Received: 17 December 2023 | Revised: 3 September 2024 | Accepted: 18 September 2024

DOI: 10.1002/ecs2.70056

ECOSPHERE
AN ESA OPEN ACCESS JOURNAL

ARTICLE

Coastal and Marine Ecology

Escape behavior of rocky-reef fish reveals the impact of spearfishing across different management regimes

Francisco J. Contreras-Drey[1,2,3] | **Natalio Godoy**[4] | **Andrés Smith**[1,2] | **Enrico L. Rezende**[1,3] | **Alejandro Pérez-Matus**[1,5] | **Rodrigo A. Estevez**[2,6] | **Ricardo Beldade**[1,5] | **F. Patricio Ojeda**[1] | **Stefan Gelcich**[1,2,3]

[1]Facultad de Ciencias Biológicas, Pontificia Universidad Católica de Chile, Santiago, Chile

[2]Instituto Milenio en Socio-ecología costera (SECOS), Facultad de Ciencias Biológicas, Pontificia Universidad Católica de Chile, Santiago, Chile

[3]Center of Applied Ecology and Sustainability (CAPES), Facultad de Ciencias Biológicas, Pontificia Universidad Católica de Chile, Santiago, Chile

[4]The Nature Conservancy, Santiago, Chile

[5]Millennium Nucleus for the Ecology and Conservation of Temperate Mesophotic Reef Ecosystems (NUTME), Estación Costera de Investigaciones Marinas (ECIM), Las Cruces, Facultad de Ciencias Biológicas, Pontificia Universidad Católica de Chile, Santiago, Chile

[6]Centro de Investigación e Innovación para el Cambio Climático, Facultad de Ciencias, Universidad Santo Tomás, Santiago, Chile

Correspondence
Francisco J. Contreras-Drey
Email: fjcontreras@uc.cl

Funding information
ANID-Millennium Science Initiative Program, Grant/Award Number: ICN 2019-015; Agencia Nacional de Investigación y Desarrollo, Grant/Award Numbers: BECAS/DOCTORADO NACIONAL, 21242280, PIA/BASAL FB0002; Fondo Nacional de Desarrollo Científico y Tecnológico, Grant/Award Numbers: 1230982, 1210216, 1221534, 3150138

Handling Editor: Sean P. Powers

Abstract

Flight initiation distance (FID), the distance at which an organism begins to flee from an approaching threat, is a major component of antipredator escape behavior and a potential indicator of threat perception in fishes. In this study, we analyzed the FID of three important rocky-reef fish species targeted by spearfishers, which are of commercial and recreational importance. We tested predictions that FID to a diver threat increases with the following factors: (1) fish body size, (2) less restricted access regimes, and (3) increased historical fishing pressure. We studied three size ranges of three rocky-reef fish species, in three different access regimes (i.e., open access, territorial user rights for fishery areas, no-take marine protected areas), and in two regions (northern and central region with different levels of fishing pressure depending on the species). We conducted an ANOVA to analyze pairwise interactions. We used the mean square criterion to select the models that best explained the variation of our response variable. Our findings indicate that FID can be distinctly elucidated by factors such as individual size, species, access regimes, and regions. Additionally, our models show that interactions involving regions and either species or size further contribute to explain FID variability. FID was higher in larger fishes and those of higher commercial value, outside marine reserves and in the region with the highest historical fishing pressures (based on landings data). This study supports the predictions that increased FID is associated with the threat posed by spearfishing activities. Furthermore, our findings indicate that spearfishing may already be altering the behavior of rocky-reef fishes on the north-central coast of Chile.

KEYWORDS
antipredator behavior, artisanal fishery, flight initiation distance, rocky-reef fish, TURFs

INTRODUCTION

Overfishing—the deployment of excessive levels of fishing effort—is one of the most pressing problems for marine ecosystems globally (Callum et al., 2001; Gelcich et al., 2009; Jackson et al., 2001; Pauly et al., 2002) Assessing fish responses to overfishing is crucial for understanding changes in population dynamics and community structure (Defeo & Castilla, 2005). A useful metric to evaluate the impact of fishing is the flight initiation distance (FID), which serves as a proxy for threat perception in fish and allows inference of the stress levels they experience due to fishing pressure and habitat variations (Benevides et al., 2019; Gotanda et al., 2009; Nunes et al., 2018). This approach provides a valuable tool for fisheries management and conservation, especially in contexts where marine resources are under constant pressure due to intensive exploitation.

Spearfishing is considered a major marine resource extraction activity around the world (Allison & Ellis, 2001; Berkes, 2001). These multispecific fisheries operate in shallow subtidal zones of tropical and temperate coastal ecosystems worldwide (Crona et al., 2017; Gelcich et al., 2017; Johannes, 1978). Evidence suggests spearfishing affects reef fish abundance, diversity, body size, reproductive potential, mobility (Gelcich et al., 2008; Glaudas et al., 2006; Godoy et al., 2016; Oakley, 1984; Wilson et al., 2020), and the wider ecosystem (Godoy et al., 2010). An important, yet still understudied approach to assess the effect of this activity is to study the escape behavior of rocky-reef fish in the presence of fishing (Lima & Dill, 1990), which can be integrated with other sources of information, to inform levels of threat under different management strategies (Nunes et al., 2018).

Multiple methods can be used to quantify rocky-reef fish behavior in the presence of predators. These include visual census, landscape of fear (LOF), and FID (Blumstein, 2003; Laundré et al., 2001). The most frequently used has been FID (Nunes et al., 2018). The FID is the distance of an approaching predator at which prey first initiates an escape (Nunes et al., 2018). With this measure, it is possible to quantify one of the main components of antipredator behavior and generate a potential indicator of an animal's perception of a threat (Benevides et al., 2019; Gotanda et al., 2009). This metric has been also used as an indicator of the effects of fishing pressure on the behavior of coastal fish targeted by spear fisheries and can aid in defining species-specific spatial management strategies (Benevides et al., 2016; Januchowski-Hartley et al., 2013; Tran et al., 2016).

FID is expected to vary in space and time, depending on the fishing pressure to which the individual is exposed. Further, most studies in coastal fish species targeted by fisheries have shown higher FID in the presence of spear fishers as opposed to when they are absent (Gotanda et al., 2009). Since the FID of an individual can be influenced by its life experience (Brown, 2003), FID can be attuned according to fishing pressure (Deecke et al., 2002). In the case of constant exposure to humans that do not represent a direct threat, the individual should have a decreased FID, behavior that has been reported, for example, inside marine protected areas (MPAs) where there is a prohibition of fishing (Cooper & Whiting, 2007; Guabiroba et al., 2022; Kramer & Chapman, 1999).

In Chile, from latitude 18° S to 40° S, over approximately the last six decades, a coastal artisanal and commercial speargun fishery has targeted rocky-reef fish (Godoy et al., 2010). This fishery operates between 0 and 30 m depth and is generally associated with *Lessonia* kelp forests (Pequeño & Olivera, 2005; Pérez-Matus et al., 2007). This fishery includes a large suite of fish guilds/trophic levels including carnivores (ichthyophagous or carcinophagous), omnivores, and herbivores, the former being the most demanded and exploited (Chirichigno, 1998; Godoy et al., 2016; Medina et al., 2004; Pérez-Matus et al., 2017; Stuart-Smith et al., 2013). Important impacts have occurred on three species considered flagships for artisanal and recreational fishing: *Graus nigra*, *Semicossyphus darwini*, and *Medialuna ancietae* (which is only observed in the northern region I of Chile). These species have sharply decreased their abundance due to overexploitation because there are still no commercial or recreational regulations regarding bans, catch limits, gear restrictions, or size limits in the country (Godoy et al., 2010; Lyach & Cech, 2018). Due to the depletion of flagship fish species, a displacement of fishing has been observed to include alternative species, such as

Cheilodactylus variegatus, *Pinguipes chilensis*, and *Aplodactylus punctatus*, which is an herbivorous species that was not very popular spearfished species in the past (Godoy et al., 2010) and the core subjects of this study.

