The effects of barotrauma on the catch-and-release survival of southern California nearshore and shelf rockfish (Scorpaenidae, *Sebastes* spp.)

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Abstract: Two experiments were used to assess the effects of barotrauma on initial capture survival and short-term post-recompression survival of line-caught (range 18–225 m) southern California rockfish (*Sebastes* spp.). Occurrence of external and internal signs of barotrauma was characterized across all species. Despite species-specific differences in the extent of barotrauma observed, initial capture survival of rockfish held in a live well for a 10-min period following capture was 68% overall (19 species, n = 168). Overall 2-day survival of rockfish following recompression in cages was also 68% (17 species, n = 257). Short-term survival varied across species (range 36% to 82%), as did the occurrence of external signs of barotrauma. The degree of external signs of barotrauma was not a significant predictor of initial capture survival or short-term survival. The most significant predictor of short-term survival was surface holding time, with short-term survival increasing with decreasing surface holding time. These results suggest that rapid recompression of rockfish can significantly decrease discard mortality and could potentially enhance rockfish conservation.

Résumé : Deux expériences nous ont servi évaluer les effets du barotraumatisme sur la survie initiale à la capture et la survie à court terme après la recompression de sébastes (*Sebastes* spp.) du sud de la Californie capturés à la ligne (étendue des profondeurs de 18–225 m). Nous avons observé des signes externes et internes de barotraumatisme chez toutes les espèces. Malgré des différences spécifiques de l'importance du barotraumatisme, la survie initiale à la capture des sébastes gardés dans un vivier pendant 10 min suivant la capture est globalement de 68 % (19 espèces, n = 168). La survie globale des sébastes gardés dans des cages pendant 2 jours après la recompression est aussi de 68 % (17 espèces, n = 257). La survie à court terme varie d'une espèce à l'autre (étendue de 36 à 82 %), de même que la présence de signes externes de barotraumatisme. L'importance des signes externes de barotraumatisme ne permet pas de prédire avec assurance la survie initiale à la capture, ni la survie à court terme. La variable la plus significative pour prédire la survie à court terme est la durée de la retenue du poisson en surface, la survie augmentant en fonction inverse de la durée de la retenue en surface. Ces résultats indiquent qu'une recompression rapide des sébastes peut réduire de façon significative la mortalité lors de leur rejet à la mer et pourrait potentiellement favoriser la conservation des sébastes.

[Traduit par la Rédaction]

Introduction

Rockfish of the genus *Sebastes* are an extremely diverse group, inhabiting a variety of depths and habitats worldwide (Love et al. 2002). The majority of these species occur in the North Pacific, and historically, many have comprised major commercial and recreational fisheries. In southern California, rockfish catches have been an important component of the winter recreational fishery since the 1950s (Dotson and Charter 1998); however, there is strong evidence indicating that many rockfish populations have suffered from excessive harvest impacts over the last two decades (Love et al. 1998; Mason 1998; Butler et al. 2003). Growing concern regarding bycatch (i.e., incidentals and discards) mortality in the recreational rockfish fishery has prompted research into rockfish physiology and the effects of angling-induced barotrauma on their survival (Parker et al. 2006; Hannah and Matteson 2007). Upon rapid decompression, rockfish, which are physoclistic, suffer internal injury and positive buoyancy as a result of overexpansion of gases within the swim bladder and other highly vascularized tissues. Consequently, many discarded rockfish are unable to swim down deep enough to force recompression of gases within their bodies. Discard mortality in the recreational fishery is assumed to be high, as floating fish at the surface eventually succumb to thermal shock and (or) bird or marine mammal predation.

Recent research on Northeast Pacific coast rockfish suggests that assisted release of discards may increase postrelease survival, as external signs of barotrauma were alleviated following recompression of fish to depth (Hannah and Matteson 2007). However, several studies on other

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physoclistic species have found no correlation between degree of barotrauma and survival (Gitschlag and Renaud 1994; Rummer and Bennett 2005). External signs of barotrauma documented for a few rockfish species include stomach eversion, exophthalmia (bulging eyes), corneal gas bubbles, and subcutaneous gas bubbles (Gotshall 1964; Lea et al. 1999; Hannah and Matteson 2007). Internal signs of barotrauma have not been characterized for rockfish, but in other physoclists, these signs have included arterial embolism, swim bladder rupture, hematoma, hemorrhage, and organ torsion (Gitschlag and Renaud 1994; Rummer and Bennett 2005). The effects of internal barotrauma on immediate and delayed mortality in the field have not yet been reported, and the condition and longer-term survival of line-caught rockfish recompressed in the field is still largely unknown.

Releasing rockfish at depth aims to decrease the probability of discard mortality, but the practice can only be effective if evidence indicates that a high enough percentage of fish returned to depth recover and survive. The primary objectives of this study were (*i*) to characterize external and internal signs of angling-induced barotrauma in rockfish and (*ii*) to quantify initial survival (within 10 min of capture) and short-term (2-day) survival following recompression in cages. An understanding of postrecompression survival in rockfish will enable fisheries managers to assess the utility of catch-and-release regulations, not only in southern California, but also along the Northeast Pacific coast, and offer resource managers more accurate population parameters for stock assessments.

Materials and methods

Characterization of barotrauma and initial capture survival

Nearshore and shelf rockfish were captured by hook-and-line from the Palos Verdes peninsula (depth 30–70 m), Southeast Bank off Huntington Beach (50–90 m), at the offshore petroleum platform Gilda off the Ventura coast (55 m), and off Santa Catalina Island (18–96 m) between October 2004 and March 2006 (Fig. 1). Fishing was designed to target demersal species; all fishing lines were fished on the sea floor and arranged with one to two dropper loops tied approximately 22 cm above an 8–12 oz torpedo weight. We recorded bottom depth and the time of day that each fish was landed. Each fish was measured (standard length) and the presence of external signs of barotrauma including stomach eversion (SE), exophthalmia (EX), corneal gas bubbles (CB), subcutaneous gas bubbles (SB), and prolapsed cloaca (PC) were recorded. Handling time to measure and examine fish was kept to less than 2 min. Fish were placed in a live well or cooler with fresh seawater for 10 min, after which each fish was assessed for signs of gill ventilation as an indicator of initial capture survival. After noting survival, fish were euthanized and dissected within 24–48 h after capture. Internal signs of barotrauma were recorded as presence of visible tears in the tunica internus of the swim bladder (ST), organ torsion (OT), hemorrhage (HE), and presence and location of arterial gas embolisms in the pericardial chamber and at the swim bladder gas gland and oval (AE). Subcutaneous gas bubbles and arterial embolism were not initially documented at the onset of this experiment, thus sample sizes for these signs vary.

