, because CRFS data were gathered from official CPFV logbook records maintained by the California Department of Fish and Game, and previous studies have shown a significant correlation ($r^2 = 0.85$; $p < 0.01$) between daily catch reports from CPFV logbook records and daily CPFV catch reports of the Los Angeles Times for these species (Hill and Barnes 1998; Dotson and Charter 2003).

We compiled catch and effort data for both *Paralabrax* species for all months from 1963 to 2008 and for the entire Southern California Bight. Catch was recorded as the number of fish landed or discarded, effort was recorded as number of angler trips, and CPUE was calculated as number of fish caught per angler trip. Data were restricted to catch and effort for the CPFV fleet because (*i*) data available for the entire recreational fishery (see http://www.recfin.org) were considered unreliable (Jarvis et al. 2004) and did not provide monthly data prior to 2003; and (*ii*) data collection methods for non-CPFV fishing activities for the two databases were different and incompatible (http://data.recfin.org/forms/est2004.html).

Fig. 1. Map of the Southern California Bight, showing the location of entrapment (generating stations) and underwater visual census sites (inset shows location of study region on USA west coast).



Data prior to 1963 were excluded because of gaps and inconsistencies in reporting (Dotson and Charter 2003). We estimated the mean proportion of annual CPFV catch taken from spawning aggregations by summing the mean total catch recorded during spawning months, because both species form aggregations that persist throughout their spawning seasons (Turner et al. 1969; Erisman and Allen 2006).

Fisheries-independent data

Two sets of fisheries-independent data were used to approximate trends in population abundance of either species within the Southern California Bight (Fig. 1): entrapment surveys (1980–2008) and underwater visual censuses (1974–2008). Electrical generating stations utilizing once-through cooling systems occur along the southern California coastline and entrain a wide variety of fishes in their cooling waters during normal operating activities. We obtained data on the abundance, masses, and lengths collected during routine entrapment surveys at three electrical generating stations (El Segundo, Huntington Beach, San Onofre) in the region from 1980 to 2008 (Miller et al. 2009; Field et al. 2010). Among the three plants, an average of 37 surveys per year and a total of 1086 surveys were conducted during the 29-year period. The entrapment rate was derived to standardize across differences in cooling water flow among power plants and years. Entrapment data were used to estimate fish biomass per unit water volume circulated and calculate annual means of fish biomass (kg·10^6 m^{-3}).

Underwater visual censuses of adult (≥25 cm TL) kelp bass conducted at two rocky reef sites (King Harbor breakwater, Palos Verdes Point) in southern California from 1974 to 2008 were used to assess long-term trends in abundance. Fish abundance at these sites has been surveyed quarterly using SCUBA continually since 1974 following standard band-transect methodology described in previous studies (Stephens et al. 1984; Pondella et al. 2002). Thirty-four replicate transects were attempted per quarter at King Harbor and 12 per quarter at Palos Verdes Point. From 1974 through 2008, 4797 transects (median = 135 per year) were completed at King Harbor, and 1475 transects (median = 44 per year) were completed at Palos Verdes Point. Fish density (number of fish·100 m^{-2}) was used to approximate abundance, and mean annual density was calculated for both sites for all years. Data on barred sand bass from these two sites were excluded, because neither site is the primary habitat of adult barred sand bass (i.e., ecotone habitat and offshore sand flats).

We assumed that entrapment surveys were sufficient to approximate population abundance in both species, since these data have been used in numerous studies (e.g., Brooks et al. 2002; Jarvis et al. 2004; Miller et al. 2009) to assess population trends in *Paralabrax* and other coastal marine fishes in southern California. Similarly, we assumed that underwater visual census data provided useful estimates of population abundance in kelp bass, since these data were collected in the known adult habitat and have been used repeatedly to assess population trends in this species (e.g., Stephens et al. 1984; Love et al. 1996*b*). Since entrapment surveys targeted fish slightly smaller than average size of sexual maturity (22–24 cm TL; Love et al. 1996*b*) in both barred sand bass (mean = 18.6 ± 0.6 cm TL) and kelp bass (mean = 19.2 ±

Table 1. Annual trends in fishing effort by the commercial passenger fishing vessel (CPFV) fleet and fisheries and populations of barred sand bass and kelp bass in southern California from 1963 to 2008.

Data set	*n*	AR	*z*	*p*
CPFV fishing effort, 1995–2008	14	0.92	–2.41	0.008
Barred sand bass catch, 2000–2008	9	0.97	34.00	<0.001
Barred sand bass CPUE, 2000–2008	9	0.91	28.00	<0.001
Barred sand bass entrapment biomass, 1980–2008	29	0.82	–4.96	<0.001
Kelp bass catch, 1963–2008	36	0.99	–4.98	<0.001
Kelp bass CPUE, 1963–2008	36	0.96	–7.25	<0.001
Kelp bass entrapment biomass, 1980–2008	29	0.78	–5.32	<0.001
Kelp bass density (King Harbor), 1980–2008	29	0.97	–4.92	<0.001
Kelp bass density (Palos Verdes), 1980–2008	29	0.95	–3.63	<0.001

Note: AR, autoregression statistic; *n*, number of years.

0.5 cm TL), it is possible they provided biased estimates of population size. Therefore, we tested their compatibility with underwater visual census data of adult kelp bass using correlation analyses (see below).

Statistical analyses and tests for hyperstability

Because of significant first-order autocorrelations, annual trends in barred sand bass and kelp bass fisheries and population abundance were analyzed using Box–Jenkins autoregressive integrated moving average (ARIMA) modeling plus Mann–Kendall test for trend analysis. A one-way analysis of variance (ANOVA) was used to test for differences in catch and effort among months. Where significant relationships were found, post hoc multiple comparisons were done using Student–Newman–Keuls tests to identify peaks in catch and CPUE. All data were log-transformed to satisfy the assumptions of parametric analyses (Sokal and Rohlf 1995).

We tested for hyperstability in both species by comparing fisheries-dependent CPUE data to fisheries-independent data on population abundance. Using the standard power curve model and following the notation of Harley et al. 2001, the catch–effort relationship is modeled by

$$(1) \qquad U_t = qN_t^{\beta}$$

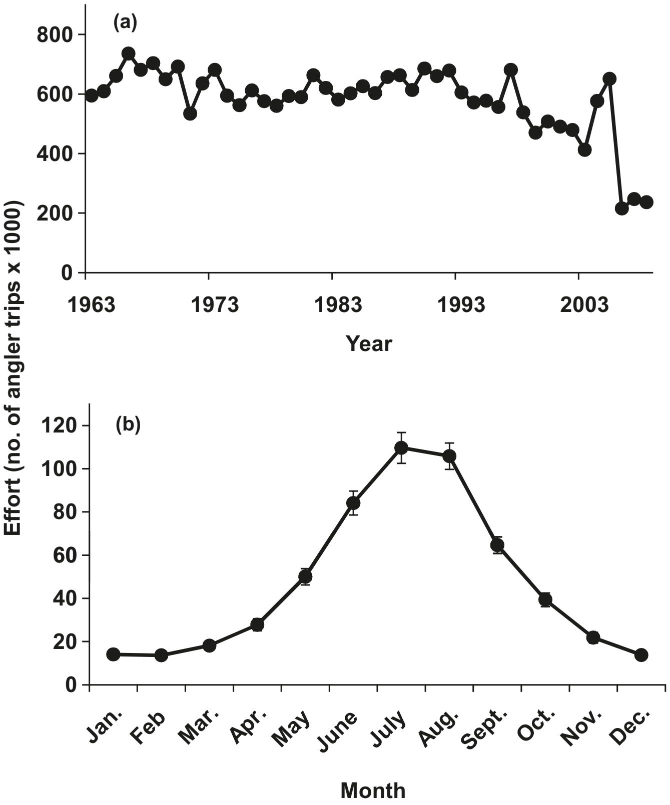
where U_t is the observed CPUE, q is the catchability coefficient, N_t is the fishery-independent estimate of true population abundance, and β is the hyperstability parameter. Taking logs of the function above yields

