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2016

This article was originally published at:
http://dx.doi.org/10.1016/j.gecco.2016.09.008

Citation for this paper:

Frid, A., McGreer, M., Haggarty, D.R., Beaumont, J. & Gregr, E.J. (2016). Rockfish size and age: The crossroads of spatial protection, central place fisheries and indigenous rights. *Global Ecology and Conservation,* 8, 170-182.
http://dx.doi.org/10.1016/j.gecco.2016.09.008

Global Ecology and Conservation 8 (2016) 170–182

Contents lists available at ScienceDirect

Global Ecology and Conservation

journal homepage: www.elsevier.com/locate/gecco

Original research article

Rockfish size and age: The crossroads of spatial protection, central place fisheries and indigenous rights

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ARTICLE INFO

Article history:
Received 18 August 2016
Received in revised form 18 September 2016
Accepted 18 September 2016
Available online 3 October 2016

Keywords:
British Columbia
Central place foraging
Fisheries
Indigenous culture and marine resources
Rockfishes
Spatial protection

ABSTRACT

Indigenous people harvest wild species for food and cultural practice, fundamentally linking biodiversity conservation and indigenous rights. Rockfishes (*Sebastes* spp.) are culturally significant to indigenous people (or First Nations) of coastal British Columbia (BC), Canada, who regulate their harvest under traditional governance structures. First Nations elders, however, have observed a decline in the body sizes and abundance of rockfishes, which coincides with increased exploitation by non-indigenous fishers. Rockfishes are vulnerable to overexploitation because fecundity and offspring quality increase with maternal size or age, yet fisheries truncate size and age structure. During 2006, 2007 and 2013–2015, we worked with the Wuikinuxv, Nuxalk, Heiltsuk and Kitasoo/Xai'Xais First Nations of BC's Central Coast, examining rockfish population characteristics at 282 of their fishing sites. We used hook-and-line gear to collect fishery independent data, and sampled landings from First Nations subsistence fishers. Spatial fishery closures served as experimental treatments. We also applied central place foraging theory to predict declines in size, age and abundance with increasing distance from recreational fishing lodges and other ports. Analyses used linear mixed models and controlled for environmental variables. Our results suggest that spatial closures for commercial and recreational fishers led to greater size and abundance of some, but not all rockfishes, possibly due to interspecific differences in the extent to which closures contain suitable habitat, effects of non-compliance, or other factors. Notably, Yelloweye Rockfish (*Sebastes ruberrimus*), a species key to indigenous diets, were 21% larger inside than outside spatial closures. Possibly reflecting cumulative fishery exploitation, however, old-aged Yelloweye Rockfish were rare. Fishery impacts on size and relative abundance decreased at sites that required longer travel times and greater fuel costs for recreational fishers to exploit, but only for the longest-lived species (size responses) and for long-lived species analysed in aggregate (abundance responses). Measures for protecting indigenous access to rockfishes include evaluation of habitat suitability and compliance within spatial closures, improved understanding of recreational fishery impacts, and treating old-age and large size structures as explicit management objectives. Our study contributes to a global effort to integrate indigenous cultural values with biological conservation.

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http://dx.doi.org/10.1016/j.gecco.2016.09.008

1. Introduction

Modern indigenous people embrace new technologies and do not isolate themselves from contemporary culture and economy, yet maintain a tradition of interconnection with wild species. Their gathering of edible and medicinal plants, their hunting and fishing, not only provide physical sustenance but also sustain worldviews that have been rooted in place for many generations. The implication is that over-exploitation and other forms of biodiversity loss threaten cultural diversity (Turner et al., 2000; Poe et al., 2014; Sangha et al., 2015). Some national governments recognize this connection, at least implicitly. Canada's constitution, for instance, grants indigenous fisheries for food, social and ceremonial (FSC) purposes priority access to marine resources (DFO, 2007a). Fulfilling this legal obligation, however, can be difficult to achieve, as indigenous, commercial and recreational fishers often target the same species (e.g. Frid et al., 2016).

Marine protected areas (MPAs) and other forms of spatial fishery closures have broad benefits for biodiversity conservation (Edgar et al., 2014). They are a management tool that can promote the recovery and sustainable use of species important to indigenous people (Zurba et al., 2012; Frid et al., 2016). Most of the world's oceans, however, still are and will likely remain open to fisheries. Thus, it is important to examine not only whether spatial closures are meeting their conservation objectives, but also what factors affect variation in fishery pressure outside closures.

Some fisheries might conform to the foraging model developed by behavioural ecologists to examine decisions made by animals foraging repeatedly from a central place, such as a nest, then returning to provision young. Theory and empirical evidence suggest that these decisions optimize travel costs, such as time and energy, and expected gain at a foraging site (Ydenberg, 2007; Houston, 2011). Fisheries expected to conform to a ''central place fishing'' model include recreational, artisanal and subsistence fisheries operating from small boats and using ports or other coastal infrastructure to repeatedly start and end fishing trips lasting a single day. The model may be less applicable to most large-scale commercial fisheries, which operate from larger live-aboard vessels that exploit numerous and distant areas before returning to port. When fishers conform to a central place fishing model, the cumulative number of trips to a site might decrease as fuel and time costs of travel increase with distance. Consequently, the impact on fish stocks of central place fishers might weaken with increasing distance from port (Stelzenmuller et al., 2008; Bellquist and Semmens, 2016; Haggarty et al., 2016a).

As a contribution to the global effort to integrate cultural values into ecosystem based management (Poe et al., 2014), we conducted a case study that connects the concepts of spatial protection, central place fishing and indigenous rights to marine resources. We focused on rockfishes (*Sebastes* spp.), which are culturally significant to the four indigenous groups (or First Nations) of British Columbia's (BC) Central Coast (Fig. 1): Heiltsuk, Nuxalk, Kitasoo/Xai'Xais and Wuikinuxv.

Conservation of rockfishes is difficult. Many species have very long lifespans and late maturity (Love et al., 2002). Like other groundfish, female rockfishes produce larvae throughout their lives, and offspring quality and annual fecundity increases with maternal size or age (Love et al., 1990; Berkeley et al., 2004a). These life history traits appear to be adaptations to long-term environmental variability. However the same traits also increase vulnerability to large-scale fisheries, which generally remove the largest and oldest individuals. The loss of females that are large and old – those that contribute the most offspring to the next generation – has been linked to the collapse of many groundfish populations (Berkeley et al., 2004b; Beamish et al., 2006; Hixon et al., 2014).