Analysis

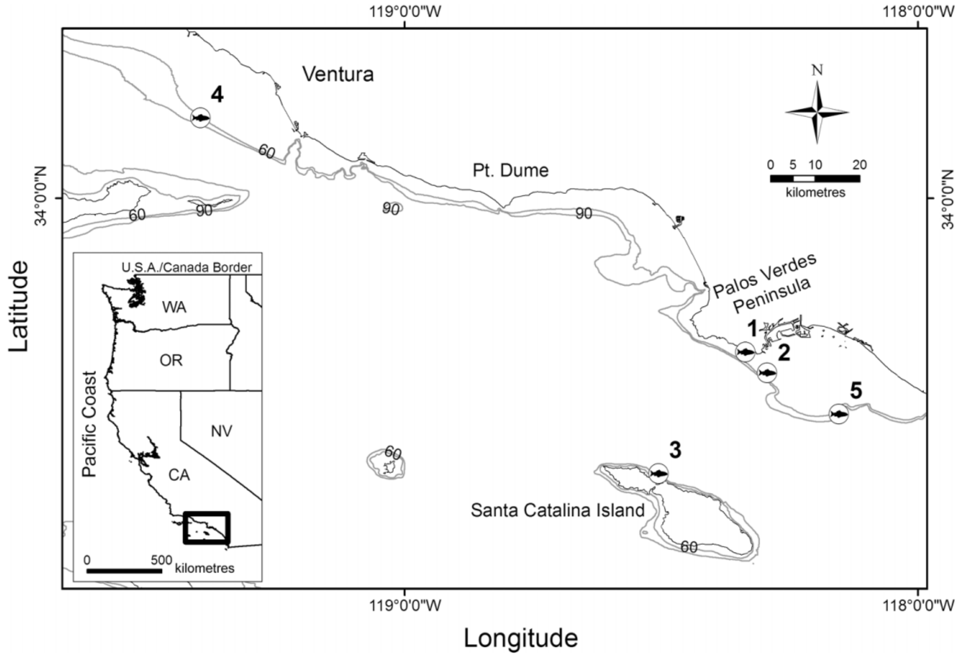
Percent occurrence and percent survival (±95% binary confidence intervals) were reported for each species and for all species combined (adjusted Wald method; Sauro and Lewis 2005). We used a general linear model (GLM, STATISTICA 7.1; StatSoft, Inc., Tulsa, Oklahoma) to examine the relationship between depth of capture and the total number of external and internal signs of barotrauma, including species in the model as a possible effect. Barotrauma effects were assessed using a Fisher exact test, comparing the proportion of survivors with and without a given sign of barotrauma. Binary logistic regression (MINITAB release 14.20; Minitab Inc., State College, Pennsylvania) was used to model the extent of barotrauma as a predictor of initial survival (barotrauma model I, external signs; barotrauma model II, internal signs). The extent of barotrauma or barotrauma category was defined by specific combinations of different signs of barotrauma observed in captured fish and was treated as a single, categorical, independent variable. The models were limited to those specific combinations of barotrauma that occurred in at least 10 fish. Additionally, survival of fish showing each specific combination of barotrauma was reported relative to fish showing no signs of barotrauma. In these models, we included only individuals for which all signs were accounted.

Characterization of barotrauma and 2-day postrecompression survival

During the summers of 2004 and 2005, nearshore and shelf rockfish were captured by hook-and-line aboard the R/V *Yellowfin* near Southeast Bank (50–89 m; Fig. 1). For each fish, we recorded bottom depth, time of capture, standard length, and the presence of external signs of barotrauma. Each fish was externally tagged for individual identification with a 4 cm long dart tag (Hallprint) and placed in a live well prior to release. Fish were then transferred to polyvinyl chloride (PVC) coated wire mesh cages (4 cm × 4 cm mesh, 1.2 m × 1.2 m × 1.5 m). Up to six cages were deployed during each trip, with as many as 12 fish per cage. Each cage was lowered to the original fish capture depth and left for 2 days on soft substratum adjacent to fished reefs. To account for differences in total surface holding duration among individuals, we recorded the exact time of each cage deployment. Two cages per trip were deployed with StowAway TidbiT temperature data loggers (Onset Computer Corp., Bourne, Mass.) to record seafloor water temperatures. Differences in water temperature between the sea floor and sea surface (i.e., temperature differential) were recorded for each trip to account for temperature change experienced by rockfish upon capture.

Two days following fish collection and recompression, each cage was pulled up to a depth of 20 m where a team of divers met the cage and assessed each fish for mortality and external signs of barotrauma. As the greatest change in pressure and, hence, gas expansion occurs within the first

Fig. 1. Fishing locations of nearshore and shelf rockfish captured by hook-and-line in southern California from depths of 18–220 m (October 2004 to August 2006): (1) White's Point outfall pipe, (2) Rockpile, (3) Ship Rock, (4) platform Gilda, and (5) Southeast Bank. Shaded lines represent 60 m and 90 m depth contours. Inset depicts southern California in relation to the Pacific coast of the United States.



10 m of the surface, this observation depth of 20 m was chosen to greatly reduce the probability of barotrauma injury resulting from the second decompression event. All dead fish and a subset of live fish per cage were saved for examination of internal barotrauma injury as described above; all remaining live fish were released.

Longer-term survival

In addition to a unique tag number, all external tags used in the cage experiments contained a phone number for reporting recaptured rockfish. To record evidence of longer-term survival, all tag returns were logged by tag identification number, species, date of recapture, location of recapture, and fisher contact.

