

Spatial dynamics of the Argentine sandperch, *Pseudoperca semifasciata* (Pinguipedidae), in temperate rocky reefs from northern Patagonia, Argentina

Leonardo A. Venerus^{A,B}, Alejo J. Irigoyen^A, David E. Galván^A
and Ana M. Parma^A

^ACentro Nacional Patagónico – Consejo Nacional de Investigaciones Científicas y Técnicas (CENPAT – CONICET), Boulevard Brown 2915 (U9120ACD) Puerto Madryn, Chubut, Argentina.

^BCorresponding author. Email: leo@cenpat.edu.ar

Abstract. The choice of appropriate conservation strategies for reef fishes depends on their mobility, degree of site fidelity and residence times. Here we report the results of a small-scale mark–recapture and resighting study conducted to investigate the spatial dynamics of the Argentine sandperch, *Pseudoperca semifasciata*. This is the flagship species of the rocky-reef fish assemblage from northern Patagonia, which has been the target of uncontrolled fishing since the early 1950s. About 19% of the fish tagged were recaptured up to four years after tagging. In total, 180 of 218 recaptured fish stayed in the reef of tagging. Thirty-six of 57 recaptures made at known locations within popular fishing areas of San José Gulf, densely covered by patchy reefs, occurred within 100 m of the tagging site, up to 793 days after tagging. Six fish were recovered more than 1 km from where they were tagged. Smaller fish were more prone to relocate, and were recovered farther from the tagging site. Fish stayed in the reefs for periods longer than a year; larger males remained longer in the same reefs. Our results indicate that relatively small reserves (in the order of a few kilometres) could be effective at protecting *P. semifasciata* populations within the northern Patagonian gulfs.

Additional keywords: external tags, movement patterns, MPAs, site fidelity, *Undaria pinnatifida*.

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Introduction

The design of marine protected areas (MPAs) needs to take into account the spatial dynamics, site fidelity and movement rates of the species to be protected (e.g. Kramer and Chapman 1999; Edgar *et al.* 2004; Chateau and Wantiez 2009). MPAs are more effective at protecting species whose individual movements are restricted to localised areas during at least part of their life-span. Both relocation of fish (i.e. a permanent shift in the position of its home range, *sensu* Robertson 1988) and migration (in which individuals do not return to the vicinity of their original position: Kramer and Chapman 1999), may increase spill-over of fish from reserves, increasing their exposure to fishing (Rowley 1994; Bohnsack 1998; Gell and Roberts 2003).

A high degree of site-attachment, typical of coral reef species (see references in Kramer and Chapman 1999; Jones 2005), also appears frequently among temperate and warm-temperate reef fishes. This is the case for many species belonging to the families Cheilodactylidae (Lowry and Suthers 1998), Cottidae (Mireles *et al.* 2012), Labridae (Barrett 1995; Arendt *et al.* 2001; Edgar *et al.* 2004; Topping *et al.* 2005; Bryars *et al.* 2012), Monacanthidae (Barrett 1995; Edgar *et al.* 2004), Pempheridae (Annese and Kingsford 2005), Pinguipedidae (Mace and Johnston 1983; Cole *et al.* 2000; Carbines and McKenzie 2004), Scorpaenidae (Matthews *et al.* 1987), Sebastidae

(Jorgensen *et al.* 2006; Green and Starr 2011), Serranidae (Lembo *et al.* 1999; Lowe *et al.* 2003; Irigoyen 2010), Sparidae (Willis *et al.* 2001; Griffiths and Wilke 2002; Parsons *et al.* 2003; Kerwath *et al.* 2007), and Syngnathidae (Connolly *et al.* 2002; Moreau and Vincent 2004). The ubiquitousness of reduced mobility in temperate reef species suggests that MPAs, as well as other spatial management strategies, may be adequate tools for protecting these species (Gunderson *et al.* 2008).

The Argentine sandperch, *Pseudoperca semifasciata* (Cuvier, 1829), is a sport trophy fish that inhabits rocky reefs along the coast of Argentina (Galván *et al.* 2009b). This species, which exceeds 1.20 m length and 25 kg weight (Elías and Burgos 1988; González 2006), has been the primary target of largely unregulated artisanal and recreational hook-and-line and spear-fisheries, and a tourist attraction for scuba divers within the northern Patagonian gulfs since the early 1950s (Sanabria 2002). Despite its economic and cultural importance, the exploitation of the rocky-reef fish assemblage along the coast of Chubut Province (42–46°S) has never been monitored or regulated. Only a 30-kg restriction per fishing licence per day has been in place since 1994 within the Peninsula Valdés Reserve, a site declared a Natural World Heritage Site by UNESCO in 1999 (Fig. 1). The inadequacy of this regulation, together with the lack of effective controls, has led to the local

