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

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1  **Abstract**

2

3      The choice of appropriate conservation strategies for reef fishes depends on

4  their mobility, degree of site fidelity and residence times. Here we report the results of

5  a small-scale mark-recapture and resighting study conducted to investigate the spatial

6  dynamics of the Argentine sandperch *Pseudopercis semifasciata*. This is the flagship

7  species of the rocky-reef fish assemblage from northern Patagonia, which has been the

8  target of uncontrolled fishing since the early 50's. About 19% of the fish tagged were

9  recaptured up to four years after tagging. In total, 180 of 218 recaptured fish stayed in

10  the reef of tagging. Thirty six of 57 recaptures made at known locations within popular

11  fishing areas of San José Gulf, densely covered by patchy reefs, occurred within 100 m

12  of the tagging site, up to 793 days since tagging. Six fish were recovered at more than

13  1 km. Smaller fish were more prone to relocate, and were recovered farther from the

14  tagging site. Fish stayed in the reefs for periods longer than a year; larger males

15  remained longer in the same reefs. Our results indicate that relatively small reserves (in

16  the order of a few kilometres) could be effective at protecting *P. semifasciata*

17  populations within the northern Patagonian gulfs.

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19  **Additional keywords:** external tags, MPA, site fidelity, movement patterns, *Undaria*

20  *pinnatifida*.

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22  **Running head:** Spatial dynamics of *Pseudopercis semifasciata.*

**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 localized 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 and Jones 2005), also appears to be frequent among temperate and warm-temperate reef fishes. This is the case of 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 *Pseudopercis 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 50´s (Sanabra 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 license per day has been in place since 1994 within

the Peninsula Valdés Reserve, a site declared Natural World Heritage Site by
UNESCO in 1999 (Fig. 1). The inadequacy of this regulation, together with the lack of
effective controls, have led to the local 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 unsuitability of size limits due to barotrauma (Venerus, Personal observation).
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 recognizable
individuals (e.g., through scars) residing during 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 in the literature for this species.

The stability of the size distribution of fishes 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. Supporting behavioural observations are however very limited.

In this paper, we analyse the spatial dynamics of adult *P. semifasciata* from two
main sources of information: (i) a small-scale tagging program conducted to study
mobility and site fidelity within San José Gulf, and (ii) 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 hypothesize that smaller fish have higher mobility and disperse more than larger individuals in search for 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. 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 Macchi[1], unpublished data). This species is a multiple spawner; its spawning season centers in November-December in Patagonia (Elías and Burgos 1988; Macchi *et al.* 1995). Although mating displays have not been observed, the low 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

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123 eggs are laid in enclosed spaces, e.g., inside crevices. In addition, the year-round

124 stability of fish abundance observed in reefs of San José Gulf (Venerus *et al*. 2008), is

125 not consistent with the occurrence of spawning migrations and/or the formation of

126 spawning aggregations; rather, it suggests that spawning may occur in the reefs or in

127 nearby soft bottom areas probably involving some form of resource- and/or female-

128 defence mechanisms. Within San José Gulf, this species occurs at low densities, even

129 in lightly exploited reefs, on the order of 1–1.5 fish per 10 m of reef ledge (Venerus *et*

130 *al.* 2008). In general, only fish >20 cm TL are found in the reefs. Grey fish are much

131 less abundant than yellow; the average ratio found in San José Gulf was 13:1 (Venerus

132 *et al.* 2008).

133

134 *Study site*

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136        Reefs are small, isolated rocky outcrops that most commonly extend between

137 >50 m and a few hundred metres on an otherwise flat, soft bottom. The commonest

138 reef topography consists in longitudinal breaks or ledges (~0.3–1.5 m high) formed

139 along the edge of submerged abrasion limestone platforms, where cavities are formed.

140        Fishing spots, each encompassing patchy reef areas of variable extension, are

141 locally known by the name of the beach or other geographical features. For this study,

142 we identified nine fishing spots within San José Gulf: Esfinge Point, Camp 39,

143 Fracasso Beach, Fracasso´s Prows, the mouth of the gulf, San Román Point, Conos

144 Point, Larralde Beach and Gales Point (Fig. 1). In the latter four we identified between

145 three and 14 reefs, distant between 120 m and 3.9 km (Fig. S1, available as

146 Supplementary Material to this paper). San José Gulf and the northern coast of Golfo

147 Nuevo are included in the Península Valdés Reserve. Although trawling and long-

148 lining are effectively banned within the gulfs, illegal commercial hook-and-line fishing

149 occurs. Recreational anglers and spear-fishers frequent the reserve and a few charter

150 boats operate from Larralde Beach, Gales Point and Puerto Pirámide (Fig. 1), mainly

151 during summer and early fall (Venerus 2006).

152

153 *Fish tagging*

154

155        Thirty-five reefs were located in San José Gulf by interviewing recreational and

156 artisanal fishers before the onset of the tagging program. A total of 1075 fish were

157    tagged during 126 fishing sessions, between October 2001 and August 2005. In

158    addition, 63 fish were tagged in reef #36, Golfo Nuevo, during 17 fishing sessions,

159    between August 2003 and December 2004. In total, 1012 yellow, 74 grey and 52

160    transitional fish were tagged. Tagging trips were scheduled opportunistically, mostly

161    restricted by weather conditions, therefore sampling effort was uneven (Tables 1 and

162    S1, the latter available as Supplementary Material to this paper). In addition to research

163    trips, we tagged fish on board of one charter boat that operates off Larralde Beach and

164    in the mouth of San José Gulf. The total angling effort exerted off Larralde Beach, in

165    which at least 14 reefs are distributed within an area of ~5 km², for example, was

166    unevenly distributed among reefs, with reefs #24 – #26 visited by the charter boat in

167    almost every fishing trip (Fig. S1, available as Supplementary Material to this paper).

168    Fish were angled with hand-lines up to ~28 m depth during research trips or with

169    rod-and-reel up to ~50 m depth during charter boat trips. They were measured to the

170    lowest cm, tagged onboard using Floy™ FD-68B anchor tags and Dennison tagging

171    guns, and immediately released. Only fish <50–55 cm TL were released during charter

172    boat trips.

173    Fish were laid on a wooden "V" shaped cradle and their eyes were covered by a

174    wet piece of fabric during tagging. Tags were inserted at the base of the dorsal fin, with

175    the gun pointing forward at an angle of ~45° with respect to the longitudinal axis of the

176    fish. Two tags were applied to each fish in reefs #36 and #11 (since January 2004 in

177    the latter) to allow individual identification underwater, using a combination of tag

178    colour, and location along the dorsal fin and body side. Since February 2004 all fish

179    were double-tagged to increase recovery rates. A total of 268 fish were double-tagged.

180    To minimise injuries produced by the swim bladder stress syndrome while allowing

181    fish to return quickly to the sea bottom, some fish were punctured with the hollow

182    needle of the tagging gun before being released (see Gotshall 1964).

183

184    *Tag recovery*

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186    Tags were recovered by us during underwater surveys of shallow reefs off

187    Esfinge Point, San Román Point, Conos Point, Fracasso Beach, Larralde Beach (San

188    José Gulf) and East Point (Golfo Nuevo), by hook-and-line in all reefs, and by

189    occasional spear-fishing (Table 1 and Fig. 1). Underwater resightings were recorded

190    during 119 visits to the reefs and ~250 hours of scuba diving (Table 1), between

October 2001 and August 2005. Our main motivation for conducting diving surveys in the same reefs of tagging 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 publicized by Internet, e-mail 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 to 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 done 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

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225  (Irigoyen *et al.* 2011, Venerus *et al.* 2013). To gather information on reef use at a finer

226  scale, a few well-identified crevices in reefs #3, #11 and # 36 were visited frequently to

227  record the presence and identity of fish in their surroundings (<2 m).

228

229  *Statistical analysis and predictions testing*

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231  Geodetic coordinates (latitude and longitude) were projected onto a Gauss-

232  Krüger grid with the software GeoCalc 3.05 to calculate distances between release and

233  recapture. When the exact recapture location was not reported but the reef was

234  identified, the position at recapture was equated to the reef's geographic centroid.