Analysis

Chi-square tests of independence were used to test for species-specific differences in both the percent occurrence of each sign of barotrauma and percent survival. Fisher exact tests and logistic regression were again used to test for barotrauma effects as described in the initial capture study. An additional logistic regression model (PROC LOGISTIC, SAS 9.1.3; SAS Institute Inc., Cary, North Carolina) tested the effects of depth, species, fish length, cage density, temperature differential, and surface holding duration on survival (overall model). For this model, we included only data for species with a sample size greater than 15. A reduced model was then designed using only significant variables from the overall model. Because several variables, including surface holding duration and temperature differential, could not be controlled in the field, we did not include interactions. To account for differences in species survival due to different temperature differentials or surface holding times, an analysis of variance (ANOVA) was used to compare temperature differential experienced by each species upon capture, and Kruskal–Wallis was used to test for differences in median surface times experienced by each species prior to recompression.

Results

Barotrauma and initial capture survival

One-hundred and sixty-eight rockfish representing 21 species were captured over a 1.5-year period from depths of 18–96 m; vermilion rockfish, *Sebastes miniatus*; greenspotted rockfish, *Sebastes chloristictus*; olive rockfish, (*Sebastes serranoides*); halfbanded rockfish (*Sebastes semicinctus*), rosy rockfish (*Sebastes rosaceous*), and honeycomb rockfish (*Sebastes umbrosus*) comprised the majority of the catch (Table 1). Initial capture survival of rockfish was 68% overall (95% confidence interval, CI: 60% to 75%).

The most common external signs of barotrauma observed in the overall catch (n = 168) were subcutaneous gas bubbles (SB, 76% of n = 157), stomach eversion (SE, 63%), and exophthalmia (EX, 52%); the most common signs of internal barotrauma were arterial embolism (AE, 68% of n = 144), hemorrhage (HE, 64%), and organ torsion (OT, 33%). The percent occurrence of each barotrauma type and the number of frequently occurring signs of barotrauma were species-specific (Table 2). Stomach eversion occurred frequently among brown rockfish (*Sebastes auriculatus*), flag rockfish (*Sebastes rubrivinctus*), greenspotted, halfbanded, honeycomb, and rosy rockfish, starry rockfish (*Sebastes constellatus*), treefish (*Sebastes serriceps*), and widow rockfish (*Sebastes ensifer*), and swim bladder tears (ST) occurred frequently (82%) only in olive rockfish. For the catch as a whole, there was a significant, yet weak, positive correlation between the number of external and internal signs of barotrauma observed in each fish (r = 0.28,

Table 1. Sample size (*n*), catch (%), and depth (m) of capture of nearshore and shelf rockfish captured by hook-and-line in southern California (initial capture survival experiment, October 2004 to March 2006).

Common name	Scientific name	*n*	Catch (%)	Depth (m)
Vermilion rockfish	*Sebastes miniatus*	35	21	35–96
Greenspotted rockfish	*Sebastes chlorostictus*	19	11	75–189
Olive rockfish	*Sebastes serranoides*	16	10	23–53
Halfbanded rockfish	*Sebastes semicinctus*	15	9	53–64
Rosy rockfish	*Sebastes rosaceous*	12	7	54–152
Honeycomb rockfish	*Sebastes umbrosus*	12	7	46–76
Widow rockfish	*Sebastes entomelas*	9	5	53
Flag rockfish	*Sebastes rubrivinctus*	9	5	55–60
Copper rockfish	*Sebastes caurinus*	7	4	53–69
Calico rockfish	*Sebastes dalli*	7	4	53
Treefish	*Sebastes serriceps*	5	3	18–53
Brown rockfish	*Sebastes auriculatus*	4	2	24–53
Starry rockfish	*Sebastes constellatus*	4	2	46–68
Chilipepper	*Sebastes goodei*	3	2	140
Greenstriped rockfish	*Sebastes elongatus*	2	1	177
Squarespot rockfish	*Sebastes hopkinsi*	2	1	61–69
Freckled rockfish	*Sebastes lentiginosus*	2	1	61–76
Bocaccio	*Sebastes paucispinis*	2	1	76–79
Kelp rockfish	*Sebastes atrovirens*	1	1	30
Yellowtail rockfish	*Sebastes flavidus*	1	1	53
Canary rockfish	*Sebastes pinniger*	1	1	53
Total		168	100	

Table 2. Percent occurrence of barotrauma in nearshore and shelf rockfish (only species with $n > 3$) following hook-and-line capture from depths of 18–189 m in southern California (initial capture survival experiment, October 2004 to March 2006).

		Occurrence of barotrauma (%)							
		External signs				Internal signs			
Common name	*n*	SE	EX	CB	PC	ST	HE	OT	No. of traumas > 50%
Olive rockfish	16	19	6	6	0	*88*	13	0	1
Treefish	5	*60*	40	20	0	20	*80*	0	2
Halfbanded rockfish	15	*67*	13	0	13	27	*60*	*53*	3
Widow rockfish	9	*100*	0	0	11	33	33	*100*	2
Brown rockfish	4	*75*	25	0	25	0	25	0	1
Calico rockfish	7	43	29	14	43	14	29	43	0
Copper rockfish	7	29	*86*	*71*	14	0	43	29	2
Flag rockfish	9	*100*	33	22	11	0	*100*	*78*	3
Starry rockfish	4	*100*	*100*	25	0	0	*100*	0	3
Honeycomb rockfish	12	*92*	42	25	8	0	*67*	17	2
Vermilion rockfish	35	40	*71*	*57*	14	6	*74*	26	3
Rosy rockfish	12	*50*	*83*	*67*	0	0	*75*	*50*	5
Greenspotted rockfish	19	*84*	*89*	*79*	11	6	*89*	32	4