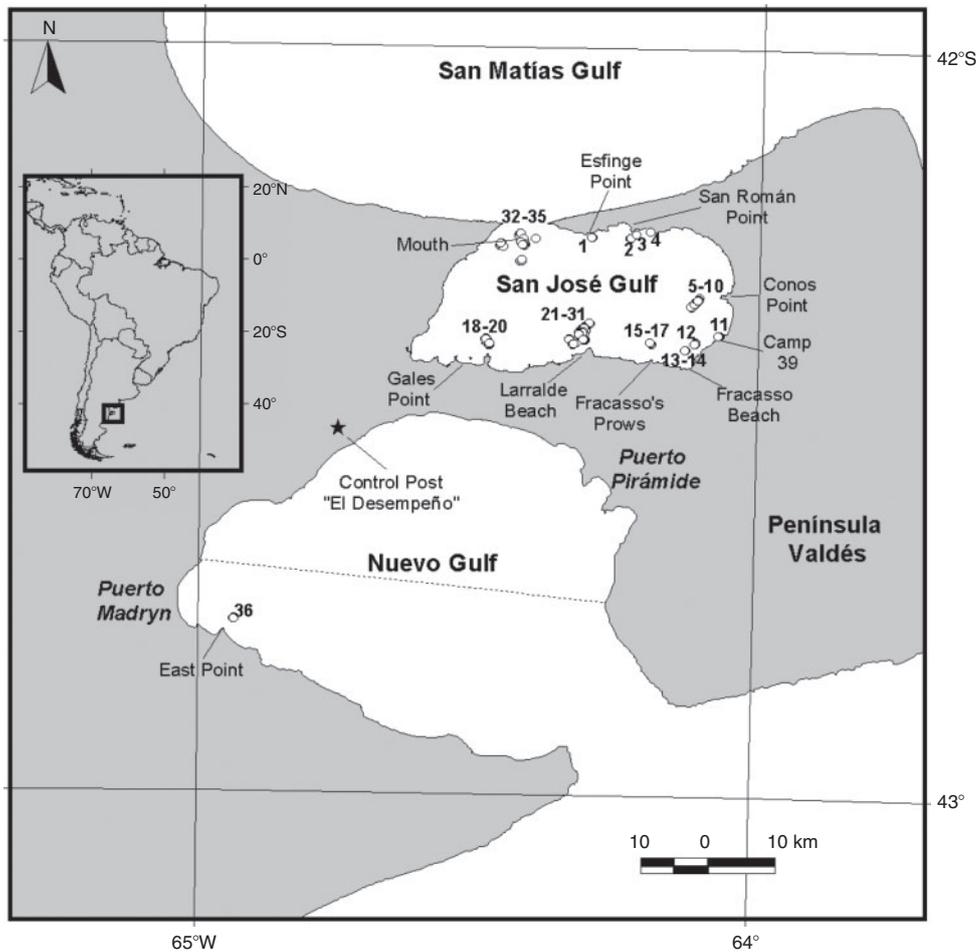


Fig. 1. Study area showing the tagging locations within Nuevo and San José gulfs, Península Valdés. The reefs are numbered and their positions are indicated by open circles. The dotted line indicates the southern limit of the reserve within Golfo Nuevo.

depletion of *P. semifasciata* in the most popular fishing spots within San José and Nuevo gulfs (Venerus 2006).

Management options are limited, given weak enforcement (Venerus 2006, 2010) and the unsuitability of size limits due to barotrauma (Venerus, pers. obs.). Marine reserves could be a suitable tool for protecting local populations of *P. semifasciata* but the effectiveness of spatial protection would depend on fish mobility. Anecdotal information as well as data from monitoring of selected reefs in San José Gulf (Venerus *et al.* 2008) suggest that *P. semifasciata* has high reef fidelity and restricted movement patterns. Local divers often report observing recognisable individuals (e.g. through scars) residing for long periods in the same reefs, often occupying the same crevices or reef areas. The general perception of anglers and spear-fishers is that fishing can easily deplete reefs of *P. semifasciata*, and that recovery of abundance takes a long time (Venerus 2006, 2010). Underwater visual censuses of *P. semifasciata* conducted in lightly exploited reefs of San José Gulf showed remarkably stable abundance and size composition over the annual cycle (Venerus *et al.* 2008). Also, recovery of abundance after documented fishing events took more than a year

(Venerus *et al.* 2008). While these findings provide indirect evidence of limited dispersal and high site fidelity for juvenile (>30 cm total length (TL)) and adult fish, no specific study of movements has been reported for this species.

The stability of the size distribution of fish in unexploited reefs and the absence of recruitment pulses reported by Venerus *et al.* (2008) suggest that recruitment to the reefs may be gradual, and dependent on the availability of adequate refuges and on density of resident fish. The fact that adult males are larger than females and change colour after reaching sexual maturity (from yellowish to grey, mostly at 50–65 cm TL) has prompted the hypothesis of a resource- or female-defence mating system (González 1998; Venerus *et al.* 2008). González (1998) speculated that grey males would actively defend a spawning territory, while yellow males, which are indistinguishable from females, would sneak into it to gain opportunistic access to females. However, supporting behavioural observations are very limited.

In this paper, we analyse the spatial dynamics of adult *P. semifasciata* from two main sources of information: (1) a small-scale tagging program conducted to study mobility and site fidelity within San José Gulf, and (2) fine-scale

underwater observations of residence patterns in a few reefs within Nuevo and San José gulfs. We also use recapture data to test a hypothesis about potential differences in mobility and residence times among chromatic phenotypes and size classes. We hypothesise that smaller fish have greater mobility and disperse further than larger individuals in search of space and refuge, while larger grey males are more strongly site-attached. We test three specific predictions: (1) fish that relocate or emigrate are smaller than those that remain in the reef; (2) smaller fish move farther from the tagging sites; and (3) grey or transitional fish have longer residence times than yellow individuals. The results are relevant to the identification of appropriate strategies for the conservation of the temperate rocky reefs from northern Patagonia.

Materials and methods

Species studied

Pseudopercis semifasciata is a long-lived (~30 years: [Elías and Burgos 1988](#); [González 2006](#)), non-schooling reef fish belonging to the family Pinguipedidae, distributed from 23°S in Brazil to 47°S in Argentina ([Menezes and Figueiredo 1985](#); [Cousseau and Perrotta 2000](#)). This species is gonochoric, sexually dimorphic (males are larger than females) and dichromatic ([Macchi et al. 1995](#); [González 1998, 2006](#)). Males with intermediate colour patterns are considered transitional ([González 2006](#); [Venerus 2006](#)). Maximum sizes for females, and for yellow and grey males are, respectively, 125 cm, 93 cm and 140 cm TL ([González 2006](#)). Females reach maturity at 37 cm TL (~3 years old: [Elías and Burgos 1988](#); [González 1998](#)) and retain their juvenile colour through adulthood ([González 1998, 2006](#)). Four yellow males ranging between 39 cm and 42 cm TL whose gonads were microscopically studied had sperm in their efferent ducts, suggesting that they were physiologically mature ([Venerus and Macchi¹, unpubl. data](#)). This species is a multiple spawner – its spawning season is primarily in November–December in Patagonia ([Elías and Burgos 1988](#); [Macchi et al. 1995](#)). Although mating displays have not been observed, the small size of the testes in relation to body mass (male gonadosomatic index between 0.02 and 0.14%: [González 1998](#)) suggests that mating pairs need to be in close proximity, or that the eggs are laid in enclosed spaces, e.g. inside crevices. In addition, the year-round stability of fish abundance observed in reefs of San José Gulf ([Venerus et al. 2008](#)) is not consistent with the occurrence of spawning migrations and/or the formation of spawning aggregations; rather, it suggests that spawning may occur in the reefs or in nearby soft-bottom areas probably involving some form of resource- and/or female-defence mechanisms. Within San José Gulf, this species occurs at low densities, even in lightly exploited reefs, on the order of 1–1.5 fish per 10 m of reef ledge ([Venerus et al. 2008](#)). In general, only fish larger than 20 cm TL are found in the reefs. Grey fish are much less abundant than yellow; the average ratio found in San José Gulf was 13 : 1 ([Venerus et al. 2008](#)).