$$(2) \qquad \log(U_t) = \log(q) + \beta \log(N_t)$$

This specification permits using regression analysis to estimate the parameter β and test its value against the null hypothesis that $\beta \geq 1$. Hyperstability is present when a one-tailed *t* test determines that β is significantly less than one. When $\beta < 1$, the curve becomes convex such that CPUE declines at a much slower rate than abundance at moderate to high population sizes but declines faster than abundance at low population sizes. Since our data contains estimation error in the both the dependent and the independent variables (log CPUE estimates and log field counts, respectively), we used reduced major axis regression to estimate the values of β.

For kelp bass, we also tested for correlation among the three fishery-independent data sets, and as the independent variables were significantly correlated, we used the first principal component axis of all three data sets as our pooled predictor (the significance of the procedure was tested by comparing the variance explained by the first principal axis against the maximum expected variation predicted by a "broken stick" distribution; see Jackson 1993). Using reduced major axis regression, we estimated β for the pooled data by regressing the log-transformed CPUE data to the log-transformed principal component.

Fig. 2. Annual (*a*) and mean monthly (*b*) trends in fishing effort by the commercial passenger fishing vessel (CPFV) fleet in southern California from 1963 to 2008. Vertical bars indicate standard error.



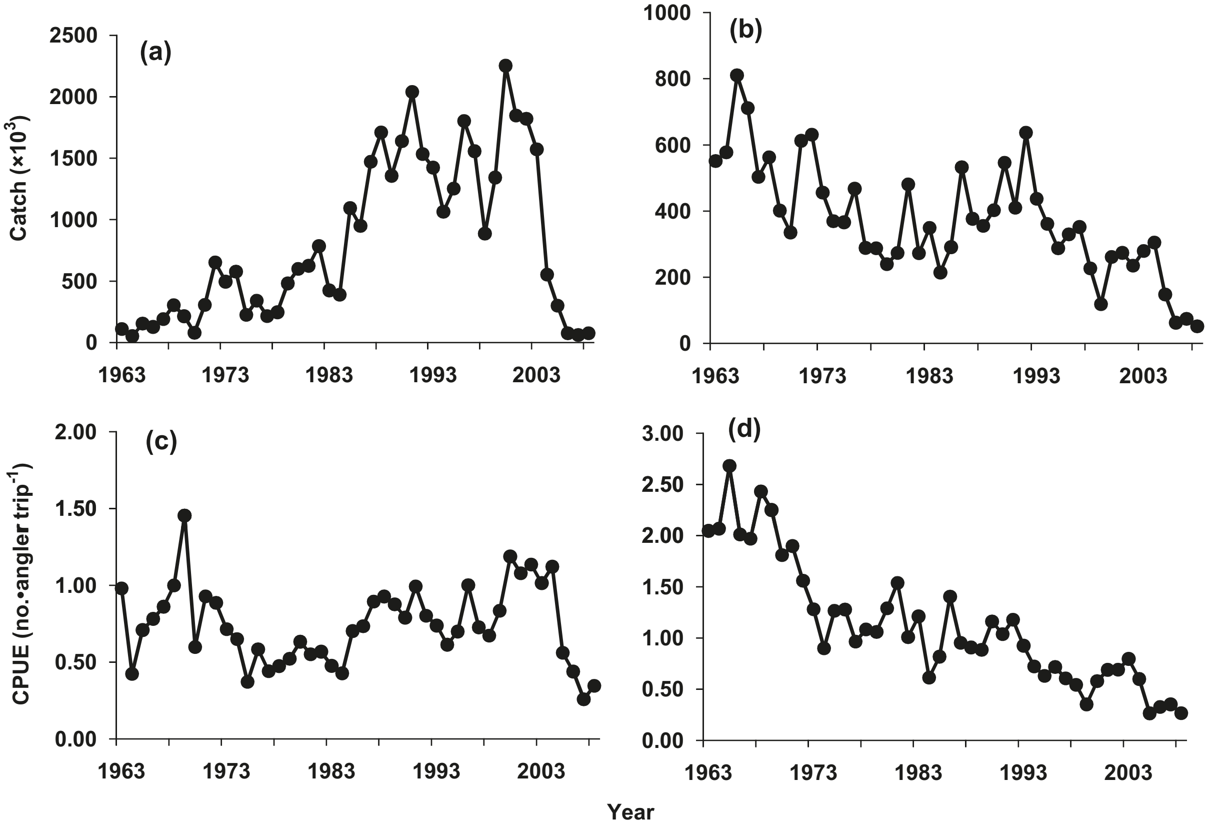
Results

Fishing effort by the CPFV fleet was relatively stable over the first 32 years of the time series, but a significant downward trend occurred from 1995 to 2008 (Table 1; Fig. 2). Differences in mean monthly fishing effort by the CPFV fleet from 1963 to 2008 were significant (Table 2; Fig. 2), with

Table 2. Monthly trends in fishing effort by the CPFV fleet and fisheries of barred sand bass and kelp bass in southern California from 1963 to 2008.

Data set	df (month)	df (error)	*F*	*p*
CPFV fishing effort, 1963–2008	11	539	84.20	<0.001
Barred sand bass catch, 1963–2008	11	539	46.60	<0.001
Barred sand bass CPUE, 1963–2008	11	539	41.62	<0.001
Kelp bass catch, 1963–2008	11	539	78.96	<0.001
Kelp bass CPUE, 1963–2008	11	539	7.24	<0.001

Fig. 3. Annual catch and catch per unit effort (CPUE) for barred sand bass and kelp bass in southern California from 1963 to 2008: (*a*) annual catch in barred sand bass; (*b*) annual catch in kelp bass; (*c*) annual CPUE in barred sand bass; (*d*) annual CPUE in kelp bass.



effort highest from June to August ($p < 0.001$). Annual catch for barred sand bass increased from 1963 to 1991, fluctuated until 2001, and declined sharply from 2002 to 2008 (Fig. 3). CPUE was relatively constant from 1963 to 2003 but decreased rapidly thereafter. Changes in annual catch and CPUE for barred sand bass were not significant from 1963 to 2008; however, both catch and CPUE decreased significantly from 2000 to 2008 (Table 1). Kelp bass catch and CPUE both decreased significantly from 1963 to 2008 (Table 1; Fig. 3).