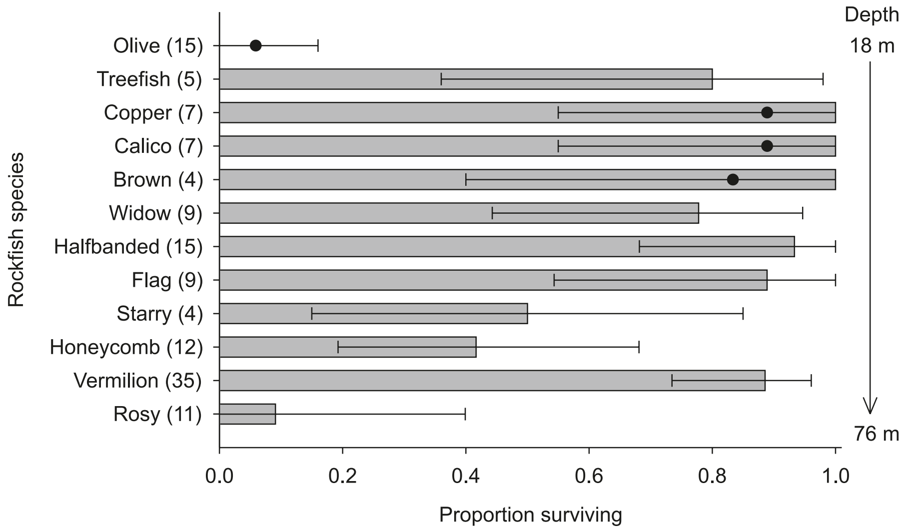
Note: Species are arranged in order of most frequent capture depth. Values in italics indicate signs of barotrauma occurring in at least 50% of individuals. SE, stomach eversion; EX, exophthalmia; CB, corneal gas bubbles; SE, stomach eversion; PC, prolapsed cloaca; ST, swim bladder tear; HE, hemorrhage; OT, organ torsion.

$p < 0.01$). The degree of barotrauma was greatest for the two species caught deepest, rosy and greenspotted rockfish. However, regardless of species, depth had a significant positive relationship with the total number of traumas observed in rockfish individuals (GLM, $n = 168$, $R^2 = 0.35$, $F = 3.61$, $p < 0.001$).

Initial capture survival varied by species (Fig. 2). Eight of 12 species (with $n > 3$) had greater than 75% initial capture survival, whereas olive and rosy rockfish had low survival. Although fish caught at deeper depths generally showed higher numbers of trauma, species caught at shallow depths showed relatively similar survival proportions as species caught in deeper depths.

Overall percent survival was significantly higher for fish

Fig. 2. Initial capture survival (±95% binary confidence intervals) of southern California nearshore and shelf rockfish (only species with $n > 3$) captured by hook-and-line from depths of 18–96 m after a 10-min holding period on deck in a live well (initial capture survival experiment, October 2004 to March 2006). Species are arranged in order of capture depth. Numbers in parentheses indicate sample sizes. Solid circles represent LaPlace Point estimates for species with survival of either 0% or 100%.



without arterial embolism (85%) than for fish with arterial embolism (58%; two-sided Fisher exact test, p = 0.002). Percent survival was also significantly higher for fish without swim bladder tears (73%) than for fish with swim bladder tears (42%; two-sided Fisher exact test, p = 0.002). Fifty-four percent of dead fish showing arterial embolism were rosy and olive rockfish, and 87% of dead fish showing swim bladder tears were olive rockfish. Externally, rockfish commonly showed five different categories of barotrauma: (*i*) the absence of all signs of barotrauma, (*ii*) the presence of only EX and CB, (*iii*) only SE, (*iv*) only SE and EX, or (*v*) all three signs together (SE, EX, and CB). Internally, rockfish commonly showed eight different categories of barotrauma: (*i*) the absence of all signs of barotrauma, (*ii*) the presence of only AE, (*iii*) only HE, (*iv*) only AE and HE, (*v*) only AE and OT, (*vi*) only AE and ST, (*vii*) only HE and OT, and (*viii*) HE, OT, and AE together. The effect of external or internal barotrauma category on initial survival was not found to be statistically significant (barotrauma model I, external signs, logistic regression, χ^2 = 8.82, df = 4, p = 0.07; barotrauma model II, internal signs, logistic regression, χ^2 = 13.71, df = 7, p = 0.06). Within barotrauma model II, fish showing both arterial embolism and swim bladder tears had significantly lower survival than fish showing no signs of barotrauma (p = 0.02, OR = 0.05); however, olive rockfish was the only species showing both AE and ST.

Barotrauma and 2-day postrecompression survival

We captured 344 rockfish comprising 17 species over seven trips. Of these, 328 fish were assessed for external signs of barotrauma, and 257 fish were recompressed to original capture depth in 42 cage deployments. A minimum of three fish and a maximum of 12 were recompressed in a single cage; the average number of fish per cage (i.e., cage density) was seven. The average capture depth was 71 m and ranged from 55 m to 81 m. Five species, vermilion rockfish, bocaccio (*Sebastes paucispinis*), and flag, squarespot (*Sebastes hopkinsi*), and honeycomb rockfish, comprised the majority (82%) of the catch (Table 3). Overall short-term survival of rockfish was 68% (95% CI: 62% to 73%). Although external signs of barotrauma were common upon capture, virtually none of the caged fish (<1%) showed external signs of barotrauma 2 days after recompression.

Of 328 fish, the most common external signs of barotrauma observed upon capture were stomach eversion (SE, 88%), exophthalmia (EX, 47%), and corneal gas bubbles (CB, 36%). The occurrence of prolapsed cloaca was not common (PC, 7%). Two days after recompression, the majority of fish were observed with cloudy corneas. Initially, the cloudy corneas were assumed to be a residual effect of ocular trauma as a result of the initial capture event, but 75% of fish having no signs of ocular trauma upon capture also showed cloudy corneas.

The extent of external signs of barotrauma observed upon capture was species-specific (Table 4). Flag, starry, and vermilion rockfish each frequently showed three signs of barotrauma. In contrast, only one sign of barotrauma, stomach eversion, frequently occurred in bocaccio and halfbanded, speckled (*Sebastes ovalis*), and squarespot rockfish. The occurrence of exophthalmia and corneal gas bubbles significantly differed among the five most abundant species (exophthalmia, χ^2 = 44.61, df = 4, $p \leq 0.001$; corneal gas bubbles, χ^2 = 24.86, df = 4, $p \leq 0.001$); however, there was no significant difference in the occurrence of stomach eversion among these species (χ^2 = 3.05, df = 4, $p > 0.05$).

Overall short-term survival (68%) was similar to that found in the initial capture survival experiment (also 68%). Two-day postrecompression survival was species-specific and ranged from 36% (95% CI: 21% to 56%) for squarespot rockfish (n = 27) to 82% (95% CI: 51% to 96%) for starry rockfish (n = 11). There was a significant difference in species survival among the five most abundant species (χ^2 = 21.6, df = 5, $p \leq 0.0001$) (Fig. 3); squarespot rockfish showed the lowest survival, whereas bocaccio showed the highest survival (95% CI: 79 to 89%). By species, there

Table 3. Sample size (*n*), catch (%), and depth (m) of capture of nearshore and shelf rockfish captured by hook-and-line in southern California (2-day postrecompression survival experiment, summer 2005 and 2006).