Study site

Reefs are small, isolated rocky outcrops that most commonly extend between >50 m and a few hundred metres on an

otherwise flat, soft bottom. The commonest reef topography consists of longitudinal breaks or ledges (~0.3–1.5 m high) formed along the edge of submerged abrasion limestone platforms, where cavities are formed.

Fishing spots, each encompassing patchy reef areas of variable extension, are known locally by the name of the beach or other geographical features. For this study, we identified nine fishing spots within San José Gulf: Esfinge Point, Camp 39, Fracasso Beach, Fracasso's Prows, the mouth of the gulf, San Román Point, Conos Point, Larralde Beach and Gales Point ([Fig. 1](#)). At the last four we identified between three and 14 reefs, between 120 m and 3.9 km apart ([Fig. S1](#), available as Supplementary Material to this paper). San José Gulf and the northern coast of Golfo Nuevo are included in the Península Valdés Reserve. Although trawling and long-lining are effectively banned within the gulfs, illegal commercial hook-and-line fishing occurs. Recreational anglers and spear-fishers frequent the reserve and a few charter boats operate from Larralde Beach, Gales Point and Puerto Pirámide ([Fig. 1](#)), mainly during summer and early autumn ([Venerus 2006](#)).

Fish tagging

Thirty-five reefs were located in San José Gulf by interviewing recreational and artisanal fishers before the onset of the tagging program. In total, 1075 fish were tagged during 126 fishing sessions, between October 2001 and August 2005. In addition, 63 fish were tagged in Reef #36, Golfo Nuevo, during 17 fishing sessions, between August 2003 and December 2004. In total, 1012 yellow, 74 grey and 52 transitional fish were tagged. Tagging trips were scheduled opportunistically, mostly restricted by weather conditions, so sampling effort was uneven ([Tables 1 and S1](#), the latter available as Supplementary Material to this paper). In addition to research trips, we tagged fish on board a charter boat that operates off Larralde Beach and in the mouth of San José Gulf. The total angling effort expended off Larralde Beach, in which at least 14 reefs are distributed within an area of ~5 km², for example, was unevenly distributed among reefs, with Reefs #24–#26 being visited by the charter boat on almost every fishing trip ([Fig. S1](#), available as Supplementary Material to this paper).

Fish were caught with hand-lines up to a depth of ~28 m during research trips or with rod-and-reel up to a depth of ~50 m during charter boat trips. They were measured to the nearest centimetre, tagged onboard using FloyTM FD-68B anchor tags and Dennison tagging guns, and immediately released. Only fish <50–55 cm TL were released during charter boat trips.

Fish were laid on a wooden 'V'-shaped cradle and their eyes were covered by a wet piece of fabric during tagging. Tags were inserted at the base of the dorsal fin, with the gun pointing forward at an angle of ~45° with respect to the longitudinal axis of the fish. Two tags were applied to each fish in Reefs #36 and #11 (since January 2004 in the latter) to allow individual identification underwater, using a combination of tag colour, and location along the dorsal fin and body side. Since February 2004 all fish were double-tagged to increase recovery rates. A total of 268 fish were double-tagged. To minimise injuries produced by the swim bladder stress syndrome while allowing

¹Dr Gustavo Macchi, Instituto Nacional de Investigación y Desarrollo Pesquero (INIDEP), Mar del Plata, Argentina.

Table 1. Tagging and recovery statistics, and diving, hook-and-line and spearing effort in rocky reefs from San José (SJ) and Nuevo (N) gulfs
–, not surveyed by scuba diving

Fishing spot	Reef ID	Mean depth (m)	No. of fish tagged and released ^A	Size range of fish tagged (cm TL)	No. of recaptures (hook-and-line or spear) ^B	No. of identified resightings ^B	No. of diving surveys	No. of hook-and-line and spear-fishing trips ^C
Esfinge Point (SJ)	1	11	7	32–62	0	0	1	3
San Román Point (SJ)	2–4	10	168 (2)	22–106	12 (12)	16 (8)	43	32
Conos Point (SJ)	5–10	16	100 (3)	30–92	9 (9)	0	1	10
Camp 39 (SJ)	11	10	76 (1)	24–88	6 (6)	67 (22)	28	22
Fracasso Beach (SJ)	12–14	14	146 (3)	29–93	24 (22)	12 (5)	19	22
Fracasso's Prows (SJ)	15–17	22	14 (2)	40–78	0	–	–	1
Gales Point (SJ)	18–20	22	207 (5)	28–84	19 (18)	–	–	19 + (96)
Larralde Beach (SJ)	21–31	19	247 (8)	30–93	82 (70)	5 (5)	2	144 + (403)
Mouth (SJ)	32–35	38	111 (11)	30–93	3 (3)	–	–	63 + (118)
East Point (N)	36	12	63 (3)	30–76	32 (25)	184 (51)	25	17

^ANumbers in parentheses indicate the number of fish that died after capture/tagging.

^BNumbers in parentheses indicate the number of different individuals recaptured or resighted. Note that some fish were recaptured and resighted, and hence are included in both counts.