Along the Chilean coast, there are MPAs, which have prohibited the commercial exploitation of reef fish species in no-take-zones. On the other hand, there are more than 800 management and exploitation areas for benthic resources, which are areas where small-scale fishery organizations have territorial use rights for fishing (TURFs) and where reef fish spearfishing is generally limited (Gelcich et al., 2012). Within MPAs and TURFs, it is possible to find greater richness and diversity of reef fish, compared to open access areas, since protection and a more restricted access regime decrease mortality derived from fishing (Gelcich et al., 2012). In MPAs and TURFs with effective surveillance, there is an increase in the abundance and size of invertebrates, algae, and also in the number of reef fish (Gelcich et al., 2012). Moreover, Gelcich et al. (2008) reported that despite the existence of low surveillance in TURFs, reef fish species were significantly more diverse and abundant and community assemblages of nontarget benthic invertebrates and reef fish were significantly different inside versus outside TURFs.

The Chilean setting, where different management areas have varying *de facto* spearfishing effort along the coast, provides a unique opportunity to explore FID in a temperate ecosystem subject to differing human pressures. Accordingly, in this study we analyzed the FID of three rocky-reef fish species important for commercial and recreational fishing: *C. variegatus*, *P. chilensis*, and *A. punctatus*. We hypothesize that FID is contingent upon the magnitude of spearfishing pressure associated with management regimes, historical levels of fishing pressure in different areas and specific locations where the fish are found, as well as the individual sizes of the individuals. We test the hypothesis through comparing FID across (1) different fish sizes; (2) areas with different fishing access regimes: open access, TURF, and one MPA (Estación Costera Investigaciones Marinas, Las Cruces); (3) administrative regions (hereafter Regions I and V) with different historical fishing pressures over reef fish.

METHODS

Study site

FID of coastal fish species *C. variegatus*, *P. chilensis*, and *A. punctatus* were measured at 16 sites distributed throughout the Valparaiso region (Region V) (zone with lower historical fishing pressure) in central Chile and 14 sites distributed in the Tarapaca region (Region I) (zone with higher historical fishing pressure) in Northern Chile (Figure 1A). Higher and lower historical fishing pressure was determined based on landing data (SERNAPESCA; Appendix S1: Figure S1) and an empirical assessment of catch-per-unit-effort (CPUE) (in kilograms/fisher/trip) provided by Godoy et al. (2016) that showed Region I was significantly higher than Region V. Figure 1B shows the frequency of visual observations where divers simulated spearfishing to measure the FID, which represents the number of instances where fish began to flee from the approaching diver threat. Data were collected in open access areas (without fisheries management for rocky-reef fish), TURFs, and one MPA. We estimated FID in subtidal zones associated with kelp forests up to 15 m depth, totaling 2418 estimates. The frequency distributions of access regimes and fish size per species are shown in Figure 1B. Open access sites in the Valparaiso region were in the town of El Tabo, Las Cruces, and Quintero. On the other hand, the open access sites in the Tarapaca region were throughout Iquique. TURF areas included those of Maitencillo, El Quisco, Valparaiso, Quintero, and Las Cruces in Region V. In Region I, the TURFs concentrate in areas adjacent to Iquique. Finally, the MPA associated with the coastal station of the Pontificia Universidad Catolica de Chile (ECIM) was assessed in Region V. Sampling took place ensuring that localities from each region were sampled iteratively. Sampling took Ca. 3 years, and localities were not resampled across different years.

Data collection

Three divers, marine biologists, experienced in spearfishing estimated FID at all sites between the end of 2015 and the beginning of 2019. Divers were trained on how to estimate FID and shared five "practice" dives to standardize methodology and discuss the method. These "practice" dives were repeated every year to ensure protocols were followed. In the "practice" dives, two divers were always submerged together, with one performing the FID measurements while the other supervised to ensure uniformity in approach and to minimize any potential variation in behavior that could influence FID. Environmental conditions during sampling were set at a minimum of 8 m visibility and between 0.8 and 1.8 m of wave height. The presence of a diver was considered an appropriate stimulus in study areas (Cooper, 2005). The divers used apnea (free-diving) to do reconnaissance and search for the species of interest. This diving method was used as it produces fewer bubbles during diving, so it allows to have less interference with the species and thus