Common name	Scientific name	*n*	Catch (%)	Depth (m)
Vermilion rockfish	*Sebastes miniatus*	73	28.5	55–86
Bocaccio	*Sebastes paucispinis*	64	25.0	57–89
Flag rockfish	*Sebastes rubrivinctus*	29	11.3	55–89
Squarespot rockfish	*Sebastes hopkinsi*	28	10.9	55–83
Honeycomb rockfish	*Sebastes umbrosus*	17	6.6	56–84
Starry rockfish	*Sebastes constellatus*	11	4.3	58–89
Speckled rockfish	*Sebastes ovalis*	11	4.3	80–84
Chilipepper	*Sebastes goodei*	7	2.7	57–84
Halfbanded rockfish	*Sebastes semicinctus*	5	1.6	59–84
Greenspotted rockfish	*Sebastes chlorostictus*	3	1.2	80–83
Olive rockfish	*Sebastes serranoides*	2	0.8	56, 83
Copper rockfish	*Sebastes caurinus*	2	0.8	56, 84
Yellowtail rockfish	*Sebastes flavidus*	1	0.4	84
Rosy rockfish	*Sebastes rosaceous*	1	0.4	82
Greenstriped rockfish	*Sebastes elongatus*	1	0.4	84
Freckled rockfish	*Sebastes lentiginosus*	1	0.4	82
Canary rockfish	*Sebastes pinniger*	1	0.4	89
Total		257	100.0	

Table 4. Percent occurrence of barotrauma in nearshore and shelf rockfish (only species with *n* > 10) following hook-and-line capture from depths of 55–89 m in southern California (2-day post-recompression survival experiment, summer 2005 and 2006).

		Occurrence of barotrauma (%)								
		External signs					Internal signs[a]			
Common name	*n*	EX	CB	SE	PC	*n*	ST	HE	OT	AE
Bocaccio	66	33	29	*92*	0	12	0	*100*	33	25
Flag rockfish	32	*63*	*59*	*84*	13	5	0	*80*	0	40
Halfbanded rockfish	41	12	7	*93*	12	0	—	—	—	—
Honeycomb rockfish	28	*57*	46	*82*	4	2	—	—	—	—
Speckled rockfish	13	8	15	*85*	23	0	—	—	—	—
Squarespot rockfish	40	25	15	*88*	15	7	43	*100*	29	29
Starry rockfish	11	*82*	*64*	*91*	0	4	25	*100*	0	*50*
Vermilion rockfish	75	*81*	*52*	*92*	0	13	8	*85*	15	*69*

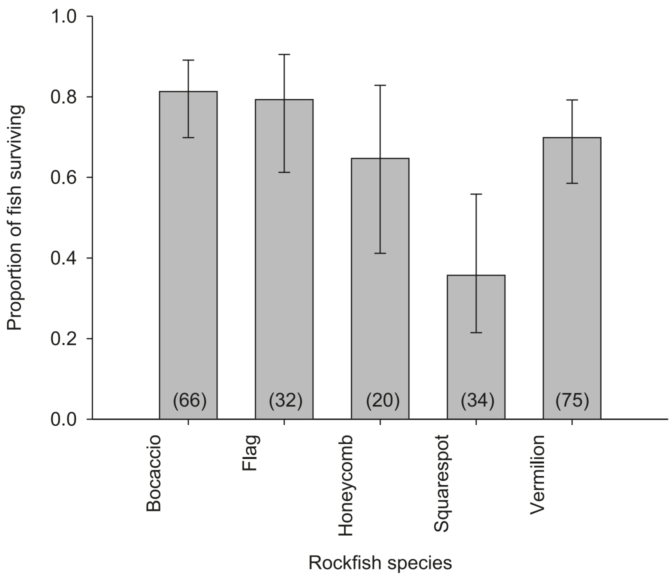
Note: Values in italics indicate signs of barotrauma occurring in at least 50% of individuals. EX, exophthalmia; CB, corneal gas bubbles; SE, stomach eversion; PC, prolapsed cloaca; ST, swim bladder tear; HE, hemorrhage; OT, organ torsion; AE, arterial embolism.

[a]Internal signs of barotrauma were assessed in a subsample of line-caught rockfish recompressed to original capture depth in cages.

were no significant differences in the proportion of survivors among fish with or without each external sign of barotrauma (two-sided Fisher exact test, $p > 0.05$). However, the results of these analyses for stomach eversion were inconclusive because sample sizes within species for fish without stomach eversion were too small. When all species were pooled, there were significantly higher mortalities in fish having stomach eversion (33%) than in fish without (0%) (two-sided Fisher exact test, $p < 0.001$), with bocaccio and vermilion and squarespot rockfish comprising 62% of these mortalities. Externally, rockfish commonly showed the same five categories of external signs of barotrauma as reported in the initial capture survival experiment. Also similar to what was reported for initial capture survival, external barotrauma category was not a predictor of 2-day postrecompression survival, although the model results in this case were much more significant (logistic regression, $\chi^2 = 1.33744$, df = 4, $p = 0.855$).

A total of 51 rockfish were dissected to assess internal signs of barotrauma (survivors, $n = 36$; dead, $n = 15$) 2 days after being recompressed in cages. Fewer dead fish than live fish were dissected because 24% of the dead fish observed in cages were completely clean carcasses that could not be assessed. Overall, 50% of fish showing organ torsion suffered mortality compared with 28% of fish without organ torsion; however, this difference was not significant (two-sided Fisher exact test, $p = 0.22$). There were also no significant differences in percent mortality for fish with and without hemorrhage, swim bladder tears, or arterial embolism (two-sided Fisher exact test, $p > 0.05$). Sample sizes

Fig. 3. Two-day survival (±95% binary confidence intervals) of the five most abundant species captured by hook-and-line in southern California from depths of 55–89 m and recompressed to original capture depth in cages (2-day postrecompression survival experiment, summer 2005 and 2006). Numbers in parentheses represent samples sizes. Percent survival was significantly different among species ($\chi^2 = 21.6$, df = 5, $p < 0.0001$).



were too small among groups of fish showing specific combinations of internal barotrauma to perform logistic regression analysis.

