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Research Article

Movements and behavior of satellite-tagged yellownose skate (*Dipturus chilensis*) and roughskin skate (*Dipturus trachyderma*) in southern Chile

Mauricio Ahumada[1], **Pedro Apablaza**[1], **Dante Queirolo**[1]
Rodrigo Wiff[2,3] **& Andrés Flores**[4]
[1]Grupo de Tecnología Pesquera, Escuela de Ciencias del Mar, Campus Curauma
Pontificia Universidad Católica de Valparaíso, Valparaíso, Chile
[2]Center of Applied Ecology and Sustainability (CAPES)
Pontificia Universidad Católica de Chile Santiago, Chile
[3]Instituto Milenio en Socio-Ecología Costera (SECOS), Santiago, Chile
[4]Independent Researcher, Viña del Mar, Chile
Corresponding author: Mauricio Ahumada (mauricio.ahumada@pucv.cl)

ABSTRACT. *Dipturus chilensis* and *D. trachyderma* are two species of skates found on the continental shelf and slope around the southern tip of South America. As another batoids, their life traits make them more susceptible to overfishing. In Chile, the skate fishery covers around twenty latitudinal degrees and is captured as a target species by artisanal vessels from the central-south zone to the Patagonian fjords (south of 41°S). Seven individuals of *D. chilensis* and three of *D. trachyderma*, 75-110 cm total length (TL), were tagged with pop-up satellite tags programmed to detach 60 days post-tagging. The skates were tracked in two areas of southern Chile, one exposed to the Pacific Ocean (Bahía Mansa) and another within the Patagonian fjords of the Chiloe inland sea (Comau Channel). Bathymetric ranges of 9-512 m and temperatures of 7.7-11.5°C for *D. chilensis* and depths of 111-513 m with temperatures of 10.5-11.5°C for *D. trachyderma* were detected. The minimum horizontal movement varied between 0.84 and 35.95 km in *D. chilensis* and 2.59 and 33.90 km in *D. trachyderma*. Notably, *D. chilensis* was found at significantly shallower depths at night, with differences between zones and higher levels of vertical activity in Comau. Both species showed daily vertical movements of up to 1.4 km, displaying movement patterns associated with different modalities of foraging. The median vertical speed was up to 0.18 TL s^{-1}, suggesting that both species could primarily utilize nektobenthic diel vertical migration to move to and from the coast.

Keywords: *Dipturus chilensis*; *Dipturus trachyderma*; elasmobranch; electronic tagging; PSATs; satellite telemetry

INTRODUCTION

Yellownose skate (*Dipturus chilensis* Guichenot, 1848) and roughskin skate (*Dipturus trachyderma* Krefft & Stehmann, 1975) are benthic elasmobranchs whose distribution has been reported around the southern tip of South America, between central Chile in the Pacific Ocean and southern Brazil in the Atlantic Ocean, in the continental shelf and slope (Agnew et al. 2000, García de la Rosa et al. 2000, Lucifora et al. 2000, Gomes & Picado 2001, Koen et al. 2001, Bustamante et al. 2012). Recently, the taxonomic classification of yellownose skate has been debated, and the skates inhabiting Chile have been considered a different species from the skates found in the Atlantic (Gabbanelli et al. 2018, 2022, Concha et al. 2019).

The yellownose and roughskin skates in Chile are found between 32 and 56°S at depths of 14-477 m and

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have been targeted by fisheries since 1979 (Vargas-Caro et al. 2015, 2017). Members of the Rajidae family, these skates are highly vulnerable to overfishing due to their life history traits, such as slow growth, large size, late maturity, and low fecundity. They show persistent abundance reductions even at low exploitation levels (Frisk et al. 2001, 2005, Dulvy & Reynolds 2002, Dulvy et al. 2021). Indeed, the yellownose skate has the lowest resilience to fishing exploitation of all fish species harvested in Chile (Wiff et al. 2018). Both species are listed as threatened by the IUCN (IUCN 2022), with roughskin skate being particularly susceptible due to its larger size and lower resilience (Dulvy & Reynolds 2002, Licandeo et al. 2007).

The skate fishery in Chile initially targeted yellownose skate but included at least six species under the generic term "skates" until 2004, with no species differentiation in the fishing logbooks. Before 1993, annual landings were below 500 t, but increased fishing efforts led to a significant rise, peaking at 5,000 t in 2003 (Quiroz et al. 2008, Vargas-Caro et al. 2015). A shift from industrial to small-scale fleets occurred in the early 2000s (Quiroz et al. 2008), followed by a decline in landings until 2012, and since then, several closures and other fishing effort restrictions have been applied in skates (Vargas-Caro et al. 2015). An artisanal gillnet and longline fleet target yellownose skate and is also caught as bycatch in the pink cusk-eel fishery (*Genypterus blacodes*). Roughskin skate is mainly captured as a secondary species (Wiff et al. 2021) or as bycatch, often discarded by both industrial and artisanal fisheries (Céspedes et al. 2005, Wiff et al. 2020, Landaeta et al. 2023).

Since 1999, fisheries and biological attributes have been collected, particularly in yellownose skate, to support a stock assessment and a management system based on the total allowable catch (TAC). However, fishing activity data is considered poor, skewed, and imprecise (Wiff et al. 2021). In the case of roughskin skate, the management of this species is only based on precautionary levels of bycatch along catches of yellownose skate. After 2006, several fishing closures were imposed on the fishery (Vargas-Caro et al. 2015). Still, the exploitation status of the yellownose skate off southern Chile was already considered severely depleted (Quiroz et al. 2011). In recent years, the TACs have been small, around 400-600 t, and have been quickly caught by the gillnet and longline fleet, resulting in a race for fishing in short fishing seasons of a few days per year.

Although biological parameters regarding growth, natural mortality and maturity are known in both species of skates, some demographic attributes are difficult to assess using data from commercial fishing operations restricted in space and time. In particular, movements, behavior, and spatial aggregation in elasmobranchs are important in proposing recovery plans in heavily depleted populations, and spatial data integrated with other ecological information improves our ability to preserve key habitats and their ecological functions (Dwyer et al. 2019). Information regarding tagging experiences will aid in improving marine reserves (Dwyer et al. 2020), the estimation of demographic parameters such as abundance and survival rates (Dudgeon et al. 2015), the study of fine-scale movement patterns (Papastamatiou et al. 2015) and habitat use patterns (Dawdy et al. 2022). Broad-scale movements can reveal migratory pathways, environmental preferences, habitat use, and residency patterns. Fine-scale movements can provide behavioral and physiological context to other studies of broad-scale movements (Andrzejaczek et al. 2018).