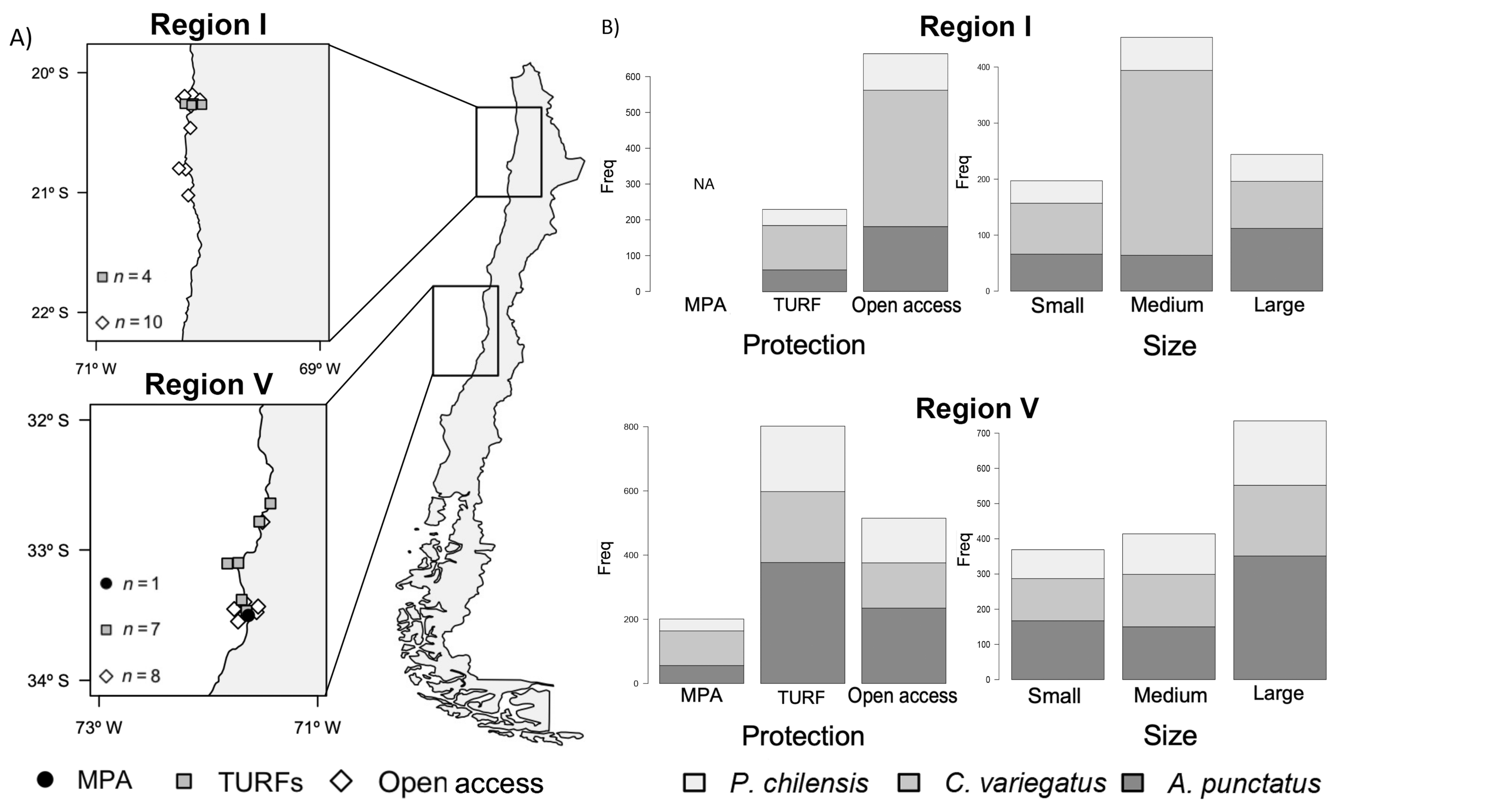

FIGURE 1 (A) Study area in Region I (higher historical fishing pressure) and Region V (lower historical fishing pressure) along the Chilean coast. (B) Frequency of fish size observations associated with access regimes (open access, territorial use rights for fishing [TURFs], marine protected areas [MPA]) in the two sampled regions of Chile.

not add an extra distraction to measure the stimulus (Gray et al., 2016). This method was utilized to parameterize the reaction of the individual, as different zones present different types of diving and fishing gear. Divers executed a deliberate exploration of the designated site, meticulously seeking the study species. Upon identifying a suitable individual, the diver approached horizontally, aligning their depth with that of the fish and positioning themselves nearly perpendicular to the fish's longitudinal axis. This approach was carried out at a velocity of approximately 0.9 m/s, following Gotanda et al. (2009).

In response to the fish displaying behaviors indicative of evasion, often coupled with an acceleration in speed and at times a change in trajectory, the observer immediately released a 2-kg diving lead, previously secured around their waist. Subsequently, a secondary marker was deployed to mark the precise location where the fish's evasion commenced. The linear distance between these two markers was measured. The recorded measurement of FID was established as the spatial separation between the fish evasion and the initial point. To ensure meticulous data acquisition, approach maneuvers were initiated at a maximum practicable distance from the focal individual. The diver registered species identity and assigned them to a size category (small 0–30 cm [0–300 g]: medium 30–40 cm [300–700 g], and large >40 cm [>700 g]). Based on Godoy et al. (2016), the medium and large sizes defined can be considered part of the sizes observed in the catch composition of commercial and recreational divers.

Observations were mostly recorded in solitary individuals, individuals observed in groups did not exceed five individuals per group, and only the first individual's FID was measured.

A total of 2418 FID records were obtained.

Fishing pressure and study species

C. variegatus (Valenciennes, 1833) is a common carnivorous fish inhabiting rocky subtidal habitats along the northern and central coast of Chile (Palma & Ojeda, 2002). It ranges from Paita (Perú) to Metri Bay in southern Chile (Chirichigno, 1974). The first official landing statistic for this species was in 1996. *C. variegatus* landings in Region I show an increase from 2009 onward, surpassing the Region V landings. These values coincide with CPUE assessments that signal significantly higher values in Region I in 2010 and 2011 (Godoy et al., 2016). The species presents high fishing pressure in Region I in the years prior to our study (Appendix S1: Figure S1).

P. chilensis (Valenciennes, 1833) is a carnivore and highly territorial fish inhabiting sandy and rocky subtidal bottoms distributed from Tumbes (Perú) to the southernmost tip of Chile (Magallanes) (Chirichigno, 1974; González & Oyarzún, 2003). Fishing for this species has been ongoing for longer than for *C. variegatus* with official records dating back to 1980. Catches have decreased in the last few years (SERNAPESCA, 2020). Higher landings of *P. chilensis* were observed in Region I than in Region V. Empirical studies from 2010 and 2011 support this pattern and signal that CPUE for this species is higher (Godoy et al., 2016). In Region V, landings have been lower and never reached the high values observed in Region I, indicating that *P. chilensis* is more intensively fished or more abundant in Region I.

A. punctatus (Valenciennes, 1833) is a common and abundant herbivorous fish mainly associated with the subtidal brown kelp *Lessonia* (Benavides et al., 1994) and distributed from northern Perú to Golfo de Arauco in southern Chile (Chirichigno, 1998; Mann, 1954). Because they are not very palatable, they have a lower fishing pressure in the country (SERNAPESCA, 2020). The official landings for *A. punctatus* show data from 1999 and low landing volumes in Region I. This species does not seem to be a significant part of the fishery in this region. In Region V, *A. punctatus* has more substantial landings, particularly around 2010, where it shows one of the highest peaks for the species. There is empirical evidence of catch in both regions (Godoy et al., 2016).

Historical context reveals that fishing pressure and landing patterns for these species have varied significantly across regions and over time (Godoy et al., 2010). The three species were selected for this study because (1) historical fishing records are more extensive in Region I than in Region V, indicating a longer history of exploitation; and (2) the selected species have more recent fishing histories, reflecting a shift due to the overexploitation of previously more abundant species.

The nationally and historically aggregated data in Appendix S1: Figure S1 are divided and allocated to the sampled regions. These regional landings are then included as qualitative factors in the "Region" variable, which categorizes regions based on higher and lower landing quantities. This approach allows for a detailed analysis of regional differences in fishing pressure and landings.

Data analysis and model selection

The following factors were selected as potential predictors of FID variability: (1) species (*A. punctatus*, *C. variegatus*, and *P. chilensis*); (2) region, with Region I representing the northern zone with the highest landings and Region V representing the southern zone with the lowest landings (SERNAPESCA, 2020); (3) body size of the observed fish (small, medium, and large size); and finally, (4) access regime (open access, TURFs, and MPA).

All factors were divided into discrete categories and present a relationship with a single response variable which is the FID (in centimeters), facilitating the interpretation of the effect of our predictors, making the individual factors more interpretable when analyzing interactions (Neter et al., 1996). Due to the robustness of our data (2418 observations), we initially performed a four-way ANOVA. To facilitate the interpretation of our models and their interaction, we used ANOVA of pairwise interaction between main effects for the selection of our models and to evaluate the variation of our response variable with our factors, by itself and by the interaction of these and a Tukey's test HSD (Tukey's honestly significant difference test) to find means that are significantly different from one another.

To visualize the distribution of our data based on the selected models, partial regressions were performed, which allowed us to control our variability under a single factor, eliminating the noise that other factors could generate in our factor of interest. The partial regressions were represented by boxplots of the adjusted estimates of our observations to facilitate their interpretation. All analyses were performed with R software version 4.2.0.

The boxplots display the five-number summary of the adjusted estimates: minimum, first quartile, median, third quartile, and maximum. Additionally, means of the adjusted estimates as individual points on the boxplots were included. Although means are not traditionally part of a boxplot, they were included to provide a clearer understanding of the central tendency of the data, especially in the context of Tukey's test. The six models mentioned in the previous paragraphs were selected, out of the 10 models run, because of their significance and their mean square that have the strongest potential to explain FID. For the visualization of our selected models, we performed partial regressions, from which we plotted the adjusted estimates to observe differences between the expected and observed values of our data.

