



# Fish assemblage associations and thresholds with existing and projected oil and gas development

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**Abstract** Energy development threatens fish and wildlife resources worldwide. This study used constrained ordinations to show fish assemblage structure associated with oil and gas well densities in the Colorado River Basin, Wyoming, but well densities explained only 6.4% of assemblage structure when compared to other factors. Threshold Indicator Taxonomic ANalysis showed significant negative threshold responses by some species to small levels of development ( $<0.15$  wells  $\text{km}^{-2}$ ), whereas positive thresholds were less distinct. Some native and imperilled species could be disproportionately affected if future oil and gas development proceeds in a manner that will impact aquatic resources. Although existing development has not substantially influenced regional fish assemblage structure, it appears to affect a subset of species. Understanding assemblage-level responses to development can help land managers determine appropriate development levels, prioritise areas for monitoring associated with future development and identify where land protection measures may be needed to offset potential risks.

**KEY WORDS:** Colorado River Basin, energy development, oil and gas, ordination, thresholds.

## Introduction

Accelerated use of fossil fuels, despite increased use of renewable resources, poses an ongoing risk to fish and wildlife (Berger & Beckmann 2010; Czúcz *et al.* 2010). For example, in the western United States, oil and gas developments have impacted sagebrush ecosystems (Walston *et al.* 2009), such as modifying mule deer, *Odocoileus hemionus* (Rafinesque), movement patterns (Sawyer *et al.* 2009), reducing the proportion of sage grouse, *Centrocercus urophasianus* Swainson, males in leks (Walker *et al.* 2007), and inciting changes in juvenile sage grouse survival and breeding territory establishment (Holloran *et al.* 2010).

Less is known about oil and gas development impacts to aquatic biota. Groundwater brought to the surface along with oil and gas (i.e. produced water) that is discharged into streams can impact water quality and is often not regulated. Water quality standards that are in place often consider constituents (e.g. ion concentrations) individually and fail to consider their interacting effects (Davis *et al.* 2009). Groundwater pumping associated with wells can alter stream flows, sometimes increasing and stabilising discharges. Changes to water quality may also alter aquatic and riparian plant communities, and,

subsequently, food web structure and aquatic ecosystem function. Surface disturbance poses additional problems, as sedimentation often occurs during road and well pad construction, for example, causing negative impacts on aquatic invertebrate diversity and density in Brazil (Couceiro *et al.* 2010). Roads and pipelines associated with development can represent barriers to fish passage, and in channel impoundments can alter flow regimes and impede fish passage (Davis *et al.* 2009; Farag *et al.* 2010). Each of these potential impacts is of concern to fishery resource managers (Dauwalter *et al.* 2010).

In the present study, fish assemblage associations and thresholds with oil and gas development were identified in the Upper Colorado River Basin in Wyoming, as well as how forecasted oil and gas development is associated with the current distributions of native fishes. The Colorado River Basin contains an endemic, species poor and imperilled native fish fauna (Tyus *et al.* 1982; Olden *et al.* 2006), therefore, understanding how development influences fish assemblages, especially identifying important development thresholds and future development threats, will help land managers regulate development and help aquatic resource managers identify endemic and imperilled species that are in areas projected for future development.

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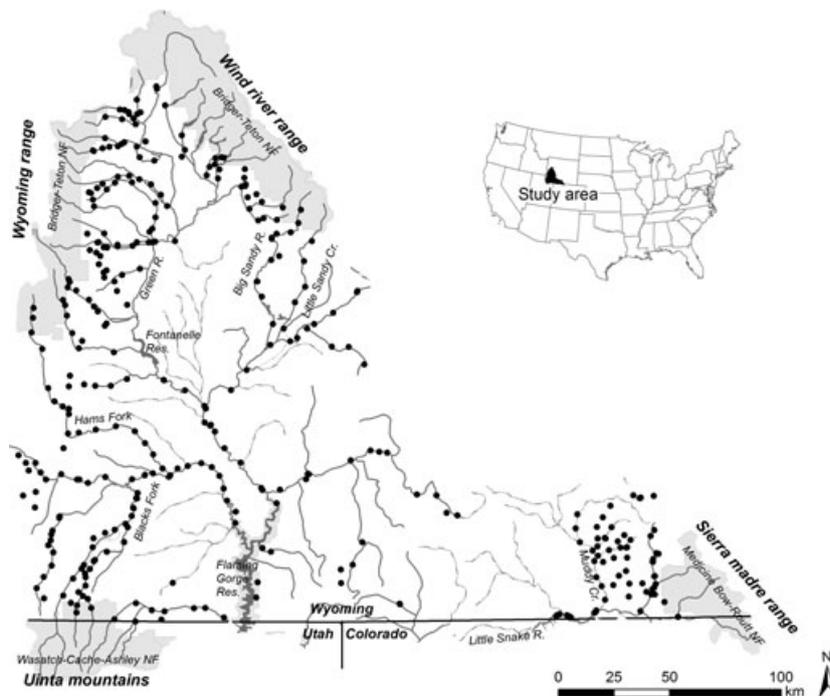
## Methods

### *Fish assemblage and environmental data*

A survey of the Colorado River Basin in Wyoming was used to evaluate fish assemblage associations and thresholds with oil and gas well densities, and to assess how current native species distributions were aligned with projected oil and gas development. Fish assemblage data were from a 2002–2006 systematic Wyoming Game and Fish Department survey of fishes in lower elevation streams of the basin (Fig. 1; Gelwicks *et al.* 2009). Streams and rivers were systematically surveyed at 354 sites located every 8–16 km and extending upstream until the fish assemblage became dominated by salmonids or cottids. Fishes were sampled using a variety of gear types depending on stream size and conductivity. In wadeable streams, fish were sampled in a 200-m reach isolated with block nets (5-mm mesh) or natural barriers (e.g. North American beaver, *Castor canadensis* Kuhl, dams). One or a combination of gear types was used to maximise sampling efficiency. A shore-based electric-fishing unit fitted with 1–4 anodes or a backpack electric-fishing unit fitted with one anode was used most often. Deeper, but still wadeable, streams were sampled with an electric fishing unit on a cataraft with one to three roving anodes. One pass was typically conducted, but if electric fishing was perceived to be poor by field

crews then a second electric fishing pass or seine haul was conducted. Streams too deep to wade were sampled with a raft electric fishing unit fitted with two fixed, boom-mounted anodes; backwaters and off-channel habitats were sampled by supplemental seining. All fishes were sorted by species and counted. Catostomids were identified following Quist *et al.* (2009), but fin clips were also taken for genetic verification of species identification (Gelwicks *et al.* 2009).