^CBesides the number of fishing trips conducted by us and charter boats, an estimated global fishing effort (minimum numbers of fishing trips) for the period October 2002 to December 2007 is provided for boat owners operating in the most popular fishing spots within San José Gulf: Larralde Beach, Gales Point and the mouth. Those estimations are based on data collected during a monitoring program conducted at the landing sites (see Venerus 2006 for further explanation).

fish to return quickly to the sea bottom, some fish were punctured with the hollow needle of the tagging gun before being released (see Gotshall 1964).

Tag recovery

Tags were recovered by us during underwater surveys of shallow reefs off Esfinge Point, San Román Point, Conos Point, Fracasso Beach, Larralde Beach (San José Gulf) and East Point (Golfo Nuevo), by hook-and-line in all reefs, and by occasional spear-fishing (Table 1; Fig. 1). Underwater resightings were recorded during 119 visits to the reefs and ~250 h of scuba diving (Table 1), between October 2001 and August 2005. Our main motivation for conducting diving surveys in the same reefs where tagging was conducted was to investigate fish residence patterns. A resighting was recorded every time an individual fish was observed in a reef on a given date by one or more divers. Visual estimates of fish size in 10-cm TL classes, along with the colour and location of tags, were recorded on plastic slates.

Tags were also recovered and reported by recreational anglers, spear-fishers and fishing-guides, who called the phone number printed on the tags or contacted our samplers at the landing sites. A brochure about the tagging program was broadly distributed and publicised by Internet, email and the local press. A system of small rewards was implemented in December 2003 in order to encourage tag reporting.

Fisheries monitoring

Information on recreational angling and spear-fishing effort (i.e. number of fishing trips) was available for the most popular fishing spots within San José Gulf, off Larralde Beach and Gales Point, and in the mouth of the gulf, from a monitoring program conducted between October 2002 and December 2007 (see details in Venerus 2006). In addition, we recorded the number of trips made by the charter boat from which we tagged

fish to each of the patchy rocky areas #21, #22, #24–#26 and #29 (off Larralde Beach), by interviewing the skipper every two or three days throughout the fishing season (Fig. S1, available as Supplementary Material to this paper).

Site fidelity

In order to estimate the distance between release and recapture sites, the boat position was recorded with a GPS each time a fish was hooked during a research trip. In general, sport fishers did not report recapture locations precisely; hence not all recaptures could be associated with a specific reef. In some cases fishers were interviewed to help locate recapture sites as accurately as possible.

An extensive census of tagged fish covering the entire reef was conducted during each diving survey in Reefs #11 and #36. The fraction of visits that resulted in a resight (from the day of tagging to the last resight) was calculated for each individual fish in order to estimate the resighting probability. Surveys of Reef #36 made during September–October were excluded because fish temporarily abandoned the reef (Irigoyen *et al.* 2011; Venerus *et al.* 2013). To gather information on reef use at a finer scale, a few well identified crevices in Reefs #3, #11 and #36 were visited frequently to record the presence and identity of fish in their surroundings (<2 m).

Statistical analysis and predictions testing

Geodetic coordinates (latitude and longitude) were projected onto a Gauss–Krüger grid with the software GeoCalc 3.05 to calculate distances between release and recapture. When the exact recapture location was not reported but the reef was identified, the position at recapture was taken to be the reef's geographic centroid.

Recapture data were used to test Predictions 1–3, derived from the hypothesis about differential movement by type and

phenotype, using randomisation tests (Manly 1991). For testing Predictions 1 and 2, recaptures for which distance moved could be estimated were selected, and fish sizes were randomly permuted with respect to distance moved under the null hypotheses that the probability of relocation/emigration (1), and the distance moved (2) were independent of fish size. Only data from four fishing spots in San José Gulf (Larralde Beach, San Román Point, Conos Point and Gales Point), in which multiple reefs were used for tagging and searching for tagged fish, were included. For testing Prediction 3, fish phenotype (yellow, transitional or grey) was permuted with respect to the number of days between tagging and the last recapture in the same reef, under the null hypothesis of independence between fish phenotype and residence time. In all cases, Monte Carlo permutations ($n = 5000$) were stratified by fishing spot because the size frequency distributions of tagged fish, the range of distances moved, and the sampling efforts were not homogeneous among sites (Table 1). Data for fishing spots that had only a few recoveries (San Román and Conos) were pooled. Gales Point and the mouth were also pooled for testing Prediction 3.

To test Prediction 1, the cumulative distribution function of the size of fish that moved >150 m, used as a rule to classify relocation/emigration from the tagging site, was compared with the 95% confidence bounds of the corresponding distribution estimated by stratified Monte Carlo permutations under the null hypothesis. Similarly, the cumulative distribution of the distance moved for fish smaller than a given threshold size was used to test Prediction 2, using different size thresholds (fish ≤ 45 cm TL, ≤ 50 cm TL, and so on). Finally, Prediction 3 was evaluated by comparing the cumulative distribution of days-in-the-reef for fish of the grey/transitional phenotype with the 95% confidence bounds of the corresponding distribution for all fish ≥ 47 cm TL under the null hypothesis. The size of 47 cm, corresponding to the smallest transitional fish, was selected to avoid confounding the effects of phenotype and fish size. In addition, we estimated the Kendall's Tau-b correlation coefficient between the residence time and fish size. The dataset used in this case contained all recoveries made in the reef of tagging, including our own and those reported by anglers and spear-fishers. We repeated the analysis by eliminating fish with short residence times (<50 days since tagging) to avoid any potential bias associated with recaptures in the initial sampling period.

Calculations were done using an *ad hoc* code programmed in R language (ver. 2.7.1, R Development Core Team 2008).

Results

Tag recovery statistics

The number of recaptures and resightings closely followed the number of angling and diving trips (Fig. S2, available as Supplementary Material to this paper).

In total, 218 fish were recaptured and/or resighted at least once, up to 1427 days after tagging. No selection bias occurred during the recovery of tags: fish sizes and proportions of chromatic phenotypes were similar for tagged and recaptured or resighted fish (Fig. S3, available as Supplementary Material to this paper). Ten fish changed from yellow to transitional or grey (minimum period elapsed = 43 days), and four transitional males were recaptured as grey.