RESULTS

We recorded the FID of 2418 individuals of *C. variegatus*, *P. chilensis*, and *A. punctatus*, for three different sizes: large ($n = 981$), medium ($n = 869$), and small ($n = 568$), in open access, TURFs, and a MPA areas, within the two regions with different fishing pressure (in the form of landings). Our study reveals that all factors and most of their interactions prove to be of significance on the FID response (Table 1). When factors are analyzed separately, fish size explains most variation in our data with the highest mean square (Msq = 152,732) and a significant variation ($F = 818.33$, $p < 2.2\text{e}{-16}$). Region comes second as the variable that mostly explains the variations of our data (Msq: 974174; $F = 521.95$, $p < 2.2\text{e}{-16}$). Protection showed a lower mean square (Msq = 358,059), but also proved to be a significant contributor ($F = 191.84$, $p < 2.2\text{e}{-16}$). Species has the lowest mean square (Msq = 114,669) among our four variables; therefore, it is the one that least explains the variation of our response variable. However, it shows statistical significance ($F = 61.44$, $p < 2.2\text{e}{-16}$). Our results reveal the importance of the four variables in explaining the variation of our response variable (FID).

Results also show that all interactions are significant, except for the region–protection interaction ($F = 2.0$, $p = 0.157574$). The interaction that most explains the

TABLE 1 ANOVA pairwise interaction between main effects and results for flight initiation distance (FID) response in size, region, species, and protection on their own and the interaction between these factors.

Factors	df	Sum of squares	Mean square	F	p
Size	2	3,054,656	1,527,328	818.33	<2.2e−16***
Region	1	974,174	974,174	521.95	<2.2e−16***
Species	2	229,339	114,669	61.44	<2.2e−16***
Protection	2	716,119	358,059	191.84	<2.2e−16***
Size–region	2	228,972	114,486	61.34	<2.2e−16***
Size–species	4	99,644	24,911	13.35	9.29e−11***
Region–species	2	418,941	209,471	110.58	<2.2e−16***
Size–protection	4	283,026	70,756	38.74	<2.2e−16***
Region–protection	1	3730	3730	2.0	0.157574
Species–protection	4	59,654	14,914	8.0	2.14e−06***
Residuals	2393	4,646,394	1942		

Note: With a given significance level of 0.05, *** indicates that results are significant. Results not significant are indicated by a blank.

variation in our data is the region–species interaction, which has the highest mean square among the interactions (Msq = 209,471) and showed high statistical significance ($F = 110.58$, $p < 2.2e{-}16$). This interaction has a higher mean square than the variable "species" by itself. Another relevant interaction is between size-region, which showed a significant mean square, although lower (Msq: 114486; $F = 61.34$, $p < 2.2e{-}16$) than that of the region--species interaction. The remaining interactions, despite showing significance ($p < 2.2e{-}16$), present lower mean squares than the mentioned interactions; therefore, they were not selected as models that explain our response variable.

Results of the different possible factors determining FID (Figure 2) show that the size factor (Figure 2A) indicates that the median of the adjusted estimates for the small sizes is around 80–90, while the mean is ~85, representing a lower FID relative to the other sizes. For the medium sizes, the median is around 90–100 and the mean is ~95, presenting a slightly higher FID than small sizes but lower than large sizes. Large sizes present the highest FID with a median around 120 and a mean of ~110.

The species factor (Figure 2B) shows that *A. punctatus* has the shortest FID compared to the other species, with a median around 80 and a mean of ~75. *P. chilensis* and *C. variegatus* present similar FID values, with medians around 100 and means of ~95.

For protection (access regime/protection) (Figure 2C), the medians and means of the FID vary depending on

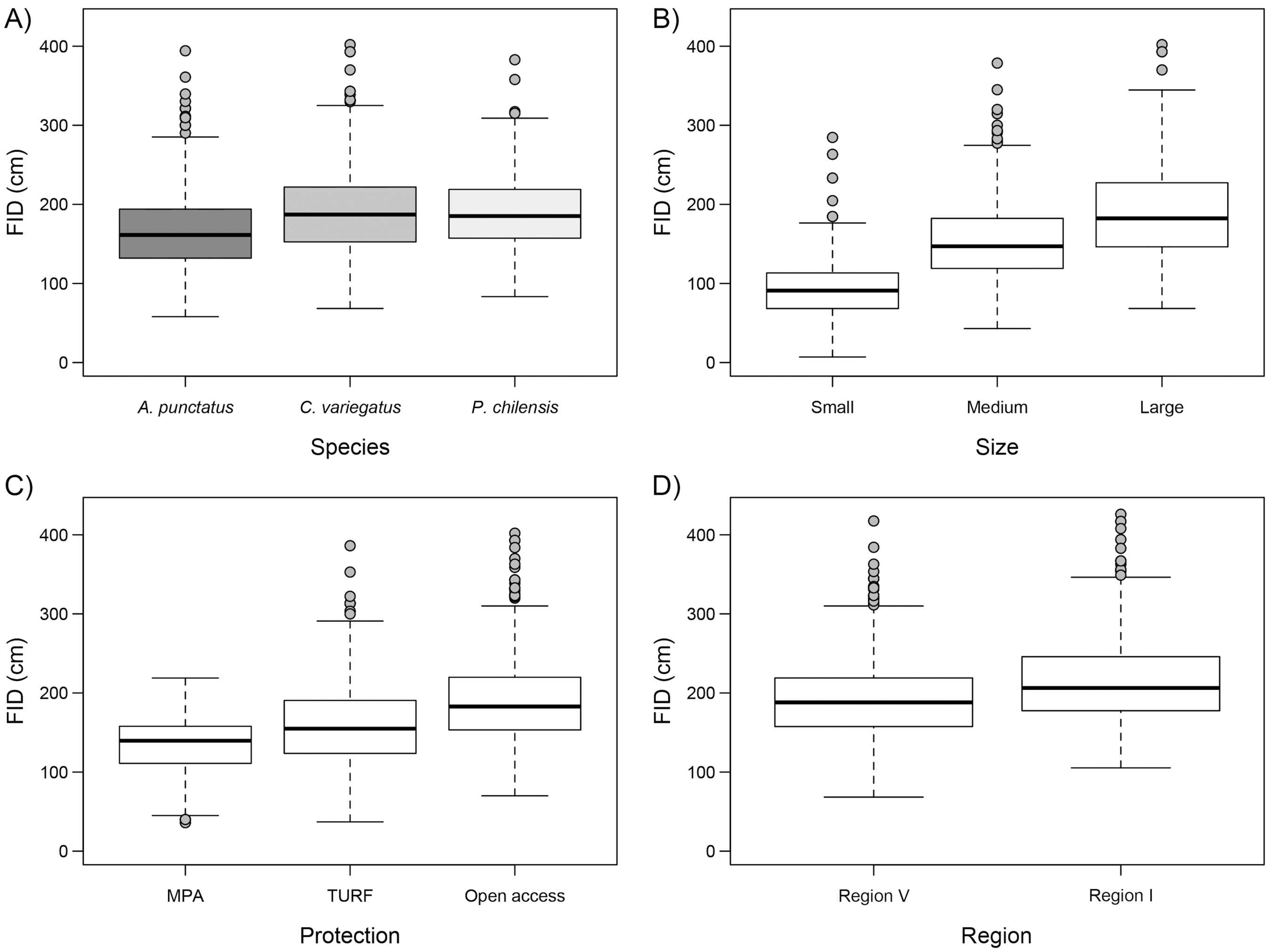

FIGURE 2 Flight initiation distance boxplot in relation to the adjusted estimates from our partial regressions: (A) species, divided into three levels: *Aplodactylus punctatus*, *Pinguipes chilensis*, and *Cheilodactylus variegatus*; (B) size, divided into three levels: small, medium, and large; (C) protection, divided into three levels: marine protected areas (MPA), territorial use rights for fishing (TURF), and open access; and (D) region, divided into two levels: Regions V and I. The midline represents the median flight initiation distance (FID) for each group. The box limits represent the interquartile range (IQR), showing where the middle 50% of the FID observations lie. The whiskers extend to the most extreme FID values that are not considered outliers. Outliers, if present, are plotted as individual points, representing FID values significantly different from the rest of the data.

the access regime. The specific values for each regime are detailed in the figure, providing a comprehensive view of how access regimes impact FID.