Fish movements are often inferred using conventional tagging, relying upon commercial fishing operations for tagging animals, which correlates with fishing fleets' spatiotemporal coverage (Bolle et al. 2005). Alternatively, pop-up satellite tags provide a useful tool for assessing movement without depending on the operation of the commercial fleet. Although the use of tracking devices is growing worldwide (Hussey et al. 2015), studies on skate movement using electronic tagging are considerably lacking (Siskey et al. 2018), focused on the north hemisphere, and still hardly affordable in developing regions.

In Chile, tagging of commercial fish species is limited to a few species and fragmented in time (Wiff et al. 2023), and pop-up satellite tags provide a suitable alternative for exploiting Chilean skates. After being released automatically, the information collected on the tag and its location is transmitted via satellite to the researcher, providing information on the individual's distribution and movement patterns and some environmental variables such as temperature, depth, and light levels.

This study aimed to test for the first time using pop-up satellite tags to describe patterns of fine-scale movements of free-ranging individuals of yellownose and roughskin skate in Chile.

MATERIALS AND METHODS

Study area and skate capture

The yellownose and roughskin skates were captured in two zones in the Los Lagos Region, southern Chile (Fig. 1). The first one, named Bahía Mansa, is in the vi-

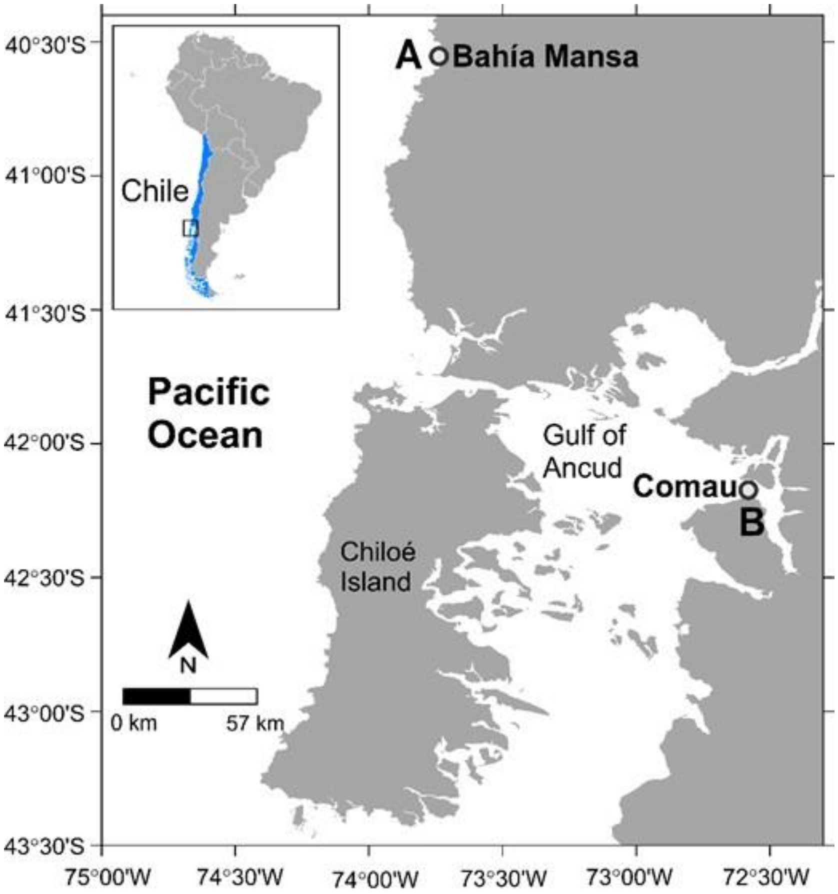

Figure 1. Map of the study area showing the location of sampling zones: A: Bahía Mansa, and B: Comau.

cinity of Bahía Mansa port (40°34'S, 73°43'W), located in open waters to the Pacific Ocean, in the area of the bifurcation of the West Wind Drift Current (or South Pacific Current) into a current with northbound (Humboldt Current System) and another one with southbound (Cape Horn Current), at the southern limit of a biogeographic transition zone. Bahía Mansa presents a relatively straight coast with a north-south orientation and coastal upwelling (Thiel et al. 2007, Strub et al. 2019).

The second sampling zone, named Comau, was located between the Patagonian fjords of the Chiloé inland sea, at the entrance of the homonymous fjord, specifically in the Comau Channel (42°16'S, 72°28'W). A zone characterized by reduced exposure to waves, which presents steep slopes, with a maximum depth of 500 m, and is under the influence of freshwater due to rain, glaciers, and rivers, with a low salinity layer up to 7 m deep and a significant tidal range (4-6 m) (Melzer et al. 2006, Häussermann & Försterra 2009, Addamo et al. 2021).

The skates were captured in artisanal boats that participate in commercial skate fishing, using bottom longline, soak times of 12 h, and Araucanian herring (*Strangomera bentincki*), whole and salted as bait in Bahía Mansa, and using fresh pieces of Chilean silverside (*Odontesthes regia*) in Comau. The skates were captured on August 21, 2021, at depths of 130 m in Bahía Mansa and on August 29 and 31, 2021, between 320 and 490 m in Comau.

Tagging and deployment

The captured skates were hoisted manually aboard, not using boat hooks, avoiding damage. Fish were deposited on deck, on a smooth surface covered with a fishing net where each hook was carefully removed.

Pop-up satellite transmitters (Wild-Life Computers, model sPAT-355H, 10 units) were used for tagging. They can be programmed for deployment times of up to 60 days, after which they automatically emerge and transmit records from the surface via satellite (Argos). Each tag was set for 60 days of time deployment. These tags allow the recording, storage, and transmission of the following data: minimum and maximum temperature and depth readings, delta (difference between min and max depth), light level for each UTC Day, and

10-min time-series depth data along the last day of deployment.