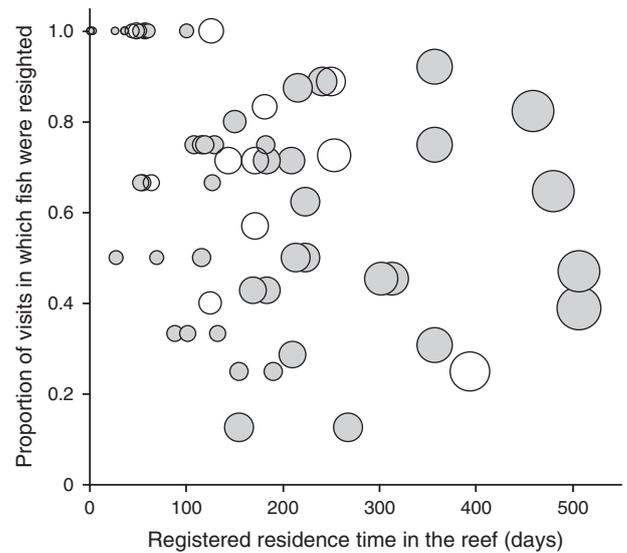


Fig. 2. Proportion of visits in which each fish was resighted versus residence time in the reef for double-tagged *P. semifasciata*. Each bubble represents one individual; the size of each bubble is proportional to the number of visits made between the first and last resighting (from 1 to 18). Data are for Reef #11 (white bubbles), surveyed by scuba 17 times between 24 January 2004 and 10 August 2005, and for Reef #36 (grey bubbles), surveyed 24 times between 11 August 2003 and 24 February 2005.

In total, 187 recaptures of 165 individuals were obtained by angling ($n = 170$) or spear-fishing ($n = 17$) between May 2002 and December 2007 (Table 1). Among the fish caught by the project staff, sixteen individuals were recaptured twice (from 54 to 1427 days at liberty) and three were recaptured three times (from 186 to 449 days at liberty). Most recaptures were made during research trips ($n = 106$); the rest were recovered by artisanal ($n = 11$) and sport ($n = 28$) fishers, and fishing guides ($n = 42$).

In total, 284 resightings of 91 fish were recorded in five reefs from San José Gulf (100 resightings) and in the reef from Golfo Nuevo (184 resightings), between January 2002 and August 2005 (Table 1). Fifty-six of those fish were repeatedly resighted (Fig. 2). More tagged fish were resighted in both gulfs, but their identity could not be established.

Site fidelity

Overall, *P. semifasciata* was strongly site-attached to the reefs. On the basis of our recaptures/resightings, and on the reports of anglers and spear-fishers, 180 fish stayed in the reef where they were tagged while an additional 20, for which the exact recapture location was not reported, remained at the same fishing spot. Another 17 fish moved between reefs within the same fishing spot, and only one individual, tagged in Conos Point, was speared at Reef #11 (Camp 39) (6.2 km away) after 104 days (Table S2, available as Supplementary Material to this paper).

The distance between release and recapture locations was estimated in 96 cases, 57 of which came from four fishing spots in San José Gulf, in which tagging and recapture surveys were conducted at several patchy reef areas (Larralde Beach, San Román Point, Conos Point and Gales Point) (Figs. 1 and S1, the latter available as Supplementary Material to this paper). Of those 57 distances, 36 were <100 m; 11 fish remained within 100 m even after a long period at large, from 6 to 26 months

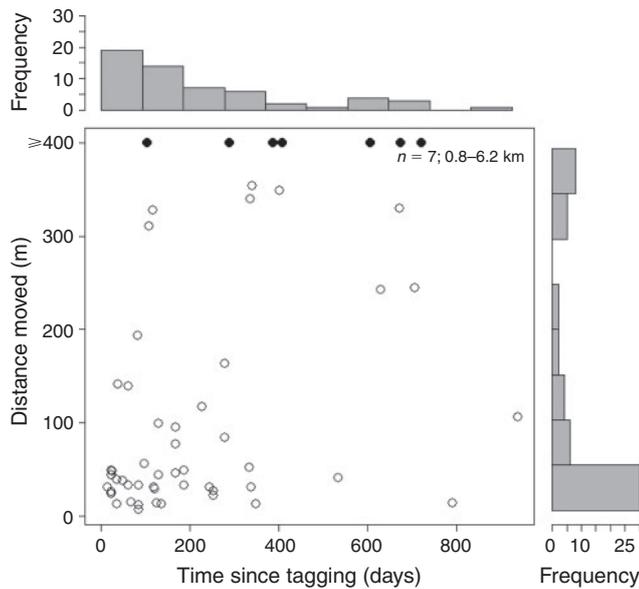


Fig. 3. Scatterplot with marginal histograms showing the estimated distance moved versus time since tagging for *P. semifasciata* in some popular fishing spots within San José Gulf ($n = 57$) (Larralde Beach, San Román Point, Conos Point and Gales Point). Solid circles represent truncated distances (≥ 400 m). The number and range of the truncated distances is indicated to their right.

(Fig. 3). Fifteen of the fish that moved > 100 m from the tagging site were caught off Larralde Beach, the most heavily fished spot, where both the number of fish tagged ($n = 247$) and the fishing effort (in total, > 540 trips were estimated for the period 2002–07) were greatest (Table 1). These conditions allowed the recovery of 28% of the fish tagged within this fishing spot.

Overall, six fish were recaptured more than 1 km from where they were tagged. Four of them were recaptured off Larralde Beach and San Román Point, in reefs that were surveyed or fished often (Table S2 and Fig. S1, available as Supplementary Material to this paper).

Smaller fish were more prone to relocate or emigrate (Prediction 1): the proportion of fish ≤ 50 cm TL among those that relocated > 150 m ($P = 0.88$; $n = 15$ of 17) was larger than for fish that moved less ($P = 0.55$; $n = 20$ of 40). That proportion was larger than the 95% upper confidence limit under the null hypothesis of no association between fish size and distance moved (Fig. 4). With respect to Prediction 2, fish ≤ 45 cm TL were recaptured within 150 m in a smaller proportion ($P = 0.38$; $n = 8$ of 21) than larger fish ($P = 0.89$; $n = 32$ of 36). That proportion was smaller than the 95% lower confidence limit under the null hypothesis (Fig. 4).