The MPA is the one that presents the lowest FIDs within our study areas, with a mean close to what was expected within our regressions. The TURFs present a similar mean to MPA. Finally, the open access areas are the ones that present a higher FID; they are the ones that present the highest difference between the observed and the expected, as well as the one that presents the highest number of outliers toward the positive peaks. For the region factor (Figure 2D), differences between the north (higher fishing pressure) and the south (lower fishing pressure) are observed with the north presenting higher FID. This assumption is based on historical landing data and fishing activity reports where higher fishing pressure in the north, and for more years, provides a rationale for the observed differences in FID.

The visualization of our two models, with interaction of selected factors, that explain most of the variation in our data show that the species–region model (Figure 3A) indicates that the highest FID measurements are found in Region I. For *C. variegatus*, the median FID is around 60 with a mean >50, and for *P. chilensis*, the median is around 40 with a mean <50. *Aplodactylus punctatus* presents the lowest FID in both regions, with a median around 20 and a mean ~25. The trend of the FID associated with the three species remains similar to when this variable was measured alone.

For the size–region interaction (Figure 3B), it is possible to observe that Region I shows the highest FIDs for large sizes, with a median around 120 and a mean >100. Medium sizes have a median around 100 and a mean ~100, while small sizes show similarities between both regions, with a median around 80 and a mean ~85.

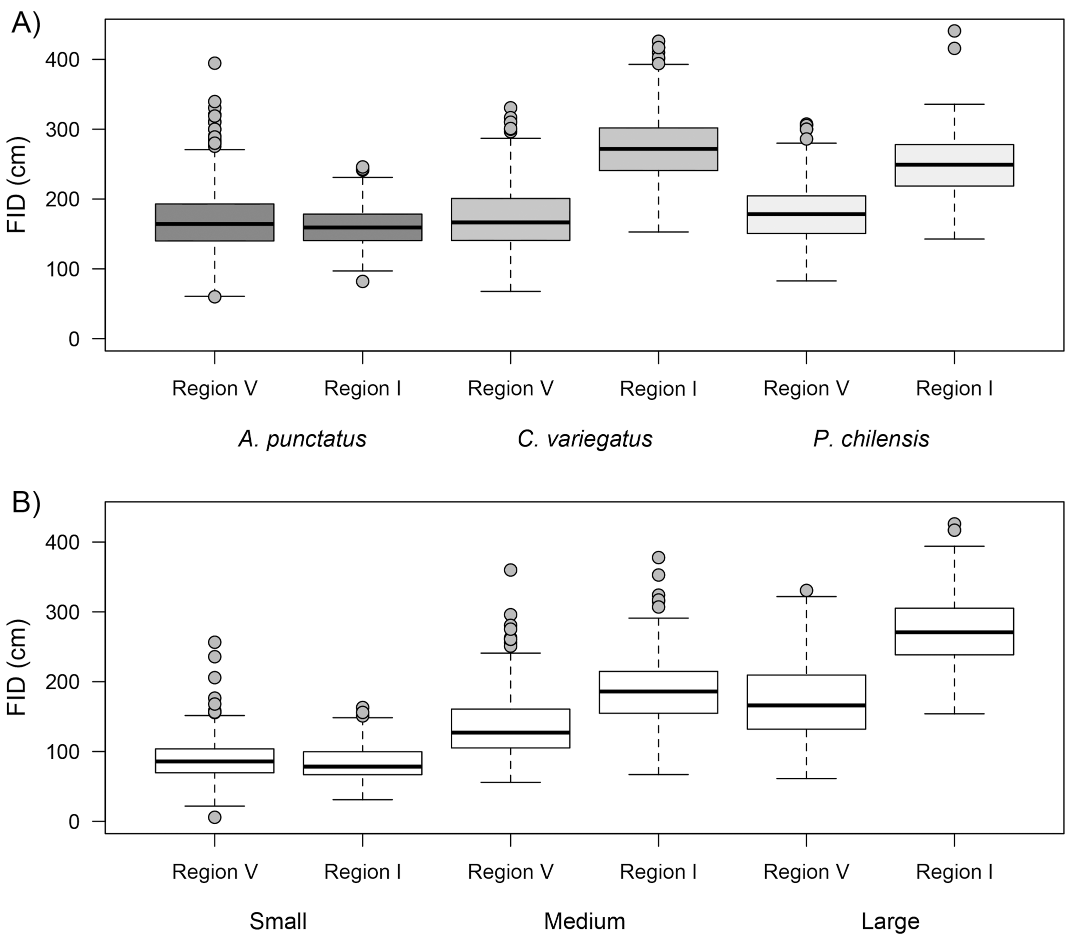

FIGURE 3 Flight initiation distance (FID) boxplot in relation to the adjusted estimates from our partial regressions with interacting factors: (A) interaction between region and species; (B) interaction between region and size. The midline represents the median FID for each group. The box limits represent the interquartile range (IQR), showing where the middle 50% of the FID observations lie. The whiskers extend to the most extreme FID values that are not considered outliers. Outliers, if present, are plotted as individual points, representing FID values significantly different from the rest of the data.

DISCUSSION

Our results show that FID differed significantly in relation to access regimes, fish body size, species identity, and historical fishing pressure. These findings support previous studies (Sbragaglia et al., 2023) and indicate that the FID can be useful as an indicator of fishing or anthropogenic disturbances associated with different access regimes. Specifically, the size–region interaction revealed that larger fish in regions with higher historical fishing pressure exhibited higher FIDs, supporting our hypothesis about the impact of historical fishing pressure. The species–region interaction showed significant variations in FID among species, with *A. punctatus* exhibiting the lowest FID across both regions, which aligns with our expectations based on species-specific behavior and vulnerability to fishing. Results support that FID can be used as a proxy of spearfishing pressure that plays an important role as a structuring agent of coastal ecological systems in Chile.

In relation to our results associated with size, theory has proposed that as size of an organism increases, the reaction to threats would increase; therefore, the measurement of FID in larger individuals (adults) should increase (Gotanda et al., 2009; Grant & Noakes, 1987). In fact, Rogers and Sargent (2001) generated a model that predicts the increase in fish reaction with increasing fish size. Literature has suggested that the increase in fish size is directly associated with the focal size of the fish and the developmental stage of the organism (large/late adult, medium/adult, and small/juvenile). As large fish present with a larger focal eye aperture, they are able to better identify the threat (Olden et al., 2006; Sbragaglia et al., 2018; Sogard, 1997). Our results showed differences in FID when comparing medium and large sizes of our three species (González & Oyarzún, 2003). Smaller sizes showed the lowest FID, with distances significantly shorter than those recorded for medium and large size fish; however, there were no differences in the interaction with other factors. Thus, small individuals show similar behavior between regimes, independent of the type of species and the area where they are fished. Previous studies have proposed that this could be explained by the fact that juvenile individuals have not yet assimilated the imprint of humans as a threat and there is no behavioral development as in larger individuals because smaller fish are not targeted by spearfishermen (Abrahams, 2000).

