
Extirpation and Recolonization in a Metapopulation of an Endangered Fish, the Tidewater Goby

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Abstract: *The tidewater goby (Eucyclogobius newberryi), an endangered species in the United States, occurs in a series of isolated coastal wetlands in California. Using historical presence-absence data and our own surveys, we estimated annual rates of extirpation and recolonization for several populations of the goby in southern California. As predicted, large wetlands had lower rates of extirpation than small wetlands. There was a negative but statistically nonsignificant correlation between recolonization rate and distance to the nearest northerly source population. Populations at small sites were sensitive to drought, presumably because droughts can eliminate suitable habitat at small wetlands. Populations in small wetlands have declined over time, even after accounting for variation in stream flow, supporting the species' endangered status. Our study emphasizes the need to understand metapopulation dynamics for conserving species where the unit of conservation is a local population. It is also emphasizes the importance of not treating metapopulations as identical units. Finally, our results provide a means for describing the decline of a species that is complex in time and space and provide insight into how to target protection measures among metapopulations.*

Extirpación y Recolonización de una Metapoblación de un Pez Amenazado, el Goby de Mareas

Resumen: *El Goby de mareas (Eucyclogobius newberryi) es una especie amenazada en los Estados Unidos que ocurre en una serie de humedales costeros aislados en California. Utilizando datos históricos de presencia y ausencia, así como nuestros propios datos, estimamos la tasa anual de extirpación y recolonización de varias poblaciones del goby en el Sur de California. A como se predijo, los humedales grandes tuvieron tasas de extirpación mas bajas que los humedales pequeños. Existió una correlación negativa, aunque no estadísticamente significativa entre la tasa de recolonización y la distancia a la población fuente norteña mas cercana. Las poblaciones en sitios pequeños fueron susceptibles a temporadas de seca, presumiblemente debido a que las secas pueden eliminar hábitat viable en humedales pequeños. Las poblaciones en humedales pequeños han disminuído a lo largo del tiempo, aún después de considerar la variación del flujo en arroyos, soportando el estatus de amenaza para las especies. Nuestro estudio enfatiza la necesidad de entender las dinámicas de metapoblaciones para conservar especies donde la unidad de conservación es una población local. También enfatiza la importancia de no tratar metapoblaciones como unidades idénticas. Finalmente, nuestros resultados proveen un medio para describir el declive de una especie compleja en tiempo y espacio y provee ideas sobre como abarcar medidas de protección entre metapoblaciones.*

Introduction

When a threatened species occurs as a metapopulation, with local populations linked by migration, understanding its dynamics is a critical step in its conservation (Hanski & Simberloff 1997). The classic metapopulation model (Levins 1970) consists of a set of extinction-prone local populations, assumes that all local populations are equal, and does not consider their spatial arrangements. Most real populations do not have a classic metapopulation structure (Harrison & Taylor 1997), and recent developments in metapopulation theory have focused on more realistic models (Hanski & Gyllenberg 1993; Hanski et al. 1994; Hastings & Harrison 1994).

The tidewater goby (*Eucyclogobius newberryi*) is a small, benthic fish occurring in shallow estuaries in California. The goby was listed as an endangered species in 1994 (U.S. Fish and Wildlife Service 1992, 1994). Tidewater gobies occur as a metapopulation along the California coast because extensive areas of unsuitable coastline separate suitable habitats (estuaries). In contrast to some metapopulation spatial arrangements, the local populations occur in linear sequence.

Migration rates among local populations of tidewater gobies are unknown, but because the goby lacks a marine phase, dispersal among estuaries seems improbable. There is some genetic evidence that movement among local populations is extremely limited, with low heterozygosity within populations and genetic divergence among geographic regions (Crabtree 1985). Some apparently suitable sites have remained unpopulated for many years, and successful reintroductions into Malibu Lagoon in 1990 (Manion 1993; Swift et al. 1993) and Waddell Creek in 1991 (Brown & Swenson 1994) suggest that some long-term absences could be the result of low recolonization rates. Such low migration rates could make the tidewater goby metapopulation particularly susceptible to extinction. Recent observations, however, suggest that floods may facilitate recolonization by transporting individuals to wetlands to the south (Lafferty et al. 1999).