In the overall model, cage density, depth, and fish length had no significant effect on survival (Table 5) and, hence, were removed from the model. Mean values for each variable and species in the model are reported in Table 6. Species, surface holding duration, and temperature differential were significant predictors of survival in the reduced model (Table 5). Surface holding duration and temperature differential showed a negative relationship with the predicted probability of 2-day postrecompression survival (Fig. 4). The odds of mortality 2 days after recompression increased 1.7 times with every 10 min increase in surface holding time (e.g., $1/0.95^{10}$; Table 5). The odds of mortality 2 days after recompression increased 1.96 times with every 1 °C increase in seafloor–surface temperature differential (e.g., $1/0.51^{1}$).

There was no significant difference in median surface holding duration among species (Kruskal–Wallis, $H = 2.96$, $p = 0.56$) and no significant difference in average seafloor–surface temperature differential experienced among species (ANOVA, $F = 0.60$, $p = 0.66$).

Longer-term survival

Of the 125 fish released alive from cages at 20 m 2 days after capture, 3% were recaptured by local anglers near the areas where they were released. Two of eight honeycomb rockfish, two of 41 bocaccio, and one of 40 vermilion rockfish that were released alive were recaptured. Days at liberty for the recaptured honeycomb rockfish were 14 and 208 days. The third recaptured fish, a bocaccio, was reported after 28 days at liberty. The second recaptured bocaccio was reported approximately 90 days after the last tagging event; however, the angler provided no other additional information (i.e., tag number, date of capture) and so actual days at liberty are unknown. The vermilion rockfish was at liberty for 447 days.

Discussion

Barotrauma and initial capture survival

Despite species-specific differences in the types and degree of angling-induced barotrauma, most rockfish showed greater than 75% initial capture survival, suggesting that degree of barotrauma is not a good predictor of mortality within the first 10 min of capture. Other studies report high initial capture mortality as a result of gas bubble formation and exhaustion (Feathers and Knable 1983; Kieffer 2000; Stephens et al. 2002). However, in this study, the initial survival of rockfish overall did not appear dependent on the presence of gas bubbles. Beyer et al. (1976) reported that some bubbles present in the blood could be tolerated by coho salmon (*Onchorhynchus kisutch*), whereas large gas bubbles in vital areas such as the heart were lethal. Rosy and olive rockfish comprised the majority of dead fish with arterial embolism, suggesting these species may be more susceptible to lethal arterial embolisms than other species.

Exhaustion may restrict the ability of the opercular muscles to pump water past the gills and may also account for species-specific differences in initial capture mortality (Kieffer 2000). All of the olive rockfish and many rosy rockfish were moribund directly upon capture, suggesting that these two species may be susceptible to exhaustion. This exhaustion, in combination with the high incidence of arterial embolism observed in dead individuals, may account for the higher initial capture mortality of these two species relative to the other rockfish species.

Intraspecific variability in barotrauma responses of fish captured at similar depths are likely due to differences in the relative volume of the swim bladders when fish are caught (Arnold and Walker 1992; Rummer and Bennett 2005; Parker et al. 2006). For example, extent of barotrauma will vary depending on whether the fish is neutrally buoyant at the depth of capture (Parker et al. 2006). Further, interspecific variability in swim bladder morphology may also influence interspecific variation in the occurrence of swim bladder tears. During examination of internal signs of barotrauma, olive rockfish swim bladders were found to be relatively thin compared with the more robust swim bladders observed in vermilion, copper, and brown rockfish. Given the high occurrence of swim bladder tears in olive rockfish observed in this study relative to the other species, a thinner swim bladder may be more prone to severe rupture than a robust swim bladder, as seen in other species (Feathers and Knable 1983). Although olive rockfish showed high mortality and high occurrence of swim bladder tears, all other rockfish with swim bladder tears lived except for two ($n = 17$). Nevertheless, longer-term survival may be compromised by structural damage to the swim bladder and (or) other organs (Parker et al. 2006).

Barotrauma and 2-day postrecompression survival

The species-specific differences in external signs of barotrauma reported in this study appear to be related to species

Table 5. Logistic regression results of the overall and reduced models of 2-day survival of rockfish captured by hook-and-line in southern California from depths of 55–89 m and recompressed in cages to original capture depth (2-day postrecompression survival experiment, summer 2005 and 2006).

Predictor of survival	df	β	X^2	p	OR
Overall model					
Species	4	—	11.23	0.024*	—
Surface time (min)	1	–0.626	9.69	0.002*	0.94
Depth (m)	1	–0.0277	2.22	0.136	0.97
Fish length (SL, cm)	1	0.0419	0.99	0.319	1.04
Cage density	1	–0.0462	0.26	0.614	0.96
Temperature difference (°C)	1	–0.6512	7.57	0.006*	0.52
Reduced model					
Species	4	—	19.76	0.001*	—
Surface time (min)	1	–0.0566	8.6312	0.003*	0.95
Temperature differential (°C)	1	–0.6705	8.4990	0.004*	0.51

Note: Asterisks (*) indicate significance at $p < 0.05$. df, degrees of freedom; OR, odds ratio; SL, standard length.

differences in body morphology and also to the degree of vertical movement within the water column. For example, species that showed few signs of barotrauma (e.g., bocaccio and squarespot, speckled, and halfbanded rockfish) can be characterized as having relatively elongate, laterally compressed bodies and occurring in schools up off the seafloor (Love et al. 2002). In contrast, flag, honeycomb, vermilion, and starry rockfish, which are all relatively deep-bodied and more demersal, showed a high degree of barotrauma. Species that show a high degree of barotrauma might be expected to have low survival following recompression relative to those species showing very few external signs of barotrauma; however, we did not observe this trend. Further, barotrauma category (e.g., specific combinations of external signs of barotrauma) was not a significant predictor of survival. Although the presence of specific external signs of barotrauma was not a clear indication of 2-day postrecompression survival, as has been found in other species (Gitschlag and Renaud 1994; Rummer and Bennett 2005), the absence of a specific sign of barotrauma may be more telling. For instance, 2-day postrecompression survival was significantly higher for fish without stomach eversion.