Similar to our results, other studies using FID as an indicator of fishing pressure predicted that FID increases with increasing danger based on the presence of a diver (using a speargun or some fishing gear) (Cooper & Whiting, 2007). Individuals from a species may gain information about a threat based on experience, whereby they may modify and adapt their antipredator responses to a threat, reflecting this in variations of the FID (Sbragaglia et al., 2018). Our results show the largest FID was recorded in open access areas. Nonexistent regulations in open access areas could be generating an increase in FID, as organisms face a greater number of encounters with spearfishers (Gaynor et al., 2018). Both in the TURFs and in the MPA, FID was similar probably due to the fact that in both these regimes fishing is limited or totally banned (Stankowich, 2008; Weston et al., 2012). Similar effects have been described in the literature for "no take zones" in tropical ecosystems (Januchowski-Hartley et al., 2011; Petit et al., 2022).

Different studies such as that of Kramer and Chapman (1999) show that large- and/or medium-sized fish have limited home ranges and tend not to move between areas, especially territorial rocky-reef fish (Palma & Ojeda, 2002). From our results, we infer that the home ranges of the species studied would be contained to the spatial scales used in our study (open access, TURFs, and MPA), generating a behavioral response within these areas, in direct relation between the access regime and FID (Baudains & Lloyd, 2007; Cooper & Whiting, 2007).

At the species level, the largest FID were recorded for *C. variegatus*, followed by *P. chilensis* and finally *A. punctatus*. *C. variegatus* has the highest commercial value so we would predict a higher FID, as increased exposure to divers may increase sensitization to disturbance cues (Gotanda et al., 2009). An example of this has been shown by Paton et al. (2017), who show that hunting pressure exacerbates behavioral impacts in migratory moose, which coincides with our results. In contrast, *A. punctatus* presents the lowest FID. This may be explained by the evolution of the coastal reef fish fishery, where this species has been only recently included in the fishery (Godoy et al., 2016; SERNAPESCA, 2020). If the species presents a recent period of extraction, it may mean that it is not yet related to a long-term constant disturbance; therefore, it may facilitate tolerance and habituation to this activity and present lower FID (Wheat & Wilmers, 2016). On the other hand, our results show that the region factor significantly predicts the variation of FID. Although the data suggest that greater fishing activity is associated with higher fish FID, it is important to note that this conclusion should be verified with more refined time series and detailed data on fishing pressure (Beckerman, 1991; Blumstein, 2016; Wilson et al., 2020). In addition, future research could consider the impact of social behavior (whether fish are in groups or solitary), the type of substrate, or the activity state of the fish (foraging vs. resting) on FID.

Our results show the most significant interactions between factors are the species/regions and size/regions interactions (Figure 3). The results observed for the species–regions interaction show that the species *A. punctatus* has the lowest FIDs among all the species for both regions. Of the three studied fishes, *A. punctatus* is the least preferred by fishers mostly because of its herbivorous habits mainly consuming the brown kelp *Lessonia*, thus making the fish less edible to humans (Cáceres et al., 1994; Madin et al., 2010; Ruz et al., 2018).

C. variegatus has higher FID in the north than in the south; this coincides with SERNAPESCA data on levels of artisanal landings, which are higher in the north where there is a culture of consumption and fishing for this species, for a longer time than in central Chile (Godoy et al., 2016; SERNAPESCA, 2020). For *P. chilensis*, the same pattern is observed as in *C. variegatus*; in this case, a higher FID in the north coincides with the history of the fishery, which spans more than six decades of operation with good records of artisanal fishery landing data for these species (Godoy et al., 2010; SERNAPESCA, 2020). In relation to the size/region interaction, the differences in the FID may be because spearfishers target fish of a larger size and ignore small fish, given the economic retribution per unit of fishing effort (Godoy et al., 2016; Ydenberg & Dill, 1986). It is worth noting that the "medium" sizes would also be being incorporated into the commercial fishery and show high FID records. Overall, our approach in which we consider factors such as fish size, access regime, region, species, and the interactions of fishing zone with target sizes and species, as categorical variables, proved useful to explore FID.

CONCLUSIONS

The results of this study suggest that spearfishing does have a significant effect on the behavior of individuals of the three commercial coastal fish species studied. This is evident in the larger sizes, but it is also possible to observe this pattern in medium-sized fishes that are also targeted by fishers. Results suggest fish can behave and have human-based imprinting in the development of escape behaviors. Importantly, results also build a knowledge base for the management of these species as they allow to infer that TURFs and MPA could be effective tools for the management and conservation of these ecologically important species within temperate rocky reefs.

AUTHOR CONTRIBUTIONS

Francisco Contreras-Drey, Natalio Godoy, and Stefan Gelcich conceived the ideas and designed the methodology. Andres Smith, Natalio Godoy, and Stefan Gelcich performed the fieldwork. Francisco Contreras-Drey and Enrico L. Rezende made the data analysis. Francisco Contreras-Drey and Stefan Gelcich wrote the first draft of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

ACKNOWLEDGMENTS

Funding for this research was provided by the ANID-Millennium Science Initiative Program (Project ICN 2019-015) and ANID PIA/BASAL FB0002. Additional funding was provided by the FONDECYT grant number 1230982 to Stefan Gelcich, grant number 1210216 to Alejandro Pérez-Matus, grant number 1221534 to Rodrigo Estevez, and grant number 3150138 to Natalio Godoy. Francisco J. Contreras-Drey was supported by the ANID BECAS/DOCTORADO NACIONAL 21242280. Thanks to "Tito" Santis for support in field and we thank Valentina Rebolledo-Zelada for her valuable feedback and collaboration during this research

CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data (Contreras-Drey et al., 2024) are available from Zenodo: https://doi.org/10.5281/zenodo.13888313.

ORCID

Francisco J. Contreras-Drey https://orcid.org/0000-0002-7542-3118
Enrico L. Rezende https://orcid.org/0000-0002-6245-9605
Alejandro Pérez-Matus https://orcid.org/0000-0001-9591-6721
Stefan Gelcich https://orcid.org/0000-0002-5976-9311

REFERENCES

Abrahams, M. V. 2000. "The Interaction Between Antipredator Behavior and Antipredator Morphology: Experiments with Fathead Minnows and Brook Sticklebacks." *Canadian Journal of Zoology* 73: 2209–15.

Allison, E. H., and F. Ellis. 2001. "The Livelihoods Approach and Management of Small-Scale Fisheries." *Marine Policy* 25: 377–388.

Baudains, T. P., and P. Lloyd. 2007. "Habituation and Habitat Changes Can Moderate the Impacts of Human Disturbance on Shorebird Breeding Performance." *Animal Conservation* 10(3): 400–407.

Beckerman, S. 1991. "Barí Spear Fishing: Advantages to Group Formation?" *Human Ecology* 19: 529–554.

Benavides, A. G., J. M. Cancino, and F. P. Ojeda. 1994. "Ontogenetic Change in the Diet of *Aplodactylus punctatus* (Pisces: Aplodactylidae): An Ecophysiological Explanation." *Marine Biology* 118: 1–5.

Benevides, L., J. de Nunes, T. L. A. Costa, and C. L. S. Sampaio. 2016. "Flight Response of the Barber Surgeonfish, *Acanthurus bahianus* Castelnau, 1855 (Teleostei: Acanthuridae), to Spearfisher Presence." *Neotropical Ichthyology* 14: e150010.

Benevides, L. J., G. C. Cardozo-Ferreira, C. E. L. Ferreira, P. H. C. Pereira, T. K. Pint, and C. L. S. Sampaio. 2019. "Fear-Induced Behavioral Modifications in Damselfishes Can be Diver-Triggered." *Journal of Experimental Marine Biology and Ecology* 514-515: 34–40.

Berkes, F. 2001. *Managing Small-Scale Fisheries: Alternative Directions and Methods*. Ottawa, ON: International Development Research Centre.

Blumstein, D. T. 2003. "Flight-Initiation Distance in Birds Is Dependent on Intruder Starting Distance." *The Journal of Wildlife Management* 67(4): 852–57.