In recent decades, First Nations elders have observed a decline in the body sizes and abundance of rockfishes at their traditional fishing sites of BC's Central Coast. These declines coincide with a period of rapid expansion of commercial fisheries that began in the late 1970s. The expansion ''outpaced management's effort controls'' until more conservative fishery restrictions were implemented in the early 2000s (Yamanaka and Logan, 2010). Despite recent reductions in commercial fishery mortality, rockfish recovery may take decades (Berkeley et al., 2004b) and the impact of recreational fisheries is largely unknown. First Nations, therefore, remain concerned about their reduced access to rockfishes in general and to Yelloweye Rockfish (*Sebastes ruberrimus*) in particular. Yelloweye Rockfish are highly prized in traditional diets and recognized by Canada's Species at Risk Act as a species of special conservation concern (DFO, 2015).

The impact of fisheries on rockfish reproductive potential (O'Farrell and Botsford, 2006) is a general problem for which spatial fishery closures may provide partial solutions (Berkeley et al., 2004b; Hixon et al., 2014). Consistent with this notion, the relative abundance and sizes of rockfishes have increased over time inside spatial closures (Keller et al., 2014; Starr et al., 2015). Accordingly, between 2004 and 2007 Fisheries and Oceans Canada (DFO) established a network of Rockfish Conservation Areas (RCAs)—spatial closures aimed to promote rockfish recovery in British Columbia. RCAs exclude commercial and recreational hook-and-line fisheries and bottom trawl fisheries (Yamanaka and Logan, 2010). Indigenous FSC fisheries, which have legal priority (DFO, 2007a) and regulate under traditional governance structures (Trosper, 2003; Lepofsky and Caldwell, 2013), are allowed within RCAs. Central Coast First Nations are working with provincial and federal governments to ensure that RCAs, future MPAs and other forms of fishery management meet their objectives for fisheries sustainability and bio-cultural conservation (Canada-British Columbia, 2014; MaPP, 2015).

To address the conservation concerns of First Nations and inform management decisions, we designed a field study that tested predictions from the hypothesis that spatial variation in fishery pressure affects the average size, age and abundance of rockfishes. To a lesser extent, we also examined Lingcod (*Ophiodon elongatus*), which overlap spatially with rockfishes and are also culturally significant to First Nations. Though much shorter-lived and faster to recover than most rockfishes, Lingcod are also easy to overfish (Berkeley et al., 2004b).

Our first prediction was that average length and age would be greater inside than outside RCAs, which in BC's Central Coast were established in 2004 and 2005. We also predicted that relative abundance, as estimated by catch-per-unit effort (CPUE),

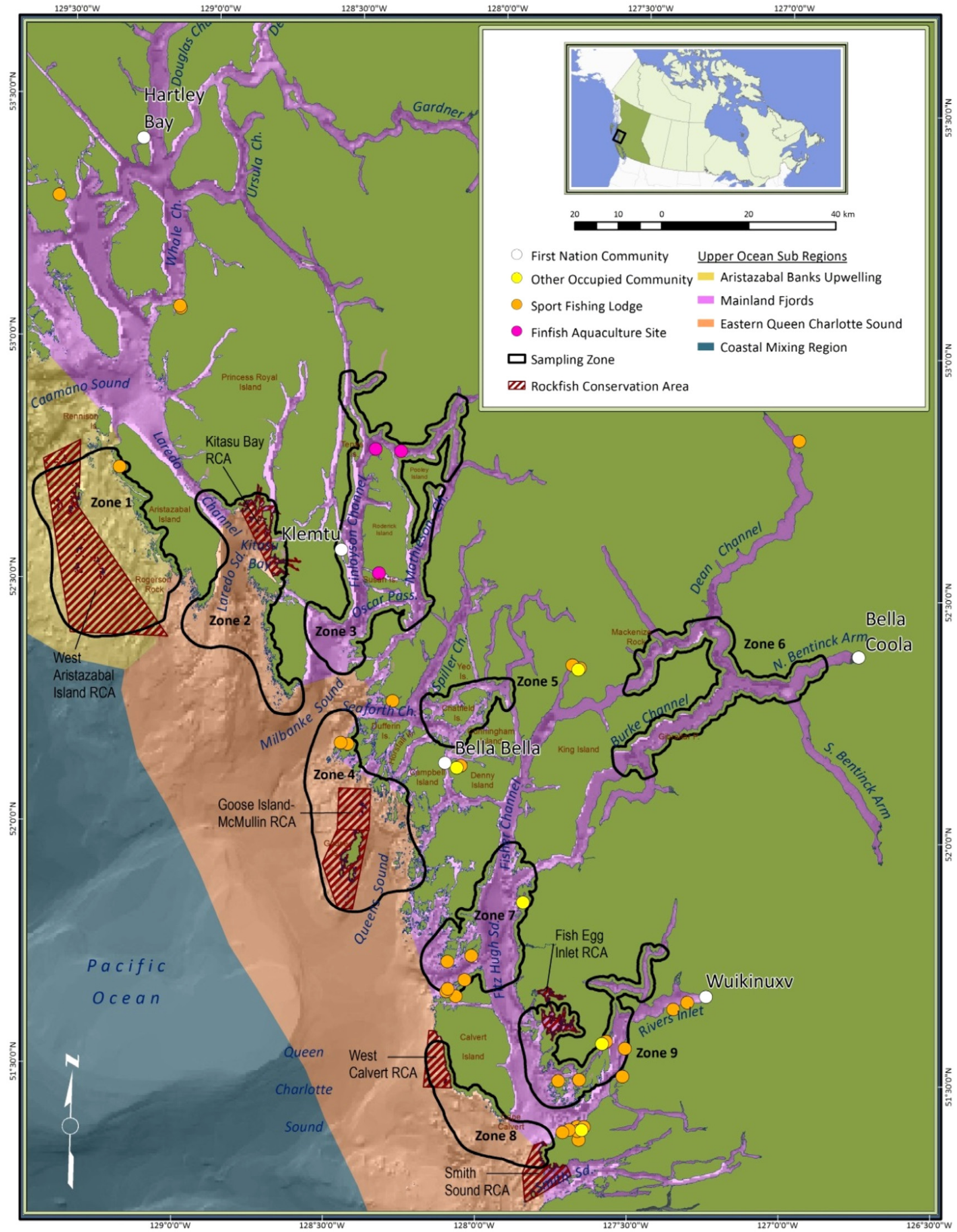

Fig. 1. Study area map, including the locations of fishery bases, Rockfish Conservation Areas, and Ocean Subregions. Sampling zones, rather than actual sampling sites, are displayed to protect sensitive locations used by First Nations. Numbers of sites sampled per zone (zn) were: zn1 = 21, zn2 = 43, zn3 = 32, zn4 = 110, zn5 = 15, zn6 = 24, zn7 = 8, zn8 = 13, zn9 = 16. The Heiltsuk, Wuikinuxv, Kitasoo/Xai'Xais, and Nuxalk First Nation reside, respectively, in Bella Bella, Wuikinuxv, Klemtu and Bella Coola. Also shown is Hartley Bay, where the Gitga'at First Nation resides.

would be greater inside than outside RCAs, but this effect would be weaker for long-lived species (e.g. Yelloweye Rockfish) than for shorter-lived species (e.g. Lingcod). The rationale is that long-lived species are more vulnerable to overfishing and require longer recovery from over-exploitation (Berkeley et al., 2004b).