Biomass of barred sand bass and kelp bass estimated from entrapment surveys both declined significantly from 1980 to 2008 (Table 1; Fig. 4). The mean annual density of kelp bass from underwater visual censuses increased in the late 1970s at both sites, peaking at 13.5 fish·100 m^{-2} at King Harbor in 1981 and at 14 fish·100 m^{-2} at Palos Verdes in 1979 (Fig. 4). Following these peaks, a significant negative trend over time was observed at King Harbor from 1980 to 2008 and Palos Verdes from 1980 to 2008. Kelp bass abundance also displayed a strong correlation between the two census sites (Table 3).

Between 1963 and 2008, mean monthly catch and mean monthly CPUE of barred sand bass were significantly higher during the spawning months from June to August ($p < 0.001$) than in other months (Table 2; Fig. 5). This equated to a mean of 80.6% of the total annual catch harvested during spawning aggregation periods. However, a marked decrease in the summer peak in CPUE occurred after 2004. Differences in mean monthly catch of kelp bass were significant from 1963 to 2008 (Table 2; Fig. 5). Peak catch for kelp bass occurred during the spawning season of May to September ($p < 0.001$), which summed to equal 79.8% of total annual catch. Differences in mean monthly CPUE for kelp bass were also significant, with peak values occurring during May to August ($p < 0.01$), although less pronounced than for barred sand bass and markedly reduced after 2004.

Annual and monthly trends in these data establish the decline of regional fisheries and populations of barred sand and kelp bass and provide evidence that persistent targeting of spawning aggregations contributed to the declines. The

Fig. 4. Annual population trends for barred sand bass and kelp bass as estimated from entrapment surveys (1980–2008) and underwater visual censuses (1974–2008): (*a*) biomass of barred sand bass from entrapment surveys; (*b*) biomass of kelp bass from entrapment surveys; (*c*) density of adult kelp bass from underwater visual censuses at King Harbor; (*d*) density of adult kelp bass from underwater visual censuses at Palos Verdes. Vertical bars indicate standard error.

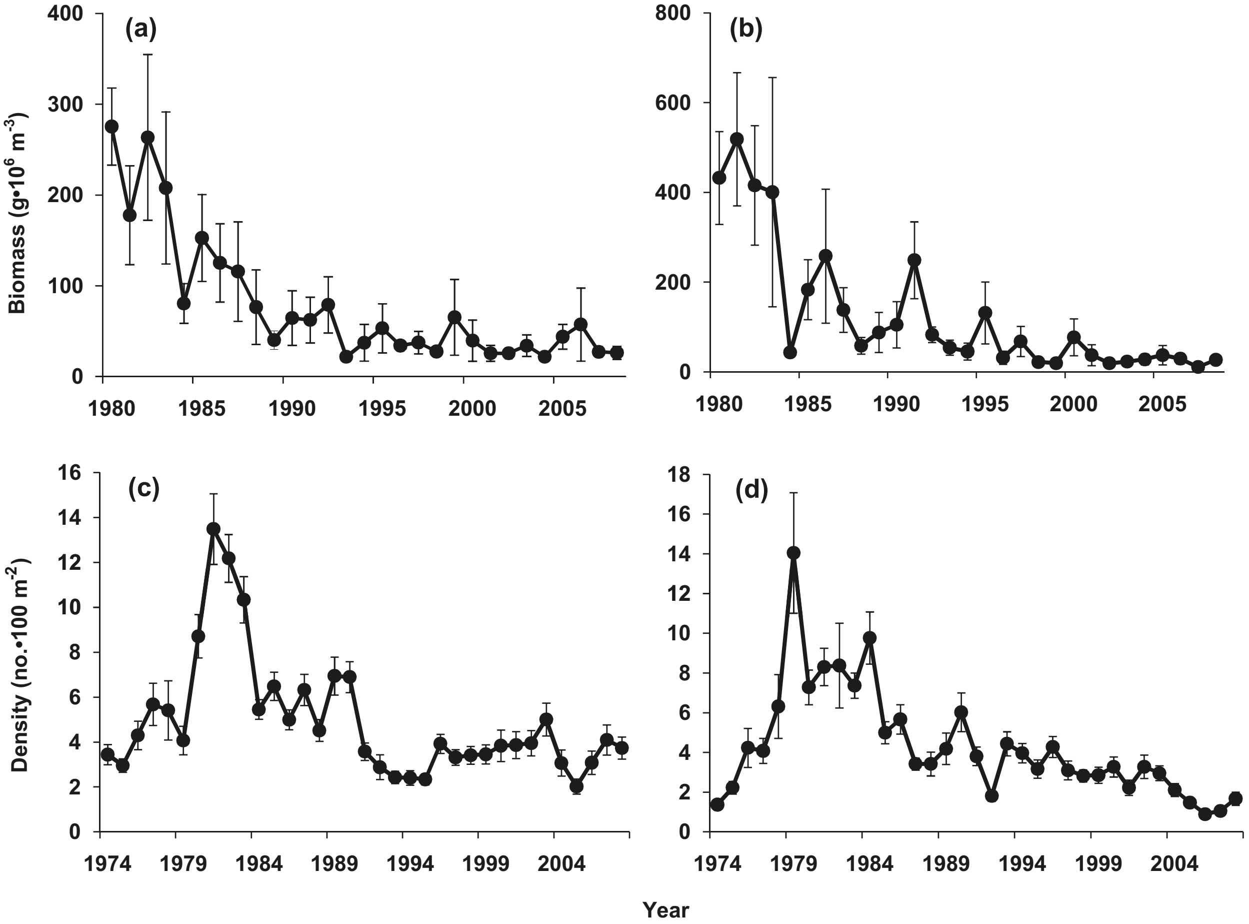


Table 3. Summary of results from correlation analyses of fisheries-independent data sets on population abundance of kelp bass in Southern California.

Data set	*n*	*r*	*t*	*p*
Density (King Harbor) vs. density (Palos Verdes), 1974–2008	33	0.65	3.78	<0.001
Density (King Harbor) vs. entrapment biomass, 1980–2008	29	0.84	7.86	<0.001
Density (Palos Verdes) vs. entrapment biomass, 1980–2008	29	0.70	4.91	<0.001

remainder of our analysis demonstrates hyperstability was present in these fisheries, and therefore, CPUE data were insufficient to track the status of either stock. In the case of the kelp bass, all three fishery-independent variables were significantly correlated (Table 3). As a result, we combined these three variables into a first principal component axis that summarized 84.6% of the variation in the complete data set (a significant axis according to the broken stick distribution test). We also found a significant relationship between the log-transformed CPUE data and the log-transformed data of the principal component axis (Table 4). The relationship was similar to that of the individual variables (nonlinear and convex in shape; Fig. 6), and produced a beta value of 0.459, indicating hyperstability.

For barred sand bass, log-transformed CPUE data were uncorrelated with log-transformed data from entrapment surveys (Table 4), meaning that as the entrapment numbers have declined, CPUE has remained constant, particularly at moderate and high population abundance levels (Fig. 6). The lack of correlation between CPUE and stock data is an extreme form of hyperstability; CPUE data for the barred sand bass provided no signal of the decline of the fish stock for the majority of the sample period. Only in recent years, after 2003, have CPUE values seriously declined.