Total length (TL), disc width (DW), total weight (TW), species, and sex were recorded from each captured individual. Nine females and one male were captured. All the sizes of the yellownose and roughskin skates were smaller than the size at 50% of maturity ($L_{50\%}$) of 106 and 86 cm for females and males of yellownose skate and 215 cm for females of roughskin skate (Licandeo et al. 2006, 2007). For *D. chilensis*, the size range varied between 75 and 104 cm, while for *D. trachyderma*, between 89 and 110 cm (Table 1).

The tags were fixed to the pectoral fin at 2.5 cm from the edge, approximately at 2/3 distance between the end of the rostrum and the distal end of the pectoral fin, using a 6 cm long metal needle, disinfected with alcohol and monofilament polyamide 0.9 mm Ø, fixed with 1/16" aluminum fishing line crimps. Two Petersen discs, one on each side of the fin, were used to reinforce the tag and to prevent muscle damage (Fig. 2). Before the release, each tagged skate was sprayed with an anti-inflammatory and antibiotic (oxytetracycline and hydrocortisone) at the place of installation of the tag.

When each skate was released, the seabed's geographical position and depth were recorded. The tagged individuals were carefully deposited in the water and observed until they moved away from the boat. Three people carried out the measurement, weighing, tagging, and releasing process, which lasted a maximum of 5 min for each skate.

Data analysis

During the entire monitoring, the vertical movements were analyzed per individual, as maximum daily vertical displacements (MDV), regarding the difference between the record of the maximum and minimum swimming depths per day. The records of depth at each interval of 10 min during the last days of deployment, before the release of each tag, were analyzed in terms of swimming depth (SWD) and of the depth difference between consecutive 10 min intervals in absolute value (DSD).

The total daily vertical movements (TVM) were estimated in terms of the sum of the depth difference between consecutive periods of 10 min, in absolute value, per a 24 h UTC day. The minimum horizontal movement (MHM) was estimated according to the distance between each animal's release position and the place where the tag appears on the sea's surface (pop-off location).

Neither the first nor the last daily record was taken into account to avoid considering the minimum depths associated with the individual's marking or the tag's release. If a tag was released before 60 days, the data was analyzed for possible causes.

The SWD was modeled using a Generalized Mixed Model (GLMM) with a Gaussian distribution and identity as a link function based on the covariates: day/night, area (as fixed effects) and each individual (random effect), the DSD ($\ln_{(DSD+1)}$, without considering zero values) was also modeled using the same fixed and random effects. Day/night hours were assigned according to modeling based on latitude and declination information for Chiloé, according to available information at https://sunrise.maplogs.com. The model selection was performed using the Akaike information criterion (AIC) (Zuur et al. 2009). The estimates were made with Restricted maximum likelihood (REML) using the nlme library (R Core Team 2022).

RESULTS

All the tags (10) emerged and transmitted the data to the Argos satellite system. The transmission was carried out in eight tags according to the time set for deployment 60 days after the tagging. Two tags emerged after 39 and 41 days in Bahía Mansa, a male (02CM) and a female (04CF) of yellownose skate. The tag of individual 02CM was released after spending more than one day at the same depth (±4 m), probably due to the skate death. The satellite tag of female 04CF indicated positions located on land, for which reason it is presumed that it was captured. For male 02CM, the records of the last 24 h before the release of the tag were eliminated. For skate 04CF, records in 10 min intervals were eliminated after the last greater difference of 4 m depth between successive intervals.

Vertical movement

The tagged skates were distributed between 9 and 512 m yellownose skate and 111 and 513 m roughskin skate. The depth data recorded by the skates indicate that in Bahía Mansa, the skates moved to depths between 10 and 221 m, while those tagged in Comau in a wider range, between 9 and 513 m (Fig. 3, Table 2).

The ranges of swimming temperatures and maximum daily temperature variations were narrow: 7.7-11.5 and 0-2.7°C for the yellownose skate and 10.5-11.5 and 0-0.6°C for the roughskin skate (Table 2).

The MDV per individual was 338 m in yellownose skate (05CF) and 305 m in roughskin skate (08TF), with 89 and 138 m medians. Ninety-five percent of the MDVs were less than 277 and 249 m for yellownose and roughskin skates.

The records of the last days of liberty of the skates indicated that the individuals had TVM of up to 1.4 km

Table 1. Summary details of the tagged rays by zone and date of tagging. DC: *D. chilensis*, DT: *D. trachyderma*. F: female, M: male, TL: total length (cm), DW: disc width (cm), TW: total weight (kg), LON: longitude and LAT: latitude: catch position, depth (m): depth of release.

Zone	Date	Species	Sex	ID	TL	DW	TW	LON	LAT	Depth
Bahía Mansa	08/21/2021	DC	F	01CF	100	79	8.4	73°51’W	40°35’S	130
Bahía Mansa	08/21/2021	DC	M	02CM	80	61	4.9	73°52’W	40°35’S	130
Bahía Mansa	08/21/2021	DC	F	03CF	96	76	7.6	73°52’W	40°35’S	134
Bahía Mansa	08/21/2021	DC	F	04CF	104	83	8.7	73°52’W	40°35’S	134
Comau	08/29/2021	DC	F	05CF	75	67	2.2	73°31’W	42°11’S	491
Comau	08/29/2021	DC	F	06CF	84	65	6.0	73°31’W	42°11’S	491
Comau	08/29/2021	DC	F	07CF	102	79	10.8	73°31’W	42°11’S	490
Comau	08/29/2021	DT	F	08TF	110	83	10.1	73°31’W	42°11’S	490
Comau	08/31/2021	DT	F	09TF	89	72	5.6	73°37’W	42°10’S	320
Comau	08/31/2021	DT	F	10TF	101	81	8.1	73°38’W	42°11’S	348

Figure 2. A male yellownose skate (*D. chilensis*) tagged with a pop-up satellite transmitter (PSAT, 02CM) before release.

(06CF and 08TF), with a mean of 512.4 m for yellownose skate and 761.6 m for roughskin skate. The skates 06CF and 08TF had the highest mean TVM, 1,160.2 and 1,156.3 m (Fig. 4). Both skate species showed vertical activity day and night.