To better understand factors affecting the current status of rockfishes and Lingcod outside RCAs, we applied the framework of central place fishing and hypothesized that areas farther from a fishery base (e.g. recreational fishing lodges, coastal communities) would have lower cumulative fishing impacts than closer areas. Based on prior studies, we assumed that such distance effects would reflect primarily impacts from recreational fishers (Bellquist and Semmens, 2016; Haggarty et al., 2016a) and, to a lesser extent, from indigenous fishers regulated by traditional governance structures. We predicted that average length, age and CPUE would increase with distance from the nearest fishery base. Given that species with longer lifespans are more vulnerable to overfishing, however, we expected the effect of distance to nearest fishery base on CPUE to be stronger for longer-lived than for shorter-lived species.

Finally, given the importance of maintaining old-age structure to the sustainability of groundfishes (Berkeley et al., 2004b; Beamish et al., 2006; Hixon et al., 2014), we described ages for the two longest-lived and culturally most significant species in our analysis, Quillback (*Sebastes maliger*) and Yelloweye Rockfishes, at sites important to indigenous fishers.

2. Methods

While our focus was on fishery related-predictors, environmental and habitat factors also affect the abundance, size and age of Lingcod and rockfishes. Lingcod and most rockfishes prefer structurally complex rocky habitats (Cass et al., 1990; Love et al., 2002). Some rockfishes undergo ontogenetic habitat shifts such that older, larger fish are found deeper than younger fish (Love et al., 2002). Further, tides, currents and seasons may affect distribution and behaviour (Carlson and Barr, 1977; Tolimieri et al., 2009). Accordingly, our study design controlled for seasonality and included habitat and environmental variables as predictors.

Field sampling took place from small boats ($\leq$8 m long) during 2006, 2007 and 2013–2015. It encompassed early spring to fall (March–October) at a total of 282 sites spread throughout BC's Central Coast (Fig. 1). Thirty seven percent of sites were within Rockfish Conservation Areas established in 2004 or 2005, while the remainder were open to all fisheries. Our methods focused on older juveniles and adults (i.e. total length $>$15 cm).

We used fishery independent methods to estimate catch per unit effort (CPUE) and collect body size and age data at sites that First Nations identified – through marine planning processes (MaPP, 2015), workshops, structured interviews, or informal discussions – as important to FSC fisheries for rockfishes and Lingcod. That is, First Nations identified areas where they currently fish, or fished historically prior to local declines, for these species. Implicitly, this focused our sampling on the rocky substrates preferred by rockfishes and Lingcod (Cass et al., 1990; Love et al., 2002). For fishery independent sampling ($N = 236$ sites), we used rods equipped with standardized lures (tailed jigs weighing 227 g or anchovy-shaped lures weighing 284–312 g) to fish demersally at depths of 10–200 m (mean = 47 m). The most common depth ranges were 31–50 m (37%) and 51–75 m (28%). Seven percent of samples were 76–100 m deep and 4% were deeper. Sampling duration was 30 min for the first three years of the study (73% of samples), but reduced to 15 min starting in 2014. The shorter samples allowed us to cover more sites with limited field time, and analyses account for differences in duration. Sampling time counted only when hooks fished near the bottom (i.e., time stopped while the hook was lowered, raised, or out of the water). When more than one fisher was involved, sampling duration equalled the sum of their times. CPUE was standardized as the number of fish caught per 15 min of sampling (i.e., catches obtained during 30 min samples were divided by 2).

We also collected body size and age data opportunistically from the catch of indigenous FSC fishers ($N = 46$ sites). We either participated in the fishery, or fishers made their catch and information available to us. FSC fishers used baited hooks on longlines or hook-and-line gear with un-baited hooks and a diversity of jigging lures. They fished at depths of 5–120 m (mean 49 m).

Longline sets consisted of 550–1100 m lengths of groundline equipped with 100–200 circle hooks (generally size 14/0) on gagnions spaced by 3–5 m. Pacific cod (*Gadus macrocephalus*), Pacific octopus (*Enteroctopus dofleini*) or Pacific salmon (*Oncorhynchus* spp.) were used as bait and soak times were two to three hours. Fishing depths ranged from approximately 50–100 m (mean 84 m). Longline sets targeted Pacific halibut (*Hippoglossus stenolepis*) and encompassed soft substrates (e.g., sand or mud) primarily, but included isolated rocky habitats where rockfishes were caught.

2.1. Site variables

At each sampling site we recorded geographic position, date, time and depth of sampling. For fishery independent samples we also recorded sampling duration.

Based on location we determined whether sites were inside or outside RCAs (DFO, 2007b) and – to control for broad-scale variation in oceanographic conditions – we assigned each site to one of the following upper ocean subregions: Aristazabal Banks Upwelling, Eastern Queen Charlotte Sound, or Mainland Fjords (BCMCA, 2011).

After field data collection, we characterized habitats using a spatial model that used random forest classification of bathymetric and oceanographic data to predict, with 20 m^2 resolution, the following physical characteristics: substrate type (rock, mixed coarse, sand, or mud), rugosity (an index of structural complexity), and maximum bottom speeds for tides and currents (Haggarty, 2015; Gregr et al., 2016). Locations in the field and in the spatial model were matched closely when jigging from a stationary boat, the method producing most of our data (96% of sites and 81% of specimens). The match, however, was coarser for FSC longlines (4% of sites and 19% of specimens), which spanned up to one linear km (and thus multiple model cells). Because we targeted the rocky habitat preferred by rockfishes, soft substrates encompassed only 34% of sites.

Next, we measured distances required to travel by boat between each of our sampling sites and fishery bases: coastal infrastructure where fishers initiate boat travel to reach fishing grounds. Such infrastructure included recreational fishing lodges, coastal communities, and finfish aquaculture sites. Locations were obtained from databases from the BC government (http://geobc.gov.bc.ca/base-mapping/atlas/bcnames/gaz.html) and the Marine Planning Partnership (http://mappocean.org/science-and-planning-tools/marine-planning-portal/). We measured distances using the ArcMap 10.1 GIS platform; we designated land and water as high and low cost layers, respectively, and calculated distances for lowest cost paths (i.e., those a boat would travel around shorelines). Our definition of fishery base did not include forestry camps, as most are transient, or abandoned infrastructure that might have been a fishery base in the past. Analyses could not consider spatial variation in commercial fisheries because those data were unavailable to us.