Blumstein, D. T. 2016. "Habituation and Sensitization: New Thoughts About Old Ideas." *Animal Behavior* 120: 255–262.

Brown, G. E. 2003. "Learning About Danger: Chemical Alarm Cues and Local Risk Assessment in Prey Fishes." *Fish and Fisheries* 4: 227–234.

Cáceres, C. W., L. S. Fuentes, and F. P. Ojeda. 1994. "Optimal Feeding Strategy of the Temperate Herbivorous Fish *Aplodactylus punctatus*: The Effects of Food Availability on Digestive and Reproductive Patterns." *Oecologia* 99: 118–123.

Callum, M., J. A. Roberts, F. Bohnsack, J. Gell, P. Hawkins, and R. Goodridge. 2001. "Effects of Marine Reserves on Adjacent Fisheries." *Science* 294: 1920–23.

Chirichigno, N. 1974. "Clave para identificar los peces marinos del Perú." Instituto del Mar del Perú, Informe No. 44, Callao, Perú. 387 pp.

Chirichigno, N. 1998. "Clave para identificar los peces marinos del Perú." Segunda Edición. Instituto del Mar del Perú, Informe No. 44, Callao, Perú. 496 pp.

Contreras-Drey, F. J. 2024. "Dataset: Escape Behavior of Rocky Reef-Fish (Version 1)." Zenodo. https://doi.org/10.5281/zenodo.13888313.

Cooper, W. E., Jr. 2005. "When and how Do Predator Starting Distances Affect Flight Initiation Distances?" *Canadian Journal of Zoology* 83: 1045–50.

Cooper, W. E., and M. J. Whiting. 2007. "Effects of Risk on Flight Initiation Distance and Escaped Tactics in Two Southern African Lizard Species." *Acta Zoologica Sinica* 53: 446–453.

Crona, B., S. Gelcich, and Ö. Bodin. 2017. "The Importance of Interplay between Leadership and Social Capital in Shaping Outcomes of Rights-Based Fisheries Governance." *World Development* 91: 70–83.

Deecke, V. B., P. J. B. Slater, and J. K. B. Ford. 2002. "Selective Habituation Shapes Acoustic Predator Recognition in Harbour Seals." *Nature* 420: 171–73.

Defeo, O., and J. C. Castilla. 2005. "More than One Bag for the World Fishery Crisis and Keys for Co-Management Successes in Selected Artisanal Latin American Shellfisheries." *Reviews in Fish Biology and Fisheries* 15: 265–283.

Gaynor, K. M., C. E. Hojnowski, N. H. Carter, and J. S. Brashares. 2018. "The Influence of Human Disturbance on Wildlife Nocturnality." *Science* 360: 1232–35.

Gelcich, S., J. Cinner, C. J. Donlan, S. Tapia-Lewin, N. Godoy, and J. C. Castilla. 2017. "Fishers' Perceptions on the Chilean Coastal TURF System After Two Decades: Problems, Benefits, and Emerging Needs." *Bulletin of Marine Science* 93(1): 53–67.

Gelcich, S., M. Fernandez, N. Godoy, A. Canepa, L. Prado, and J. C. Castilla. 2012. "Territorial User Rights for Fisheries as Ancillary Instruments for Marine Coastal Conservation in Chile." *Conservation Biology* 26: 1005–15.

Gelcich, S., N. Godoy, and J. C. Castilla. 2009. "Artisanal Fishers' Perceptions Regarding Coastal Co-Management Policies in Chile and Their Potentials to Scale-Up Marine Biodiversity Conservation." *Ocean & Coastal Management* 52(8): 424–432.

Gelcich, S., L. Prado, N. Godoy, and J. C. Castilla. 2008. "Add-on Conservation Benefits of Marine Territorial User Rights Policy in Central Chile." *Ecological Applications* 18: 273–281.

Glaudas, X., C. T. Winne, and L. A. Fedewa. 2006. "Ontogeny of Anti-Predator Behavioral Habituation in Cottonmouths (*Agkistrodon piscivorus*)." *Ethology* 112: 608–615.

Godoy, N., S. Gelcich, J. C. Castilla, M. Lima, and A. Smith. 2016. "Artisanal Spear Fishery in Temperate Nearshore Ecosystems of Chile: Exploring the Catch Composition, Revenue, and Management Needs." *Marine and Coastal Fisheries* 8: 436–447.

Godoy, N., S. Gelcich, J. A. Vasquez, and J. C. Castilla. 2010. "Spearfishing to Depletion: Evidence From Temperate Reef Fishes in Chile." *Ecological Applications* 20: 1504–11.

González, P., and C. Oyarzún. 2003. "Diet of the Chilean Sandperch, *Pinguipes chilensis* (Perciformes, Pinguipedidae) in Southern Chile." *Journal of Applied Ichthiology* 19: 371–75.

Gotanda, K. M., K. Turgeon, and D. L. Kramer. 2009. "Body Size and Reserve Protection Affect Flight Initiation Distance in Parrotfishes." *Behavioral Ecology and Sociobiology* 63: 1563–72.

Grant, J. W., and D. L. Noakes. 1987. "Escape Behaviour and Use of Cover by Young-of-the-Year Brook Trout, *Salvelinus fontinalis*." *Canadian Journal of Fisheries and Aquatic Sciences* 44(8): 1390–96.

Gray, A. E., I. D. Williams, K. A. Stamoulis, R. C. Boland, K. C. Lino, B. B. Hauk, and R. K. Kosaki. 2016. "Comparison of Reef Fish Survey Data Gathered by Open and Closed-Circuit SCUBA Divers Reveals Differences in Areas With Higher Fishing Pressure." *PLoS One* 11: 1–18.

Guabiroba, H. C., C. C. Vilar, H. T. Pinheiro, and J. C. Joyeux. 2022. "Limited Human Access Is Linked to Higher Effectiveness in a Marine Sanctuary." *Journal of Environmental Management* 311: 114838.

Jackson, J. B. C., M. X. Kirby, W. H. Berger, K. A. Bjorndal, L. W. Botsford, B. J. Bourque, R. H. Bradbury, et al. 2001. "Historical Overfishing and the Recent Collapse of Coastal Ecosystems." *Science* 80(293): 629–637.

Januchowski-Hartley, F. A., N. A. Graham, D. A. Feary, T. Morove, and J. E. Cinner. 2011. "Fear of Fishers: Human Predation Explains Behavioral Changes in Coral Reef Fishes." *PLoS One* 6(8): e22761.

Januchowski-Hartley, F. A., N. A. J. Graham, J. E. Cinner, and G. R. Russ. 2013. "Spillover of Fish Naïveté From Marine Reserves." *Ecological Letters* 16: 191–97.

Johannes, R. E. 1978. "Traditional Marine Conservation Methods in Oceania and Their Demise." *Annual Review of Ecology and Systematics* 9(1): 349–364.

Kramer, D. L., and M. R. Chapman. 1999. "Implications of Fish Home Range Size and Relocation for Marine Reserve Function." *Environmental Biology of Fishes* 55: 65–79.

Laundré, J. W., L. Hernández, and K. B. Altendorf. 2001. "Wolves, Elk, and Bison: Reestablishing the 'Landscape of Fear' in Yellowstone National Park, USA." *Canadian Journal of Zoology* 79(8): 1401–9.

Lima, S. L., and L. M. Dill. 1990. "Behavioral Decisions Made under the Risk of Predation: A Review and Prospectus." *Canadian Journal of Zoology* 68(4): 619–640.

Lyach, R., and M. Čech. 2018. "A New Trend in Central European Recreational Fishing: More Fishing Visits but Lower Yield and Catch." *Fisheries Research* 201: 131–37.