Discussion

Barred sand bass and kelp bass stocks in southern California have collapsed, based on the criteria set by several organizations and fisheries studies (Hutchings 2001; Worm et al. 2006; FAO 2009). The biomass of barred sand bass and kelp bass from entrapment surveys has decreased by 90% or more since 1980, and kelp bass densities from visual surveys have declined by 79% over the same time period.

Fig. 5. Mean monthly catch and catch per unit effort (CPUE) trends for barred sand bass and kelp bass in southern California from 1963 to 2008: (*a*) catch of barred sand bass; (*b*) catch of kelp bass; (*c*) CPUE of barred sand bass; (*d*) CPUE of kelp bass.

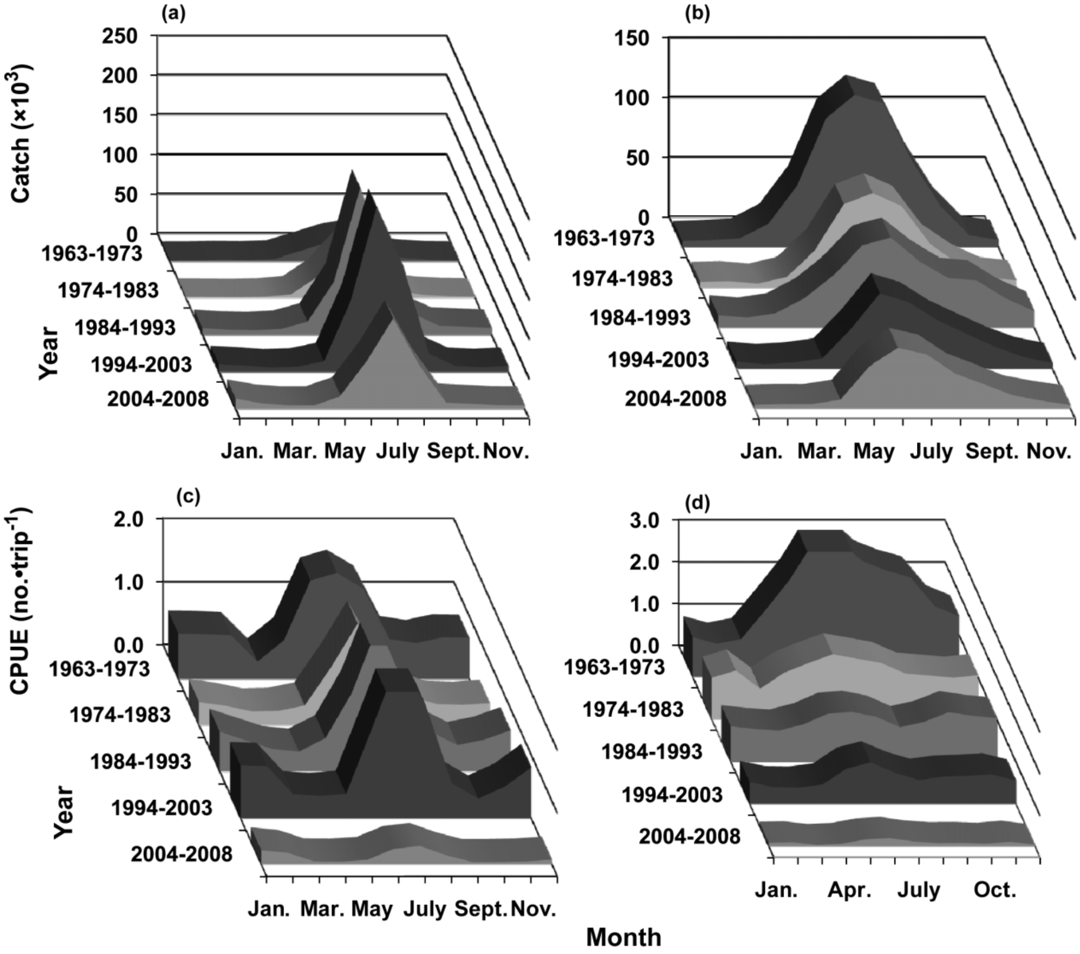


Table 4. Summary of results from reduced major axis regressions and hypothesis tests for hyperstability.

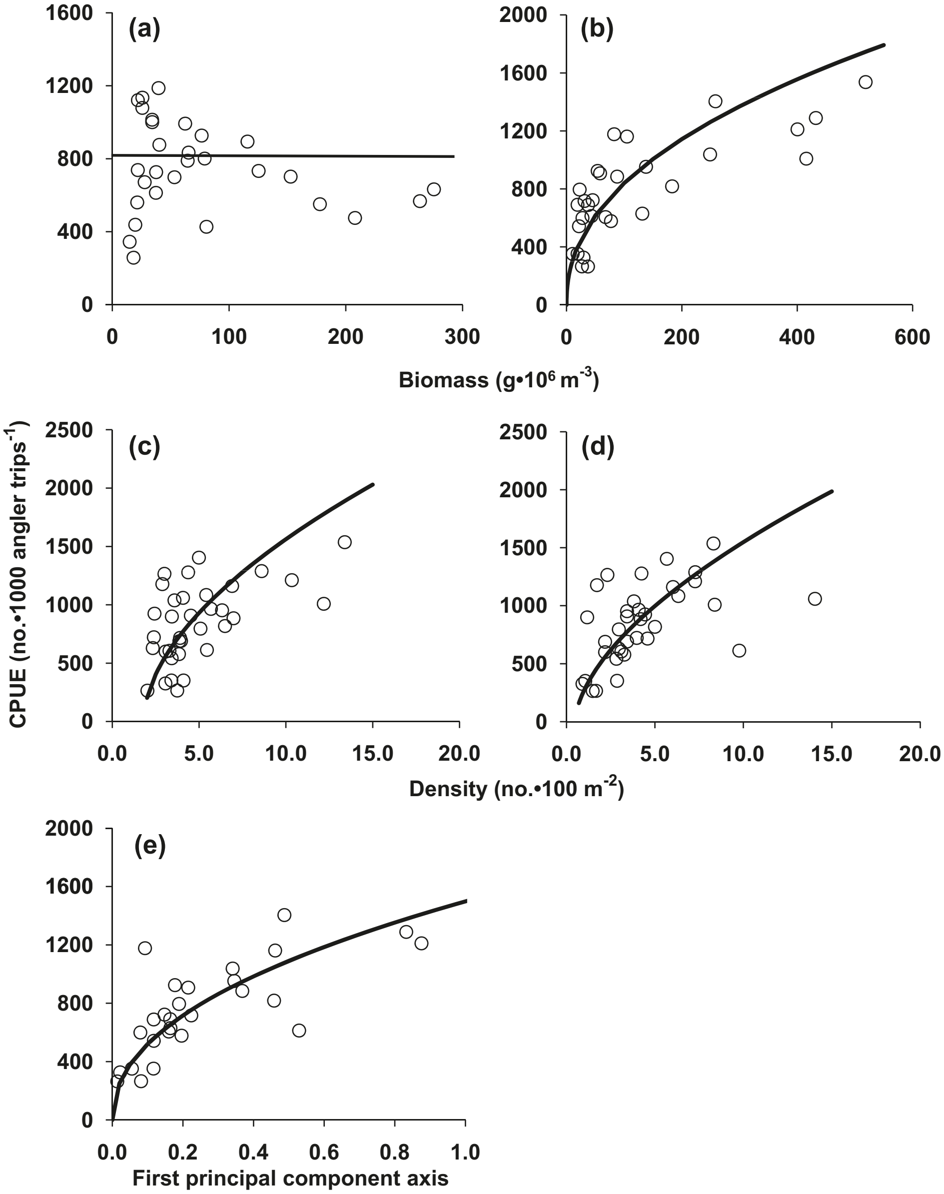
							H_0: $\beta = 1$	
Data set	*n*	r^2	*p*	α	β	SE (β)	*t*	*p*
Barred sand bass								
CPUE vs. entrapment biomass, 1980–2008	29	0.00	0.99	—	—	—	—	—
Kelp bass								
CPUE vs. entrapment biomass, 1980–2008	29	0.56	<0.001	4.69	0.44	0.06	9.81	<0.001
CPUE vs. density (King Harbor), 1974–2008	33	0.27	<0.001	5.13	0.55	0.08	5.51	<0.001
CPUE vs. density (Palos Verdes), 1974–2008	33	0.39	<0.001	5.72	0.59	0.08	5.17	<0.001
CPUE vs. first principal axis, 1974–2008	29	0.66	<0.001	7.31	0.46	0.05	10.51	<0.001