2.2. Biological variables

For each specimen caught we recorded species, depth of capture, total length, body depth, gape width, weight, sex, and maturity. To age rockfish, we collected sagittal otoliths which were aged by the Sclerochronology Laboratory at DFO's Pacific Biological Station using the burnt otolith section method (Maclellan, 1997). To age Lingcod, we collected the fourth to eighth rays of the second dorsal fin, which were aged by the same lab, but sample sizes were insufficient for analysis. For sites where fishery-independent sampling took place, CPUE was estimated as the number of fish caught per 15-min of sampling; the CPUE of rockfishes and Lingcod obtained from systematic surveys reflects the density of these species (Haggarty and King, 2006).

2.3. Statistical analyses

We tested predictions using linear mixed models (LMMs: Zuur et al., 2009) implemented with the 'lme' package (Pinheiro and Bates, 2000) in R version 3.2.4. Random effects were selected a priori. They consisted of categorical variables required as statistical controls but not central to our predictions, and therefore were not reduced through model selection procedures. Predictors treated as fixed effects consisted of categorical and continuous variables that tested our predictions, or of continuous variables required as statistical controls. Fixed effects lacking explanatory power were eliminated via AIC model selection (Burnham and Anderson, 2002), while holding random effects constant. When competing models were deemed not to be different (i.e. $\Delta AIC < 2$), we selected the most parsimonious model. For visual displays of estimated responses, confidence intervals (95%) were derived from standard errors around the model's predictions (i.e. from the variance–covariance matrix of the model's predictions), rather than around individual parameters (Pinheiro and Bates, 2000). Visual inspection of quantile–quantile plots, residuals vs fitted plots, and correlation values between variables, were used to verify the assumptions of normality, homogeneity, and variable independence, respectively. Some sampling locations were <1 km apart, which raises issues of potential lack of independence between sites. Thus, in all models we accounted for the spatial autocorrelation of residuals by using a Gaussian correlation structure derived from the latitude and longitude of each sampling site (Pinheiro and Bates, 2000).

A subset of the analyses we performed examined length or age of specimens in response to RCA status and distance to nearest fishery base, while controlling for other factors. We ran separate LMMs for four species with adequate sample sizes (i.e., >60 observations): Yelloweye Rockfish, Quillback Rockfish, Copper Rockfish (*Sebastes caurinus*) and Lingcod (length only). These models included the following nested random effects: substrate (rock vs. soft substrates), fishing gear (baited longlines vs. un-baited lures), and upper ocean subregion. Fixed effects were distance to nearest fishery base, RCA status (inside vs. outside an RCA), sampling period (2006–2007 vs. 2013–2015), the two-way interaction between RCA and sampling period (except for age of Copper Rockfish, as the model would not converge when including this interaction), maximum bottom tidal speed, maximum bottom current speed, rugosity, and depth. Sampling period was included to account for potential increases in cumulative fishery effects over time outside RCAs, and the sampling period by RCA interaction was included to account for differences in RCA age at the time of sampling (see Molloy et al., 2009). All models examining age or length pooled data from fishery independent methods and FSC fisheries.

A separate LMM examined log-transformed catch per unit effort ($\log(\text{CPUE} + 1)$), as estimated from fishery independent data, in response to RCA status and distance to nearest fishery base, while controlling for other factors. CPUE was calculated separately for two species lifespan categories: long-lived species with maximum lifespans of 79–121 years, and shorter-lived species with maximum lifespan of 25–64 years (Table 1). Nested random effects in the model were fishing gear, upper ocean subregion, substrate, and season. Season was included to account for seasonal behaviours that might affect catchability (Carlson and Barr, 1977); it consisted of spring (March-1 to May-31), summer (June-1 to August-31) and fall (September-1 to Oct-31). Fixed effects in the model were lifespan category, distance to nearest fishery base, RCA status, sampling period, the two-way interaction between RCA status and sampling period, maximum bottom tidal speed, maximum bottom current speed, rugosity, median depth of sampling, and two-way interactions between lifespan category and RCA status and between lifespan category and nearest fishery base. The latter two interactions tested our predictions, respectively, that RCA effects would be weaker for longer- than shorter-lived species and that nearest fishery base effects would be stronger for longer- than for shorter-lived species.

Table 1
Species analysed and their maximum recorded lifespans (Love et al., 2002; Beamish et al., 2006; DFO, 2015).

Common name	Scientific Name	Max. recorded lifespan (yrs)
Lingcod	*Ophiodon elongatus*	25
Black Rockfish	*Sebastes melanops*	50
Copper Rockfish	*Sebastes caurinus*	50
Greenstriped Rockfish	*Sebastes elongatus*	54
Redstripe Rockfish	*Sebastes proriger*	55
Vermillion Rockfish	*Sebastes miniatus*	60
Yellowtail Rockfish	*Sebastes flavidus*	64
China Rockfish	*Sebastes nebulosus*	79
Silvergray Rockfish	*Sebastes brevispinus*	82
Canary Rockfish	*Sebastes pinniger*	84
Quillback Rockfish	*Sebastes maliger*	95
Tiger Rockfish	*Sebastes nigrocinctus*	116
Yelloweye Rockfish	*Sebastes ruberrimus*	121

Table 2
Best linear mixed models (as determined by AIC model selection) describing variation in age, length and CPUE.

Response variable	Predictor	Coefficient	Std error	DF	t-value	p-value
Length of Yelloweye Rockfish	Intercept	26.053	8.668	77	3.006	0.0036
	RCA (out relative to in)	−10.313	4.110	77	−2.509	0.0142
	Depth	0.359	0.096	77	3.751	0.0003
	Distance to fishery base	0.610	0.188	77	3.238	0.0018
Age of Yelloweye Rockfish	Intercept	16.063	3.424	54	4.692	<0.0001
	Max. bottom tidal speed	0.803	0.354	54	2.267	0.0274
Length of Quillback Rockfish	Intercept	77.608	29.122	218	2.665	0.0083
	Rugosity	−51.006	29.139	218	−1.750	0.0814
	Tide	0.149	0.045	218	3.319	0.0011
	Depth	0.098	0.011	218	8.993	<0.0001
	Distance to fishery base	0.033	0.020	218	1.694	0.0917
Age of Quillback Rockfish	Intercept	21.648	3.349	142	6.464	<0.0001
	Sampling period (2013–15 relative to 2006–7)	−6.516	2.250	142	−2.896	0.0044
	Depth	0.146	0.051	142	2.866	0.0048
Length of Copper Rockfish	Intercept	35.624	1.477	100	24.127	<0.0001
Age of Copper Rockfish	Intercept	43.282	8.084	78	5.354	<0.0001
	Max. bottom current speed	0.275	0.137	78	2.008	0.0482
	RCA (out relative to in)	−3.717	1.440	78	−2.581	0.0117
	Distance to fishery base	−0.469	0.138	78	−3.402	0.0011
	Max. bottom tidal speed	−1.388	0.430	78	−3.226	0.0018
Length of Lingcod	Intercept	69.281	1.215	95	57.015	<0.0001
CPUE	Intercept	0.292	0.105	442	2.77	0.0058
	Distance to fishery base	0.00523	0.00313	442	1.671	0.0954
	RCA	0.214	0.0713	442	3.00	0.0029
	Species lifespan	0.311	0.114	442	2.727	0.0067
	Depth	−0.002	0.00097	442	−2.066	0.0394
	Dist. to fishery base *X* species lifespan	−0.0105	0.0041	442	−2.571	0.0105
	RCA *X* species lifespan	−0.2908	0.0940	442	−3.09	0.0021

3. Results

We present results in terms of the best models determined by AIC model selection (i.e., not statistical significance: Burnham and Anderson, 2002) and describe average responses. Variability around these averages is detailed by 95% confidence intervals in Figs. 2–5 and standard errors for coefficients reported in Table 2.