During the last days of monitoring, the skates' SWD was located between 19.5 and 512.5 m (yellownose skate, mean: 199.5 m) and between 139 and 506.5 m (roughskin skate, mean: 288 m). Six individuals of yellownose skate were located deeper during daylight than in the nightlight (Table 3, Fig. 5).

The results of the GLMM model to explain the SWD indicated that the zone and day/night factors were significant, with a 5% type I error (P = 0.024) in a model with interaction (Table 4). Model results indicate that the skates were located deeper in Comau than in Bahía Mansa (differences of 192.6 m), with a preference during the night for 5.8 m shallower waters than the day, with an interaction effect between night and Comau. With a 5% type I error rate, the results of the GLMM model explaining DSD indicated that the fixed effect of the zone was significant (P = 0.023), showing higher activity levels in Comau compared to Bahía Mansa. Additionally, a significant interaction between night and Comau (P = 0.001) suggests a preference for nocturnal activity in Comau.

A 95% of the DSD were less than 19.5 and 20.5 m for yellownose skate and roughskin skate with maximums of 69 (04CF) and 56 m (08TF) by specie. Likewise, maximum sequences of depth differences of 115 (05CF) and 104.5 m 30 min^{-1} (08TF) for yellownose skate and roughskin skate were recorded. In terms of TL by individual, the median ascent velocities varied between 0.01-0.18 TL s^{-1} for yellownose skate and between 0.05-0.12 TL s^{-1} for roughskin skate, while the range of median descent velocities was similar: 0.01-0.17 and 0.05-0.11 TL s^{-1} for both species.

The patterns of the time-depth profiles, according to depth recorded per 10 min, were described in terms of shape and variability (coefficient of variation, CV%) by grouping into four groups according to i) lower (01CF, 03CF; CV < 10%), ii) low (09TF and 10TF; 10% < CV < 20%), iii) high (05CF, 06CF, and 08TF; 20% < CV < 30%) and iv) higher (02CM, 04CF, and 07CF; CV > 30%) (Fig. 6). The roughskin skates had high or low CV%. The skates 09TF and 10TF moved between 200 and 300 m depth, mainly with periods of increased vertical activity (maximum vertical changes in depth of 32 and 36 m per 10 min), with a predominant type V

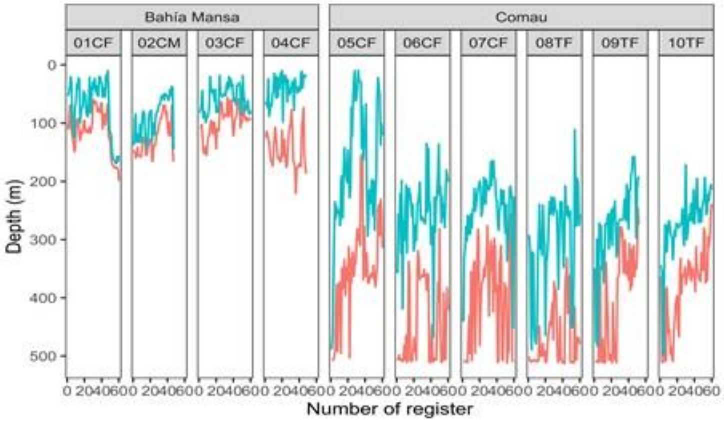

Figure 3. Bathymetric profile by individual tagged. The blue line represents the minimum depth registers per day. The red line represents the maximum depth registers per day.

Table 2. Minimum (MIN), maximum (MAX), and maximum daily differences (MAXD) in temperature of swimming (TMP, °C) and swimming depth (SWD, m) by species: DC: *D. chilensis*; DT: *D. trachyderma* and skate.

ID	Species	TMP			SWD		
		MIN	MAX	MAXD	MIN	MAX	MAXD
01CF	DC	7.7	11.4	1.3	10	199	95
02CM	DC	8.0	10.8	1.6	37	168	168
03CF	DC	8.8	11.3	1.4	18	155	84
04CF	DC	8.2	11.3	2.7	10	221	186
05CF	DC	10.7	11.5	0.4	9	507	338
06CF	DC	10.7	11.5	0.6	135	511	308
07CF	DC	11.0	11.5	0.2	164	512	292
Total DC		**7.7**	**11.5**	**2.7**	**9**	**512**	**338**
08TF	DT	10.8	11.5	0.6	111	513	305
09TF	DT	10.6	11.5	0.5	157	512	273
10TF	DT	10.5	11.5	0.5	172	511	232
Total DT		**10.5**	**11.5**	**0.6**	**111**	**513**	**305**
Total		**7.7**	**11.5**	**2.7**	**9**	**513**	**338**

pattern in the ray 09TF and with an active vertical movement followed by a period of less movement in the ray 10TF. The female 08TF had constant activity, with wider vertical displacements, in a V shape, between approximately 150 and 500 m, and maximum depth changes of 56 m per 10 min (Figs. 6b-c).

For yellownose skate, skates 01CF and 03CF, tagged in Bahía Mansa, barely changed depth for four days, remaining at depths of 180 and 100 m (Fig. 6a). The skates 05CF and 06CF, tagged in Comau, had more activity with vertical depth variations of up to 61 and 41.5 m per 10 min, V-shaped vertical swimming patterns mainly, with swimming at depths mostly corresponding to those detected on the Comau Fjord margins (Fig. 6c).

The skates 02CM, 04CF, and 07CF had a U-shaped vertical swimming pattern (Fig. 6d). The swimming depths of the 02CM and 04CF skates had high CV%, with ranges between 50-100 and 50-150 m, where 04CF had maximum depth changes of 69 m per 10 min. The 07CF ray had two characteristic lapsus, remaining at 220 and 500 m depths.

Horizontal movement

The MHM between the tagging point and the pop-off location of each satellite tag varied between 0.84 and 35.95 km. Two females tagged in Comau (*D. chilensis*: 05CF and *D. trachyderma*: 09TF) had the higher MHM, 35.95 and 33.90 km, after 60 days of liberty (0.60 km per day). The skates with lower MHM were also tagged in Comau, 07CF (0.84 km) and 08TF (2.59 km) (Table 5).

A consistent pattern was not detected between the tagging point's relative position and the pop-off location.