Oil and gas well densities and important covariates were measured from landscape scale spatial data that were processed in a geographic information system (GIS). Oil and gas wells were from an existing database (USGS 2004), and densities were measured both within a 0.5-km buffer and within the contributing drainage basin upstream of each sample site. Other important natural landscape and anthropogenic variables thought to influence fish assemblages in the basin were also included in the ordinations to explain variation that may mask associations with oil and gas well densities. These variables were measured for each stream segment in the National Hydrography Dataset Plus (1:100 000 scale) (USEPA & USGS 2005): mean annual flow ( $\text{m}^3 \text{s}^{-1}$ ), stream slope ( $\text{m m}^{-1}$ ); mean annual air temperature ( $^{\circ}\text{C}$ ) from Parameter-Elevation Regressions on Independent Slopes Model (PRISM) 800-m Normals (1971–2000; PRISM Climate Group, Oregon State University); percent riparian cover in a variable width buffer based on



**Figure 1.** Fish survey sites ( $n = 354$ ) in the Upper Colorado River Basin, Wyoming sampled from 2002 to 2006.

stream order (Ruefenacht *et al.* 2005) and riparian vegetation classes in the LANDFIRE existing vegetation types data set (USFS 2009); extent of connected stream habitat (km) between probable fish passage barriers (Gelwicks *et al.* 2009); road density ( $\text{km km}^{-2}$ ) both in a 0.5-km buffer and in the contributing drainage basin [CENSUS 2000 Topologically Integrated Geographic Encoding and Referencing (TIGER) system roads data]; percent converted land in a 0.5-km buffer and in the contributing drainage basin [developed, pasture/hay, and cultivated crops classes, National Land Cover Dataset (NLCD) 2001, U.S. Geological Survey, Sioux Falls]; and percent water in the contributing drainage basin (water class, NLCD 2001, U.S. Geological Survey, Sioux Falls). Fish assemblages have been shown to be influenced by these factors within the study region (Martinez *et al.* 1994; Quist *et al.* 2006; Compton *et al.* 2008; Dauwalter *et al.* 2011b). All spatial data were viewed and processed in ArcGIS 9.3 software (ESRI, Redlands, CA, USA).

#### *Fish assemblage associations with oil and gas well density*

Fish assemblage relations with oil and gas well density in the Upper Colorado River Basin in Wyoming were evaluated using canonical correspondence analysis (CCA), which is a direct gradient analysis that uses a unimodal species model to explain variation in species composition using environmental variables (ter Braak 1986). Exploratory analysis showed maximum gradient length in the fish data (beta diversity) to be 4.8 and that using a unimodal ordination model was appropriate (Lepš & Šmilauer 2003; p. 51). A partial CCA (pCCA) allows variation attributable to certain environmental variables to be factored out to focus on the variables of interest. The associations between fish assemblage structure and all natural and anthropogenic environmental variables were evaluated using a pCCA, while also including eight-digit hydrologic unit code drainage basin (HUC 8; USGS & USDA 2009) as a conditional covariate to reduce the potential effect of spatial autocorrelation in the fish data. A second pCCA was then used to assess the specific effects of oil and gas well density in a 0.5-km buffer and in the contributing drainage basin, while partialling out, or conditioning on, the effects of all other covariates (including HUC 8). The species matrix used in the ordinations was comprised of  $\log_{10}(X + 1)$  transformed relative abundances of species that occurred in >3% of all sites sampled. The significance of pCCA axes (comparing the full model to the reduced model) and individual environmental variables was determined using permutation tests with 9999

permutations. Environmental variables and pCCA axes were considered significant at  $P \leq 0.05$ . Variance partitioning was then conducted to determine the fraction of variance in fish assemblage structure explained by the two oil and gas density variables, all other covariates, and variance indistinguishable between the two variable sets (Økland 1999). The ordinations were done using the VEGAN package in 'R', v2.14.1 (Dixon 2003; R Development Core Team 2011).

#### *Species and assemblage thresholds with oil and gas well density*

Canonical correspondence analysis is based on a unimodal model of species responses to environmental gradients, and while exploratory analyses suggested a unimodal ordination model was more appropriate than a linear model (e.g. principal component analysis or redundancy analysis), not every species in a community can be expected to have the same type of response to a stressor. Likewise, multivariate analyses can obscure responses of taxa with low frequency of occurrence and threshold-type responses to environmental gradients, and aggregate indices (e.g. species richness) can be insensitive to anthropogenic disturbances. Threshold Indicator Taxa ANalysis (TITAN) was developed to overcome these issues (King & Baker 2010; Baker & King 2010), and it was used to identify individual fish species and assemblage thresholds with oil and gas development in the Colorado River Basin, Wyoming.

Threshold Indicator Taxa ANalysis uses indicator species scores that integrate occurrence, abundance and directionality to identify species responses to environmental variables. Indicator species analysis is a widely accepted measure used to explain how groups of sample units explain species distributions (Dufrene & Legendre 1997). Scores are computed for each taxon for each group as the product of cross-group relative abundance (proportion of abundance across all sample units belonging to group  $i$ ) and within-group frequency of occurrence (proportion of sample units in group  $i$  with a positive abundance value). That is, occurrence frequency in a group is used to weight a taxon's relative abundance by how consistently it is observed in each group; a large abundance value in a group results in higher scores only if that taxon occurs with regularity in that group. To identify species-specific thresholds, TITAN identifies the optimum value of the environmental variable that partitions samples (sites) to maximise indicator species scores, similar to how classification and regression trees use a deviance reduction measure to partition sample units at a value of an environmental variable (De'ath & Fabricius 2000). To identify assemblage-level thresholds,

original indicator scores are then standardised as  $z$  scores [(individual score – mean)/SD] relative to the mean and SD of permuted samples along the environmental gradient. Standardisation using  $z$  scores emphasises relative changes in indicator scores and increases the contribution of rare species that often are down-weighted in other analyses (e.g. ordinations) despite having high sensitivity to the environmental gradient (Baker & King 2010). Cumulative  $z$  scores of species that collectively increase (or decrease) in response to the environmental variable indicate assemblage-level responses, and bootstrapping is used to estimate uncertainty of species-specific and assemblage-level thresholds.