235  Recapture data were used to test predictions 1–3, derived from the hypothesis

236  about differential movement by type and phenotype, using randomization tests (Manly

237  1991). For testing predictions 1 and 2, recaptures for which distance moved could be

238  estimated were selected, and fish sizes were randomly permutated with respect to

239  distance moved under the null hypotheses that the probability of relocation/emigration

240  (1), and the distance moved (2) were independent of fish size. Only data from four

241  fishing spots in San José Gulf (Larralde Beach, San Román Point, Conos Point and

242  Gales Point), in which multiple reefs were used for tagging and searching for tagged

243  fish, were included. For testing prediction 3, fish phenotype (yellow and transitional or

244  grey) was permutated with respect to the number of days between tagging and the last

245  recapture in the same reef, under the null hypothesis of independence between fish

246  phenotype and residence time. In all cases, Monte Carlo permutations (n = 5000) were

247  stratified by fishing spot because the size frequency distributions of fish tagged, the

248  range of distances moved, and the sampling efforts were not homogeneous among sites

249  (Table 1). Fishing spots that had only a few recoveries (San Román and Conos) were

250  pooled in one group. Gales Point and the mouth were also pooled for testing prediction

251  3.

252  To test prediction 1, the cumulative distribution function of the size of fish that

253  moved >150 m, used as a rule to classify relocation/emigration from the tagging site,

254  was compared to the 95% confidence bounds of the corresponding distribution

255  estimated by stratified Monte Carlo permutations under the null hypothesis. Similarly,

256  the cumulative distribution of the distance moved for fish smaller than a given

257  threshold size was used to test prediction 2, using different size thresholds (fish ≤45 cm

258  TL, ≤50 cm TL, and so on). Finally, prediction 3 was evaluated by comparing the

259 cumulative distribution of days-in-the-reef for fish of the grey/transitional phenotype

260 with the 95% confidence bounds of the corresponding distribution for all fish ≥47 cm

261 TL under the null hypothesis. The size of 47 cm, corresponding to the smallest

262 transition fish, was selected to avoid confounding the effects of phenotype and fish

263 size. In addition, we estimated the Kendall´s Tau-b correlation coefficient between the

264 residence time and fish size. The data set used in this case contained all recoveries

265 made in the reef of tagging, including our own and those reported by anglers and

266 spear-fishers. We repeated the analysis by eliminating fish with short residence times

267 (<50 days since tagging) to avoid any potential bias associated with recaptures in the

268 initial sampling period.

269　　　Calculations were done using an *ad-hoc* code programmed in R language

270 (version 2.7.1, R Development Core Team 2008).

271

272 **Results**

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274 *Tag recovery statistics*

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276　　　The number of recaptures and resightings closely followed the number of

277 angling and diving trips (Fig. S2, available as Supplementary Material to this paper).

278　　　A total of 218 fish were recaptured and/or resighted at least once, up to 1427

279 days after tagging. No selection bias occurred during the recovery of tags: fish sizes

280 and proportions of chromatic phenotypes were similar for tagged and recaptured or

281 resighted fish (Fig. S3, available as Supplementary Material to this paper). Ten fish

282 changed from yellow to transitional or grey (minimum time period elapsed = 43 days),

283 and four transitional males were recaptured as grey.

284　　　A total of 187 recaptures of 165 individuals were obtained by angling (n = 170)

285 or spear-fishing (n = 17) between May 2002 and December 2007 (Table 1). Among the

286 fish angled by the project staff, sixteen individuals were re-caught twice (from 54 to

287 1427 days at liberty) and three were re-caught three times (from 186 to 449 days at

288 liberty). The majority of recaptures were made during research trips (n = 106); the rest

289 were recovered by artisanal (n = 11) and sport (n = 28) fishers, and fishing guides (n =

290 42).

291　　　In total, 284 resightings of 91 fish were recorded in five reefs from San José Gulf

292 (100 resightings) and in the reef from Golfo Nuevo (184 resightings), between January

10

293  2002 and August 2005 (Table 1). Fifty-six of those fish were repeatedly resighted (Fig.

294  2). More tagged fish were resighted in both gulfs, but their identity could not be

295  established.

296

297  *Site fidelity*

298

299     Overall, *P. semifasciata* was strongly site-attached to the reefs. Based on our

300  recaptures/resightings, and on the reports by anglers and spear-fishers, 180 fish stayed

301  in the same reef of tagging while an additional 20, for which the exact recapture

302  location was not reported, remained at the same fishing spot. Another 17 fish moved

303  between reefs within the same fishing spot, and only one individual, tagged in Conos

304  Point, was speared at reef # 11 (Camp 39) (6.2 km far) after 104 days (Table S2,

305  available as Supplementary Material to this paper).

306     The distance between release and recapture locations was estimated in 96 cases,

307  57 of which came from four fishing spots in San José Gulf, in which tagging and

308  recapture surveys were conducted at several patchy reef areas (Larralde Beach, San

309  Román Point, Conos Point and Gales Point) (Figs. 1 and S1, the latter available as

310  Supplementary Material to this paper). Of those 57 distances, 36 were <100 m; 11 fish

311  remained within 100 m even after a long period at large, from 6 to 26 months (Fig. 3).

312  Fifteen of the fish that moved >100 m from the tagging site were caught off Larralde

313  Beach, the most heavily fished spot, where both the number of fish tagged (n = 247)

314  and the fishing effort (in total, >540 trips were estimated for the period 2002 – 2007)

315  were greatest (Table 1). These conditions allowed recovering 28% of the fish tagged

316  within this fishing spot.

317     Overall, six fish were recaptured farther than 1 km in our study. Four of them

318  were recaptured off Larralde Beach and San Román Point, in reefs that were surveyed

319  or fished often (Table S2 and Fig. S1, available as Supplementary Material to this

320  paper).

321     Smaller fish were more prone to relocate or emigrate (prediction 1): the

322  proportion of fish ≤50 cm TL among those that displaced >150 m (p = 0.88; n = 15 of

323  17) was larger than for fish that moved less (p = 0.55; n = 20 of 40). That proportion

324  was larger than the 95% upper confidence limit under the null hypothesis of no

325  association between fish size and distance moved (Fig. 4). With respect to prediction 2,

326  fish ≤45 cm TL were recaptured within 150 m in a smaller proportion (p = 0.38; n = 8

327    of 21) than larger fish (p = 0.89; n = 32 of 36). That proportion was smaller than the

328    95% lower confidence limit under the null hypothesis (Fig. 4).

329

330    *Residence patterns*

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332        Fish were repeatedly resighted and/or recaptured in the same reefs, mainly in

333    reefs #11 and #36, the reefs most intensely surveyed by scuba. More than 70% of the

334    individuals resighted were registered in more than half of the visits (Fig. 2). This

335    indicates that at least some fish stay in the reefs during periods exceeding the year. For

336    example, a transitional fish 55 cm TL was resighted 14 times and hand-lined twice in

337    reef #36, between October 2003 and January 2005 (459 days after tagging). In total,

338    there were 15 fish that could not be individually identified because they had a single

339    tag but, based on their tag colour, they could have migrated from other reefs. However,

340    a few records with wrong combinations of fish size and tag colour indicate that

341    misidentifications of tag colour can not be ruled out.

342        Overall, the distribution of residence periods (i.e., maximum number of days a

343    fish was recorded in the same reef) declined exponentially since about 200 days after

344    tagging (Fig. 5). Yellow fish showed a median residence period of 150 days (quartiles

345    = 67 and 253 days), while grey and transitional fish were registered for longer periods:

346    median residence time = 239 days (quartiles = 112 and 453 days). About 23% of the

347    grey or transitional fish stayed in the reefs longer than a year, compared to <7% for

348    yellow fish. The proportion of grey or transitional fish that remained in the reefs for

349    shorter periods (from 100 to 600 days) was lower than the 95% confidence bound

350    estimated under the null hypothesis of no association between phenotype and residence

351    time (Fig. 4). This result did not change even when 21 fish resighted or recaptured in

352    the same reef immediately after tagging (<50 days since tagging) were excluded from

353    the analysis. The number of days spent in the same reef was uncorrelated with fish size

354    (n = 107, Kendall´s Tau-b = 0.028; P = 0.677), so it was unlikely that the phenotype

355    effect detected when testing prediction 3 was actually a size effect.