Factors affecting age or length varied according to species. For Yelloweye Rockfish, total length ($N = 88$) was, on average, 10.3 cm (21%) longer inside than outside RCAs and increased with depth and distance from the nearest fishery base (Table 2; Table S1; Fig. 2). For instance, the LMM estimated that their total length was, on average, 24.4 cm (58%) greater at 45 km than at 5 km from the nearest fishery base (Fig. 2(c)), and 21.5 cm (59%) greater at 90 m than at 30 m depths (Fig. 2(b)). The effect of distance from nearest fishery base was driven by both finfish aquaculture sites (nearest in 48% of samples) and recreational fishing lodges (nearest in 40% of samples). Ages for this species ($N = 61$) increased with maximum bottom tidal speed but did not respond to other predictors (i.e. fixed effects) in the model (Table 2; Table S1; Fig. 2).

For Quillback Rockfish, total length ($N = 230$) increased with distance from the nearest fishery base, depth and maximum bottom tidal speed; it decreased at sites with greater rugosity (Table 2; Table S1; Fig. 3). For instance, the LMM estimated

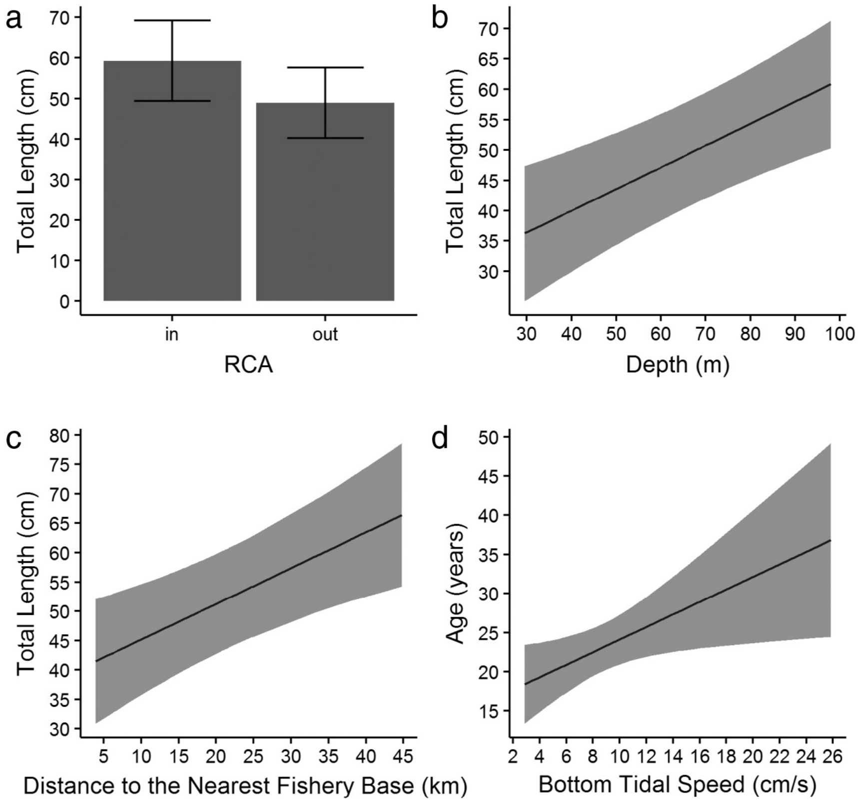

Fig. 2. Age and length of Yelloweye Rockfish in relation to predictors (fixed effects), as estimated by the best linear mixed models (Table 2). Bands or whiskers are 95% confidence intervals. Fixed effects not displayed below were held constant at median values or at "outside" status for RCA.

that their total length was, on average, 1.3 cm (13.9%) greater at 45 km than at 5 km from the nearest fishery base (Fig. 3(a)), and 5.9 cm (18.4%) greater at 90 m than at 30 m depths (Fig. 3(b)). The effect of distance from nearest fishery base was driven primarily by recreational fishing lodges (nearest in 58% of samples) and secondarily by communities (nearest in 31% of samples). Ages for this species ($N = 150$) declined, on average, by 6.5 years between the 2006–2007 and the 2013–2015 sampling periods (Table 2; Table S1; Fig. 3(e)). This change reflected a lower proportion of older fish during 2013–2015 (Fig. 6(a)), possibly as a consequence of increased fishery exploitation since 2007. Ages of Quillback Rockfish also increased with depth. Average age, for instance, was 8.8 years older at 90 m than at 30 m depth (Table 2; Table S1; Fig. 3(f)).

Total lengths of Copper Rockfish ($N = 107$) and Lingcod ($N = 103$), did not respond to any predictors (i.e. fixed effects) in our analysis (Table 2; Table S1). Copper Rockfish ages ($N = 86$) were, on average, greater inside than outside RCAs by 3.7 years, and increased at sites with faster bottom currents. Age for this species, however, decreased with distance to the nearest fishery base and bottom tidal speed (Table 2; Table S1; Fig. 4). The effect of distance from nearest fishery base was driven almost entirely by recreational fishing lodges (nearest in 98% of samples).

CPUE responded to distance from the nearest fishery base, but the effect was positive for long-lived species and negative for shorter-lived species ($N = 236$ per species lifespan category). The LMM estimated that CPUE of longer-lived species was, on average, 47% greater at 45 km than at 5 km from the nearest fishery base. In contrast, the average CPUE of shorter-lived was 42% lower at 45 km than at 5 km from the nearest fishery base. The effects of distance from nearest fishery base were driven primarily by recreational fishing lodges (nearest in 70% of samples) and, to a much lesser extent, by communities (nearest in 20% of samples). CPUE was lower inside than outside RCAs for longer-lived species, but shorter-lived species had a higher CPUE inside than outside RCAs. For all species, CPUE decreased with depth (Table 2; Table S1; Fig. 5).