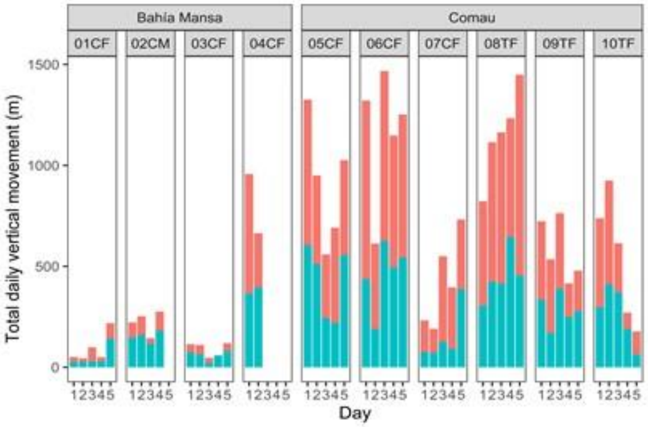

Figure 4. Total daily vertical movements (m) per skate. Red bars represent movements during the day, and blue bars represent movements during the night.

Table 3. Median of depth differences (DSD, m) and median of swimming depth (SWD, m) during the day and the night. DC: *D. chilensis*; DT: *D. trachyderma*.

ID	Species	Median of DSD		Median of SWD	
		Day	Night	Day	Night
01CF	DC	0	0	175	174
02CM	DC	0	0	117	67
03CF	DC	0	0.5	89	89
04CF	DC	0	0.5	85	106
05CF	DC	0	5.5	204	171
06CF	DC	3.5	2.5	329	312
07CF	DC	0	0	410	246
Total DC		**0.0**	**0.0**	**175**	**171**
08TF	DT	6.0	2.5	352	337
09TF	DT	1.5	0.5	247	258
10TF	DT	1.5	2.0	228	244
Total DT		**10.5**	**11.5**	**111**	**513**
Total		**7.7**	**11.5**	**9**	**513**

In Comau, the pop-off locations were located towards the Comau Fjord (08TF, 06CF) and the Gulf of Ancud in the Chiloé inland sea (05CF, 09TF, and 10TF) without a pattern about the distance of the coast (Fig. 7). In Bahía Mansa, the pop-off locations were located at a higher and lesser distance from the coast from the tagging point.

DISCUSSION

Regarding habitat conditions occupied by both skate's species, the temperature range per day UTC evidenced slight changes in temperature, with differences mainly associated with the study area, with wider thermal ranges in Bahía Mansa than in Comau. Thus, the individuals of yellownose skate, the species captured in both study areas, occupied temperatures of 7.7-11.4°C in Bahía Mansa and 10.7-11.5°C in Comau. The wider range of temperature in Bahía Mansa (3.7°C) was detected in a narrower depth range than in Comau (Fig. 3), a zone with higher mixing in the water column, according to the characteristics of the water in the fjord, which presents a superficial layer of low salinity and stability of salinity and temperature deeper than 20 m (Addamo et al. 2021). The thermal structure in Comau is almost homogeneous due to the vertical mix resulting from strong winds, tidal currents, and the absence of a thermocline and halocline, which affects the low stability of the water column (Sievers 2006).

The maximum daily depth differences indicated vertical displacements of up to 338 m in yellownose skate and of up to 305 m in roughskin skate, with lesser

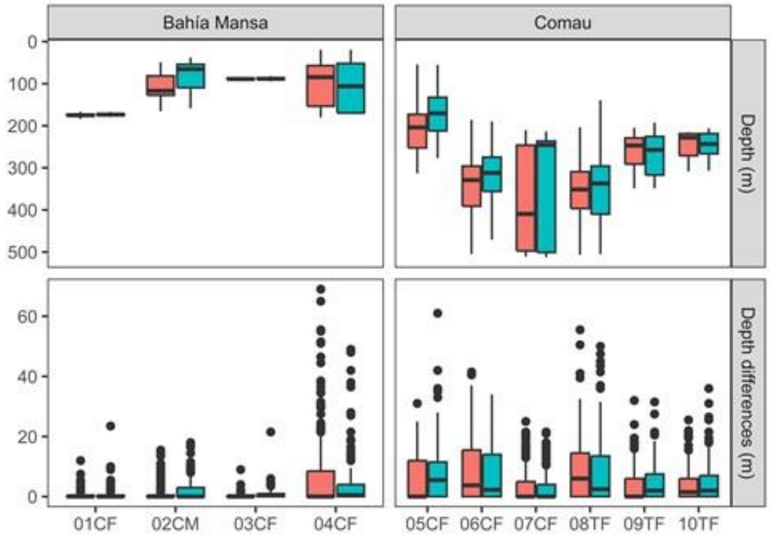

Figure 5. Box plots of the individual depth (swimming depth) between day and night (m). Red box: day, blue box: night.

Table 4. Results of Generalized Linear Mixed Model to explain a) swimming depth (SWD) recorded per 10 min per tag for *D. chilensis* and b) difference of depth (DSD) recorded per 10 min per tag for *D. chilensis*. St. Dev.: standard deviation.

a) DC data (n = 4,827)				b) DC data (n = 2,210)		
Random effects:			Random effects:			
Groups		St. Dev.				St. Dev.
ID (Intercept)		67.235				0.487
Residual		66.179				0.659
Fixed effects:			Fixed effects:			
	Estimate	Std. Error	*P*	Estimate	Std. Error	*P*
(Intercept)	118.430	33.664	0.000	1.142	0.245	0.000
Comau	192.576	51.416	0.013	1.255	0.374	0.020
Night	-5.828	2.594	0.024	0.053	0.038	0.172
Comau*Night	-23.053	3.861	0.000	-0.193	0.056	0.001

depth differences in Bahía Mansa than in Comau (Fig. 3), which is associated with the higher depth and topographic complexity of the fjord area. The Comau Fjord extends approximately north-south (orientation 346° from its north). It is characterized by a U-shaped with very steep slopes, with maximum depths of 500 m at its central axis (Häussermann & Försterra 2009, Addamo et al. 2021), so the depth patterns of both species in that area could indicate periodic movements in an east-west direction inside or at the mouth of the fjord (10 km wide), from its maximum depth up to 111 m, except for skate 05CF, which reached shallower waters, with a minimum depth of 9 m. In the Bahía Mansa area, bottom depth varied between 80-200 m, and patterns for yellownose skate seem to indicate movements in east-west directions following the bottom topography.