356        A seasonal trend in resightings was observed in Golfo Nuevo but not in San José

357    Gulf, paralleling trends in the numbers of fish censused in reefs #36 and #11,

358    respectively (Venerus *et al.* 2008, Irigoyen *et al.* 2011, Venerus *et al.* 2013). Tagged

359    fish disappeared from reef #36 in September-October, along with a sharp drop in total

360    fish counts, and reappeared since 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; coincidently with slighter fluctuations in 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 associated with crevices all year round and some were repeatedly encountered roaming in the same reef area or associated to 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 were observed simultaneously associated to the same crevice, and one grey male was recorded entering two different crevices along the same day, at the start of the reproductive season. Further, in reef #36, two individuals re-occupied 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 reefs or nearby and moved <100 m from the tagging site during time 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 represent the proportion of fish that moved less and stayed within patchy reef areas.

The gradual return of fish to the 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 of one yellow fish that had been displaced by us 1.1 km in the reef of tagging, 289 days later is also suggestive of this possibility.

395    Dispersal capabilities were also studied for the blue cod *Parapercis colias,*

396    another pinguipedid species from temperate waters. Cole *et al*. (2000) reported that

397    90% of tagged blue cod were resighted within 100 m of the release point up to 31

398    months after tagging. Mace and Johnston (1983) found that 53 blue cod (~72% of the

399    fish recaptured) were caught in the same headland or reef where they had been tagged,

400    while 21 fish had displaced distances of up to 41.7 km from the tagging site. Carbines

401    and Mackenzie (2004) also observed that up to 65% of all recaptures after one year

402    occurred within 1 km of their release site, and that a small fraction of the tagged fish

403    displaced longer distances of up to 156 km, in southern New Zealand. These evidences

404    support the hypothesis that adult blue cod form resident subpopulations on the scale of

405    a few kilometres in enclosed waterways due to limited migration and restricted home

406    ranges on the temporal scale of one year, which was reinforced by dietary evidence

407    (Rodgers and Wing 2008). This general pattern agrees with our results for *P.*

408    *semifasciata*. However, the relationship between mobility and fish size was less clear

409    in *P. colias* compared to *P. semifasciata*. Mace and Johnston (1983) reported that no *P.*

410    *colias* >30 cm TL were recaptured at significant distances from where they had been

411    tagged (maximum length of *P. colias* is >50 cm TL, Ayling and Cox, 1987; and size at

412    first maturity is 21–25 cm TL, Rapson, 1956). In turn, Cole *et al*. (2000) did not find

413    any obvious relationship between dispersal distance and fish size. However, all

414    resightings of fish >35 cm TL in that study occurred within 150 m from the tagging

415    site, suggesting that larger fish were home-ranging. Differently, Rapson (1956) found

416    that among 18 fish that had moved more than 1.6 km, 16 were larger than 30 cm TL

417    when tagged, which suggested the opposite pattern (i.e., larger fish move longer

418    distances). Finally, Carbines (2004) found only a weak relationship between fish size

419    and distance moved in *P. colias*.

420

421    *Residence patterns*

422

423    Multiple recaptures and resightings of fish over the annual cycle indicate that *P.*

424    *semifasciata* have long residence times in the reefs that may exceed one year (Fig. 5).

425    Furthermore, the observations of several fish occupying the same crevice or roaming in

426    the same reef area over successive resightings, indicate that site-attachment also occurs

427    at the within-reef scale (Table 2). The longest periods during which fish were

428    registered in the same reef area in this study probably underestimate the actual

429 residence times for several reasons. First, a high tag shedding rate of 0.0040 day$^{-1}$ has

430 been estimated for *P. semifasciata* (Venerus *et al.*, 2013), which would appreciably

431 reduce recoveries over time. Under that tag shedding rate, the probability that a fish

432 retains at least one tag after 200 days is 0.70 for a double-tagged fish and 0.45 for a

433 single-tagged fish. In addition, many of the fish resighted with a single tag could not be

434 unequivocally identified underwater, which affected more than 240 resightings.

435 Second, the reliability of tag identification by scuba decreased with time as external

436 tags became fouled after a few months. Third, as we continued tagging over the course

437 of the study, fish tagged later in the study had less time to be resighted.

438 The occurrence of long residence times in *P. semifasciata* is consistent with the

439 generally stable occupation pattern described by Venerus *et al*. (2008) in San José

440 Gulf. In that study, fish abundance fluctuated between 17 and 33% around its mean. By

441 contrast, the abundance of *P. semifasciata* in reef #36 of Golfo Nuevo fluctuated

442 markedly; fish disappeared from the reef coincidentally with the seasonal presence of

443 dense thickets of *U. pinnatifida* covering the reef ledges and blocking the entrances to

444 the crevices (Irigoyen *et al.* 2011). This transitory loss of habitat observed particularly

445 in low-relief reefs, the preferred habitat for this species (Galván 2008), could lead fish

446 to relocate to deeper reefs free of *U. pinnatifida* during late winter and early spring.

447 Indeed, the only fish caught far from the reef of tagging in Golfo Nuevo was angled at

448 approximately 30 m depth in late winter, when the density of *U. pinnatifida* is highest

449 (Irigoyen 2010).

450 Finally, longer residence times for grey and transitional males are consistent with

451 the hypothesis of a female-defence or resource-defence mating system associated with

452 the reefs (González 1998; Venerus *et al*. 2008).

453

454 *Management implications*

455

456 The high site fidelity registered in this study implies that no-take reserves could

457 be effective for the conservation of local populations of *P. semifasciata.* Relatively

458 small reserves (in the order of a few kilometres) could protect most fish within their

459 limits. Restricted mobility and long residence, on the other hand, could limit fishery

460 benefits through spill-over. Given that smaller fish were more prone to relocate or

461 emigrate, spill-over from closed areas would be expected to be mostly of yellow

462 individuals smaller than 45–50 cm LT.

463    Reserves could also protect other species of the assemblage targeted by anglers

464    and spear-fishers. The Argentine seabass *Acanthistius patachonicus*, for example, also

465    showed strong site fidelity and long residence times in reefs from Golfo Nuevo

466    (Irigoyen 2010).

467    When our tagging program initiated, San José Gulf was free of *U. pinnatifida*.

468    At present, the alien species has heavily colonized the southern coast of the gulf. Based

469    on our results, reserves aimed at protecting *P. semifasciata* should include reef areas at

470    depths greater than 20 m, deeper than the range occupied by *U. pinnatifida.*

471    Despite its strong association with refuges, *P. semifasciata* is an active predator

472    that consumes soft-bottom prey in similar proportions to transient prey and to prey

473    from rocky-bottoms (Galván *et al.* 2009a). Reserves should also include soft bottom

474    areas used for foraging, which have been found to support, at least partially, the

475    production of rocky reef fish populations (Galván *et al.* 2008, 2009a).

476

491

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694 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.

695 Fracasso's Prows, Gales Point and the mouth of San José Gulf were not surveyed by scuba diving (indicated by a dash).

| Fishing Spot | Reef ID | Mean depth (m) | Number of fish tagged and released[a] | Size range of fish tagged (cm TL) | Number of recaptures (hook-and-line or spear)[b] | Number of identified resightings[b] | Diving surveys | 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 |

696

697 [a] In parenthesis, numbers that died after capture/tagging.

23

698    [b] In parenthesis, number of different individuals recaptured or resighted. Note that some fish were recaptured and resighted, and hence are

699    included in both counts.

700    [c] Besides the number of fishing trips conducted by us and charter boats, an estimated global fishing effort (minimum numbers of fishing trips)

701    for the period Oct 2002 to Dec 2007 is provided for boat owners operating in the most popular fishing spots within San José Gulf: Larralde

702    Beach, Gales Point and the mouth. Those estimations are based on data collected during a monitoring program conducted at the landing sites

703    (see Venerus 2006 for further explanation).

704 Table 2: Repeated use of crevices by *P. semifasciata* in San José and Nuevo gulfs. $C_x$: associated to crevice x; DAL: days at liberty associated to

705 the same crevice; individual code composed of chromatic phenotype (Y: yellow, G: gray, Tr: transitional) and fish size at tagging (cm TL); R:

706 resighted; T: date of tagging.