Threshold Indicator Taxa ANalysis was applied to the fish assemblage data from the Upper Colorado River Basin in Wyoming to identify important species-specific and assemblage-level thresholds associated with oil and gas development. The same fish assemblage matrix (including the rare species) with  $\log_{10}(X + 1)$  transformed relative abundances described previously for the ordinations was used for the TITAN analysis, which was replicated twice with two variables: oil and gas well density within a 0.5-km buffer and well density within the cumulative upstream drainage basin. Species-specific thresholds to well densities were estimated by recursively partitioning samples across all values of well density and computing indicator species scores for each partitioned group. As described previously, threshold well densities (one threshold each for the two variables) were estimated to be the value at which indicator scores were maximised across samples. A total of 250 permuted estimates of species-specific threshold values was used to estimate the probability ( $P$  value) that an equal or larger indicator value could be obtained from random data;  $P$  values  $\leq 0.05$  were used to assess the significance of species-specific thresholds. Five hundred bootstrapped estimates were used to generate diagnostic indices for species-specific thresholds: purity and reliability. Purity is the proportion of bootstrap-estimated directional responses (+ or –) that agree with the observed response; pure indicators are consistently assigned the same response direction to the environmental variable (well density) regardless of abundance and the frequency distributions resulting from resampling of original data (Baker & King 2010). Reliability is the proportion of bootstrap estimates whose threshold values consistently result in  $P$  values below a user-defined probability level; reliable indicators are those with repeatable and consistently large maximum indicator values (Baker & King 2010). Reliable values were estimated to have  $P < 0.05$ . Negative assemblage-level thresholds were determined using the sums of negatively responding species ( $z^-$ ), and positive thresholds were determined using the sums

of positively responding species ( $z^+$ ). In each case, the assemblage-level threshold was estimated to be the well density at which the sum of  $z$  scores was maximised. The well density resulting in maximum sum( $z^-$ ) or sum( $z^+$ ) values correspond to the maximum aggregate change in frequency and abundance across species. Bootstrapped replicates were used to estimate the 5th and 95th percentiles associated with assemblage-level thresholds. The TITAN analysis was conducted using R v2.14.1 (R Development Core Team 2011) using the code provided by Baker and King (2010).

#### *Future oil and gas development threats to native fishes*

How native species might be threatened by future oil and gas development was evaluated by comparing known occurrences with anticipated and unrestricted forecasts of oil and gas development for Wyoming developed by Copeland *et al.* (2009, Fig. 2). Both forecasts were made using a spatially explicit Random Forest (Breiman 2001) model of oil and gas development potential that predicted producing versus non-producing wells as a function of six predictor variables: aeromagnetic, isostatic gravity and Bouguer gravity anomalies; geology; topography; and bedrock depth (Fig. 2b); the model had 81% cross-validated classification accuracy (Copeland *et al.* 2009). The spatial predictions of development potential (ranging from 0 to 1) and published projections from federal land management agencies were then used to develop anticipated and unrestricted build-out scenarios. The anticipated scenario was based on a 20-year reasonable foreseeable development projection from U.S. Bureau of Land Management (BLM) resource management plans (Fig. 2c). The unrestricted scenario allowed development in the upper quartile of development potential (model predictions = 0.75–1.0; Fig. 2d); the unrestricted scenario was used in addition to the anticipated scenario because BLM projections of development are often conservative (Copeland *et al.* 2009). Wells were placed into 1-km<sup>2</sup> landscape units with the highest potential first, then the next highest and so on while accounting for the number of existing wells and up to the maximum density of wells (16 ha<sup>-1</sup>). Development was constrained to occur outside of protected lands (e.g. national parks, designated wilderness, ‘no surface occupancy’ BLM lands). For the anticipated scenario, 95 867 wells were allocated per BLM field office. For the unconstrained scenario, 260 953 wells were allocated in areas with only high development potential (predictions from 0.75–1.0). The threat of future oil and gas development under each scenario to native fish species was then evaluated. Perceived threat of development to

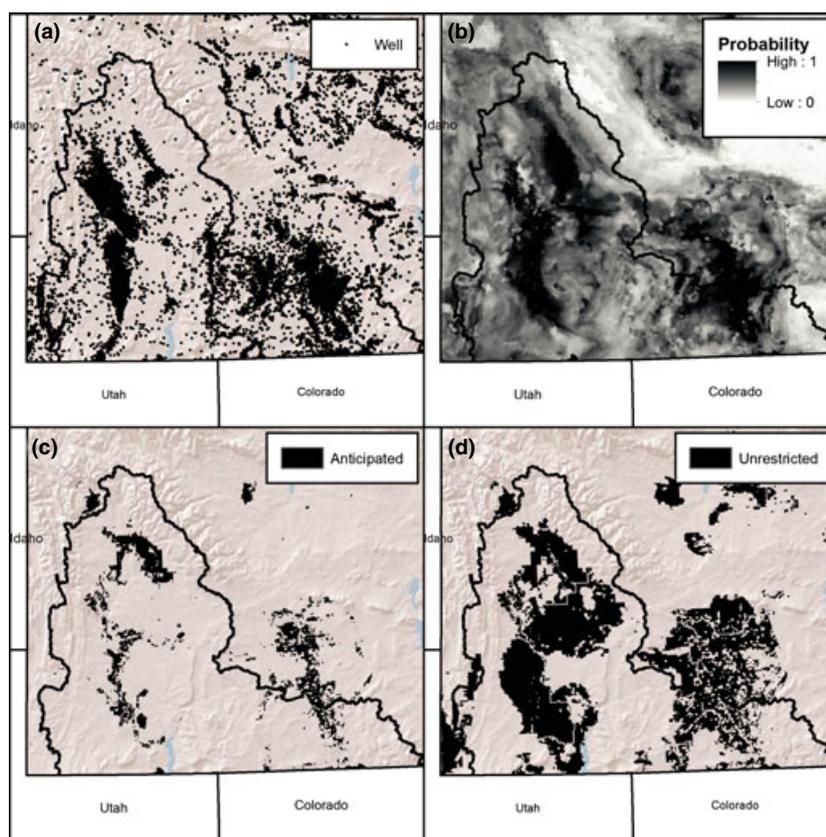
native species was determined by computing the percent of sites where each species occurred that intersected a landscape unit predicted for future oil and gas development under each scenario.

