



Annual occupation pattern of temperate rocky reefs by the Argentine sandperch *Pseudopercis semifasciata* in San José Gulf Marine Park, Argentina

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Abstract The Argentine sandperch, *Pseudopercis semifasciata* (Cuvier), is the target of unregulated recreational and artisanal fisheries within the northern Patagonian gulfs of Argentina. Being a reef species, the applicability of conventional large-scale assessment and management approaches appear limited. A more suitable alternative might be offered by spatial approaches, but their effectiveness would depend on the species' degree of mobility. Underwater visual censuses were used to study the annual occupation pattern of shallow rocky reefs by *P. semifasciata* to evaluate the possible occurrence of spawning migrations and the potential of reserves to protect the stocks. The abundance of *P. semifasciata* was greatest in winter, intermediate in autumn and lowest in spring and summer, but densities were relatively stable and oscillated ± 17 –31% around the overall mean for each reef. There was no evidence of spawning migrations as no demographic changes were observed throughout the year. Young sandperches (< 1 year old) were never observed on the reefs. Implications of the results for the management of this species are discussed.

KEYWORDS: generalized linear models, northern Patagonia, rocky reef fish, spawning migrations, underwater visual censuses.

Introduction

The occupation pattern and use made of reefs by reef fish populations have direct consequences for their monitoring and management, to the extent that they determine their spatial distribution, movement rates and exposure to fishing. The Argentine sandperch, *Pseudopercis semifasciata* (Cuvier 1829) (Pisces, Pinguipedidae), is a popular sport trophy, reef fish in the northern Patagonian gulfs of Argentina: San Matías, San José (SJG) and Nuevo (NG) (Fig. 1), where it is found in coastal low-relief rocky reefs formed by small scattered fronts of hard substrata. This species has been targeted by recreational anglers and spear-fishers for more than 50 years, and is also a tourist attraction for divers (Sanabra 2002), mainly because of its large size (more than 1 m long and 20 kg). The estimated recreational landings estimated for the 2002, 2003 and 2004 fishing seasons (summer months) in the two most popular fishing spots within SJG (off Tehuelche Point

and the mouth of the gulf) were 965 ± 160 fish, equivalent to 3461 ± 583 kg (Venerus 2006). Annual commercial landings from the Argentine shelf averaged 2660 t between 1992 and 2002 [official statistics SAGPyA, <http://www.sagpya.mecon.gov.ar> (last accessed Jan 2008)].

Despite its economic and cultural importance, the exploitation of this long-lived species (maximum age: *c.* 30 years) (Elías & Burgos 1988; González 2006) and of other rocky reef fishes has not been regulated except for a restriction of 30 kg of fish per fishing license per day for San José Gulf Marine Park and Península Valdés. Nowadays, it is becoming increasingly difficult to find big sandperches in the vicinity of Puerto Madryn and Puerto Pirámide, the most important coastal tourist centres in the region (Fig. 1). Fishers have expressed concerns about the decreased catch rates and fish sizes, sharing a perception that reefs can be easily depleted of sandperch by fishing.

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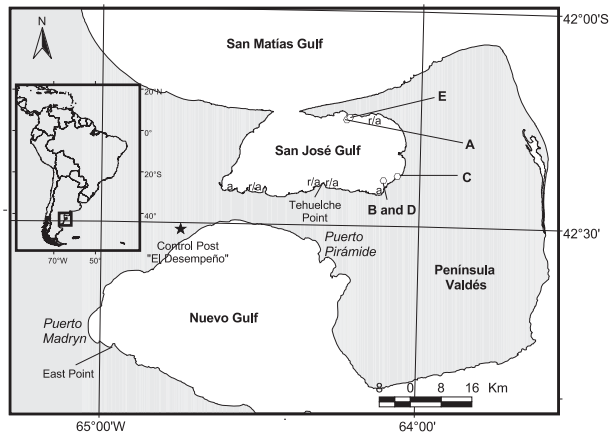


Figure 1. Map of the study area showing the location of the monitored reefs (A – E) and the beaches from which recreational (r) and artisanal (a) fishers operate within San José Gulf Marine Park.

The sandperch's association with the reefs, together with the weak enforcement capabilities of the fisheries administration, limit the applicability of conventional assessment and management approaches (Venerus 2006). A lack of knowledge about the ecology and spatial dynamics of *P. semifasciata* has hampered the development of alternative management strategies tailored to the characteristics of the species. Aside from a few studies on the age, growth and reproduction (Elías & Burgos 1988; Macchi, Elías & Burgos 1995; González 1998, 2006), little is known about its life history and mating system. The distribution of *P. semifasciata* larvae along the Argentine shelf suggested that the reproductive grounds would be small and associated with irregular and/or rocky bottoms (Venerus, Machinandarena, Ehrlich & Parma 2005). Furthermore, the concentration of larvae in limited areas suggested the possibility that sandperches left the reefs temporarily to form spawning aggregations, similar to many reef fishes. Alternatively, still consistent with the observed larval distribution, the Argentine sandperch could reproduce in the reefs (González 1998), or in adjacent soft-bottom areas. Anecdotal information from old-time skippers that used to trawl along narrow flat areas surrounded by irregular bottoms, in the northern Patagonian shelf, tells about large hauls of sandperch made during the summer. However, no clear seasonal pattern in the large-scale distribution of sandperch was apparent in a series of trawl surveys conducted by Instituto Nacional de Investigación y Desarrollo Pesquero (INIDEP) between 1970 and 2002 (L. Venerus, unpublished data).