**Reef # 36**

| Id Code | DAL | 2003 Oct 6 | Oct 27 | 2004 Dec 2 | Jan 15 | Feb 10 | Feb 13 | Mar 4 | Mar 20 | Abr 28 | Jun 1 | Jun 28 | Jul 23 | Jul 26 | Ago 20 | Sep 13 | Oct 13 | Nov 2 | Dec 6 | Dec 28 | 2005 Jan 11 | Jan 28 | Feb 24 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Y42 | 153 | T | | R | R | | R | | $C_a$ | | $C_a$ | | | R | $C_a$ | | | | | | | | |
| Y45 | 25 | | | | | | | | | | T | $C_a$ | $C_a$ | | | | | | R | | | | |
| Y47 | 36 | | | | | | | | | T | R | | | R | | | | | $C_a$ | $C_a$ | $C_a$ | | 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 | $C_c$ | $C_c$ | $C_c$ | | | | | | | | | | | | | |

**Reef # 11**

| Id Code | DAL | 2004 Jan 24 | Jan 25 | Mar 8 | Mar 28 | May 10 | May 28 | Aug 29 | Aug 5 | Aug 15 | Oct 16 | Oct 2 | Oct 3 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| G64 | 58 | T | | | R | R | R | R | $C_d$ | $C_d$ | $C_d$ | $C_{de}$ | $C_{de}$ |

**Reef # 3**

| Id Code | DAL | 2002 Aug 16 | Oct 18 | Dec 09 | 10 | 2003 Feb 13 | Apr 15 |
|---|---|---|---|---|---|---|---|
| G86 | 242 | $C_f$ | $C_f$ | $C_f$ | T/$C_f$ | $C_f$ | $C_f$ |

**Figure captions**

Figure 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.

Figure 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; with its size 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 Jan 2004 and 10 Aug 2005, and for reef #36 (grey bubbles), surveyed 24 times between 11 Aug 2003 and 24 Feb 2005.

Figure 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.

Figure 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 (5,000 replicates). The solid lines represent the empirical cumulative distribution.

Figure 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 registered 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 ore one tag, assuming a constant tag shedding rate (based on results by Venerus *et al.* 2013).
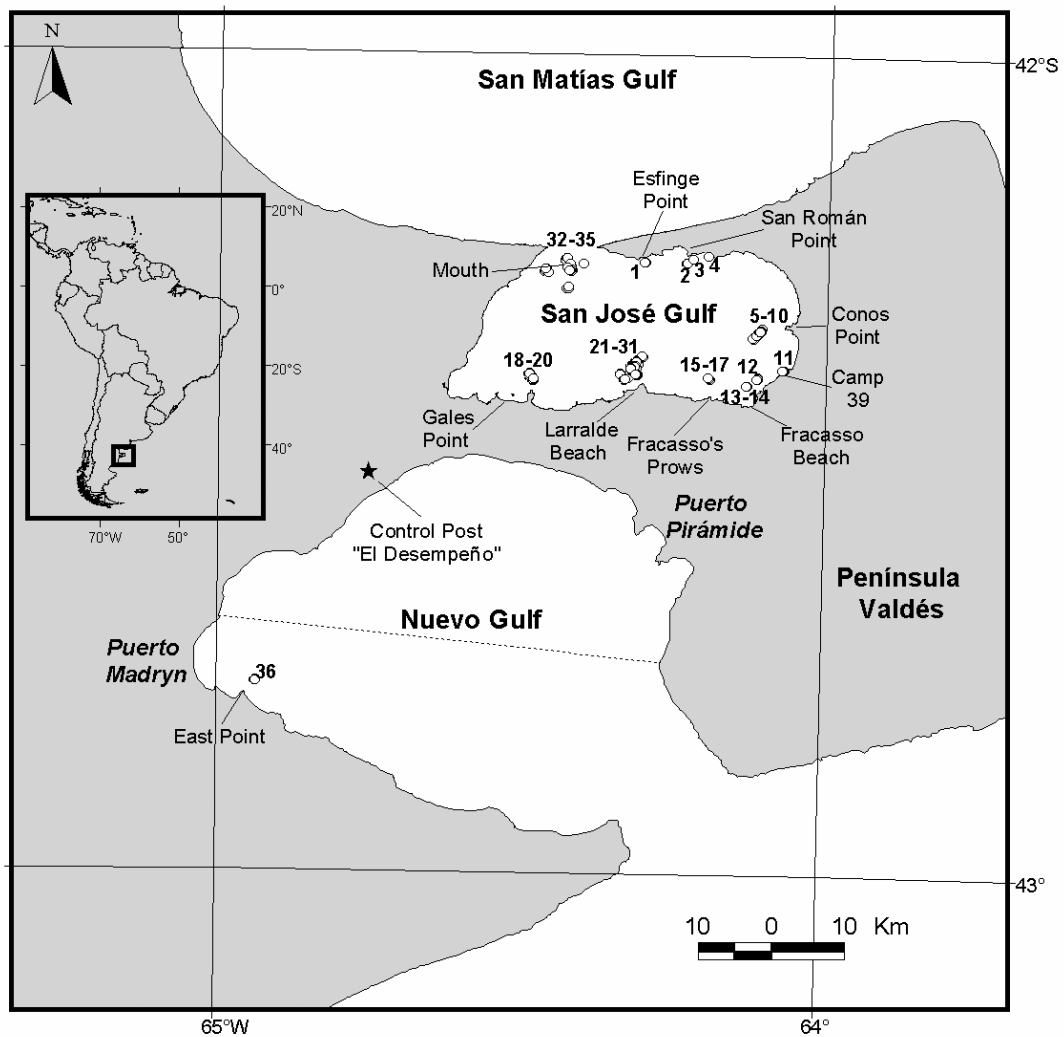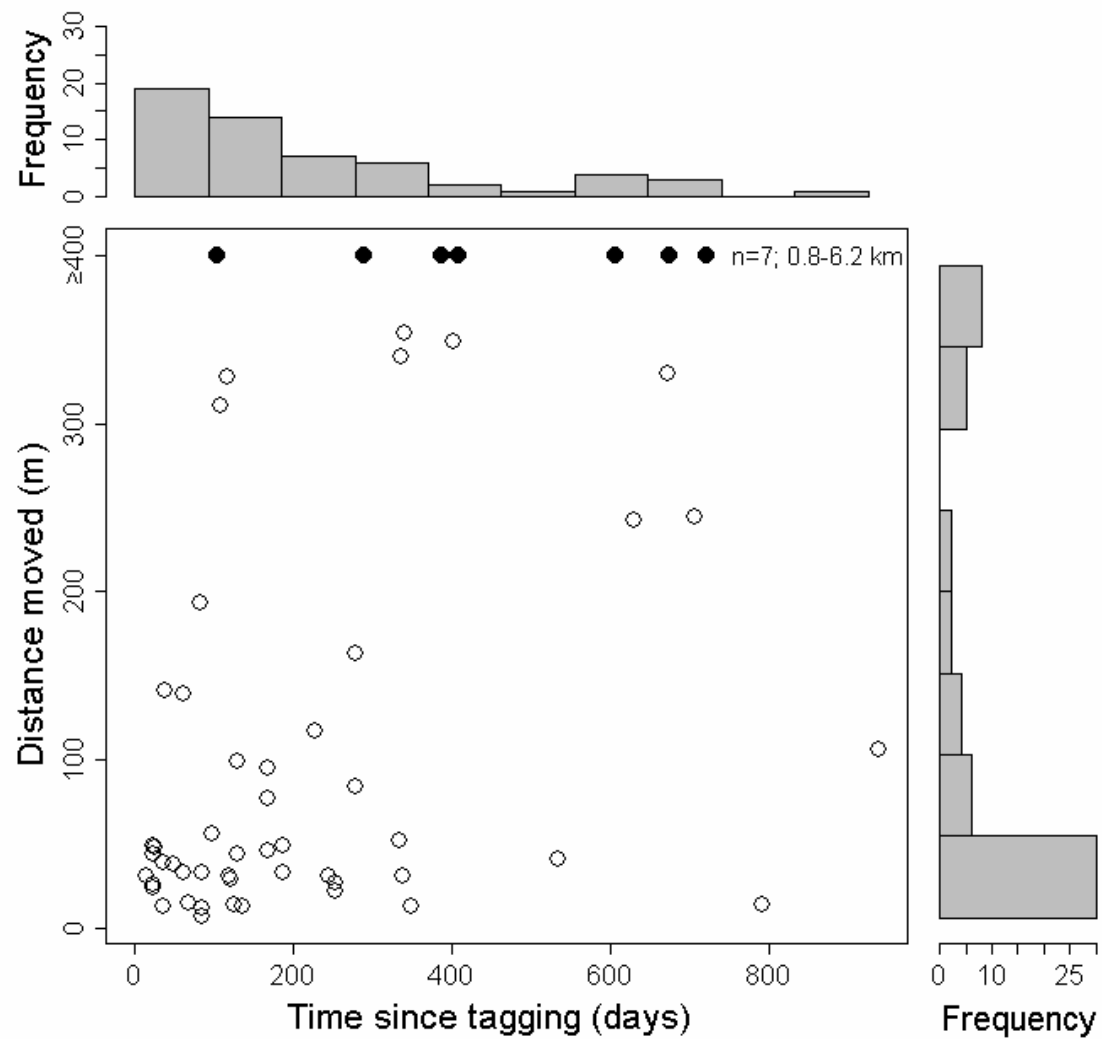
Venerus et al.