## Results

The Wyoming Game and Fish Department database contained occurrences of eight native species and 20 non-native species (Table 1). Of the 354 sites sampled, fish were collected only at 285 sites. Of the native fishes, the mountain sucker, *Catostomus platyrhynchus* (Cope), and the mottled sculpin, *Cottus bairdii* Girard, occurred most frequently at 60% and 47% of the 285 sites, respectively (Table 1). For non-native fishes, the white sucker, *C. commersonii* (Lacépède), occurred at 64% of sites and the redbreast shiner, *Richardsonius balteatus* (Richardson), at 56%. Burbot, *Lota lota* L., and kokanee, *Oncorhynchus nerka* (Walbaum), were collected at two sites (<1%), and smallmouth bass, *Micropterus dolomieu* L., was collected at only three sites (1%). Burbot, Bonneville cutthroat trout *O. c. Utah* (Richardson), channel catfish, *Ictalurus punctulatus* (Richardson),

kokanee, longnose sucker, *C. catostomus* Forster, leatherside chub, *Snyderichthys copei* (Jordan & Gilbert), smallmouth bass, and Yellowstone cutthroat trout, *O. c. bouvieri* (Jordan & Gilbert), occurred at <3% of sites and were omitted from the pCCAs owing to their rare occurrences.

Stream size and stream gradient represented the dominant environmental gradient influencing fish assemblage structure in the study area (pCCA Axis 1 in Fig. 3;  $P < 0.001$ ). Colorado River cutthroat trout, *O. c. pleuriticus* (Cuvier), and brook trout, *Salvelinus fontinalis* (Mitchill), occurred most often in small, high gradient streams and non-native common carp, *Cyprinus carpio* L., sand shiner, *Notropis stramineus* (Cuvier), Utah chub, *Gila atraria* (Girard), and native roundtail chub, *G. robusta* Baird & Girard, and flannelmouth sucker, *C. latipinnis* Baird & Girard, were more abundant in larger, low gradient rivers. Human disturbance was a significant secondary factor influencing fish assemblage structure, with lake chub, *Couesius plumbeus* (Agassiz), Utah chub, fathead minnow, *Pimephales promelas* (R.), and creek chub, *Semotilus atromaculatus* (Mitchill), being most abundant at sites with high road densities in



**Figure 2.** Existing oil and gas wells (a), oil and gas well development potential (b), anticipated oil and gas build-out scenario (c), and unrestricted build-out scenario (d) in the Upper Colorado River Basin, Wyoming. Development potential and build-out scenarios from Copeland *et al.* (2009).

**Table 1.** Fishes collected during a survey of 285 stream sites by Wyoming Game and Fish Department in the Upper Colorado River Basin, Wyoming

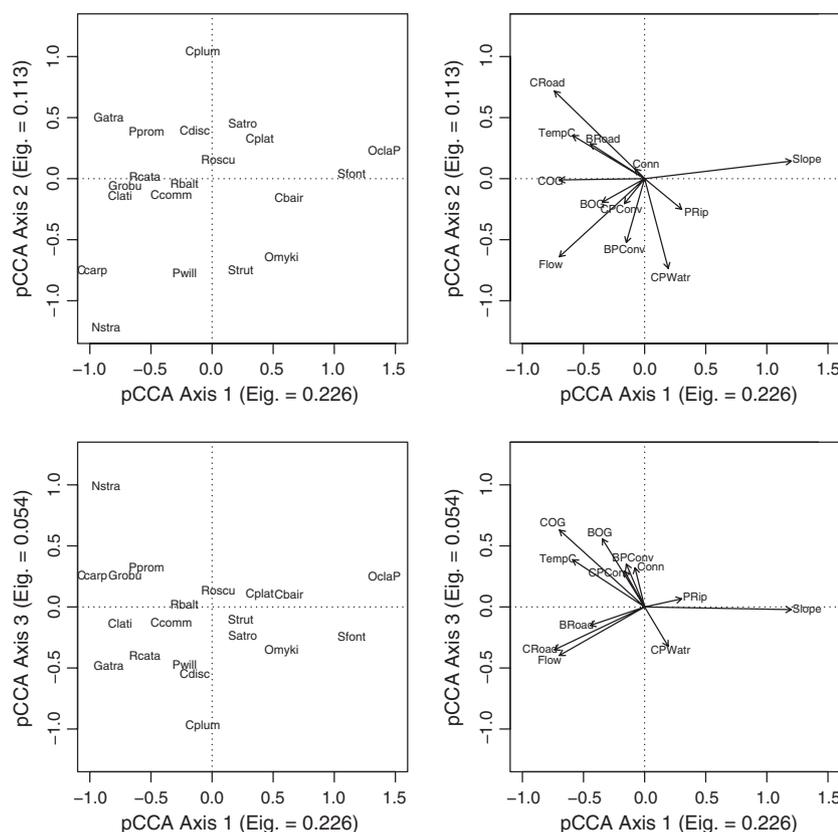
Native or introduced	Common name	Scientific name	Wyoming status (federal status)	Percent occurrence	
Native	Colorado pikeminnow*	<i>Ptychocheilus lucius</i> Girard	Extirpated (E)	0.0	
	Humpback chub*	<i>Gila cypha</i> Miller	Extirpated (E)	0.0	
	Bonytail*	<i>Gila elegans</i> Baird and Girard	Extirpated (E)	0.0	
	Roundtail chub*	<i>Gila robusta</i> Baird and Girard	NSS1	9.5	
	Speckled dace	<i>Rhinichthys osculus</i> (Girard)		30.5	
	Kendall Warm Springs dace*	<i>Rhinichthys osculus thermalis</i>	NSS1	0.0	
	Razorback sucker*	<i>Xyrauchen texanus</i> (Abbott)	Extirpated (E)	0.0	
	Bluehead sucker	<i>Catostomus discobolus</i> Cope	NSS1	7.0	
	Flannelmouth sucker	<i>Catostomus latipinnis</i> Baird and Girard	NSS1	28.4	
	Mountain sucker	<i>Catostomus platyrhynchus</i> Cope	NSS3	60.4	
	Colorado River cutthroat trout*	<i>Oncorhynchus clarkii pleuriticus</i> (Cope)	NSS2	8.8	
	Mountain whitefish	<i>Prosopium williamsoni</i> (Girard)	NSS4	10.5	
	Mottled sculpin	<i>Cottus bairdii</i> Girard	NSS4	46.7	
	Introduced	Common carp	<i>Cyprinus carpio</i> Linnaeus		9.5
		Creek chub	<i>Semotilus atromaculatus</i> Rafinesque		9.5
		Lake chub	<i>Couesius plumbeus</i> (Agassiz)		6.7
Leatherside chub		<i>Snyderichthys copei</i> (Jordan and Gilbert)		1.4	
Utah chub		<i>Gila atraria</i> (Girard)		7.7	
Fathead minnow		<i>Pimephales promelas</i> (Rafinesque)		38.6	
Longnose dace		<i>Rhinichthys cataractae</i> (Valenciennes)		13.0	
Redside shiner		<i>Richardsonius balteatus</i> (Richardson)		56.5	
Sand shiner		<i>Notropis stramineus</i> (Cope)		3.9	
Longnose sucker		<i>Catostomus catostomus</i> Forster		1.4	
Utah sucker		<i>Catostomus ardens</i> Jordan and Gilbert		0.0	
White sucker		<i>Catostomus commersonii</i> Lacépède		63.5	
Bonneville cutthroat trout		<i>Oncorhynchus clarkii Utah</i> (Suckley)		0.7	
Snake River cutthroat trout		<i>Oncorhynchus clarkii bouvieri</i> (Jordan and Gilbert)		2.5	
Rainbow trout		<i>Oncorhynchus mykiss</i> Walbaum		20.0	
Kokanee salmon		<i>Oncorhynchus nerka</i> (Walbaum)		0.7	
Brook trout		<i>Salvelinus fontinalis</i> (Mitchill)		15.8	
Brown trout		<i>Salmo trutta</i> Linnaeus		24.2	
Burbot		<i>Lota lota</i> (Linnaeus)		0.7	
Channel catfish		<i>Ictalurus punctatus</i> (Rafinesque)		2.1	
Smallmouth bass		<i>Micropterus dolomieu</i> Lacépède		1.0	
Paiute sculpin		<i>Cottus beldingii</i> Eigenmann and Eigenmann		0.0	