The depth records per UTC day indicated that the TVM reached up to 1.4 km per skate in both species (Fig. 4). Similar situations were reported in other benthic skates, such as *Dipturus batis*, a species with TVM of up to 1.8 km (Wearmouth & Sims 2009). In yellownose skate and roughskin skate, both species do not show differences in TVM, at least in their maximums, even though the larger relative size of roughskin skate (08TF: 110 cm) could lead one to suppose a greater swimming capacity than yellownose skate (05CF: 75 cm). However, the similarity of TVM was obtained for the last days of liberty, which would require more time to prove any correlation between TVM and the size of the skates.

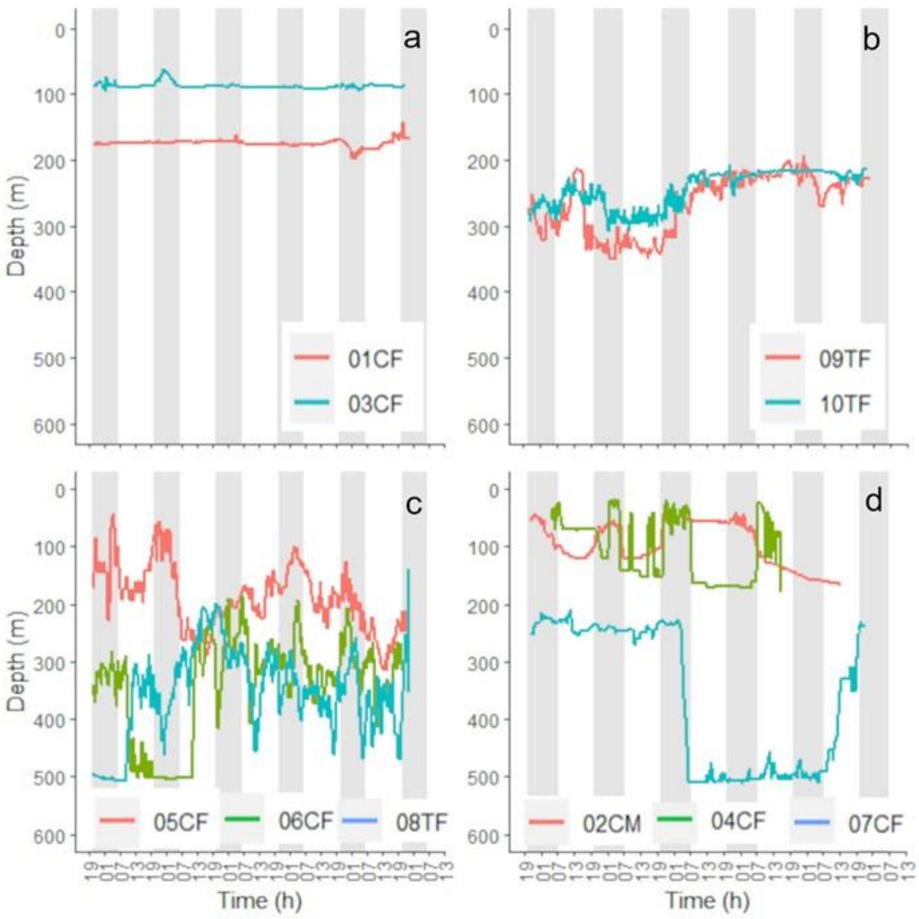

Figure 6. Time-depth profiles of electronically tagged individual skates, according to their variability (CV%), in light/shade the day/night: a) lower (CV < 10%), b) low (10% < CV < 20%), c) high (20% < CV < 30%) and d) higher (CV > 30%).

Table 5. Summary of the minimum horizontal movement per tagged ray. DC: *D. chilensis*; DT: *D. trachyderma*, F: female, M: male, DTAG: date of tagging, DPOP: day of release of tag, Days: number of days between the date of tagging and date of release of tag, and Dist: distance between tagging and release positions (km).

Zone	Species	Sex	ID	DTAG	DPOP	Days	Dist	Dist/Days
Bahía Mansa	DC	F	01CF	08/23/2021	10/23/2021	60	19.72	0.33
Bahía Mansa	DC	M	02CM	08/23/2021	10/10/2021	39	14.70	0.38
Bahía Mansa	DC	F	03CF	08/23/2021	10/23/2021	60	6.75	0.11
Bahía Mansa	DC	F	04CF	08/23/2021	10/12/2021	41	8.04	0.20
Comau	DC	F	05CF	08/29/2021	10/29/2021	60	35.95	0.60
Comau	DC	F	06CF	08/29/2021	10/29/2021	60	10.25	0.17
Comau	DC	F	07CF	08/29/2021	10/29/2021	60	0.84	0.01
Comau	DT	F	08TF	08/29/2021	10/29/2021	60	2.59	0.04
Comau	DT	F	09TF	08/31/2021	10/31/2021	60	33.90	0.57
Comau	DT	F	10TF	08/31/2021	10/31/2021	60	7.16	0.12

The shape of the time-depth profiles revealed different patterns among the skates (Fig. 6). The vertical displacement patterns in elasmobranchs and other predators have been associated with different foraging modalities for pelagic predators that follow their prey vertically. A U-shaped pattern, like the one observed in skates 02CM, 04CF, and 07CF (with higher variability, CV > 30%), could correspond to the active