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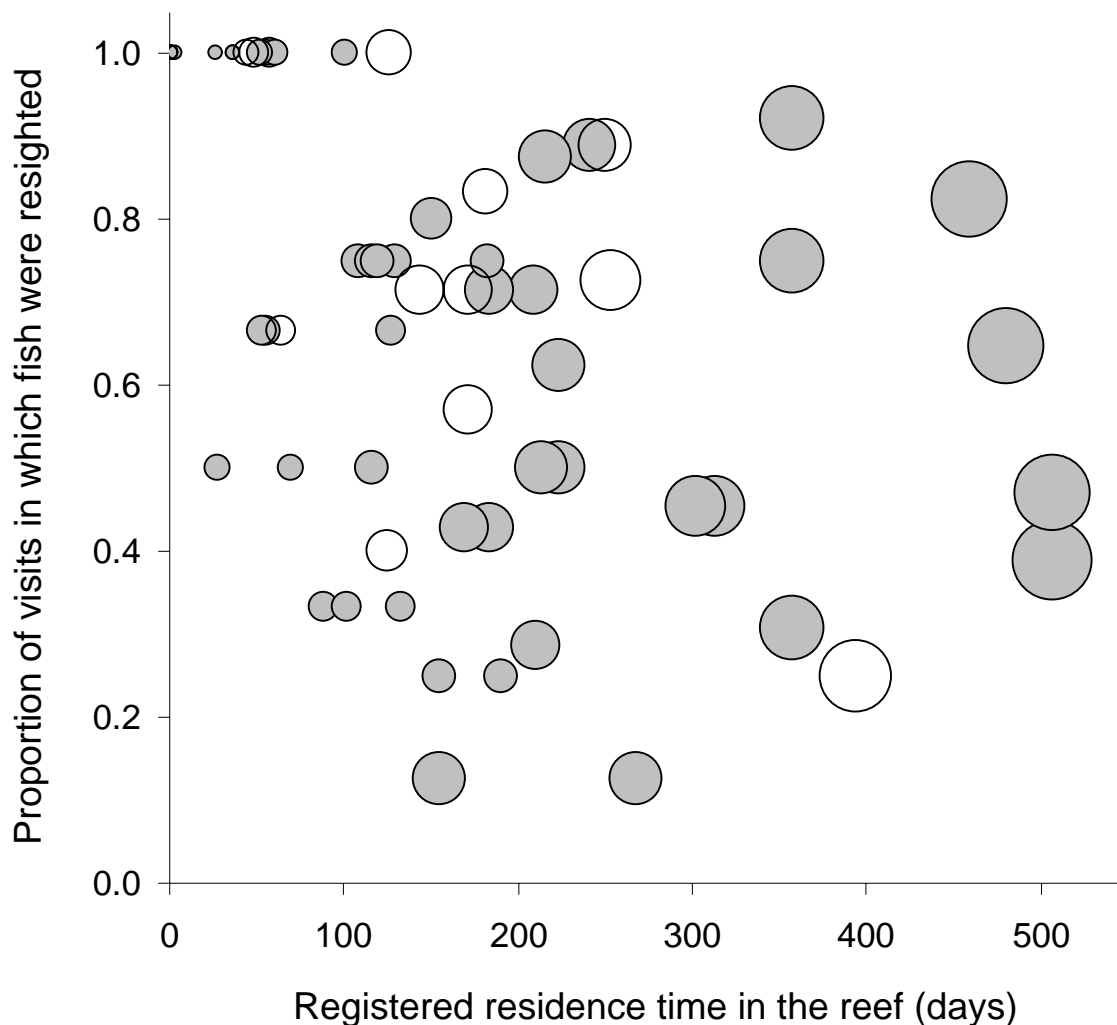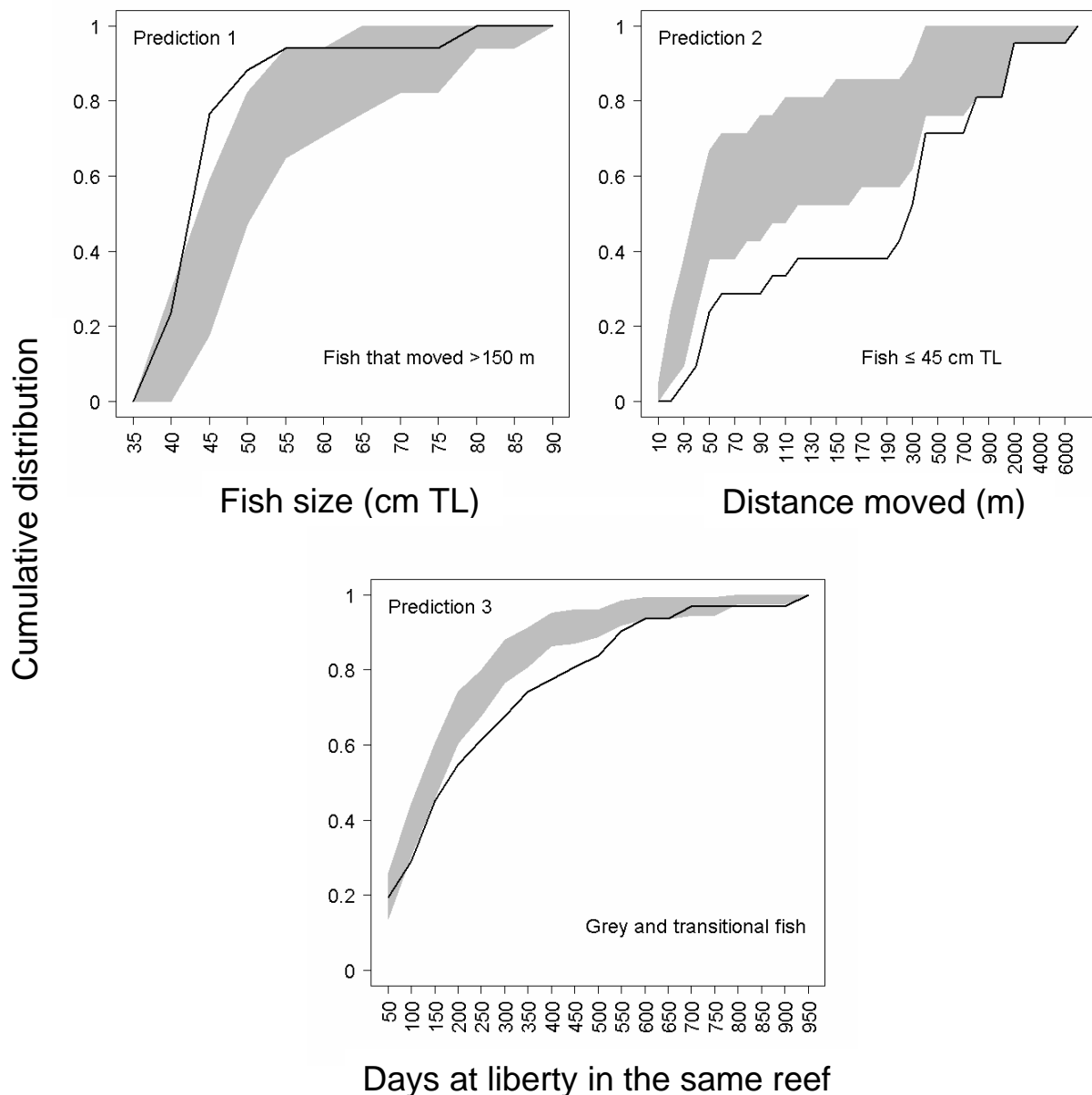
Venerus et al.