To understand the metapopulation dynamics of the tidewater goby, we investigated factors associated with extirpation and recolonization of local populations. Extrapolating from island biogeography theory (MacArthur & Wilson 1967), we predicted (1) that populations in large wetlands would experience lower extirpation rates than populations in small wetlands. Because the goby lacks a dispersal phase, we predicted (2) that recovery rates of extirpated local populations would be low and diminish with increasing distance from the nearest source population. Noting the large number of extirpations in Los Angeles County and the San Francisco Bay area, two of the most developed areas in the state, and the continued degradation of tidewater goby habitat as development has continued along the coast,

we predicted (3) that population persistence has declined. Because some wetlands containing gobies dried up during the 1987–1992 drought in California and gobies are unable to move to better habitats during low-flow years, we also predicted (4) a positive association between years with high stream flow and the presence of gobies.

To evaluate these predictions, we first compiled historical presence-absence data from the southern group of populations (the goby's historical range is split into aggregations of populations in northern California, San Francisco Bay, Santa Cruz, and south of San Luis Obispo). We then determined rates of extirpation and recolonization at each site where four or more observations were available. We chose this cut-off because it struck the best balance between our desire to reduce error in the estimates and our need to include a sufficient number of sites. Error in our estimates (particularly those with few observations) might have made it more difficult for us to obtain significant results in some cases. The estimated rates of extirpation and recolonization allowed us to determine expected probabilities of presence or absence. Comparing the expected probabilities with whether the population was actually present or absent allowed us to quantify how much a particular year at a particular site deviated from expectation. We then categorized wetlands by size and obtained historical stream flow records to determine how these factors have affected goby populations.

Tidewater gobies live in low-flow, shallow, brackish portions of coastal streams, marshes, lagoons, and estuaries between the Smith River in northern California and Agua Hedionda Lagoon in southern California (Swift et al. 1989; Capelli 1998). These habitats are usually small in area, ranging from a few square meters to a few square kilometers. They nearly always lack continual tidal flow due to the seasonal formation of a sand barrier at the mouth of the estuary (Swift et al. 1989). Where they occur, tidewater gobies are often one of the most abundant fish species (Lafferty & Altstatt 1995) and are able to survive the dramatic changes in salinity and dissolved oxygen related to irregular tidal and freshwater inputs (Swift et al. 1989). They are small (4–5 cm) predators that feed on benthic invertebrates such as ostracods, amphipods, and insect larvae (Irwin & Soltz 1984; Swenson & McCray 1996). Males excavate mucus-lined burrows of 10–20 cm in coarse sand and care for one clutch of 300–500 eggs, which develop in about 10 days (Swenson 1995). Spawning occurs almost year-round, with spring and fall peaks (Goldberg 1977). Mortality appears to increase after spawning, and individuals typically live only 1 year (Swift et al. 1989), although some may overwinter upstream (Irwin & Soltz 1984).

Despite the broad physical tolerance of this species, as few as half of the original populations still exist, with most extirpations having occurred in southern California and San Francisco Bay (Swift et al. 1989). Habitat loss

and degradation, a consequence of land-use practices such as conversion of coastal wetlands to marinas, highway and railroad construction, freshwater diversions, grazing, breaching of coastal lagoons, and flood control practices appear to have led to several permanent extirpations (Lafferty et al. 1996).

Methods

Historical Data

The U.S. Geological Survey (USGS) Internet site (<http://waterdata.usgs.gov/nwis-w/us>), provides stream gauge data for a large number of locations across the United States. We obtained daily records of stream flow (feet³/second) from 1941 through 1995 for Carpinteria Creek, California. This was approximately the middle of the latitudinal range of our sites and was the only source of information with a record for all years. We condensed the data into yearly averages. These flows had strong positive associations with the fragmentary records available from other sites. Therefore, we used this single site as a representation of the region's relative annual variation in stream flow. In addition to annual variation in stream flow, there is large among-site variation in flows associated with watershed area and other factors.

We compiled over 250 historical records of presence-absence at 48 sites from our own data, museum collections, gray literature, and unpublished reports (Swift et al. 1989, 1993; Lafferty & Altstatt 1995; Lafferty et al. 1999; data available upon request). The oldest records dated from the 1890s, but most records dated from after 1940. The high abundance often achieved by tidewater gobies and their habit of sitting on the bottom in shallow water make determining presence or absence easier than for other fishes in these habitats. We analyzed data from only those 37 sites with four or more records. Our main concern about these data was the possibility of false absences. Although this sort of error is not completely avoidable, we critically evaluated the data records and eliminated several cases where an absence might represent insufficient search effort.