Old-aged Quillback and Yelloweye rockfishes, the longest-lived and culturally most significant species in our data, were rare (Fig. 6). Average ages of Yelloweye Rockfish (23.0 yrs) and Quillback Rockfish (27.3 yrs) were, respectively, 19.0% and 28.7% of maximum known ages (121 yrs and 95 yrs). Further, 56.7% of Quillback Rockfish but only 16.4% of Yelloweye Rockfish in our sample exceeded the generation time (i.e., mean age of reproductive females) reported 10 years ago (22.8 yrs for Quillback: Yamanaka et al., 2006a; 32.5 yrs for Yelloweye: Yamanaka et al., 2006b). Thus age truncation for Yelloweye Rockfish, possibly reflecting cumulative fishery exploitation, appears to be high at our study sites.

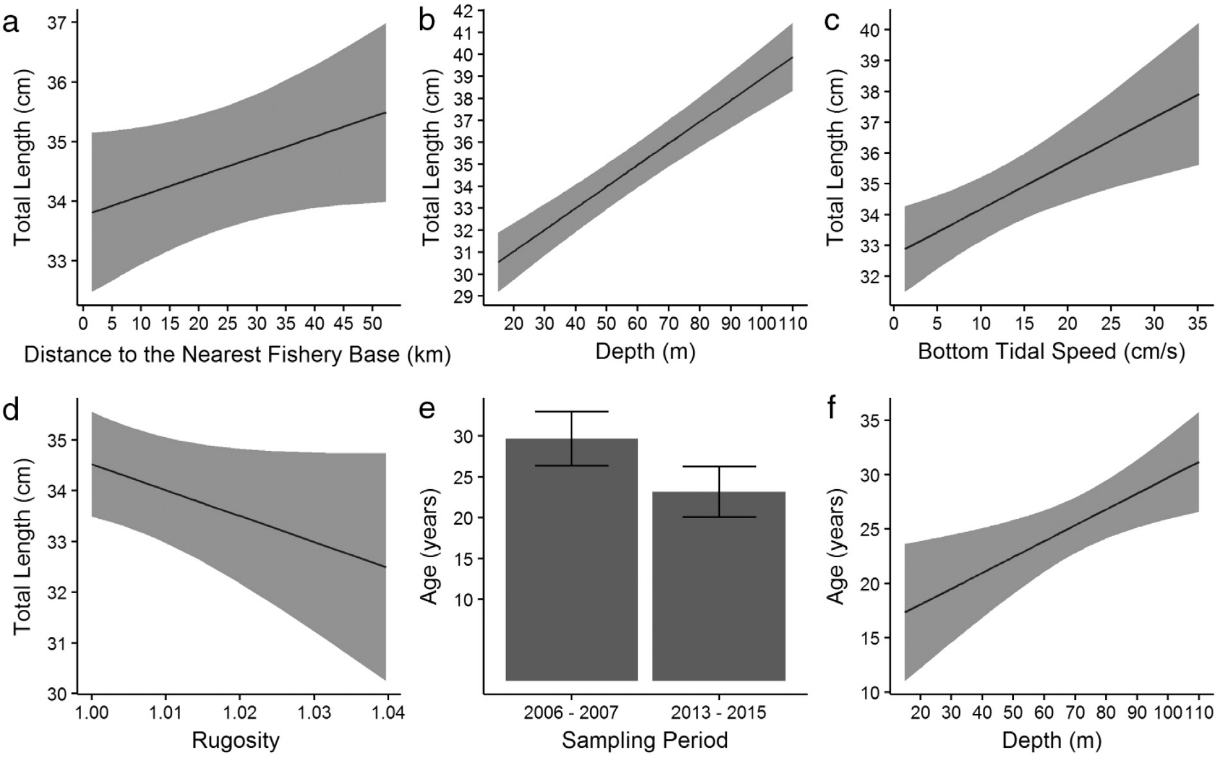

Fig. 3. Age and length of Quillback Rockfish in relation to predictors (fixed effects), as estimated by the best linear mixed models (Table 2). Bands or whiskers are 95% confidence intervals. Fixed effects not displayed below were held constant at median values or for the 2013–2015 sampling period.

Table 3
Species or species groups for which data supported, or failed to support, predictions.

Prediction	Supported:	*Not* supported:
Positive RCA effect on length	Yelloweye Rockfish	Quillback Rockfish Copper Rockfish Lingcod
Positive RCA effect on age	Copper Rockfish	Yelloweye Rockfish Quillback Rockfish
Positive RCA effect on CPUE, but weaker effect for longer- than shorter-lived species	Shorter-lived species aggregated	Longer-lived species aggregated (negative effect)
Positive effect of distance to nearest fishery base on length	Yelloweye Rockfish Quillback Rockfish	Copper Rockfish Lingcod
Positive effect of distance to nearest fishery base on age		Yelloweye Rockfish Quillback Rockfish Copper Rockfish (negative effect)
Positive effect of distance to nearest fishery base on CPUE, but stronger effect for longer- than shorter-lived species.	Longer-lived species aggregated	Shorter-lived species aggregated (negative effect)

4. Discussion

In response to conservation concerns by First Nations, we tested predictions from the hypothesis that spatial variation in fishery pressure affects the size, age and abundance of rockfishes and Lingcod, while controlling for environmental variables. Support for our predictions was mixed and varied according to species (Table 3).

Spatial protection led to greater size, age and abundance of some, but not all species, possibly due to interspecific differences in movement behaviour. For instance, Lingcod generally make larger movements than most rockfishes (Freiwald, 2012); the lack of positive size response to spatial protection by this species could potentially reflect large home ranges that extend beyond the boundaries of RCAs (Martell et al., 2000). Also, species with moderate home range sizes might be more likely to immigrate into a reserve and stay within than species with smaller or larger home ranges (Molloy et al., 2009). Further analyses that consider the patch sizes and distribution of suitable habitat (i.e. rocky reefs) within RCAs are needed to examine the extent to which these hypotheses explain the species differences to spatial protection that we observed