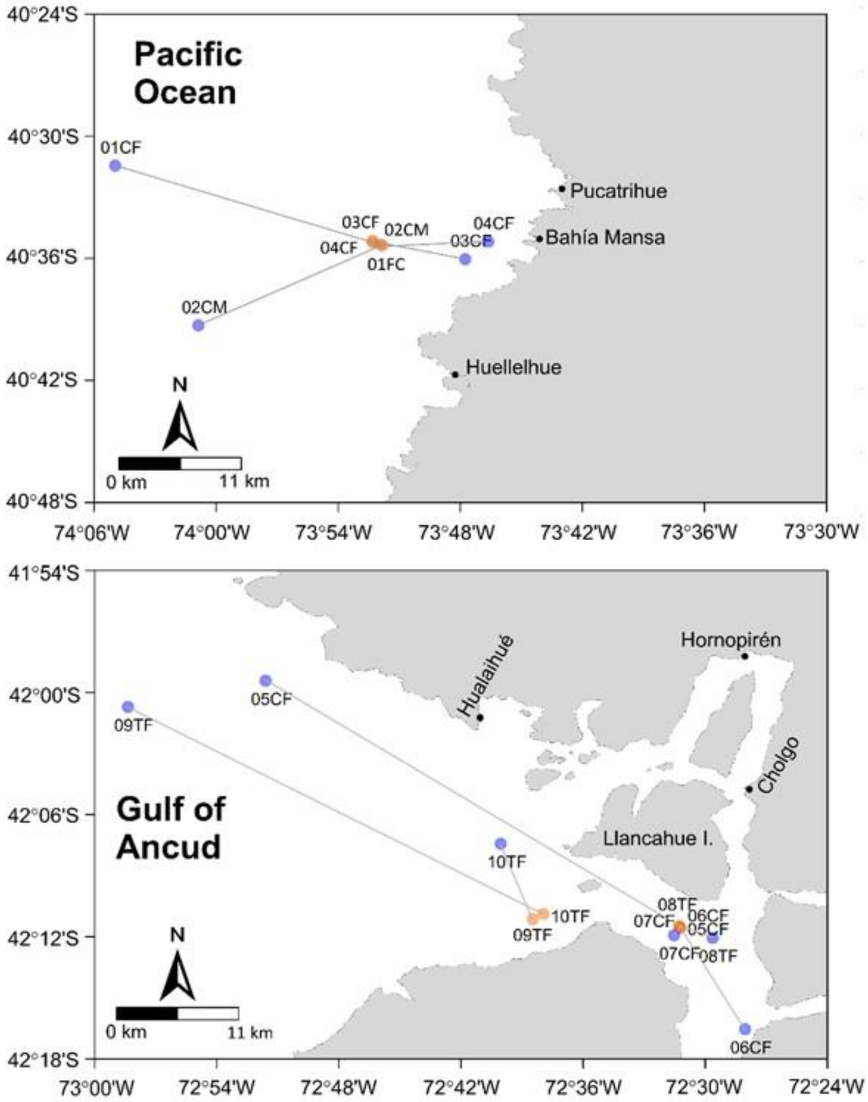

Figure 7. Map of the study area: Bahia Mansa (upper) and Comau (lower), showing the tagging (red) and pop-off locations (blue) by tagging code.

predation of aggregated prey in horizontal layers, with skates maintaining a relatively constant depth for a time before shifting between depths. In contrast, the V-shaped patterns, as those observed in skates 05CF, 06CF, 08TF, and 09TF, associated with high and low variability (10% < CV < 30%) where the skates constantly change depth, have been associated with transit or search for prey to increase the probability of detecting olfactory clues (Queiroz et al. 2017). Based on the results, our data indicate that the pattern for yellownose skate in both regions was one of predation and searching (types U and V), with two individuals exhibiting lower mobility in Bahía Mansa (CV < 10%). In contrast, the roughskin skate in both regions displayed behavior associated with searching (type V).

The results of the GLMM indicate that yellownose skate showed a significant preference for shallower waters at night, and it shows a significant change of vertical activity only in interaction with the zone. The occurrence of DVM in elasmobranchs is a pattern commonly linked to foraging, and diving deeper during the day than at night is the most common strategy across species (Hammerschlag et al. 2016). For benthic rays, this behavior has also been observed in *Raja microocellata* and *R. montagui* (Humphries et al. 2017, Lavender 2021a). The different depths between day/night have been associated with the preference for shallower waters to be used for feeding or a feeding modality based on more active predation. In comparison, the deeper waters are used as a refuge, a resting place, or for a diet based on more opportunistic predation (Braun et al. 2021, Lavender 2021a).

It has been suggested that during the deeper phase, the skates would present limited movement or immobility due to their propensity to bury themselves or a passive behavior in the vicinity of the seabed (Kotwicki & Weinberg 2005, Queirolo et al. 2012), which would be related to changes in the metabolic rate, where being located deeper (lower temperature) would allow rest and digestion or would be the result of adaptive behavior to avoid predators. In comparison, at a lower depth (higher temperature), the metabolic rate increase would act as a driver for the increase in foraging.

In our case, the low-temperature variation about depth, especially in Comau, makes it unlikely that temperature variation triggers a change in the metabolic rate in both species. In addition, it should be noted that in the Atlantic Ocean, yellownose skate (as *D. chilensis*) has been reported as a top predator, being considered a species with a trophic level of 4.5, one of the highest estimates for ray species (Belleggia et al. 2016, Flowers et al. 2020), and its diet corresponding mainly to teleost, as well as crustaceans (Lucifora et al. 2000, Bellegia et al. 2016, Lamilla, 2016), making it unlikely that day/night depth differences are a predator avoidance strategy.

Alternatively, DVM could be related to preference for certain types of prey. The trophic information of yellownose skate comes mainly from studies carried out from individuals captured in the Atlantic Ocean (Lucifora et al. 2000, Koen et al. 2001, Bellegia et al. 2016) and according to the size range of yellownose skate captured in this study (75-104 cm TL), the diet of the skates would be based on teleost, such as *Macruronus magellanicus* (Gadidae) or *Sebastes oculatus* (Scorpaenoidei) (Belleggia et al. 2016, Lamilla 2016), species that could modulate variation of the bathymetric preference of skates between day and night and between both areas. It must be noticed that although there are no reports of DVM for *M. magellanicus* or *S. oculatus*, it has been reported in other species of the same genus, such as *M. novaezelandiae* or *S. flavidus* (Bulman & Blaber 1986, Stanley et al. 1999).