Note: Dashes (—) indicate no data exist, because the reduced major axis regression did not produce a significant relationship.

Recreational catch and CPUE of barred sand bass decreased 97% and 70%, respectively, from 2000 to 2008. Kelp bass catch has declined 95% since a peak in catch was recorded in 1965, and CPUE has declined by 90% over that period. The current collapse of *Paralabrax* fisheries in southern California is not surprising, since peaks in recreational catch exceeded earlier peaks in commercial catch that resulted in a commercial closure in 1953 (Young 1963). Moreover, the trends observed in *Paralabrax* have been reported for several other recreational fisheries in southern California and thus point to a general decline of the sport fishing industry in the region (Dotson and Charter 2003; Sweetnam 2010).

The combined evidence from this study indicates that persistent overfishing of seasonal spawning aggregations by recreational fisheries brought about the collapse of barred sand bass and kelp bass stocks in southern California. Both species aggregate to spawn during the summer months, which coincides with the peak season of the CPFV fishery in southern California. The CPFV has long targeted spawning aggregation sites for barred sand bass and kelp bass, because they occur at the same locations and during the same months each year and thus are viewed as easy opportunities for novice anglers to catch large numbers of fishes (Love et al. 1996*a*). Daily catch by single vessels can be immense during aggre-

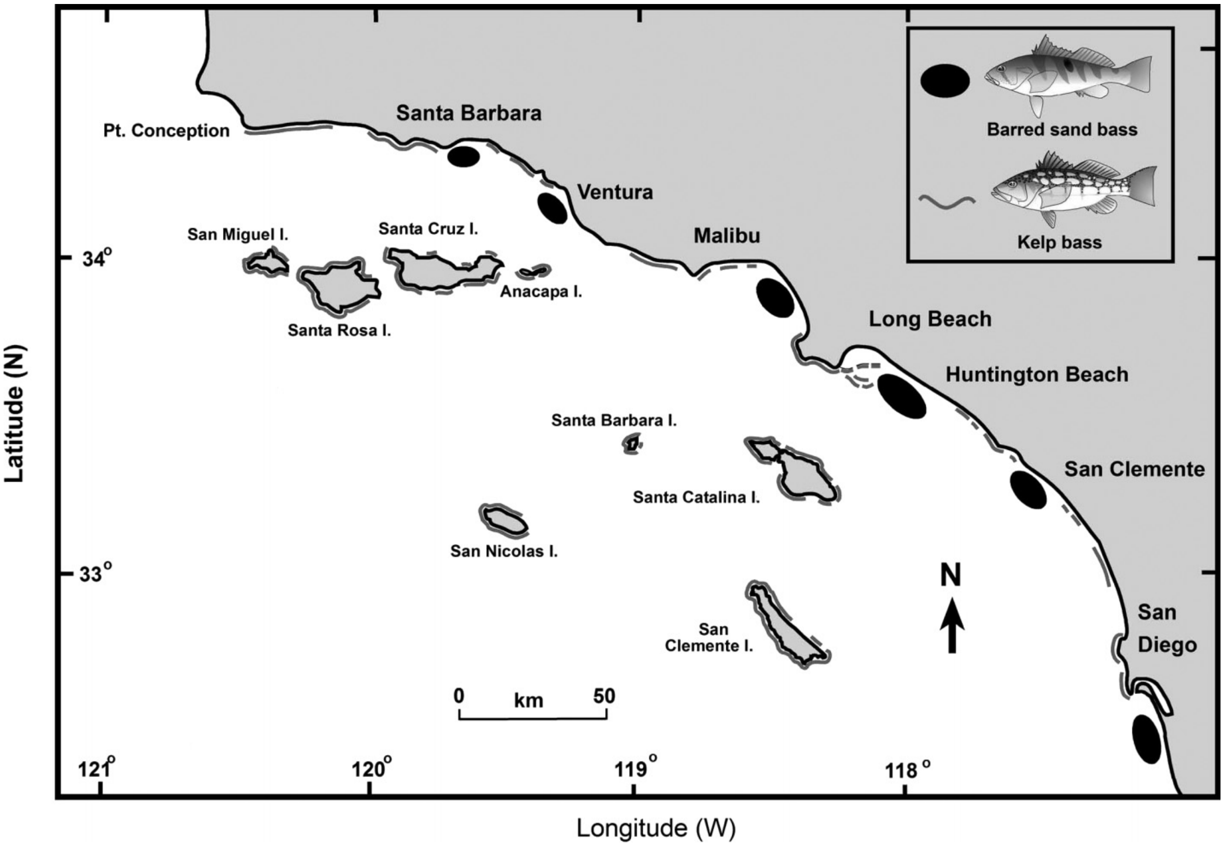
Fig. 6. Relationship between annual catch per unit effort (CPUE) of the recreational fishery and fishery-independent proxies of population abundance for barred sand bass and kelp bass: (*a*) CPUE vs. entrapment biomass in barred sand bass; (*b*) CPUE vs. entrapment biomass in kelp bass; (*c*) CPUE vs. adult density in kelp bass at King Harbor; (*d*) CPUE vs. adult density in kelp bass at Palos Verdes; (*e*) CPUE vs. first principle component axis in kelp bass.



gation periods, as fishers are permitted to land up to 10 *Paralabrax* each per day, and each CPFV can hold as many as 100 persons. As a result, CPUE for both species is disproportionately high at aggregation sites (Love et al. 1996*a*; CRFS database 2005–2007), and more than 80% of mean annual catch is harvested during aggregation months (this study; Dotson and Charter 2003). This type of fishing behavior is typical of aggregation-based fisheries, and there is overwhelming evidence that such activities are unsustainable and have contributed to global declines in fish spawning aggregation sites and aggregating species (Sadovy and Domeier 2005; Sadovy de Mitcheson et al. 2008; Sadovy de Mitcheson and Erisman 2011). Consistent with such trends, the seasonal peaks in catch and CPUE that long coincided with the spawning aggregation months of both species have declined substantially over time. Although declines in catch for both *Paralabrax* species may be partially explained by a decline in fishing effort by the CPFV fleet since the late 1990s (Sweetnam 2010), effort remained relatively constant from the 1960s to the mid-1990s, while catch and CPUE in kelp bass and stock abundances in both species began to decline in the early 1980s.