Stomach eversion may occur as a result of swim bladder leaks or ruptures. Although visible swim bladder tears were not common for the catch as a whole, we did observe many fish with partially deflated swim bladders, suggesting that escapement of gas at high pressure likely occurred during ascent. Although the mechanism by which swim bladders reseal after overinflation is not well understood, this may explain why not all rockfish with stomach eversion showed visible tears in the swim bladder wall. Delayed mortality in fish with stomach eversion may be a result of internal organ torsion associated with the occurrence of stomach eversion and (or) internal organ damage resulting from the overinflated swim bladder crushing organs (Keniry et al. 1996; Rummer and Bennett 2005). Fifty percent (4 of 8 fish) exhibiting organ torsion died versus only 26% (11 of 42 fish) without organ torsion. Low sample size among fish with organ torsion (n = 8) may explain why this difference was not significant. Further analyses of internal signs of barotrauma as predictors of postrecompression survival could not be conducted because of low sample sizes among dead specimens (n = 15).

Rummer and Bennett (2005) reported that internal organ damage of red snapper (*Lutjanus campechanus*) increased with depth of capture because of the progressive expansion of the swim bladder from posterior to anterior regions of the body cavity. Although not specifically tested, it is likely that swim bladder rupture thresholds and the space allowable for swim bladder expansion may also vary across rockfish species. Thus, the extent of organ damage in rockfish may differ among species with different body shapes and (or) swim bladder morphologies, even at similar capture depths. For example, squarespot rockfish (low survival) and bocaccio (high survival) frequently showed stomach eversion. Squarespot rockfish were observed as having thinner swim bladder morphology similar to that of olive, widow, and halfbanded rockfish, and three of six fish showed swim bladder tears. In contrast, bocaccio were observed to have relatively thicker swim bladders. Bocaccio swim bladders may rupture only minutely, allowing gas escapement into the body cavity at high pressure, which would force the stomach out of the mouth but nevertheless, leave the swim bladder visibly intact. Only one of 12 bocaccio showed swim bladder tears. It is important to note that swim bladder ruptures, although common in some species, may not be deleterious, at least in the short term. Several studies indicate a remarkable ability of physoclistic species to repair ruptured swim bladders within a few days or even hours (Burns and Restrepo 2002; Nichol and Chilton 2006; Parker et al. 2006).

In the initial capture survival experiment, the degree of barotrauma in rockfish was partially attributed to depth; however, depth was not a significant predictor of 2-day postrecompression survival of rockfish. Depth has been shown in numerous studies to significantly affect postrelease survival in other physoclistic species (Wilson and Burns 1996; Morrissey et al. 2005; St. John and Syers 2005). Nevertheless, because rockfish exhibit a wide range of foraging behavior (e.g., benthic ambush predators versus water-column planktivores) and were observed to differ in swim bladder morphology as discussed above, depth effects on rockfish survival corresponding to the incidence and degree of barotrauma are likely to differ by species (Lea et al. 1999; Parker et al. 2006; Hannah and Matteson 2007).

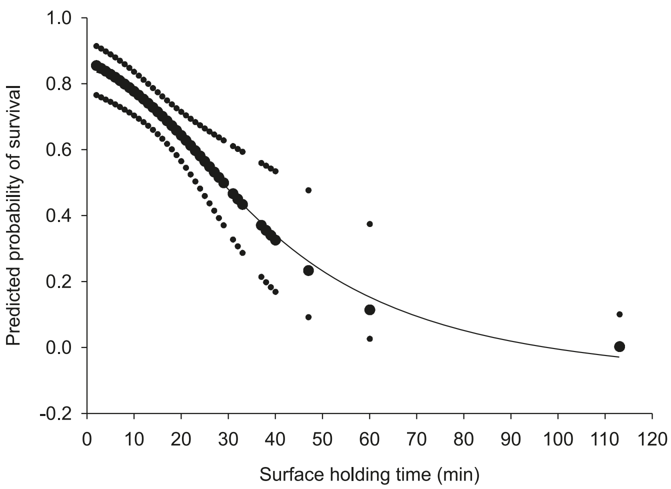
In addition to depth, fish size was not a significant predictor of 2-day postrecompression survival. It has been hypothesized that smaller fish may be more susceptible to gas embolism because of the relationship between critical blood vessel size and the size of expanded bubbles in the blood (Beyer et al. 1976), and thermal shock may occur more quickly in smaller fish than in larger fish (Davis 2002); however, other studies report no effect of fish length on short-term survival (Gitschlag and Renaud 1994; Collins et al. 1999).

Cage density was not found to affect 2-day postrecompression survival; nevertheless, we cannot dismiss that

Table 6. Species catch-and-release summary data (mean ± standard deviation, SD) for the five most abundant rockfish captured by hook-and-line in southern California and recompressed to original capture depth in cages (2-day postrecompression survival experiment, summer 2005 and 2006).

Common name	Standard length (cm)	Depth (m)	Cage density	Temperature differential (°C)	Surface holding duration (min)
Bocaccio	35.2 (7.4)	83.3 (4.3)	7 (2)	9.7 (0.7)	14.4 (6.7)
Flag rockfish	21.5 (2.7)	69.9 (13.1)	8 (2)	9.4 (0.6)	13.6 (9.3)
Honeycomb rockfish	16.3 (1.7)	76.7 (10.8)	8 (3)	8.2 (0.7)	14.9 (9.1)
Squarespot rockfish	19.9 (1.3)	70.2 (12.0)	7 (2)	9.3 (0.7)	21.5 (21.2)
Vermilion rockfish	24.3 (4.0)	63.8 (11.5)	7 (2)	9.0 (1.0)	16.0 (9.7)
Overall mean (±1 SD)	26.0 (8.1)	72.4 (12.9)	7 (2)	9.2 (0.9)	15.8 (11.3)

Fig. 4. Predicted probability (±95% confidence interval) of rockfish 2-day postrecompression survival as a function of surface holding time (min) (2-day postrecompression survival experiment, summer 2005 and 2006). The probability curve is based on the five most abundant rockfish captured during the 2-day cage trials; $n = 211$ fish).



observed cage abrasion and potentially high stress levels due to the confinement of the cages may have contributed to some mortality (Gliniak et al. 2006). The presence of scavengers such as crustacean zooplankton or hagfish, as suggested by the clean carcasses of several fish, may have further exacerbated stress levels in other fish that had not suffered immediate mortality (Stepien and Brusca 1985).