In this study, the ascent and descent speeds associated with bathymetric movements are found to be one to two orders of magnitude lower than the optimal swimming speeds reported for skates in relation to body length (BL, expressed as Disc length), such as *Leucoraja erinacea* (1.25 BL s^{-1}) and *Raja eglanteria* (~1.25-1.5 BL s^{-1}) (Di Santo & Kenaley 2016, Di Santo et al. 2017). The lower relative speed (<1/3 BL s^{-1}) and lower energy consumption have been associated with the substitution of swimming by walking on the seabed using pelvic fins, characteristic of nektobenthic DVM in *L. erinacea* (Lucifora & Vassallo 2002, Koester et al. 2003, Humphries et al. 2017). In conclusion, despite our data being expressed in terms of TL, they also indicate that both species of skates exhibit speeds lower than the optimal, during vertical movements, suggesting they could primarily migrate to and from the coast using a nektobenthic DVM modality. This behavior results in movement patterns that differ from those of pelagic animals, which show rapid ascents and descents to and from the same depth. Instead, the skates' movements are mainly tortuous, following the seabed profile (Fig. 6).

For roughskin skate, the information on trophic behavior is very scarce. In Chile, for the Valdivia and Puerto Montt area, through the analysis of nine stomachs, has been reported a diet based mainly on bony fish (*M. magellanicus*, *Paralichthys* sp.) (Lamilla 2016). Although the number of individuals tagged in this study was very low, this species does not show clear indications of bathymetric changes or activity changes associated with day/night, which could be attributed to a different trophic dynamic than the yellownose skate.

The results indicate that the skates had MHM between 0.8 and 35.9 km. They were tagged and liberated after 39 and 60 days, without important differences between yellownose skate (0.84-35.9 km) and roughskin skate (2.59-33.9 km). These records can be compared with other reports for benthic rays, standardizing the MHM for 30 days, being greater than the ranges reported in *Dipturus batis*: (0-1.81 km 30 d^{-1}) (Wearmouth & Sims 2009) and comparable to the recorded in *Beringraja binoculata* (0.5-37.7 km 30 d^{-1}) and *Amblyraja hyperborea* (7.46-27.57 km 30 d^{-1}) (Peklova et al. 2014, Farrugia et al. 2016). It must be noticed that a maximum of 36 km after 60 days of liberty was detected for both species (05CF and 09TF); however, only along the last four and five days of liberty, the vertical distance for both skates was 2.29 and 4.55 km, respectively, which suggests a higher level of activity than indicated by the MHM. As another example, in *B. binoculata,* the spatial movement by MHM was underestimated (205 km) because the pop-up suggested a distance of 2,000 km (Farrugia et al. 2016).

Population dynamics is the result of individual movements, which in some cases present the behavior named philopatry, which can be defined as the existence of individuals who frequently return or remain within the home range, places of birth, or other specific localities (Flowers et al. 2016). Low horizontal displacements observed in yellownose and roughskin skates can be associated with philopatry. However, the duration of this study (60 days) does not provide sufficient evidence to determine "residence" (to remain in one location for at least 12 months) or "seasonal residence" (to remain in an area for only several months at a time, at least three months), while the nature of the data does not allow us to specify whether the individuals made long migration to return to the location where they were tagged, a behavior known as "site fidelity" (Chapman et al. 2015).

In this context, it should be noted that site fidelity and seasonal residence have been reported in species of the genus *Dipturus* (*D. batis*, *Dipturus cf. intermedia*, *D. intermedius*) (Wearmouth & Sims 2009, Neat et al. 2014, Lavender et al. 2021b). Likewise, it has been proposed that the smaller species (yellownose skate) might not present extensive migrations, in contrast to the roughskin skate, which would be correlated with a pronounced genetic isolation in yellownose skate, inferred by microsatellite analysis in the Chilean coasts, which endangers the survival of the species in the Patagonian fjords of southern Chile, since it would depend almost exclusively on self-recruitment (Vargas-Caro et al. 2017). However, in this study, the data do not indicate correlations between the horizontal movements and species, and its duration (max. 60 days of liberty for skates) makes it unlikely that extensive migrations will occur in such a period.

It should be noted that species of skates with large-scale movements, such as *Leucoraja ocellata* (more than 1,000 km) and *Raja clavata* (up to 276 km), have been reported (Hunter et al. 2006, Frisk et al. 2019), so it is discussed whether the common belief that benthic rays have small home ranges, do not migrate seasonally, and move long distances only before maturity is due to biases produced by the use of conventional tags, which do not provide behavioral data during the period of liberty, instead of satellite tags (Siskey et al. 2018). For yellownose skate and roughskin skate, a migration dynamic with mature females moving annually between the egg-laying and breeding habitat for transitional periods (Patagonian fjords of southern Chile) and the adult habitat (open waters to the Pacific Ocean) (Vargas-Caro et al. 2017) has been suggested, in terms of a behavior known as natal or regional philopatry (Flowers et al. 2016). The results revealed by pop-up tags indicate an important activity for skates below the $L_{50\%}$ size for a short temporal scale of 60 days between the Comau Fjord and the Gulf of Ancud, and it suggests that the juvenile could also migrate for high distances. Extending the study to longer periods, including the tagging of smaller juvenile individuals and mature females, would allow the generating of information to specify eventual migratory movements.

The skate fishery in Chile operates on a small scale, targeting a depleted stock within a very narrow temporal window and limited spatial areas. Its management faces data quality issues (Wiff et al. 2021), consistent with the global finding that 46.8% of elasmobranch species suffer from data deficiencies (Dulvy et al. 2021). These issues raise alert signals regarding the status of their populations.

Spatial approaches for the stock assessment or initiatives to establish marine reserves need an understanding of how individual elasmobranch movements correlate with their population structure (Chapman 2015). The present study is the first to track the movements of yellownose skate and roughskin skate with electronic tags. Our results indicate that using pop-up satellite tags is a feasible tagging tool for recording data independent of Chile's commercial skate fishing activity. We provide first-hand insight into the fine-scale movements in both skate species. This method allows information generation during the days of liberty of each individual, reducing biases inherent in conventional tagging methods.

Credit author contribution

M. Ahumada: conceptualization, validation, methodology, formal analysis, writing-original draft; Pedro Apablaza: data curation, review and editing; D. Queirolo: funding acquisition, project administration, supervision, review, and editing; R. Wiff & A. Flores: formal analysis, review, and editing. All authors have read and accepted the published version of the manuscript.

Conflict of interest

The authors declare no potential conflict of interest in this manuscript.

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