The timing of observed population declines in both species suggests that changes in regional environmental conditions also had a major effect. Using similar data as this study, Brooks et al. (2002) demonstrated that many fish stocks, including *Paralabrax* species, in the Southern California Bight have declined since the late 1970s and attributed this to a regional decline in productivity associated with a shift to an alternate (i.e., warm-water) climatic regime (Bograd and Lynn 2003; McGowan et al. 2003). Similarly, a few investigations have noted declines in densities and frequencies of *Paralabrax*

Fig. 7. Map of Southern California Bight, showing locations of spawning (and fishing) sites for barred sand bass and kelp bass. Locations of barred sand bass aggregations were identified from catch data summarized by the California Department of Fish and Game from the California Recreational Fishery Survey (CRFS) from June to August (2004–2008), whereas locations of kelp bass aggregations were derived from the regional distribution of kelp beds and rocky reefs as summarized by the Marine Life Protection Act Initiative (http://southcoast.marinemap.org/marinemap/).



larvae over the last two decades (Moser et al. 2001; Stephens and Pondella 2002). For kelp bass, it is also possible that populations declined in response to decreased kelp (*Macrocystis pyrifera*) densities, since there is a positive relationship between kelp density and larval recruitment (Carr 1989). However, adult kelp bass show no relationship to kelp density, and recent increases in kelp canopy sizes along the coast have occurred without associated increases in kelp bass populations (Holbrook et al. 1990; Parnell et al. 2010).

The reliance on fisheries data to assess stock condition (see Allen and Hovey 2001*a*, 2001*b*) meant that collapses in both species were masked by hyperstability, which resulted from the combined effects of the aggregating behavior of fish and the persistent targeting of spawning aggregations by recreational fishers. Catch and CPUE of both fisheries remained high for several decades because of the persistent harvesting of fish from summer spawning aggregations. In fact, catch and CPUE for barred sand bass increased steadily between the 1970s and 1990s as the fishery gained in popularity and vessels became increasingly familiar with the timing and location of aggregation sites (Allen and Hovey 2001*a*; Love 2006). As a result, both fisheries were deemed sustainable in fishery assessments conducted during that period (e.g., Ono 1992; Read 1992). Yet, while incredible numbers of fish were removed from aggregations each year (e.g., over 2 million barred sand bass landed by the CPFV fleet in 1999), population abundance was decreasing because of overfishing and regional climatic changes. Consequently, the relationship between CPUE and population abundance was disproportional in both species of *Paralabrax*. CPUE data in barred sand bass were completely insensitive to changes in population size and continued to increase as abundance declined, indicating that fishers were capable of locating aggregations and maintaining high catch rates even when populations had reached historically low levels. These scenarios created the illusion that harvest levels for both species were sustainable and stock abundances were stable, and as a result, resource managers did not react to or even recognize the collapses. To date, no changes in the management of either species have been implemented to mitigate further declines or hasten their recovery, even though the targeted protection of spawning aggregations has stimulated the recovery of other aggregating species in southern California (see Allen et al. 2007; Pondella and Allen 2008).

Differences in the rate of decline between the two species of *Paralabrax* may be related to the size, duration, and distribution of their spawning aggregations. Barred sand bass form transient spawning aggregations of tens to hundreds of thousands of fish at six main areas during July and August each year (Fig. 7), whereas during nonspawning periods, they are more dispersed along inshore habitats (Love et al. 1996*a*; Allen and Hovey 2001*a*; Jarvis et al. 2011). The predictability in the timing and location of barred sand bass aggregations and the massive size of each aggregation allowed fishers to maintain high CPUE for many years until fish abundance at the few known aggregation sites became so sparse that both catch and CPUE suddenly collapsed. The hyperstability of this population was so extreme that even the power function model failed to capture its shape, as CPUE remained very high while the entrapment biomass steadily declined. It was only until the last few years that the population collapse started to become reflected in declining CPUE values. Conversely, kelp bass form resident spawning aggregations of tens to several hundreds of fish at most rocky reef and kelp bed sites throughout southern California, and they also aggregate outside the spawning season (Young 1963; Erisman and Allen 2006). Consequently, fishing effort and catch was distributed more broadly in time and space (Love et al. 1996*a*), and catch and CPUE declined steadily over time as aggregation sites were serially depleted and fishers moved to other aggregation sites to maintain high catch rates. Claro et al. (2009) found similar results in a study of long-term fisheries trends in reef fishes that form spawning aggregations in Cuba, such that species showed differential responses to fishing pressure according to their spawning behavior. Specifically, those species that aggregate at a small number of spawning sites during brief, predictable periods showed significantly greater declines compared with those with prolonged, less predictable spawning aggregation patterns.

In summary, this study provides further empirical evidence that fisheries targeting fish spawning aggregations can exhibit hyperstability. Our results demonstrate that simple fishery-dependent proxies such as CPUE should be used with caution when estimating stock condition in fishes that form spawning aggregations and be given low weight when fishery-independent data are available. While nonlinear relationships between stock and CPUE can be accounted for in statistical analyses, the difference across species of the nature of the nonlinearities in our results confirms the importance of directly estimating this relationship whenever possible. CPUE data collected from fisheries are useful and essential for managing aggregation-based fisheries, as they can be used to identify aggregation periods and determine the degree to which fisheries target aggregations. However, such measures are inappropriate as sole determinants of stock condition for aggregating fishes, because they overestimate biomass and stock productivity and give the false impression that fishing levels are sustainable when true abundance is declining (this study; Crecco and Overholtz 1990; Sadovy and Domeier 2005). The consequences of relying on such indices can be devastating, providing resource managers with little or no warning of an imminent fishery or population collapse (Rose and Kulka 1999; Clark 2001; Post et al. 2002).

Direct, fishery-independent surveys of population abundance are essential to monitor stock condition in fishes that form spawning aggregations and avoid costly management errors associated with hyperstability. However, fishery-independent indices of abundance of aggregating fishes are also susceptible to producing biased estimates (Wilberg et al. 2009), particularly given the strong temporal and spatial variations in the distribution and abundance of fish that characterize most aggregating species (Colin et al. 2003). In addition, the appropriate survey methods (e.g., underwater visual censuses, multibeam sonar transects, ichthyoplankton trawls) vary considerably among species, depending on differences in the timing, duration, and size of aggregations; local environmental conditions; and habitat type (Sadovy et al. 2005; Foote 2009). Nevertheless, once optimized for a particular species or location, the data obtained should provide informative and accurate estimates of population abundance. Moreover, as methods are developed to incorporate hyperstability and temporal and spatial variations in abundance into stock assessment models of aggregating species (Wilberg et al. 2009), resource managers will be able to set more appropriate harvest limits, better detect and respond to population declines prior to a collapse, and properly evaluate fishery and population responses to management actions (Colin et al. 2003; Sadovy et al. 2005). The importance of effective monitoring for aggregating fishes cannot be overstated, given that few aggregations are managed worldwide and most have either declined or disappeared altogether (Sadovy de Mitcheson et al. 2008).