Residence patterns

Fish were repeatedly resighted and/or recaptured in the same reefs, mainly in Reefs #11 and #36, the reefs most intensely surveyed by scuba. More than 70% of the individuals resighted were recorded in more than half of the visits (Fig. 2). This indicates that at least some fish stay in the reefs for periods longer than a year. For example, a transitional fish 55 cm TL was resighted 14 times and hand-lined twice in Reef #36 between October 2003 and January 2005 (459 days after tagging).

In total, there were 15 fish that could not be individually identified because they had a single tag but, on the basis of their tag colour, could have migrated from other reefs. However, a few records with wrong combinations of fish size and tag colour indicate that misidentifications of tag colour cannot be ruled out.

Overall, the distribution of residence periods (i.e. maximum number of days a fish was recorded in the same reef) declined exponentially from ~ 200 days after tagging (Fig. 5). Yellow fish showed a median residence period of 150 days (quartiles = 67 and 253 days), while grey and transitional fish were recorded for longer periods: median residence time = 239 days (quartiles = 112 and 453 days). About 23% of the grey or transitional fish stayed in the reefs longer than a year, compared with $< 7\%$ of yellow fish. The proportion of grey or transitional fish that remained in the reefs for shorter periods (100–600 days) was lower than the 95% confidence bound estimated under the null hypothesis of no association between phenotype and residence time (Fig. 4). This result did not change even when 21 fish resighted or recaptured in the same reef immediately after tagging (< 50 days since tagging) were excluded from the analysis. The number of days spent in the same reef was uncorrelated with fish size ($n = 107$, Kendall's Tau- $b = 0.028$, $P = 0.677$), so it was unlikely that the phenotype effect detected when testing Prediction 3 was actually a size effect.

A seasonal trend in resightings was observed in Golfo Nuevo but not in San José Gulf, paralleling trends in the numbers of fish censused in Reefs #36 and #11, respectively (Venerus *et al.* 2008, 2013; Irigoyen *et al.* 2011). Tagged fish disappeared from Reef #36 in September–October, along with a sharp drop in total fish counts, and reappeared in November–December. The disappearance of fish coincided with the seasonal peak in the abundance of drifting individuals of the invasive kelp *Undaria pinnatifida*, which get stuck onto reefs, physically obstructing the refuges. By contrast, in Reef #11, which was free of *U. pinnatifida*, the number of resightings fluctuated without a clear seasonal trend; coincidentally with rather subtle seasonal fluctuations in fish abundance observed in San José Gulf (Venerus *et al.* 2008).

Repeated resightings of fish also allowed us to examine the spatial dynamics at the within-reef scale. Fish were observed to be associated with crevices all year round and some were repeatedly encountered roaming in the same reef area or associated with the same refuge. Six yellow, one transitional and three grey fish were repeatedly observed for up to eight months in the vicinity of well identified crevices in Reefs #36, #3 and #11 (Table 2), resting outside the crevices, patrolling close to their entrance or hidden inside. More than one fish was observed simultaneously associated with the same crevice, and one grey male was recorded entering two different crevices on the same day, at the start of the reproductive season. Further, in Reef #36, two individuals reoccupied the same crevice after returning to the reef in late spring and summer, once the reef was clear of *U. pinnatifida* (Table 2).

Discussion

Site fidelity

The general pattern observed in the tag recoveries indicates that *P. semifasciata* is strongly site-attached: most fish stayed in the