Extirpation and Recolonization Rates

We estimated site-specific extirpation and recolonization probabilities from records of presence and absence. Because gobies were reintroduced into Malibu Lagoon, we calculated separate estimates for before and after reintroduction and averaged them. We first constructed an empty, two-dimensional matrix by using possible annual extirpation and recolonization probabilities (ranging from 0 to 1 at 0.1 intervals) as row and column headings. Each of the 121 cells in the resulting matrix, therefore, corresponded to a unique pair of extirpation (row)

and recolonization (column) probabilities. For each cell, then, we used the methods of Clark and Rosenzweig (1994) to find the likelihood that the corresponding pair of probabilities could explain the observed data. We then divided the value of each cell by the sum of the likelihoods (so that the sum of all the cells equaled 1).

We used two methods to summarize the expected probability of extirpation and recolonization for a site. First, we multiplied each possible extirpation probability by the sum of the likelihoods across recolonization space. For example, if the likelihood of annual extirpation being 0, 0.1, 0.2, and >0.2 summed (across all probabilities of recolonization) to 0.1, 0.6, 0.3, and 0, respectively, then the expected estimate for extirpation was the sum of the products, or 0.12. We used the same approach to estimate the expected rate of recolonization. For our second method, we solved numerically for the parameter values that yielded the maximum likelihood of producing the observed data. Both estimates correlated strongly. Because maximum likelihoods tended to be unrealistically extreme values (often 0 or 1), and expected values tended to be too moderate (nearer 0.5), we averaged the two estimates into a single parameter. The maximum likelihood, expected value, and average all produced qualitatively similar results in the analyses.

Deviations from the Expected Probability of Occurrence

To assess the accumulated effects of habitat degradation and to correlate variation in rainfall with extirpation and recolonization, we needed a method for determining how population dynamics varied from year to year while controlling for site-specific variation in extirpation and recolonization. For sites that had at least one extirpation or recolonization, we estimated the extent to which each observed record represented a better or worse year than expected for that particular site. Absences yielded negative deviations, whereas years when gobies were present had positive deviations. The magnitude (-1 to 1) of these deviations depended on the probability of extirpation and recolonization at a site as well as whether the population was present or absent during previous surveys. To estimate these deviations, we used simulations to generate 1000 presence-absence time series for each survey at each site and then determined how the observed values deviated from the average of the simulations. The simulations constructed a hypothetical complete history for the population, constrained by the known values from sampled dates.

The following is an example of our approach. Consider a population for which gobies were present in 1972 and absent in 1981; the estimated site-specific probabilities of extirpation and recolonization were 0.5 and 0.2, respectively. The probability of a new absence equals the product of the probability of extirpation and 1 minus the probability of recolonization, or $(0.5)(1 -$

0.2) = 0.4 in this example. We know that 1981 was a bad year, but how bad was it given the probability of extirpation and recolonization at the site and the presence of gobies in 1972? At the first time step (1973), we generate a random number between 0 and 1, say 0.2. Because 0.2 is less than the probability of a new absence, the simulated population disappears in 1973. At the next time step (1974), we generate another random number, say 0.1. Because this is less than the probability for recolonization, the population recovers. We continue to run the model until the year 1981. A single iteration might produce the following simulated 10-year time series of presence (p) and absence (a): papaappap. We then reseed the random number generator and iterate the model again. In this case, we would likely obtain a different presence-absence time series (e.g., paappapaa). We then repeat the simulation again. Recall that the historical data, with blanks for missing years, were p - - - - - a. We obtain an average "expected presence" for 1981 by setting each presence to 1 and each absence to 0, summing across the 1000 simulated time series and dividing by 1000. In the previous example, for instance, consider that the average expected probability of occupying the site in 1981 was 0.4. We then compare this with the observed absence by subtracting the expected probability of occurrence from zero. The difference between the expected and the observed would be -0.4 , indicating a relatively bad year in 1981. We call this the "deviation from expected probability of occurrence." We then repeat this process for the next observation at the site.