\* listed as imperilled by the American Fisheries Society (Jelks *et al.* 2008). Federal status E = endangered.

the upstream drainage basin (pCCA Axis 2 in Fig. 3;  $P < 0.001$ ). Sand shiner, common carp, mountain whitefish, *Prosopium williamsoni* (Girard), brown trout, *Salmo trutta* (L.), and rainbow trout, *O. mykiss* (Walbaum), were more abundant where there were more lentic water bodies (lakes and reservoirs) in the upstream drainage basin, more converted land in the stream buffer, and in larger streams and rivers (pCCA Axis 2 in Fig. 3). Oil and gas development explained a smaller, but still significant, amount of fish assemblage structure, where sand shiners, fathead minnows, common carp, and roundtail chub were more abundant in areas with high well densities (pCCA Axis 3 in Fig. 3;  $P < 0.001$ ). All environmental variables included in the pCCA explained

significant variation in fish assemblage structure ( $P < 0.050$ ), except percent riparian buffer ( $P = 0.079$ ), and variance inflation factors were all  $< 1.8$  indicating linear independence among covariates.

Fish assemblage structure was significantly associated with oil and gas well densities, both within a 0.5-km buffer and within the contributing drainage basin, in the Colorado River Basin, Wyoming. Oil and gas well densities in a 0.5-km buffer ranged from 0 to 3.7 km<sup>-2</sup> across sites, and from 0 to 1.1 km<sup>-2</sup> within the contributing drainage basins. Associations between species relative abundance and well densities included binomial, wedge-shaped and unimodal patterns (Fig. 4). As revealed by the pCCA focusing solely on the oil and gas