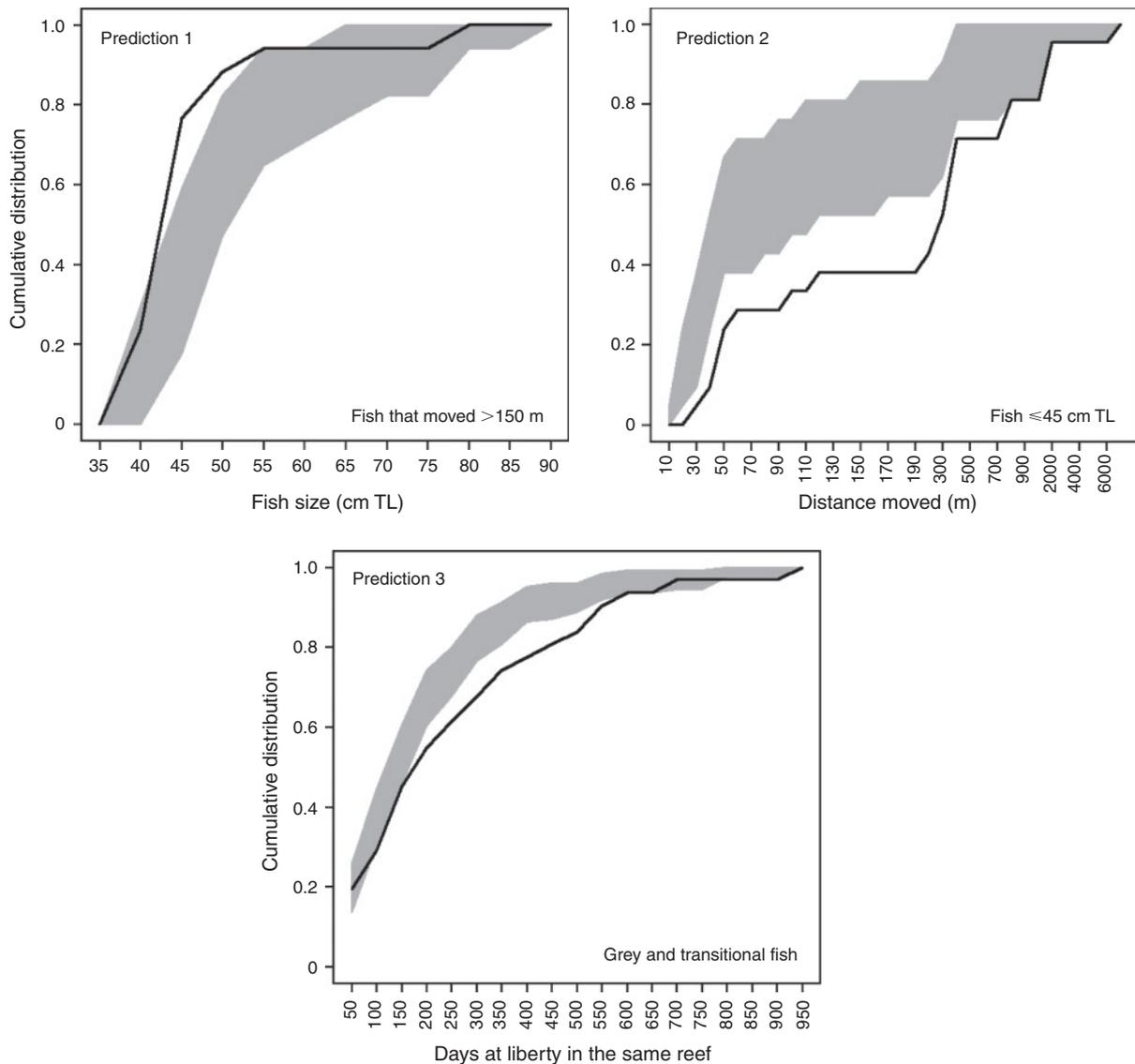


Fig. 4. Evaluation of three predictions about mobility patterns in *P. semifasciata*: (1) fish that relocate or emigrate are smaller than those that remain in the reef; (2) smaller fish move farther from the tagging sites; (3) grey or transitional fish have longer residence times than yellow individuals. Shaded areas represent 95% confidence regions for cumulative distributions under the null hypothesis, approximated by Monte Carlo permutations (5000 replicates). The solid lines represent the empirical cumulative distribution.

reefs or nearby and moved <100 m from the tagging site during periods that exceeded a year. Fewer individuals, mainly yellow fish ≤ 45 cm TL, moved longer distances between reefs of up to 6.2 km in 104 days. Most fish that displaced >100 m from the tagging site were recaptured off Larralde Beach. Because other fishing spots were sampled less intensively, the distribution of recoveries over-represents the proportion of fish that moved shorter distances and stayed within patchy reef areas.

The gradual return of fish to Reef #36 during summer, once the reef was clear of *U. pinnatifida*, suggests the possibility of homing. While no planned relocation experiments have been conducted to investigate this possibility, the recapture 289 days later of a yellow fish that had been displaced by us by 1.1 km from the reef where it was tagged is also suggestive of this possibility.

Dispersal capabilities have also been studied for the blue cod, *Parapercis colias*, another pinguipedid species from temperate waters. Cole *et al.* (2000) reported that 90% of tagged blue cod were resighted within 100 m of the release point up to 31 months after tagging. Mace and Johnston (1983) found that 53 blue cod (~72% of the fish recaptured) were caught in the same headland or reef where they had been tagged, while 21 fish had displaced distances of up to 41.7 km from the tagging site. Carbines and McKenzie (2004) also observed that up to 65% of all recaptures after one year occurred within 1 km of their release site, and that a small fraction of the tagged fish displaced longer distances (up to 156 km) in southern New Zealand. This evidence supports the hypothesis that adult blue cod form resident subpopulations on the scale of a few kilometres in enclosed waterways due to limited migration and restricted home ranges on the temporal

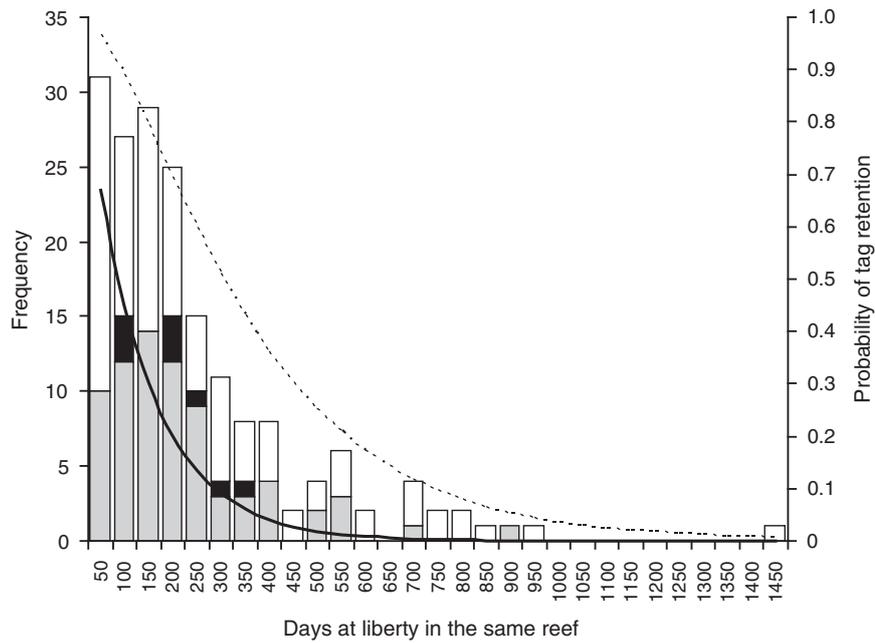


Fig. 5. Frequency distribution of days at liberty for fish recaptured (white bars), resighted (grey bars) or both (black bars) in the same reef of tagging within San José and Nuevo gulfs. Only the last record was included for fish recorded multiple times. Fish double- and single-tagged were considered. For reference, the solid and dotted lines show, respectively, the probability that a double-tagged fish retains the two tags or one tag, assuming a constant tag-shedding rate (based on results by Venerus et al. 2013).