Analyses

To simplify the analysis of wetland size, we categorized wetlands as large or small, based on the typical surface area of their lagoons (Table 1). We compared rates of extirpation and recolonization between large and small wetlands using a one-tailed, unpaired *t* test for extirpation (we expected small wetlands to have higher rates of extirpation) and a two-tailed, unpaired *t* test for recolonization. To calculate the effect of isolation on recolonization, we first estimated the distance to each northerly source population, excluding those populations not known to contain gobies since 1980. We measured the northerly distance (following the contour of the coastline) because dispersal most likely follows the longshore currents that flow north to south (or west to east along much of Santa Barbara County) (Lafferty et al. 1999). We then tested for an association between distance and recolonization with a Pearson's correlation analysis. We analyzed habitat degradation and stream flow independently by performing a multivariate analysis in which the dependent variable was the deviation from the expected probability of occupying a site and the independent variables were wetland size, year, and stream flow (counting each sampling event as an independent

event). We excluded populations known to be extinct since 1980 from the multivariate analysis and *t* test because we expected that the presence of gobies at these sites was no longer dependent on wetland size or stream flow.

Results

The average estimated annual rates of extirpation and recolonization (0.37 and 0.48) were higher than we expected and suggest a dynamic system. Judging by the broad distribution of the likelihood estimates over the parameter space evaluated, however, these estimates are not precise and would be better used for broad comparisons than for accurate description of individual sites. In nearly half of the populations, extinction rates were greater than recolonization rates. There was a significant negative association between extirpation and recolonization rates ($R = -0.498$, $n = 37$, $p < 0.01$), suggesting that the populations most likely to be extirpated were also unlikely to recover quickly. As predicted, annual rates of extirpation were lower for large than small wetlands (Fig. 1, 0.24 vs. 0.43, one-tailed *t* test, $p = 0.01$). Annual rates of recolonization were not different between large and small wetlands (0.56 vs. 0.52, two-tailed *t* test, $p = 0.71$).

The predicted negative association between rates of recolonization and the distance from the next northerly wetland was not significant ($R = -0.19$, $n = 32$, $p > 0.05$). Incorporating information on wetland size into this analysis did not substantially improve this association.

There was a significant positive association between deviations from the expected probability of occurrence and high stream flows (Table 2). There was a significant interaction term between wetland size and the effect of stream flow on deviations resulting from the stronger negative effect of flow on populations in small habitats (Table 2). Although there was no significant change in deviations over time independent of stream flow (Table 2), there was a significant interaction term between wetland size and the effect of date on deviations (Table 2), resulting from a negative effect of date (year) on small habitats and a slightly positive effect on large habitats.

Discussion

The high rates of extirpation and recolonization suggest that we can expect some tidewater goby populations, particularly small ones, to disappear and become recolonized. The high recolonization rates suggest that there may be more gene flow among populations than initially expected. Although Crabtree's (1985) allozyme results might reflect low levels of dispersal among tidewater

Table 1. Estimates of recovery and extirpation for the tidewater goby populations surveyed.