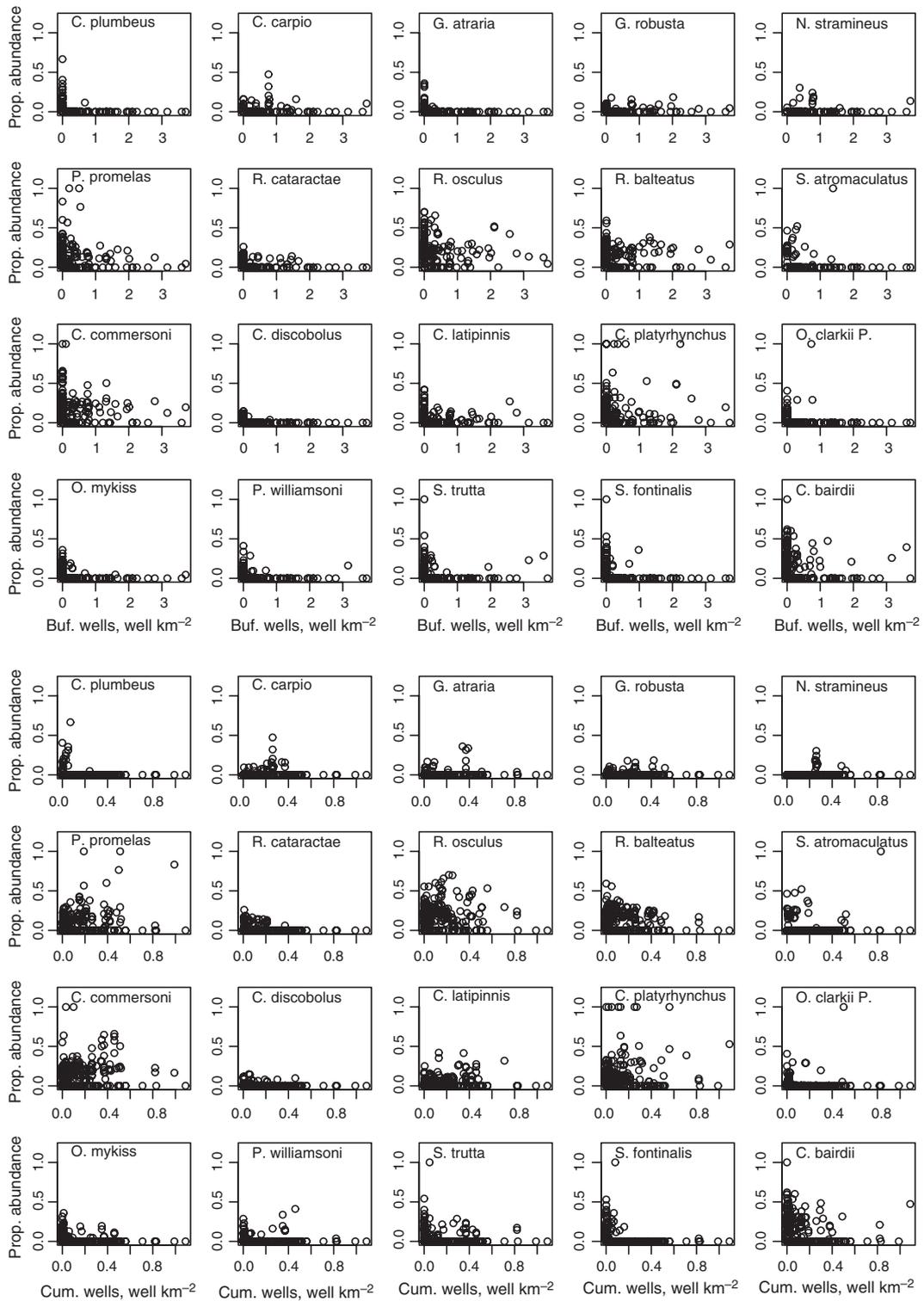


**Figure 3.** Biplots of partial canonical correspondence analysis (pCCA) axes 1 and 2 (top panels), and axes 1 and 3 (bottom panels) summarising fish assemblage structure (relative abundance) in relation to several environmental gradients in the Upper Colorado River, Wyoming. Species codes are first letter of genus then first four letters of specific epithet. Variables codes are: CRoad = road density in upstream drainage basin; BRoad = road density in 0.5-km buffer; TempC = mean annual air temperature; Conn = extent of connected stream habitat; Slope = stream gradient; COG = oil and gas well density in upstream drainage basin; BOG = oil and gas well density in 0.5-km buffer; CPCov = percent converted land in upstream drainage basin; BPCov = percent converted land in 0.5-km stream buffer; Flow = mean annual discharge; CPWatr = percent water in upstream drainage basin; PRip = percent riparian vegetation. EIG = eigenvalue.

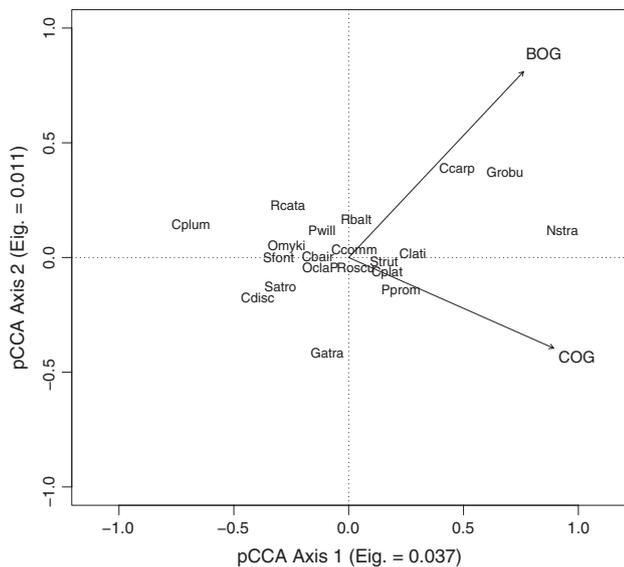
well density variables, the non-native common carp and sand shiner and native roundtail chub had higher relative abundances in areas with high oil and gas well densities within a 0.5-km buffer; non-native lake chub and Utah chub and native bluehead sucker, *C. discobolus* Cuvier, were more abundant at sites with lower well densities in a 0.5-km buffer (Fig. 5). Non-native sand shiners were more abundant when well densities within the contributing drainage basin were high, whereas non-native lake chub and longnose dace, *Rhinichthys cataractae* (Val.), were less abundant. The pCCA axis 1 was significant ( $P < 0.001$ ) whereas axis 2 was not ( $P = 0.151$ ). Oil and gas well density in a 0.5-km buffer was significantly related to fish assemblage structure ( $P < 0.002$ ), as was oil and gas well density within the contributing drainage basin ( $P < 0.001$ ). Variance partitioning showed the two oil and gas variables together uniquely explained only 6.4% of the total explainable variance in fish assemblage structure across sites, the covariates (natural landscape

and other anthropogenic variables) explained 86.3% of the explainable variance, and the remaining 7.3% was indistinguishable between the two variable sets (Table 2).

Four negative indicator species and four positive indicators species had threshold responses to oil and gas well densities in a 0.5-km buffer as identified by the TITAN analysis. Even small amounts of development impacted negative indicator species, as the sum( $z^-$ ) scores peaked slightly above 0.0 wells  $\text{km}^{-2}$  in a 0.5-km buffer (Fig. 6a) and the assemblage-level threshold (median of species-specific thresholds) was 0.15 wells  $\text{km}^{-2}$  (Table 3). Four species declined, that is had negative  $z$  scores ( $z^-$ ), at low levels of oil and gas development (0–0.3 wells  $\text{km}^{-2}$ ) with high purity ( $>0.95$ ) and reliability ( $>0.90$  of bootstrap replicates at  $P < 0.05$ ); two species were native (mottled sculpin, bluehead sucker) and two were non-native salmonids (brook trout, rainbow trout) (Fig. 6c; Online Appendix).



**Figure 4.** Biplots of oil and gas well densities, within a 0.5-km buffer (top 20 panels) and in the cumulative upstream drainage basin (bottom 20 panels), and fish species relative abundance in the Upper Colorado River, Wyoming.



**Figure 5.** Biplot of partial canonical correspondence analysis (pCCA) axes 1 and 2 summarising fish assemblage structure (relative abundance) in relation to oil and gas well density in a 0.5-km buffer (BOG) and in the contributing drainage basin (COG) in the Upper Colorado River, Wyoming. Species codes are first letter of genus then first four letters of specific epithet. EIG = eigenvalue.

**Table 2.** Variance in fish assemblage structure attributable to oil and gas well density, natural and anthropogenic influences (covariates), and shared variance in the Upper Colorado River Basin, Wyoming

Factor	Number of variables	∑ canonical eigenvalues	% variance	Mean% per variable
Oil and gas well density	2	0.048	6.4	3.2
Natural and anthropogenic variables (covariates)	11	0.645	86.3	7.8
Oil and gas ∩ covariates	13	0.055	7.3	0.6

For the positive indicator species, the plot of  $\text{sum}(z+)$  scores had a broad curve indicating a less distinct assemblage-level threshold for positively responding species (Fig. 6a); the estimated peak was  $0.73 \text{ wells km}^{-2}$  but with a broad inter-quartile range (Table 3). The four positive indicator species ( $z+$ ) with high purity and reliability included one native species, the roundtail chub (Fig. 6c).