Table 2. Examples of repeated use of crevices by *P. semifasciata* in San José and Nuevo Gulfs

C_x, associated with crevice x; DAL, days at liberty associated with the same crevice; individual code composed of chromatic phenotype (Y, yellow; G, grey; Tr, transitional) and fish size at tagging (cm TL); R, resighted; T, date of tagging

(a) Reef #36		2003						2004						2005											
ID code	DAL	Oct 6	Dec 27	Jan 2	Jan 15	Feb 10	Feb 13	Mar 4	Mar 20	Apr 28	Jun 1	Jun 28	Jul 23	Jul 26	Aug 20	Sep 13	Oct 13	Nov 2	Dec 6	Dec 28	Jan 11	Jan 28	Feb 24		
Y42	153	T		R	R			C _a			C _a			R	C _a										
Y45	25										T	C _a	C _a								R				
Y47	36									T	R			R							C _a	C _a		R	
Y47	161										T	C _a	C _a	R	C _a						C _a	C _a	R	R	
Y51	70										T	R									C _a	C _a	R	C _a	
Y67	44							T	R	R	R	R	R	R	R	R					R	R	C _b	C _b	C _b
Tr55	189		T	R	R	R	R	R	R	R	R	R	C _b	C _b	R						R	C _b	C _b	C _b	
G75	78		T			C _c	R	C _c	C _c	C _c															

(b) Reef #11		2004											
ID code	DAL	Jan 24	Jan 25	Mar 8	Mar 28	May 10	May 28	May 29	Aug 5	Aug 15	Aug 16	Oct 2	Oct 3
G64	58	T			R	R	R	R	C _d	C _d	C _d	C _{de}	C _{de}

(c) Reef #3		2002			2003		
ID code	DAL	Aug 16	Oct 18	Dec 09	Feb 10	Apr 13	Apr 15
G86	242	C _f	C _f	C _f	T/C _f	C _f	C _f

scale of one year, which was reinforced by dietary evidence (Rodgers and Wing 2008). This general pattern agrees with our results for *P. semifasciata*. However, the relationship between mobility and fish size was not as clear in *P. colias* as in *P. semifasciata*. Mace and Johnston (1983) reported that no *P. colias* >30 cm TL were recaptured significant distances from where they had been tagged (maximum length of *P. colias* is >50 cm TL (Ayling and Cox 1987) and size at first maturity is 21–25 cm TL (Rapson 1956)). In turn, Cole *et al.* (2000) found no obvious relationship between dispersal distance and fish size. However, all resightings of fish >35 cm TL in that study occurred within 150 m from the tagging site, suggesting that larger fish were home-ranging. On the other hand, Rapson (1956) found that, among 18 fish that had moved more than 1.6 km, 16 were larger than 30 cm TL when tagged, which suggested the opposite pattern (i.e. larger fish move longer distances). Finally, Carbones (2004) found only a weak relationship between fish size and distance moved in *P. colias*.

Residence patterns

Multiple recaptures and resightings of fish over the annual cycle indicate that *P. semifasciata* have long residence times (which may exceed a year) in the reefs (Fig. 5). Furthermore, observations of several fish occupying the same crevice or roaming in the same reef area over successive resightings indicate that site-attachment also occurs at the within-reef scale (Table 2). The longest periods during which fish were recorded in the same reef area in this study probably underestimate the actual residence times, for several reasons. First, a high tag-shedding rate of 0.0040 day⁻¹ has been estimated for *P. semifasciata* (Venerus *et al.* 2013), which would appreciably reduce recoveries over time. According to that tag-shedding rate, the probability that a fish retains at least one tag after 200 days is 0.70 for a double-tagged fish and 0.45 for a single-tagged fish. In addition, many of the fish resighted with a single tag could not be unequivocally identified underwater, which affected more than 240 resightings. Second, the reliability of tag identification by scuba decreased with time as external tags became fouled after a few months. Third, as we continued tagging over the course of the study, fish tagged later in the study had less time to be resighted.

The occurrence of long residence times in *P. semifasciata* is consistent with the generally stable occupation pattern described by Venerus *et al.* (2008) in San José Gulf. In that study, fish abundance fluctuated between 17% and 33% around its mean. By contrast, the abundance of *P. semifasciata* in Reef #36 of Golfo Nuevo fluctuated markedly; fish disappeared from the reef coincidentally with the seasonal presence of dense thickets of *U. pinnatifida* covering the reef ledges and blocking the entrances to the crevices (Irigoyen *et al.* 2011). This transitory loss of habitat, observed particularly in low-relief reefs, the preferred habitat for this species (Galván 2008), could lead fish to relocate to deeper reefs free of *U. pinnatifida* during late winter and early spring. Indeed, the only fish caught far from the reef of tagging in Golfo Nuevo was caught at ~30 m depth in late winter, when the density of *U. pinnatifida* is highest (Irigoyen 2010).

Finally, longer residence times for grey and transitional males are consistent with the hypothesis of a female-defence

or resource-defence mating system associated with the reefs (González 1998; Venerus *et al.* 2008).

Management implications

The high site fidelity recorded in this study implies that no-take reserves could be effective for the conservation of local populations of *P. semifasciata*. Relatively small reserves (in the order of a few kilometres) could protect most fish within their limits. Restricted mobility and long residence, on the other hand, could limit fishery benefits through spill-over. Given that smaller fish were more prone to relocate or emigrate, spill-over from closed areas would be expected to be mostly of yellow individuals smaller than 45–50 cm LT.

Reserves could also protect other species of the assemblage targeted by anglers and spear-fishers. The Argentine seabass, *Acanthistius patachonicus*, for example, also showed strong site fidelity and long residence times in reefs from Golfo Nuevo (Irigoyen 2010).

When our tagging program started, San José Gulf was free of *U. pinnatifida*. At present, the invasive species has heavily colonised the southern coast of the gulf. On the basis of our results, reserves that are designed to protect *P. semifasciata* should include reef areas at depths greater than 20 m, deeper than the range occupied by *U. pinnatifida*.

Despite its strong association with refuges, *P. semifasciata* is an active predator that consumes soft-bottom prey in similar proportions to transient prey and to prey from rocky substrates (Galván *et al.* 2009a). Reserves should also include soft-bottom areas used for foraging, which have been found to support, at least partially, the production of rocky reef fish populations (Galván *et al.* 2008, 2009a).

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