Site ^a	Size ^b	Distance ^c	Recolonization ^d			Extirpation ^d		
			Exp	ML	average	Exp	ML	average ^e
San Luis Obispo	large	36	0.33	0.06	0.2	0.49	0.06	0.28
Pismo	large	8	0.72	1.00	0.86	0.35	0.00	0.17
Sta Maria	large	18	0.74	1.00	0.87	0.32	0.00	0.16
Shuman	small	18	0.69	1.00	0.84	0.36	0.00	0.18
San Antonio	large	4	0.70	1.00	0.85	0.34	0.00	0.17
Sta Ynez	large	13	0.74	1.00	0.87	0.30	0.00	0.15
Honda	small	10	0.27	0.02	0.24	0.67	0.95	0.81
Jalama	small	28	0.57	0.67	0.62	0.66	1.00	0.83
Cojo	small	11	0.68	1.00	0.84	0.37	0.00	0.19
St. Augustine	small	8	0.12	0.00	0.06	0.63	1.00	0.82
Agujas	small	1	0.50	0.49	0.50	0.58	0.56	0.57
Bulito	small	1	0.29	0.13	0.21	0.53	0.19	0.36
Sta Anita	small	2	0.73	1.00	0.87	0.32	0.00	0.16
Alegria	small	2	0.73	1.00	0.87	0.31	0.00	0.16
Caliente	small	2	0.34	0.22	0.28	0.51	0.24	0.38
Gaviota	large	2	0.66	0.63	0.65	0.48	0.26	0.37
Hondo*	small	7	0.09	0.00	0.05	0.62	1.00	0.81
Quemado	small	11	0.35	0.33	0.34	0.66	0.99	0.83
Refugio	small	3	0.33	1.00	0.67	0.37	0.00	0.19
Tecolote	small	15	0.46	0.37	0.42	0.58	0.43	0.51
Bell	small	0.3	0.74	1.00	0.87	0.32	0.00	0.16
Carp SM*	large	12	0.07	0.00	0.04	0.59	1.00	0.80
Carp Cr.	small	13	0.49	0.09	0.29	0.54	0.08	0.31
Ventura	large	23	0.72	1.00	0.86	0.32	0.00	0.17
Santa Clara	large	7	0.60	0.43	0.52	0.47	0.18	0.33
Ormond	large	13	0.46	0.09	0.27	0.40	0.00	0.20
Mugu*	large	8.5	0.09	0.00	0.05	0.43	0.04	0.24
Malibu	large	40	0.40	0.50	0.45	0.40	0.02	0.21
Aliso	large	119	0.41	0.00	0.21	0.47	0.02	0.25
San Juan*	small	9	0.07	0.00	0.04	0.45	0.11	0.28
San Mateo	large	21	0.51	0.26	0.39	0.45	0.10	0.28
San Onofre	small	1	0.67	0.82	0.75	0.52	0.77	0.65
Los Flores	small	16	0.72	1.00	0.86	0.33	0.00	0.17
Aliso Cyn.	small	0.6	0.32	0.21	0.27	0.48	0.00	0.24
French	small	0.2	0.54	0.25	0.29	0.68	1.00	0.84
Cockleburrr	small	1	0.25	0.25	0.40	0.45	0.00	0.23
Sta Margarita	large	2.4	0.26	0.11	0.19	0.51	0.28	0.40
Average		12	0.47	0.49	0.48	0.47	0.28	0.37

^aSites represent those areas where four or more observations were available. A complete list of sites and samples is available upon request from K.D.L. An asterisk indicates that we believe the population is permanently extirpated.

^bWetlands are large (>10,000 m²) or small based on the typical surface area of the coastal lagoon.

^cDistance is in kilometers from the nearest (regularly extant) population located up-coast (north).

^dExp is the expected value of the parameter based on all likelihoods; ML is the parameter corresponding to the parameter pair with the maximum likelihood for producing the observed series of presence and absence.

^eAverage between Exp and ML.

goby populations, he based his analysis on samples taken from sites that were much more broadly dispersed than ours, indicating fixed differences only among large geographic regions. More recent molecular data suggest frequent gene flow on smaller spatial scales (D. Jacobs et al., unpublished data), which is consistent with our results.

Our analyses indicate that the persistence of tidewater goby populations was affected by wetland size and annual variation in stream flow. In small wetlands, tidewater gobies did better in wet than in dry years. Wet years led to a larger usable habitat area, better water quality,

and, perhaps most important, a lower chance of drying up. Conversely, variation in stream flow had little effect in large habitats, even in dry years. The restriction of local populations to single wetlands, coupled with the limited ability of individuals to move voluntarily to more favorable habitats, made goby populations in small wetlands especially susceptible to environmental stochasticity, particularly droughts. Unfortunately for the goby, the time it most needs to leave a habitat—during a drought—is when it is least able to leave. Thus, large wetlands probably provided a persistent refuge even during unfavorable conditions.