Seventy-five percent of fish showed cloudy corneas 2 days after recompression, but fish were observed bumping into the sides of the cages during cage retrievals. We conclude that cloudy corneas were likely a symptom of keratitis as a result of cage abrasion because even fish without initial ocular trauma exhibited cloudy corneas after recompression (St. John and Syers 2005). Recompression appeared to reverse or alleviate external signs of barotrauma observed in rockfish upon capture, which has also been noted in previous studies (St. John and Syers 2005; Parker et al. 2006; Hannah and Matteson 2007). Still, it is unclear whether ocular trauma may result in long-term visual impairment.

Rapid recompression of line-caught rockfish can reduce the extent of injury caused by arterial embolism and hemorrhaging and thereby increase survival. In this study, surface holding time was found to have a significant effect on recompression survival. Fish held at the surface for 10 min or less had a 78% probability of survival following recompression, and this probability of survival increased to 83% if fish were released within 2 min of landing. Parker et al. (2006) reported 97% survival (up to 21 days) of black rockfish (*Sebastes melanops*) recompressed within 30 s of decompression (from 4 atm) in pressure chambers. Surface holding duration may explain species-specific differences in survival in our study. Of the five most abundant species caught (e.g., bocaccio and vermilion, flag, honeycomb, and squarespot rockfish), squarespot rockfish showed the lowest survival. It is possible that surface holding duration may have affected squarespot rockfish survival because these fish were held at the surface an average 5 min longer than the other four species (Table 6). This difference in surface holding duration, although not statistically significant, may have been biologically significant.

Fish held at the surface for long periods of time may also experience thermal stress (Feathers and Knable 1983). Reduced blood flow as a result of intravascular bubble formation following decompression may be especially detrimental in warmer surface waters where oxygen demand is higher and oxygen concentration is lower. Feathers and Knable (1983) reported a synergistic effect of barotrauma and surface temperature on mortality of released largemouth bass (*Micropterus salmoides*). Because of the physiological effects of temperature on rockfish and the negative affect of increased temperature differential on short-term survival, it is possible that postrelease survival probabilities relative to surface holding duration may increase during winter months when sea surface temperatures differ less from seafloor temperatures.

Longer-term survival

Although tag recaptures were few, they provided evidence of longer-term postrelease survival (at least up to 1.5 years) in line-caught rockfish following recompression. Although these data provide no indication of actual delayed mortality following release, other studies document delayed capture mortality following recompression up to the first several days of release (Gitschlag and Renaud 1994; Wilson and Burns 1996; Lowe et al. 2007). For example, 93% of line-caught rockfish that were acoustically tagged at the surface, recompressed to depth, and monitored for a 2-year period were detected within the first 2 days after their release (Lowe et al. 2007). Subsequently, the decline in detections leveled out 6 days after release. Cage recompression studies on line-caught red snapper and red grouper (*Epinephelus morio*) found that delayed mortality continued up to 10 days, although the majority of deaths occurred within the first 2 days (Gitschlag and Renaud 1994; Wilson and Burns 1996).

Fisheries management implications

The results of this research provide evidence of both short-term and long-term postrelease survival of line-caught southern California nearshore and shelf rockfish recompressed to capture depth (from 55 to 89 m). Findings suggest that the utility of recompression devices is high if used within minutes of capture. A variety of assisted release (i.e., recompression) methods, including inverted weighted milk crates and "fish descenders", currently exist to return overinflated fish to depth following capture (Theberge and Parker 2005). Although the use of recompression devices would not be practical for a strictly catch-and-release fishery, recompression would provide a practical means for decreasing discard mortality of incidentally caught rockfish.

Between 1993 and 2002, an estimated two million rockfish were discarded in southern California (Pacific States Marine Fisheries Commission 2007). Fifty-eight percent of fish were discarded from private boats. Dwarf species (i.e., honeycomb, squarespot, and halfbanded rockfish) comprise a large proportion of rockfish discards (M. Horeczko, California Department of Fish and Game, 4665 Lampson Avenue, Los Alamitos, CA 90720, USA, personal communication), which likely suffer high mortality. These species are now among the common rockfish caught in southern California (Love et al. 1998), although they are seldom kept by fishers because of their small size. The practice of using assisted release in the recreational rockfish fishery may help restore rockfish diversity on rocky reefs that have suffered decades of intense fishing pressure, which in turn would help to increase ecosystem function and resilience to fishery collapse (Worm et al. 2006).

Minimum size limits have not been considered as a management tool for rockfish because of the perceived high release mortality attributed to barotrauma (J. Ugoretz, California Department of Fish and Game, 20 Lower Ragsdale Drive, Monterey, CA 93940, USA, personal communication), but federal and state mandates outlined in the Magnuson Fishery Conservation and Management Act (MFCMA) [301 (a)(9)] and the Marine Life Management Act (MLMA) [7056(d)] require a reduction in groundfish bycatch (i.e., incidental catch + discards) mortality. Some studies have evaluated the effectiveness of deflating swim bladders to increase survival of overinflated fish by relieving excess gas with a hypodermic needle ("venting"), which enables fish to swim to depth on their own following release (Bruesewitz et al. 1993; Keniry et al. 1996; Collins et al. 1999). However, venting is still controversial because the results of these studies are not definitive and experience in using this method is necessary to avoid accidental puncture of vital organs (Kerr 2001). Implementation of less invasive assisted release methods would increase the practicality of size limits as an alternative to current nearshore and shelf rockfish regulations. Nevertheless, for minimum size limits to be effective in conserving rockfish stocks, fish that are recompressed to depth after capture must live long enough to reach size at maturity. For long-lived species such as rockfish, it may be important to consider cumulative mortality risk, which increases exponentially with every recapture (Bartholomew and Bohnsack 2005). Based on rockfish recapture rates from this study and those reported from the Nearshore Groundfish Tagging Project, rockfish recapture rates in southern California appear low (3%; Hanan and Associates Inc. 2006). Furthermore, the possibility of subsequent mortality of a recaptured immature fish is likely offset by the decrease in overall fishing mortality that would be provided by implementing recompression. Other factors, including vision impairment and (or) angling-induced physiological impacts on growth and reproduction that may decrease rockfish longevity following capture and recompression, need further exploration.

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