By contrast, more species appeared to have threshold responses to oil and gas development within the upstream drainage basin. Again,  $\text{sum}(z-)$  scores peaked near  $0.0 \text{ wells km}^{-2}$  indicating that any amount of

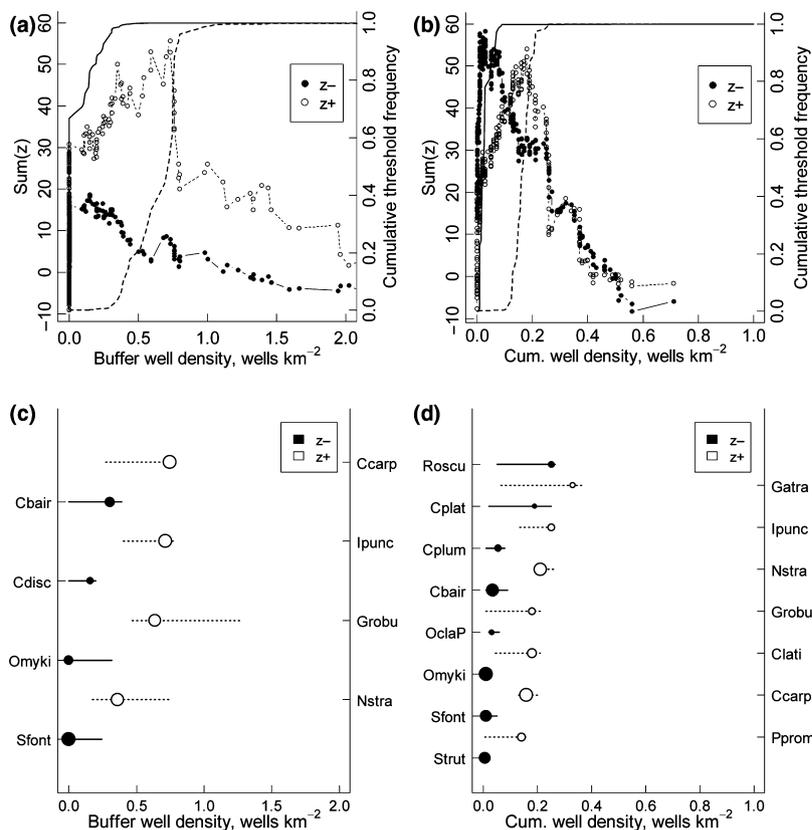
upstream development begins to impact negative indicator species (Fig. 6b, Table 3). Eight species that had negative threshold responses ( $z-$ ) between  $0.0$  and  $0.25 \text{ wells km}^{-2}$  with high purity ( $>0.95$ ) and reliability ( $>0.90$  at  $P < 0.05$ ), four of which were native and three others were introduced salmonids (Fig. 6d). The distribution of  $\text{sum}(z+)$  scores indicated a less distinct threshold for positive indicator species (Fig. 6b), with eight positive indicator species – two that were native – having high purity and reliability; the assemblage-level threshold was estimated to be  $0.18 \text{ wells km}^{-2}$  (Table 3).

Among the eight native species collected, the roundtail chub and flannelmouth sucker occurred most often in areas likely to be developed for oil and gas in the future regardless of the development scenario (Fig. 7). Both species have an imperilled status (Table 1). By contrast, the cold-water Colorado River cutthroat trout had a low percent of occurrences in areas likely to be developed in both scenarios. The percent of sites currently occupied by flannelmouth sucker, bluehead sucker, and roundtail chub at risk to development increased most (27, 25, and 22%, respectively) between the anticipated and unrestricted development scenarios.

**Discussion**

This study documented how fish assemblage structure is associated with oil and gas development across a broad landscape. Fish assemblage structure was not as strongly related to oil and gas development in the Colorado River Basin, Wyoming as it was to other natural and anthropogenic factors. However, there were still significant associations with development, including negative ones, and evidence of negative threshold responses by some species to low levels of development. Although negative effects appear to not be pervasive across the entire regional fish assemblage, there appears to be some potential for individual development projects to have negative impacts on a subset of the assemblage. In addition, the native roundtail chub and bluehead sucker have declined in distribution (~50% of historical distributions; Bezzerides & Bestgen 2002); they were only collected at ~5% of all sites sampled (out of 354), and those sites were in areas projected for future development. Thus, future development projects could have a disproportionate impact on these species’ ranges in Wyoming.

Other studies have also shown oil and gas development to only have subtle effects of fish assemblage structure at the landscape scale. Davis *et al.* (2010) found no significant differences in fish assemblage structure metrics between coal-bed natural gas development sites and control sites in tributaries to the Powder and



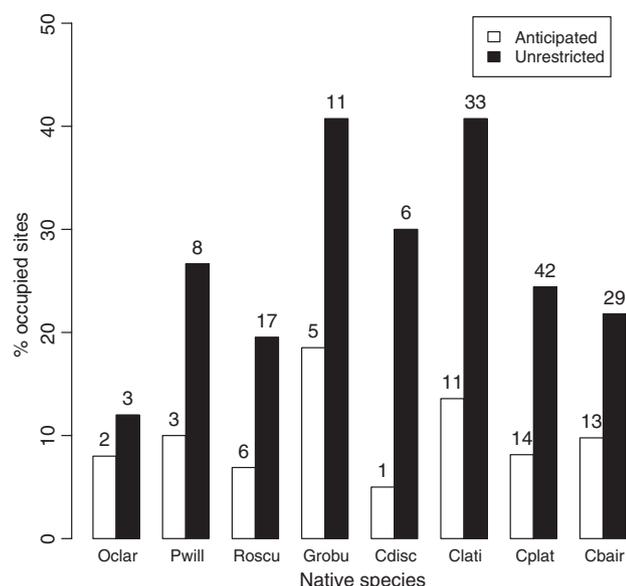
**Figure 6.** Threshold Indicator Taxa ANalysis (TITAN) results showing fish assemblage threshold responses to oil and gas well densities in a 0.5-km buffer (panels a, c) and in the cumulative upstream drainage basin (panels b, d). Panels a and b show sum( $z^-$ ) and sum( $z^+$ ) scores for negative (filled circles) and positive (open circles) indicator species, respectively, across all thresholds for oil and gas well densities. Lines are cumulative frequency distributions for oil and gas well density thresholds for negative (solid) and positive (dashed) indicator species across 500 bootstrapped replicates. Panels c and d show pure (>0.95) indicator species plotted in increasing order with respect to oil and gas well densities. Filled circles indicate negative indicator species ( $z^-$ ) and open circles indicate positive indicator species ( $z^+$ ). Symbol sizes are proportional to  $z$  scores. Horizontal lines indicate 5th and 95th percentiles among 500 bootstrapped replicates. Species codes are first letter of genus then first four letters of specific epithet.