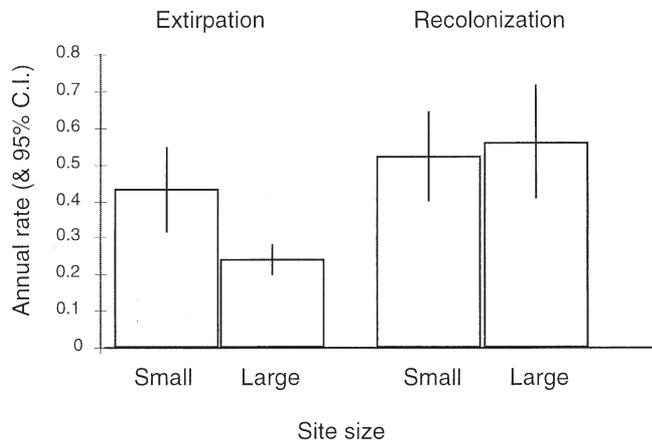


Figure 1. Estimated annual rates of extirpation and recolonization for small and large wetlands. Rates are the average between the maximum likelihood and the expected of the likelihoods (see methods). Error bars indicate 95% confidence intervals of the means.

One alternative explanation commonly given for our observation of lower extirpation rates in large compared to small habitats is that stochastic variation in birth and death rates is less likely to lead to extirpation in large populations (Schoener 1991). For the tidewater goby, however, this explanation may not apply. Even the smallest wetland typically supports populations of tidewater gobies numbering in the hundreds (Lafferty & Altstatt 1995), far more than are needed to overcome the effects of demographic stochasticity (Goodman 1987).

The tidewater goby metapopulation appears to be most similar to a core-satellite type of metapopulation, in which core populations in large wetlands are relatively stable and satellite populations in small wetlands may become extinct in unfavorable years (Bleich et al. 1990; Gotelli 1991; Hanski & Gyllenberg 1993). In the time covered by our data, however, size alone did not guarantee persistence. Many of the largest wetlands in California, such as the Salinas River, Elkhorn Slough, Morro Bay, San Francisco Bay, and Mugu Lagoon, have lost tidewater gobies, in some cases due to large-scale alteration of the habitat.

Stream flow, date, and wetland size explained only a portion (12%) of the variation in goby population dynamics. This is due in part to our limited ability to accurately estimate site-specific extirpation and recolonization rates. Habitat degradation and introduced predators, however, may also have led to extirpations. Tidewater gobies usually occur in habitats where large piscivorous fishes are rare or absent. Several extirpations of tidewater gobies in the San Francisco Bay area followed the invasion of rainwater killifish (*Lucania parva*; Hubbs & Miller 1965; Leidy 1984) and yellowfin goby (*Acanthogobius flavimanus*; Brittan et al. 1970). Similarly, the introduction of squawfish (*Ptychocheilus grandis*) may have extirpated gobies from Morro Bay. Presently, we are concerned about the effect that African clawed frogs (*Xenopus laevis*) might have on tidewater gobies in the Santa Clara River (Lafferty & Page 1997).

The U.S. Fish and Wildlife Service has proposed de-listing tidewater gobies in all areas but Orange and San Diego counties (Aliso and South) (U.S. Fish and Wildlife Service 1999). Even though our analysis of deviations excluded populations that appear to be permanently extirpated, we found that prospects for persistence in small wetlands continue to deteriorate through time. Therefore, our results support the continued listing of this species as endangered.

Understanding the dynamics of tidewater goby metapopulations should be useful in developing a management strategy for this species. Because the tidewater goby is frequently abundant where it occurs, its population characteristics appear more similar to those of insects than large vertebrates (Murphy & Noon 1992). This means that management concerns need to concentrate at the level of the local population, not the individual fish, where present protection efforts tend to focus. Management of both small and large wetlands should include maintaining natural stream flows, protecting sand barriers at the mouths of lagoons, monitoring water quality, preventing the spread of exotic species and reintroduction. Because large wetlands support persistent core populations of tidewater gobies, these habitats should receive protection assiduously. Protection of only the large populations may not be sufficient, however, because the linear distribution of populations means

Table 2. General linear model statistics for an examination of size, year, and stream flow relating to whether the presence of gobies at sites on a particular date was better or worse than expected.*

Source	Sum of squares	df	Mean square	F ratio	p
Year	0.166542	1	0.166542	1.491241	0.223491
Flow	1.551564	1	1.551564	13.892956	0.000253
Size	1.119261	1	1.119261	10.022047	0.001794
Size × flow	0.815045	1	0.815045	7.298049	0.007508
Size × year	1.094340	1	1.094340	9.798898	0.002013
Error	21.889262	196	0.111680		

*n = 202; R = 0.345; R² = 0.119.

that small wetlands likely act as stepping stones between large, isolated populations.

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