Madin, E. M. P., S. D. Gaines, J. S. Madin, and R. R. Warner. 2010. "Fishing Indirectly Structures Macroalgal Assemblages by Altering Herbivore Behavior." *American Naturalist* 176: 785–801.

Mann, F. G. 1954. *La vida de los peces en aguas chilenas*. Invest: Veterinarias, Universidad de Chile, Santiago, Chile.

Medina, M., M. Araya, and C. Vega. 2004. "Alimentación y relaciones tróficas de peces costeros de la zona norte de Chile." *Investigaciones Marinas* 32: 33–47.

Neter, J., M. H. Kutner, C. J. Nachtsheim, and W. Wasserman. 1996. *Applied Linear Statistical Models*, 5th ed. New York, NY: The McGraw-Hill Companies, Inc.

Nunes, J. A. C. C., Y. Costa, D. T. Blumstein, A. O. H. C. Leduc, A. C. Dorea, L. J. Benevides, and F. Barros. 2018. "Global Trends on Reef Fishes' Ecology of Fear: Flight Initiation Distance for Conservation." *Marine Environmental Research* 136: 153–57.

Oakley, S. G. (1984). The effects of spearfishing pressure on grouper (Serranidae) populations in the Eastern Red Sea. In *Proceedings of the Symposium on Coral Reef Environments of the Red Sea* (pp. 341–359). King Abdulaziz University, Jeddah, Saudi Arabia.

Olden, J. D., N. L. Poff, and K. R. Bestgen. 2006. "Life-History Strategies Predict Fish Invasions and Extirpations in the Colorado River Basin." *Ecological Monographs* 76(1): 25–40.

Palma, Á. T., and F. P. Ojeda. 2002. "Abundance, Distribution and Feeding Patterns of a Temperate Reef Fish in Subtidal Environments of the Chilean Coast: The Importance of Understory Algal Turf." *Revista Chilena de Historia Natural* 75: 189–200.

Paton, D. G., S. Ciuti, M. Quinn, and M. S. Boyce. 2017. "Hunting Exacerbates the Response to Human Disturbance in Large Herbivores While Migrating Through a Road Network." *Ecosphere* 8(6): e01841.

Pauly, D., V. Christensen, S. Guenette, T. Pitcher, R. Sumaila, C. Walters, R. Watson, and D. Zeller. 2002. "Towards Sustainability in World Fisheries." *Nature* 418: 689–695. https://doi.org/10.1038/nature01017.

Pequeño, G., and F. Olivera. 2005. "Peces litorales de Chile, objeto de pesca: primer análisis de conjunto hay en la pesquería litoral una amenaza a la diversidad ictiofaunistica, que ha sido humanamente imperceptible e incalculable. Cuarta parte. Capitulo XV." In *Biodiversidad marina: valoración, uso y perspectivas, ¿Hacia dónde va Chile?* edited by E. Figueroa, 507–538. Santiago, Chile: Editorial Universitaria.

Pérez-Matus, A., A. Ospina-Alvarez, P. A. Camus, S. A. Carrasco, M. Fernandez, N. G. Gelcich, F. P. Ojeda, et al. 2017. "Temperate Rocky Subtidal Reef Community Reveals Human Impacts Across the Entire Food Web." *Marine Ecology Progress Series* 567: 1–16.

Pérez-Matus, A. L. A., A. C. Ferry-Graham, and J. A. Vásquez. 2007. "Community Structure of Temperate Reef Fishes in Kelp-Dominated Subtidal Habitat of Northern Chile." *Marine and Freshwater Research* 58: 1069–85.

Petit, I. J., C. F. Gaymer, A. M. Friedlander, and J. B. Gusmao. 2022. "Depth as a Fish Refuge From Spearfishing at Rapa Nui: Flight Behaviour in the Pacific Rudderfish *Kyphosus sandwicensis*." *Aquatic Conservation: Marine and Freshwater Ecosystems* 32: 727–740.

Rogers, L., and R. C. Sargent. 2001. "A Dynamic Model of Size-Dependent Reproductive Effort in a Sequential Hermaphrodite: A Counterexample to Williams's Conjecture." *The American Naturalist* 158(5): 543–552.

Ruz, C. S., A. F. Muth, F. Tala, and A. Pérez-Matus. 2018. "The Herbivorous Fish, *Aplodactylus punctatus*, as a Potential Facilitator of Dispersal of Kelp, *Lessonia trabeculata*, in Chile." *Journal of Experimental Marine Biology and Ecology* 500: 112–19.

Sbragaglia, V., R. Arlinghaus, D. T. Blumstein, H. Diogo, V. J. Giglio, A. Gordoa, F. A. Januchowski-Hartley, et al. 2023. "A Global Review of Marine Recreational Spearfishing." *Rev Fish Biol Fisheries* 33: 1199–1222.

Sbragaglia, V., L. Morroni, L. Bramanti, B. Weitzmann, R. Arlinghaus, and E. Azzurro. 2018. "Spearfishing Modulates Flight Initiation Distance of Fishes: The Effects of Protection, Individual Size, and Bearing a Speargun." *ICES Journal of Marine Science* 75: 1779–89.

Sogard, S. M. 1997. "Size-Selective Mortality in the Juvenile Stage of Teleost Fishes: A Review." *Bulletin of Marine Science* 60: 1129–57.

Stankowich, T. 2008. "Ungulate Flight Responses to Human Disturbance: A Review and Meta-Analysis." *Biological Conservation* 141: 2159–73.

Stuart-Smith, R. D., A. E. Bates, J. S. Lefcheck, J. E. Duffy, S. C. Baker, R. J. Thomson, and G. J. Edgar. 2013. "Integrating Abundance and Functional Traits Reveals New Global Hotspots of Fish Diversity." *Nature* 501: 539–542.

Tran, D. S. C., K. A. Langel, M. J. Thomas, and D. T. Blumstein. 2016. "Spearfishing Induced Behavioral Changes of an Un-Harvested Species Inside and Outside a Marine Protected Area." *Current Zoology* 62: 39–44.

Weston, M. A., E. M. McLeod, D. T. Blumstein, and P.-J. Guay. 2012. "A Review of Flight-Initiation Distances and Their Application to Managing Disturbance to Australian Birds." *Emu – Austral Ornithology* 112: 269–286.

Wheat, R. E., and C. C. Wilmers. 2016. "Habituation Reverses Fear-Based Ecological Effects in Brown Bears (*Ursus arctos*)." *Ecosphere* 7: e01408.

Wilson, M. W., A. D. Ridlon, K. M. Gaynor, S. D. Gaines, A. C. Stier, and B. S. Halpern. 2020. "Ecological Impacts of Human-Induced Animal Behaviour Change." *Ecology Letters* 23(10): 1522–36.

Ydenberg, R. C., and L. M. Dill. 1986. "The Economics of Fleeing From Predators." *Advances in the Study of Behavior* 16: 229–249.

SERNAPESCA (National Fisheries Service). 2020. *Anuarios estadísticos de pesca [National landing register of artisanal fisheries]*. Valparaiso: SERNAPESCA.

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

How to cite this article: Contreras-Drey, Francisco J., Natalio Godoy, Andrés Smith, Enrico L. Rezende, Alejandro Pérez-Matus, Rodrigo A. Estevez, Ricardo Beldade, F. Patricio Ojeda, and Stefan Gelcich. 2024. "Escape Behavior of Rocky-Reef Fish Reveals the Impact of Spearfishing across Different Management Regimes." *Ecosphere* 15(11): e70056. https://doi.org/10.1002/ecs2.70056