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References

Allen, L.G., and Hovey, T.E. 2001*a*. Barred sand bass. *In* California's living marine resources: a status report. *Edited by* W.S. Leet, C.M. Dewees, R. Klingbeil, and E.J. Larson. Calif. Dept. Fish Game Univ. Calif. Agric. Nat. Res. Publ. SG01-11. pp. 224–225.

Allen, L.G., and Hovey, T.E. 2001*b*. Kelp bass. *In* California's living marine resources: a status report. *Edited by* W.S. Leet, C.M. Dewees, R. Klingbeil, and E.J. Larson. Calif. Dept. Fish Game Univ. Calif. Agric. Nat. Res. Publ. SG01-11. pp. 222–223.

Allen, L.G., Pondella, D.J., II, and Shane, M.A. 2007. Fisheries independent assessment of a returning fishery: abundance of juvenile white seabass (*Atractoscion nobilis*) in the shallow nearshore waters of the Southern California Bight, 1995–2005. Fish. Res. **88**(1–3): 24–32. doi:10.1016/j.fishres.2007.07.012.

Bannerot, S.P., and Austin, C.B. 1983. Using frequency distributions of catch per unit effort to measure fish-stock abundance. Trans. Am. Fish. Soc. **112**(5): 608–617. doi:10.1577/1548-8659(1983)112<608:UFDOCP>2.0.CO;2.

Bograd, S.J., and Lynn, R.J. 2003. Long-term variability in the Southern California Current System. Deep Sea Res. Part II Top. Stud. Oceanogr. **50**(14–16): 2355–2370. doi:10.1016/S0967-0645(03)00131-0.

Brooks, A.J., Schmitt, R.J., and Holbrook, S.J. 2002. Declines in regional fish populations: have species responded similarly to environmental change? Mar. Freshw. Res. **53**(2): 189–198. doi:10.1071/MF01153.

Carr, M.H. 1989. Effects of macroalgal assemblages on the recruitment of temperate zone reef fishes. J. Exp. Mar. Biol. Ecol. **126**(1): 59–76. doi:10.1016/0022-0981(89)90124-X.

Clark, M. 2001. Are deepwater fisheries sustainable? — The example of orange roughy (*Hoplostethus atlanticus*) in New Zealand. Fish. Res. **51**(2–3): 123–135. doi:10.1016/S0165-7836(01)00240-5.

Claro, R., Sadovy de Mitcheson, Y., Lindeman, K.C., and García-Cagide, A.R. 2009. Historical analysis of Cuban commercial fishing effort and the effects of management interventions on important reef fishes from 1960–2005. Fish. Res. **99**(1): 7–16. doi:10.1016/j.fishres.2009.04.004.

Colin, P.L., Sadovy, Y.J., Domeier, M.L. 2003. Manual for the study and conservation of reef fish aggregations. Soc. Conserv. Reef Fish Agg. Spec. Publ. 1.

Crecco, V., and Overholtz, W.J. 1990. Causes of density-dependent catchability for Georges Bank haddock *Melanogrammus aeglefinus*. Can. J. Fish. Aquat. Sci. **47**(2): 385–394. doi:10.1139/f90-040.

Dotson, R.C., and Charter, R.L. 2003. Trends in the Southern California sport fishery. Calif. Coop. Oceanic Fish. Invest. Rep. **44**: 94–106.

Erisman, B.E., and Allen, L.G. 2006. Reproductive behaviour of a temperate serranid fish, *Paralabrax clathratus* (Girard), from Santa Catalina Island, California, U.S.A. J. Fish Biol. **68**(1): 157–184. doi:10.1111/j.0022-1112.2006.00886.x.

Field, J.C., MacCall, A.D., Ralston, S., Love, M.S., and Miller, E.F. 2010. Bocaccionomics: the art of living off lottery tickets. Calif. Coop. Ocean. Fish. Invest. Rep. **51**: 77–90.

FAO. 2009. The state of world fisheries and aquaculture 2008. Food and Agriculture Organization of the United Nations, Rome, Italy.

Foote, K.G. 2009. Quantitative research surveys of fish stocks. *In* Computers in fisheries research. 2nd ed. *Edited by* B.A. Megrey and E. Moksness. Springer Science + Business Media B.V., New York. pp. 145–190.

Harley, S.J., Myers, R.A., and Dunn, A. 2001. Is catch-per-unit-effort proportional to abundance? Can. J. Fish. Aquat. Sci. **58**(9): 1760–1772. doi:10.1139/f01-112.

Hilborn, R., and Walters, C.J. 1992. Quantitative fisheries stock assessment: choice, dynamics and uncertainty. Chapman and Hall, New York.

Hill, K.T., and Barnes, J.T. 1998. Historical catch data from California's commercial passenger fishing vessel fleet: status and comparison of two sources. Calif. Dep. Fish Game Mar. Reg. Tech. Rep. 60.

Holbrook, S.J., Carr, M.H., Schmitt, R.J., and Coyer, J.A. 1990. Effect of giant kelp on local abundance of reef fishes: the importance of ontogenetic resource requirements. Bull. Mar. Sci. **47**: 104–114.

Hutchings, J.A. 2001. Conservation biology of marine fishes: perceptions and caveats regarding assignment of extinction risk. Can. J. Fish. Aquat. Sci. **58**: 108–121.

Jackson, D.A. 1993. Stopping rules in principal components analysis: a comparison of heuristical and statistical approaches. Ecology, **74**(8): 2204–2214. doi:10.2307/1939574.

Jarvis, E.T., Allen, J.M., and Smith, R.W. 2004. Comparison of recreational fish catch trends to environment–species relationships and fishery-independent data in the Southern California Bight, 1980–2000. Cal. Coop. Ocean. Fish. Invest. Rep. **45**: 167–179.

Jarvis, E.T., Linardich, C., and Valle, C.F. 2011. Spawning-related movements of barred sand bass, *Paralabrax nebulifer*, in Southern California: interpretations from two decades of historical tag and recapture data. Bull. South. Calif. Acad. Sci. **109**: 123–143.

Love, M.S. 2006. Subsistence, commercial, and recreational fisheries. *In* Ecology of marine fishes: California and adjacent waters. *Edited by* L.G. Allen, D.J. Pondella II, and M. Horn. University of California Press, Los Angeles, Calif. pp. 567–594.

Love, M.S., Brooks, A., and Ally, J.R.R. 1996*a*. An analysis of commercial passenger fishing vessel fisheries for kelp bass and barred sand bass in the Southern California Bight. Calif. Fish Game, **82**: 105–121.

Love, M.S., Brooks, A., Busatto, D., Stephens, J., and Gregory, P.A. 1996*b*. Aspects of the life histories of the kelp bass, *Paralabrax clathratus*, and barred sand bass, *P. nebulifer*, from the southern California Bight. Fish Bull. **94**: 472–481.