**Table 3.** Threshold Indicator Taxa ANalysis fish assemblage-level thresholds estimated in response to oil and gas well densities within a 0.5-km buffer and within the cumulative upstream drainage basin in the Colorado River Basin, Wyoming. Percentiles estimated from 500 bootstrapped replicates.

Oil and gas well density (# km <sup>-2</sup> )	Observed	5%	50%	95%
0.5-km buffer				
Sum( $z^-$ )	0.15	0.00	0.00	0.29
Sum( $z^+$ )	0.73	0.38	0.72	0.80
Cumulative upstream				
Sum( $z^-$ )	0.03	0.01	0.02	0.07
Sum( $z^+$ )	0.18	0.13	0.17	0.21

Tongue rivers, Montana-Wyoming, USA. Among a multitude of measures, they only found magnesium, alkalinity, bicarbonate, sulphate and total dissolved solid concentrations to differ between development and

control streams, and stream conductivity to be negatively related to index of biotic integrity scores (Bramblett *et al.* 2005); these water quality constituents were negatively associated with biotic integrity in other regions (e.g. central U.S.; Dauwalter *et al.* 2003). Water produced from wells can alter groundwater below unlined storage impoundments, with increased sulphate, bicarbonate, sodium, magnesium ions and total dissolved solid concentrations from 5000 to 100 000 mg L<sup>-1</sup> (Healy *et al.* 2011). By contrast, Davis *et al.* (2010) found negative relations between number of gas wells and gas well density in the upstream catchment and native species richness, catostomid and ictalurid richness, number of long-lived species and familial richness. They concluded that although coal-bed methane development did not have a wide-spread effect on fish assemblage structure in their study area, subtle increases in ion concentrations and salinity could exacerbate naturally high salinity levels in some of their prairie streams and



**Figure 7.** Percent of native species occurrences overlapping areas predicted to be developed for oil and gas under anticipated and unrestricted build-out scenarios (from Copeland *et al.* 2009). Species codes are first letter of genus then first four letters of specific epithet. Number of occupied sites predicted for development under each development scenario noted above each bar.

decrease fish diversity as salinity intolerant species are extirpated over time.

It is unclear why some species, including native species like the roundtail chub, showed positive associations with oil and gas well densities. Dauwalter *et al.* (2011b) explained the positive association between well densities and roundtail chub in this data set to be a result of chubs having declined in distribution because altered streamflows and hydrogeomorphic processes have reduced the abundance of pool habitat (Gaeuman *et al.* 2005), and as a consequence remaining individuals now aggregate near oil and gas infrastructure (e.g. rock-armoured pipeline crossings) that artificially creates the deep pools and rocky substrates preferred by the species (Bower *et al.* 2008). Other non-native and rare species, like the common carp, were only collected in larger rivers upstream of Flaming Gorge Reservoir and in the Little Snake River near the Wyoming-Colorado border. These clustered occurrences could reflect introduction histories (*sensu* Rahel 2004) or emigrants from nearby reservoir populations and, therefore, could coincidentally be found at these sites that also have high concentrations of oil and gas wells. The sand shiner also showed a positive association; the species showed good survival in sentinel cages in fishless stream influenced by coal-bed methane produced water in the Powder River basin (Davis *et al.* 2010), but, similar to the common carp, the sand shiner was only collected in

the Little Snake River where there are numerous oil and gas wells. Future research is needed to elucidate the mechanisms behind these unexpected relationships.

While the constrained ordination revealed that oil and gas development influenced fish assemblage structure less than other environmental factors, the TITAN analysis showed some individual species to have significant threshold responses in the Colorado River Basin in Wyoming. It showed negative responding fishes (negative  $z$  scores) to have very low thresholds to oil and gas development ( $0.3\text{--}0.15$  wells.km<sup>-2</sup>), including sensitive native species (bluehead sucker) and non-native salmonid sport fishes. This suggests that development should be prohibited, or at least be done in ways that minimise aquatic impacts, in river basins with high native fish values or important recreational trout fisheries. Threshold-type responses by fish assemblages have been used to inform management of other human activities, such as harvest of riparian vegetation (Jones *et al.* 1999) and land use planning (Brenden *et al.* 2008).

Considering future threats while developing conservation plans for native species is becoming increasingly important (Wilson *et al.* 2005). Land use conversion, mining and climate change have all been considered important in conservation planning and are useful in proactive planning efforts (Williams *et al.* 2007; Theobald 2010). Copeland *et al.* (2009) used the same projections to show that future oil and gas development could result in a 7–19% decline in sage grouse populations, and they suggested that projections could be used by decision makers to minimise development impacts to the species. Future development scenarios were also coincident with a high proportion of the few sites where some native fish species occur. Although oil and gas development does not appear to have pervasive impacts on the entire regional fish community, some species have negative threshold responses and there could be localised impacts owing to differences in well development and operation. Furthermore, the difference between the two development scenarios showed that already sensitive species are most at risk if development was to proceed at levels beyond those specified in, for example, BLM resource management plans. This suggests that, where development is likely to exceed resource plan projections, land managers should carefully consider unforeseen impacts to imperilled aquatic species and existing populations should be monitored if development occurs nearby.

River catchments with high development potential and high native fish diversity can also be the focus of protective management. For example, Muddy Creek (Yampa Basin) in south-central Wyoming has been identified as a stronghold for roundtail chub, bluehead sucker and flannelmouth sucker, and is managed for native fishes

(Gelwicks *et al.* 2009; Dauwalter *et al.* 2011a). The drainage basin has some areas with high development potential. Identifying river catchments, such as Muddy Creek, that have native fish values and/or particular species with negative threshold responses could help focus land protection legislation (Saunders *et al.* 2002) or simply highlight areas where land management should be compatible with native fish goals (Williams *et al.* 2011). This is especially true where development is likely to trigger important biological thresholds and exceed development levels specified in resource management plans of land management agencies. Roundtail chub, bluehead sucker, and flannelmouth sucker were all disproportionately represented in the unrestricted development scenario. Given the status of these species, management should strive to avoid or minimise development impacts where remnant populations occur.

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