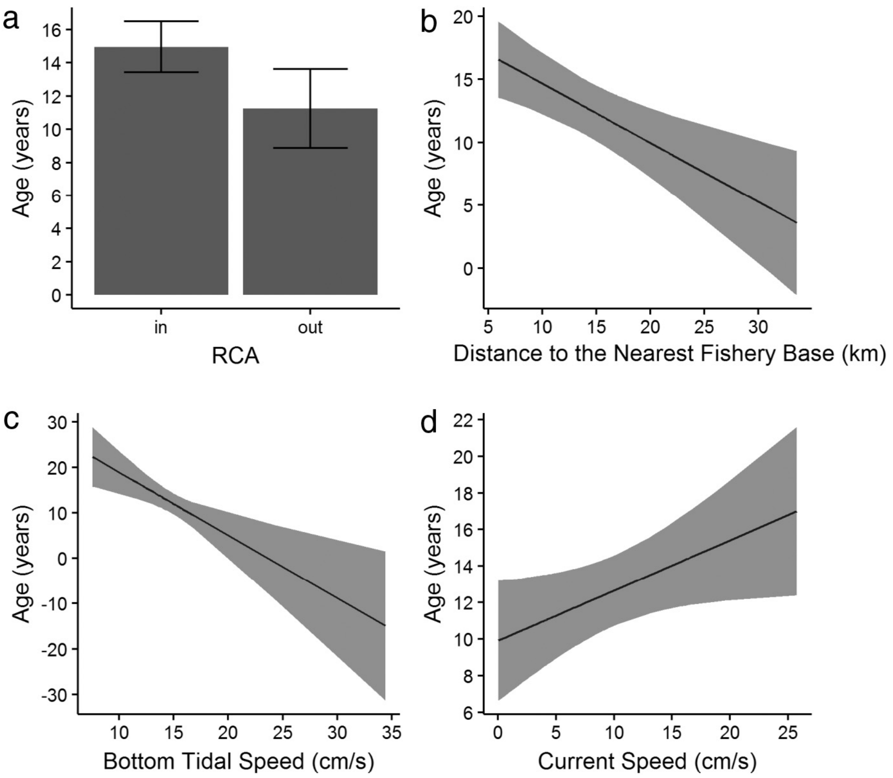

Fig. 4. Ages of Copper Rockfish in relation to predictors (fixed effects), as estimated by the best linear mixed model (Table 2). Bands or whiskers are 95% confidence intervals. Fixed effects not displayed below were held constant at median values or at "outside" RCA status.

(Haggarty et al., 2016b). Also, species with a more intense history of exploitation may show stronger responses to spatial protection than less exploited species (Molloy et al., 2009). Commercial fishery data were not available for our analyses; interspecific differences in historical and current catches from commercial fisheries outside RCAs may have contributed to unexplained variability in our results (Moffitt et al., 2011). Not mutually exclusive with these explanations, substantial lack of compliance from recreational fishers has been documented at RCAs in southern British Columbia Lancaster et al., 2015; Haggarty et al., 2016a); recreational fisher compliance rates might also be poor at our remote study area, where monitoring and enforcing resources are scarcer, and may have reduced RCA benefits for some species. (Commercial fisheries are monitored electronically and have high compliance.) Our observation that long-lived species analysed in aggregate had higher CPUE *outside* RCAs contradicts our predictions; CPUE estimates did not account for size variation within a species group and the higher abundance outside RCAs might be driven by small individuals. Also, while indigenous FSC fisheries occur almost entirely outside RCAs, the potential effect of their modest exploitation rates inside RCAs has yet to be quantified.

Consistent with central place foraging theory (e.g. Houston, 2011), fishery impacts on the size and relative abundance of rockfishes were lower farther from fishery bases – that is, at sites that required longer travel times and greater fuel costs for fishers to exploit – but this was the case only for Yelloweye and Quillback rockfishes (size responses) and for long-lived species analysed in aggregate (CPUE response). However, we did not find similar responses for Copper Rockfish, Lingcod and the shorter-lived species group. One potential explanation relates to interspecific differences in depth preferences of adults. Adults of long-lived species, including Quillback and Yelloweye rockfishes, generally occupy depths greater than 50 m (Kronlund and Yamanaka, 2001; Yamanaka et al., 2006a). In contrast, adults of shorter-lived species, including Copper Rockfish and Lingcod, generally prefer shallower depths (Richards, 1987; Haggarty and King, 2004). In fact, our data show a size increase with depth for Quillback and Yelloweye rockfishes (Figs. 2(c), 3(c)), but not for Copper Rockfish and Lingcod. This suggests that fishers targeting large individuals of long-lived species exert less effort at the shallower depth range of shorter-lived species. Proximity to recreational fishing lodges, the nearest fishery base in most cases, may amplify differences in depth-specific effort from recreational fishers. Alternatively, foraging theory predicts that, to maximize fitness, animals travelling farther to a resource patch should increase their foraging effort per trip—that is, they may forage more selectively for larger prey or not stop foraging until they accrue a greater prey load (Charnov, 1976). If central place fishers behave consistent with this model when targeting certain species, then their impact on those species might not decrease with distance from fishery bases. Data on fisher behaviour are needed to distinguish between hypotheses.

Our study has management implications relevant to Canada's legal obligation to ensure long-term access by indigenous people to species of cultural significance (DFO, 2007a). First, RCAs had measureable benefits, including for size of Yelloweye

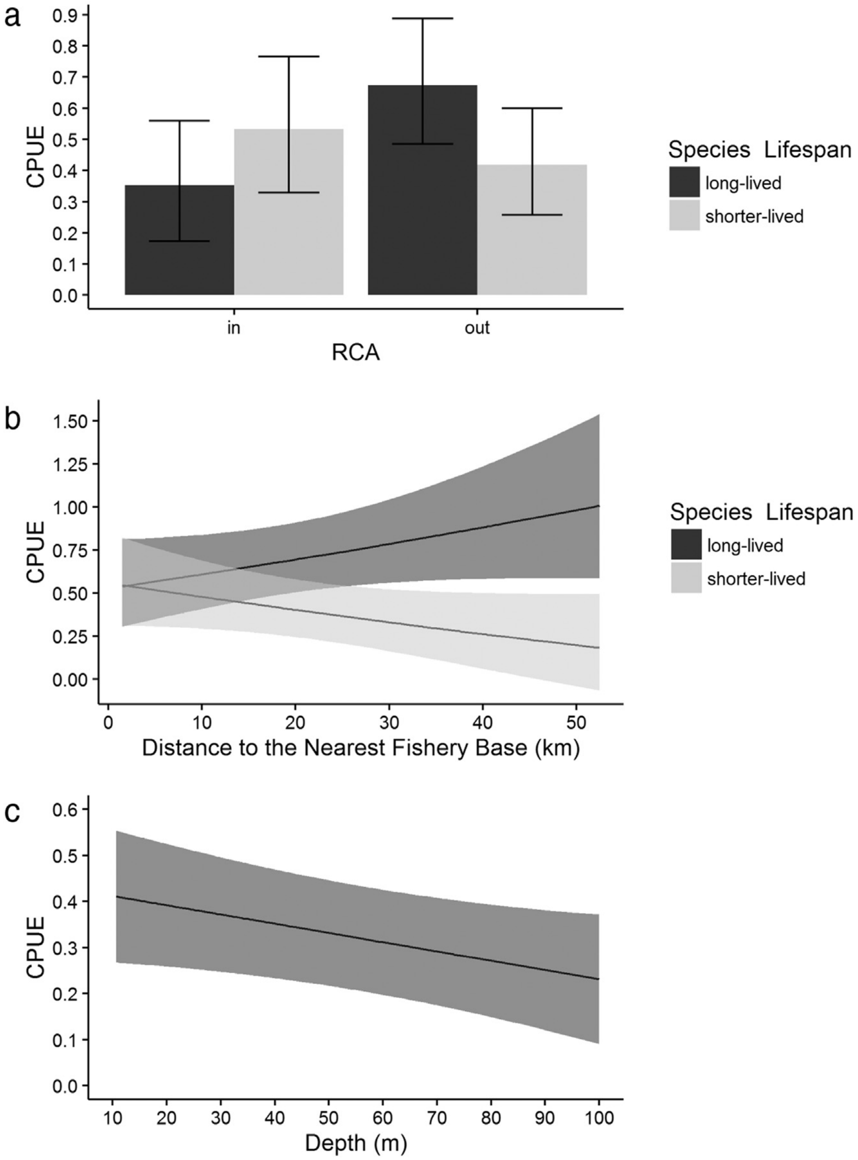

Fig. 5. CPUE in relation to predictors, as estimated by the best linear mixed model (Table 2). Bands or whiskers are 95% confidence intervals. Fixed effects not displayed below were held constant at median values or at "outside" status for RCA. We did not analyse a depth by species lifespan interaction; the lower panel, therefore, illustrates the depth effect for both lifespan categories combined.