Figure 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; with its size 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 Jan 2004 and 10 Aug 2005, and for reef #36 (grey bubbles), surveyed 24 times between 11 Aug 2003 and 24 Feb 2005.
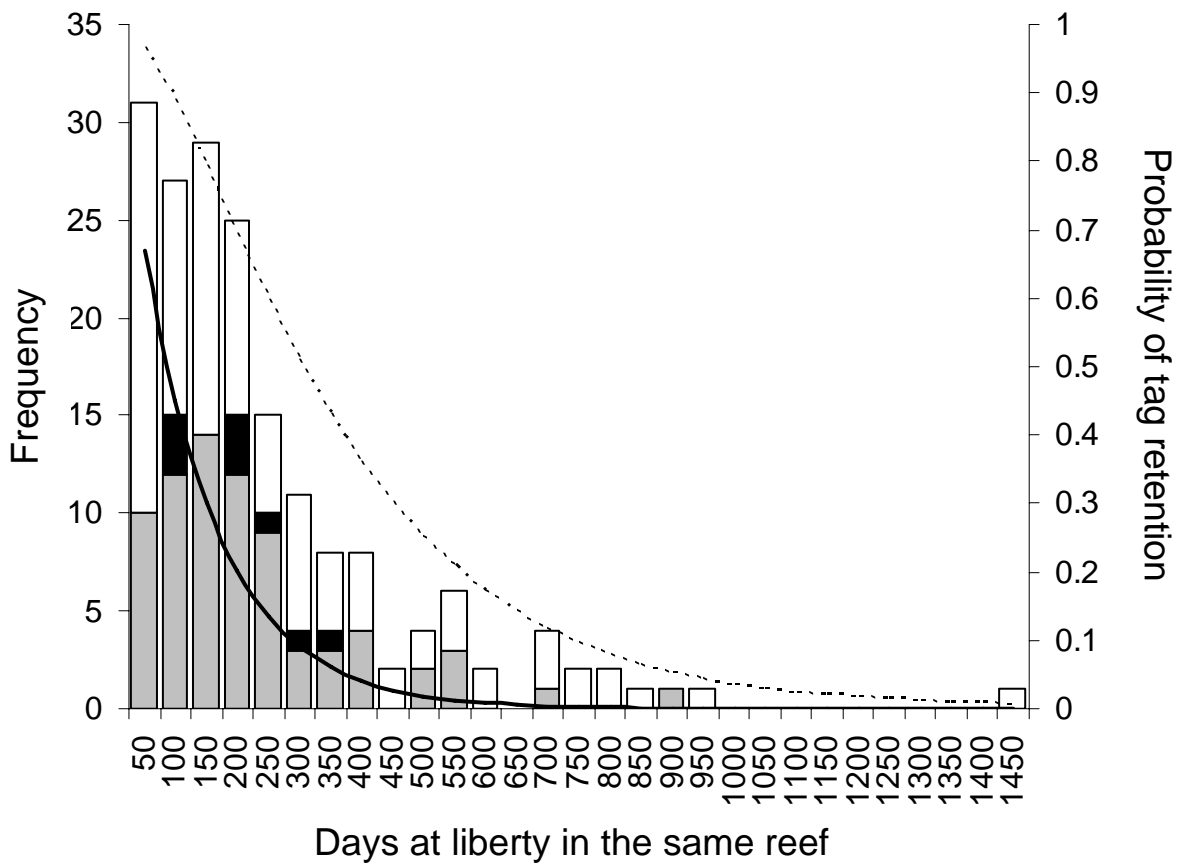
Venerus et al.

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Venerus et al.

Figure 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 (5,000 replicates). The solid lines represent the empirical cumulative distribution.

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Figure 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 registered 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 Venerus *et al.*, 2013).
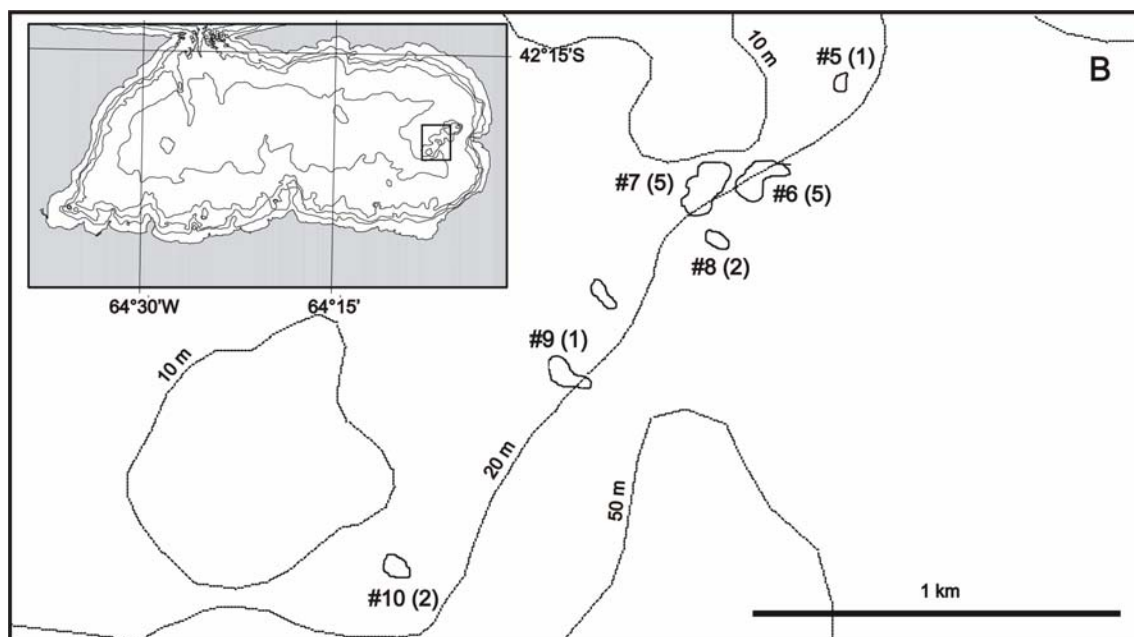
**Supplementary material for Venerus *et al*.**

Table S1: Schedule of field work by our project staff in each fishing spot within San José (SJ) and Nuevo (N) gulfs. The numbers indicate the months in which the reefs were surveyed. Underlined: angling and scuba diving; bold: scuba diving; plain: angling.