Mason, T.J., and Lowe, C.G. 2010. Home range, habitat use, and site fidelity of barred sand bass within a Southern California marine protected area. Fish. Res. **106**(1): 93–101. doi:10.1016/j.fishres.2010.07.008.

McGowan, J.A., Bograd, S.J., Lynn, R.J., and Miller, A.J. 2003. The biological response to the 1977 regime shift in the California Current. Deep Sea Res. Part II Top. Stud. Oceanogr. **50**(14–16): 2567–2582. doi:10.1016/S0967-0645(03)00135-8.

Miller, E.F., Williams, J.P., Pondella, D.J., II, and Herbinson, K.T. 2009. Life history, ecology, and long-term demographics of queenfish. Mar. Coast. Fish. Dynam. Man. Ecosyst. Sci. **1**(1): 187–199. doi:10.1577/C08-018.1.

Moser, H.G., Charter, R.L., Smith, P.E., Ambrose, D.A., Watson, W., Charter, S.R., and Sandknop, E.M. 2001. Distributional atlas of fish larvae and eggs in the Southern California Bight region, 1951–1998. Calif. Coop. Ocean. Fish. Investig. Atlas, **34**: 1–166.

Ono, D.S. 1992. Sand basses. *In* California's living marine resources and their utilization. *Edited by* W.S. Leet, C.M. Dewees, R. Klingbeil, and C.W. Haugen. University of California Sea Grant Extension Program, Davis, Calif. pp. 151–153.

Parnell, P.E., Miller, E.F., Lennert-Cody, C.E., Dayton, P.K., Carter, M.L., and Stebbins, T.D. 2010. The response of giant kelp (*Macrocystis pyrifera*) in southern California to low-frequency climate forcing. Limnol. Oceanogr. **55**: 2686–2702.

Pondella, D.J., II, and Allen, L.G. 2008. The decline and recovery of four predatory fishes from the Southern California Bight. Mar. Biol. **154**(2): 307–313. doi:10.1007/s00227-008-0924-0.

Pondella, D.J., II, Stephens, J.S., and Craig, M.T. 2002. Fish production of a temperate artificial reef based on the density of embiotocids (Teleostei: Perciformes). ICES J. Mar. Sci. **59**(Suppl.): S88–S93. doi:10.1006/jmsc.2002.1219.

Post, J.R., Sullivan, M., Cox, S., Lester, N.P., Walters, C.J., Parkinson, E.A., Paul, A.J., Jackson, L., and Shuter, B.J. 2002. Canada's recreational fisheries: the invisible collapse? Fisheries, **27**: 6–17.

Quast, J.C. 1968. Observations on the food and biology of the kelp bass (*Paralabrax clathratus*), with notes on its sportfishery at San Diego, California. *In* Utilization of kelp-bed resources in southern California. *Edited by* W.J. North and C.L. Hubbs. Calif. Dep. Fish Game Fish. Bull. 139. pp. 81–105.

Quinn, T.J., II, and Deriso, R.B. 1999. Quantitative fish dynamics. Oxford University Press, New York.

Read, D. 1992. Kelp bass. *In* California's living marine resources and their utilization. *Edited by* W.S. Leet, C.M. Dewees, R. Klingbeil, and C.W. Haugen. University of California Sea Grant Extension Program, Davis, Calif. pp. 150–151.

Rose, G.A., and Kulka, D.W. 1999. Hyperaggregation of fish and fisheries: how catch-per-unit-effort increased as the northern cod (*Gadus morhua*) declined. Can. J. Fish. Aquat. Sci. **56**(Suppl. 1): 118–127. doi:10.1139/f99-207.

Sadovy, Y., and Domeier, M.L. 2005. Are aggregation-fisheries sustainable? Reef fish fisheries as a case study. Coral Reefs, **24**(2): 254–262. doi:10.1007/s00338-005-0474-6.

Sadovy, Y.J., Colin, P., and Domeier, M. 2005. Monitoring and managing spawning aggregations: methods and challenges. SPC Live Reef Fish Bull. **14**: 25–29.

Sadovy de Mitcheson, Y.J., and Erisman, B.E. 2011. Fishery and biological implications of fishing spawning aggregations, and the social and economic importance of aggregating fishes. *In* Reef fish spawning aggregations: biology, research, and management. *Edited by* Y.J. Sadovy and P.L. Colin. Springer, New York. [In press.]

Sadovy de Mitcheson, Y., Cornish, A., Domeier, M., Colin, P., Russell, M., and Lindeman, K.C. 2008. A global baseline for spawning aggregations of reef fishes. Conserv. Biol. **22**(5): 1233–1244. doi:10.1111/j.1523-1739.2008.01020.x. PMID:18717693.

Salthaug, A., and Aanes, S. 2003. Catchability and the spatial distribution of fishing vessels. Can. J. Fish. Aquat. Sci. **60**(3): 259–268. doi:10.1139/f03-018.

Sokal, R.R., and Rohlf, F.J. 1995. Biometry: the principles and practice of statistics in biological research. 3rd ed. W.H. Freeman and Co., New York.

Stephens, J.S., Jr, and Pondella, D.J., II. 2002. Larval productivity of a mature artificial reef: the ichthyoplankton of King Harbor, California, 1974–1997. ICES J. Mar. Sci. **59**: S51–S58. doi:10.1006/jmsc.2002.1189.

Stephens, J.S., Jr, Morris, P.A., Zerba, K., and Love, M. 1984. Factors affecting fish diversity on a temperate reef: the fish assemblage of Palos Verdes Point, 1974–1981. Environ. Biol. Fishes, **11**(4): 259–275. doi:10.1007/BF00001373.

Sweetnam, D. 2010. Review of selected California fisheries for 2009: coastal pelagic finfish, market squid, red abalone, Dungeness crab, pacific herring, groundfish/nearshore live-fish, highly migratory species, kelp, California halibut, and sandbasses. Calif. Coop. Ocean. Fish. Invest. Rep. **51**: 14–38.

Turner, C.H., Ebert, E.E., and Given, R.R. 1969. Man-made reef ecology. Calif. Dep. Fish Game Fish. Bull. 146.

Walters, C. 2003. Folly and fantasy in the analysis of spatial catch rate data. Can. J. Fish. Aquat. Sci. **60**(12): 1433–1436. doi:10.1139/f03-152.

Wilberg, M.J., Thorson, J.T., Linton, B.C., and Berkson, J. 2009. Incorporating time-varying catchability into population dynamic stock assessment models. Rev. Fish. Sci. **18**(1): 7–24. doi:10.1080/10641260903294647.

Worm, B., Barbier, E.B., Beaumont, N., Duffy, J.E., Folke, C., Halpern, B.S., Jackson, J.B.C., Lotze, H.K., Micheli, F., Palumbi, S.R., Sala, E., Selkoe, K.A., Stachowicz, J.J., and Watson, R. 2006. Impacts of biodiversity loss on ocean ecosystem services. Science, **314**(5800): 787–790. doi:10.1126/science.1132294. PMID:17082450.

Young, P.H. 1963. The kelp bass (*Paralabrax clathratus*) and its fishery, 1947–1958. Calif. Dept. Fish Game Fish Bull. 122.