Rockfish. This is notable, as RCAs in southern British Columbia have yet to show similar benefits (Haggarty et al., 2016b). The regional differences in RCA responses might reflect greater cumulative impacts of non-compliance and other human stressors in the more densely populated southern coast. Non-compliance rates, however, are unknown at our study area. Quantifying these rates, coupled with greater monitoring and enforcement of RCAs, likely would enhance recovery of rockfishes (Lancaster et al., 2015; Haggarty et al., 2016a).

Second, not all species responded positively to spatial protection. This suggests that the suitability and distribution of habitats within the RCA network might not be meeting the requirements of some species (Moffitt et al., 2011). For instance, lack of high quality rocky habitat has been identified as a potential concern for some RCAs (Haggarty et al., 2016b). Further habitat analyses would inform whether RCA boundaries need modification, and help improve the design of proposed MPAs (Canada-British Columbia, 2014).

Third, outside RCAs fishery impacts on long-lived rockfishes conformed to a central place fishery model, which we interpret as primarily reflecting impacts from recreational fishers (Bellquist and Semmens, 2016; Haggarty et al., 2016a). Improved understanding and management of recreational fishing impacts on rockfishes, therefore, should complement the use of spatial fishery closures for rockfish restoration (Bellquist and Semmens, 2016).

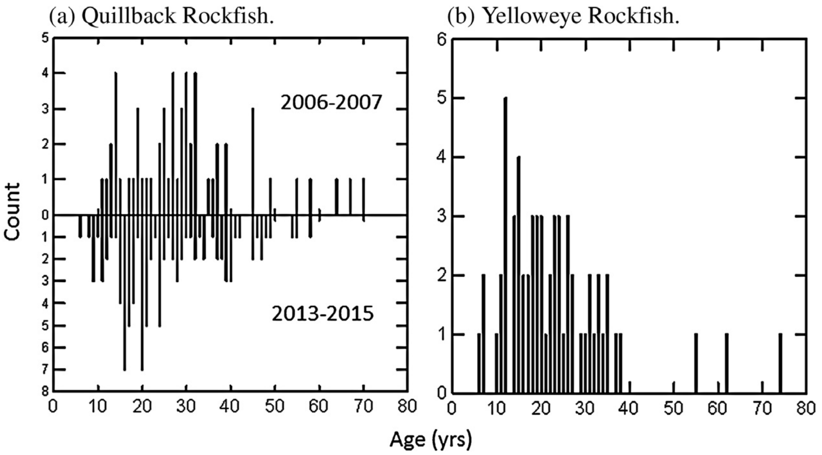

Fig. 6. Age frequency distribution for (a) Quillback and (b) Yelloweye rockfishes at sites important to indigenous fishers. Quillback ages are separated by sampling period, as the Linear Mixed Model found these to differ (Table 2). Yelloweye Rockfish ages did not differ significantly between sampling periods and are combined for all years of the study.

Finally, our data suggest that old-aged Yelloweye Rockfish were rare at sites important to indigenous fishers. Despite tremendous improvements to fishery management in the last decade (Yamanaka and Logan, 2010), stock assessment outside of RCAs continues to be based on biomass trends over time. Managers use a ratio of current biomass to biomass at maximum sustained yield to assess the status of a stock and decide on the opening or closing of a commercial fishery (e.g. DFO, 2015). Other Pacific groundfish fisheries are managed similarly (Berkeley et al., 2004b). Arguably, a biomass-based framework is inconsistent not only with the goals of ecosystem based management, which should consider size-based indirect interactions between target and non-target species (Tolimieri et al., 2013), but also may fail to safeguard the persistence of rockfishes and other groundfish. Therefore, long term access to rockfishes by indigenous people and other users is more likely to be secured if fishery management agencies in Canada and elsewhere were to treat old-age and large size structures as explicit management objectives (Berkeley et al., 2004b; Beamish et al., 2006; Hixon et al., 2014).

More generally, the loss of traditional resources has a long history of affecting the physical, mental and spiritual well-being of indigenous people throughout the world (Brody, 2001; Kuhnlein et al., 2013; Sangha et al., 2015). By providing insight into the management actions that may promote long-term access to traditional foods, our study contributes to a global effort to integrate indigenous well-being and cultural values with biological conservation (Poe et al., 2014).

Acknowledgements

Field sampling was conducted by Coastal Guardian Watchmen, fisheries staff, or FSC fishers from the Wuikinuxv, Kitasoo/Xai'Xais, Heiltsuk and Nuxalk Nations, whose indigenous right to fish precludes the need for research permits. The traditional knowledge of elders and other fishers from each First Nation community was essential for selection of our study sites and providing historical context (with special thanks to Charlie Mason and Frank Johnson). Our research was possible thanks to funding from Environment Canada's Habitat Stewardship Program for Species at Risk, the Vancouver Foundation, Tides Canada, and the Tula Foundation. The dedicated fieldwork of the following people was essential: Ernie Mason, Sandie Hankewich, Fred Brown, Clark Brown, Brian Johnson, Chris Corbett, Alex Chartrand Jr., Ernest Talio, John Sampson, Roger Harris, Richard Reid, Randy Carpenter, and Davie Wilson. For additional field contributions, we thank Julie Carpenter, Doug Neasloss, Vern Brown, Tammy Norgard, Tristan Blaine, Natalie Ban, Lauren Eckert and Twyla Bella Frid Lotenberg. Leadership from the following stewardship directors and fishery managers from First Nation communities was essential: Doug Neasloss, Megan Moody, Mike Reid, Dave Rolston and Susan Anderson-Behn. We thank DFO's sclerochronology lab for ageing specimens (special thanks to Shayne McLellan and Joanne Groot). Ken Cripps and Lynne Yamanaka provided technical advice. Natalie Ban provided insightful comments on an earlier draft.

Appendix A. Supplementary data

Supplementary material related to this article can be found online at http://dx.doi.org/10.1016/j.gecco.2016.09.008.

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