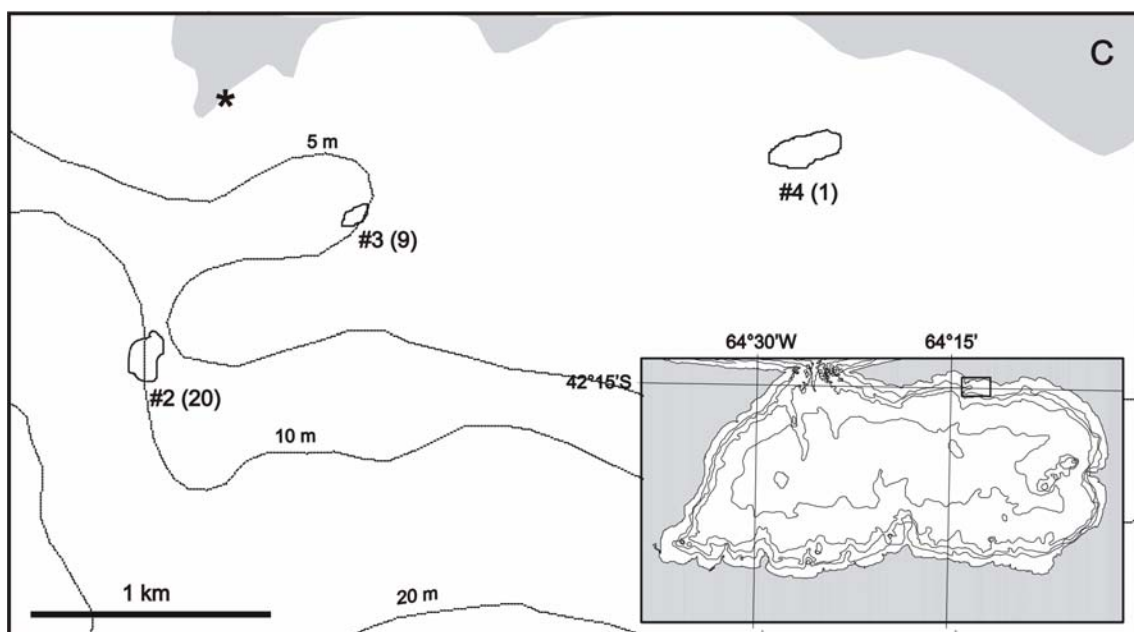| Fishing Spot | Reef ID | 2001 | 2002 | 2003 | 2004 | 2005 |
|---|---|---|---|---|---|---|
| | | | | Year | | |
| Esfinge Point (SJ) | 1 | | | 4, 7 | | 2 |
| San Román Point (SJ) | 2–4 | 10 | **1**, 2, 4, 7, 8, 10, 12 | 2, 3, 4, 7, 8, 10, **12** | 2, 4, 8 | 2, 8 |
| Conos Point (SJ) | 5–10 | | | 1, 7, 11, 12 | 1, 8, 12 | |
| Camp 39 (SJ) | 11 | | 3, 5, 7, **9**, 11, 12 | 1, 3, 5, 7, 9, 11 | 1, **3**, 5, 8, 10, **11** | 2, 8 |
| Fracasso Beach (SJ) | 12–14 | | 2, 5, 7, **9**, 11, 12 | 1, 3, 5, 7, 9, 11 | 1, 3, 5, 8 | 8 |
| Fracasso's Prows (SJ) | 15–17 | | | | 1 | |
| Gales Point (SJ) | 18–20 | | | 7, 9, 12 | 1, 12 | |
| Larralde Beach (SJ) | 21–31 | | 5, 10, 11, 12 | 1, 2, 3, 4, 7, 10, 11, 12 | 1, 2, 3, 4, 6, 8, 12 | |
| Mouth (SJ) | 32–35 | | | 1, 3, 4, 7 | 2 | |
| East Point (N) | 36 | | | 8, 9, 10, 12 | **1**, 2, 3, 4, 6, 7, 8, 9, **10**, 11, 12 | **1, 2** |

Table S2: *Pseudopercis semifasciata* recaptured >1 km from the tagging site. Individual code composed of chromatic phenotype (Y: yellow, G: gray) and fish size at tagging (cm TL). The asterisk indicates a fish angled in reef #2, displaced 1.13 km and kept 24 hrs within a cage to evaluate the effect of tagging, before being released. The location of the unknown reef within Bahía Nueva was estimated approximately based on references provided by a recreational angler.

| ID Code | Time at liberty (days) | Distance displaced (km) | Spot / reef of tagging | Recapture reef |
|---|---|---|---|---|
| Y40 | 387 | 1.05 | San Román Point / # 2 | San Román Point / # 3 |
| Y43 | 289 | 1.13 | San Román Point / * | San Román Point / # 2 |
| G80 | 606 | 1.20 | Larralde Beach / # 27 | Larralde Beach / # 25 |
| Y40 | 675 | 1.51 | Larralde Beach / # 25 | Larralde Beach / # 29 |
| G59 | 60 | 2.30 | East Point # 36 | Bahía Nueva / unknown |
| Y41 | 104 | 6.17 | Conos Point / # 6 | Camp 39 / # 11 |

| Reef | #22 | #23 | #24 | #25 | #26 | #27 | #28 | #29 | #30 | #31 |
|------|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|
| #21 | 1.09 | 1.21 | 1.67 | 2.16 | 2.40 | 2.55 | 2.61 | 3.83 | 3.49 | 3.94 |
| #22 | | 0.47 | 0.69 | 1.09 | 1.37 | 1.79 | 1.91 | 2.74 | 2.94 | 2.52 |
| #23 | | | 0.49 | 1.03 | 1.21 | 1.40 | 1.50 | 2.70 | 2.28 | 2.73 |
| #24 | | | | 0.55 | 0.74 | 1.14 | 1.28 | 2.21 | 1.84 | 2.28 |
| #25 | | | | | 0.35 | 1.20 | 1.37 | 1.68 | 1.50 | 1.87 |
| #26 | | | | | | 0.94 | 1.12 | 1.51 | 1.16 | 1.56 |
| #27 | | | | | | | 0.18 | 2.10 | 1.18 | 1.67 |
| #28 | | | | | | | | 2.24 | 1.27 | 1.75 |
| #29 | | | | | | | | | 1.14 | 0.98 |
| #30 | | | | | | | | | | 0.49 |

| Reef | #6 | #7 | #8 | #9 | #10 |
|------|------|------|------|------|------|
| #5 | 0.34 | 0.44 | 0.54 | 1.09 | 1.77 |
| #6 | | 0.12 | 0.20 | 0.74 | 1.43 |
| #7 | | | 0.15 | 0.65 | 1.34 |
| #8 | | | | 0.55 | 1.23 |
| #9 | | | | | 0.68 |

| Reef | #2 | #3 | #4 |
|------|------|------|------|
| * | 1.14 | 0.71 | 2.61 |
| #2 | | 1.05 | 3.08 |
| #3 | | | 2.11 |

| Reef | #19 | #20 |
|------|-----|-----|
| #18 | 0.45 | 0.94 |
| #19 | | 0.50 |
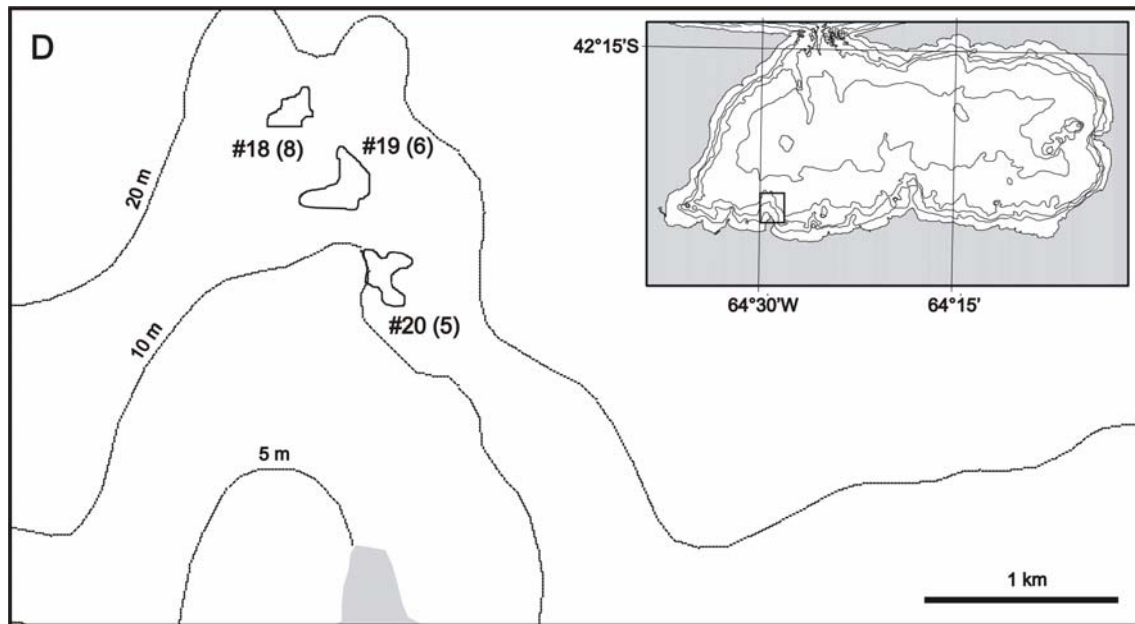
Fig. S1: Spatial distribution of patchy reef areas (filled lines) and angling effort in four fishing spots located in San José Gulf, between October 2001 and September 2005. A: Larralde Beach; B: Conos Point; C: San Román Point; and D: Gales Point. The number of trips made to each reef is shown in parenthesis. In Larralde Beach, we used italics to indicate the minimum number of trips in reefs also used by fishing guides. The asterisk in San Román Point shows the location of a cage in which some fish were observed prior to release. The table below each map shows the estimated between-reef distances, in km.
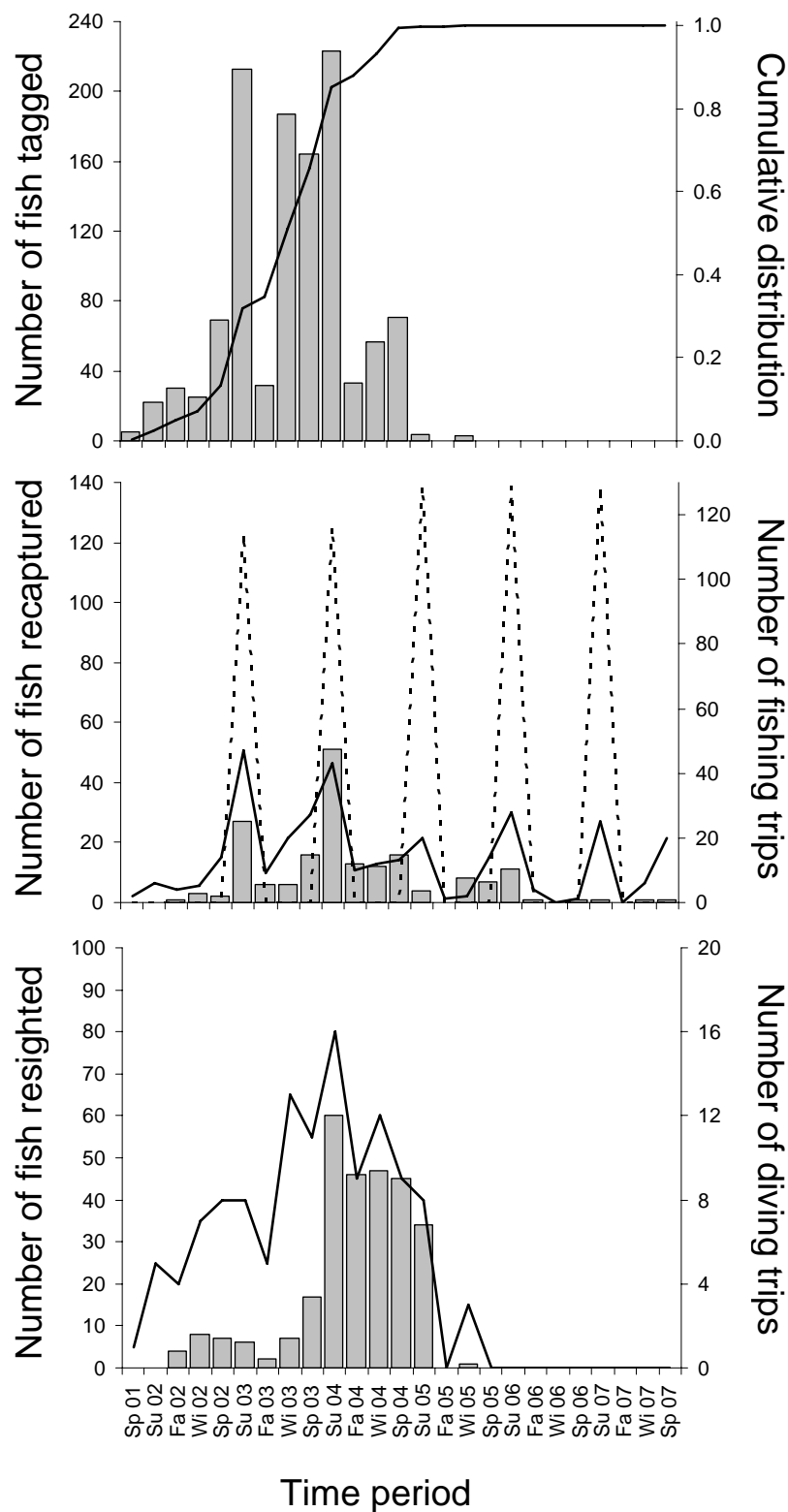
Figure S2: Number of fish tagged, recaptured and resighted in San José and Nuevo
gulfs, over the entire study (grey bars). Middle panel: the solid line shows the fishing
effort exerted by us in San José and Nuevo gulfs and by the fishing guides operating off

Gales Point, Larralde Beach and in the mouth of San José Gulf; the dotted line shows the number of fishing trips estimated for boat owners in the same three fishing spots. Lower panel: the solid line shows the number of diving trips conducted by us in the two gulfs.

Although the estimated angling effort by boat owners off Larralde Beach, off Gales Point and in the mouth of San José Gulf, during the angling season (late December to mid March), was more than twice that of research and charter trips, its impact on the number of recoveries was lower (mid panel). Resightings increased disproportionately between December 2003 and February 2005, when fish were double-tagged in reefs #11 and #36 (lower panel).
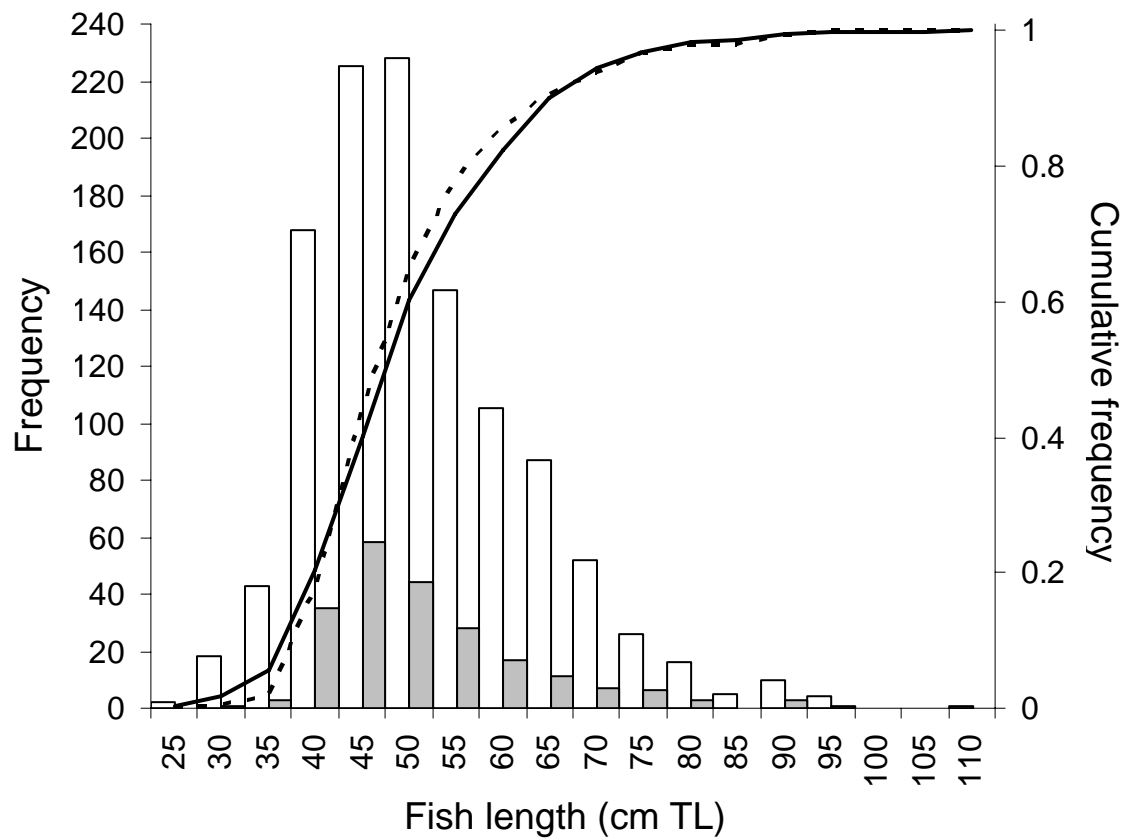
Fig. S3: Size frequency and cumulative distributions of *P. semifasciata* tagged (n = 1138) and recaptured or resighted (n = 218) within Nuevo and San José gulfs. White bars and black solid line: fish tagged; grey bars and dotted line: fish recaptured or resighted.