The Argentine sandperch is a multiple spawner with low batch fecundity and an extended reproductive

season, peaking between October and December (Macchi *et al.* 1995; González 1998). Both sexes develop into a yellow phenotype at settlement. Males later metamorphose into a grey phenotype, mostly around 50–60 cm total length (TL) (L. Venerus, unpublished data), while females maintain their juvenile colour (González 1998, 2006). The existence of sexual dimorphism and dichromatism, with males being larger than females and changing colour after reaching sexual maturity, would favour a hypothesis of a resource-defence or female-defence polygynous mating system associated with the reefs (Berglund 1997). In addition, males have small testes (González 1998), a feature commonly associated with non-communal spawning (Stockley, Gage, Parker & Moller 1997; Taborsky 1998).

The two possible spawning modalities have very different consequences for the availability of the species on the reefs. If spawning migrations occurred, at least a fraction of the mature fish would leave the reefs during the reproductive season. By contrast, if fish spawned on or near the reefs, they would spend more time around them, and their seasonal fluctuations in abundance would be less marked.

This study investigated the annual pattern of occupation of SJG rocky reefs by *P. semifasciata* using underwater visual censuses (UVCs). Size frequency distributions (SFDs) of fish and the proportion of grey and yellow phenotypes over the annual cycle were analysed in search for demographic changes that could be related to the reproductive activity. The main goal was to shed light on the association of the Argentine sandperch to the reefs, and whether they undertake reproductive migrations. These questions have relevance for monitoring sandperch populations and for evaluating the potential efficacy of spatial harvesting strategies and marine reserves for the management of this species.

Materials and methods

Study area

San José Gulf was designated a Marine Provincial Park in 1975, and a UNESCO Natural World Heritage Site in 1999. Trawling and long-lining are banned, but an unknown level of commercial hook-and-line fishing exists within the park limits. In addition, recreational anglers and spear-fishers frequent the area, mainly during summer, and a few charter boats operate from a few beaches along the gulf (Fig. 1) (Venerus 2006).

Table 1. Physical characteristics of the indicator reefs in San José Gulf Marine Park

Reef	Type	Length/ area	Depth range (m)	Horizontal visibility range (m)	Maximum tidal currents
A	I	~4000 m ²	6.5–14.5	4.50–10.50	Strong
B	II	310 m	9.0–20.5	3.75–8.75	Moderate
C	II	315 m	5.5–13.5	4.75–11.75	Low
D	II	99 m	10.0–18.0	3.75–8.50	Moderate
E	II	52 m	7.0–15.0	5.75–10.25	Strong

Reefs are formed by isolated small rocky outcrops that extend for a few hundred metres on an otherwise flat, soft bottom. They were classified into two types (I and II) based on their structure and topography. Type-I reefs are areas of irregular shape and topography, covered by scattered rocks and small platforms of no more than 1 m in height. Type-II reefs, by far the most common, are linear structures, typically low breaks or ledges (from 0.2–0.3 to 1–1.5 m high) formed along the edge of submerged abrasion limestone platforms, where cavities are formed. Five inshore reefs, one of Type I (A) and four of Type II (B, C, D and E) (Fig. 1), were monitored. These reefs were chosen based on their accessibility, presence of Argentine sandperch, shallow depth, tidal currents that allowed scuba diving, good visibility and because they were little known (Table 1). The latter was a key feature to minimise the impact of angling and spear-fishing on fish abundance or behaviour (Cole 1994; Kulbicki 1998; Davidson 2001).

Underwater visual censuses

The UVCs with scuba were conducted bimonthly at the five reefs between April 2002 and August 2004. Different UVC techniques were used according to reef type. Type-I reef (reef A) was monitored by two methods: fixed strip-transects and a much simpler roaming-diver technique adapted from Martell, Walters & Wallace (2000). Eight fixed parallel transects of variable length (25–58 m) and 4-m width were laid approximately every 6 m, covering the entire reef area. Three trained divers conducted the censuses; each was randomly assigned two or three contiguous transects of the whole set. A second census, hereafter referred to as Pinguipedidae census, was conducted to count both *P. semifasciata* and *Pinguipes brasiliensis* Cuvier on five of the transects. In both census types, each transect was replicated by two divers in the same day.

In the roaming-diver technique, two divers roamed for 5 min trying to count as many sandperches as

Table 2. Explanatory variables tested during model fitting

Explanatory variable	Justification
Diver	Factor (3). (RL)
Horizontal visibility	Numerical. Relative index of horizontal visibility, measured with a 24 cm Secchi disk immediately after the censuses were finished. (TRL)
Order of census	Factor (3). It represents the disturbance level generated by successive censuses. In reef A it was defined as the order of replication of an entire census series (first or second). (TL)
Reef	Factor (4). (L)
Season	Factor (4). Summer (January to March), Autumn (April to June), Winter (July to September) and Spring (October to December). (TRL)
Swimming speed	Numerical. Travelled distance (m)/rounded min. (TL)
Tidal amplitude	Numerical. Height difference (m) between the flow tide and the ebb tide. (TRL)
Tidal state	Numerical. Time (min) to the closest quiet tide (flow or ebb tide) corrected by the quotient between the tidal amplitude and the maximum tidal amplitude for the whole sampling period (2002–2004) in SJG. (L)
Type of census	Factor (2). <i>Pseudoperca semifasciata</i> and Pinguipedidae census. (T)
Year	Factor (3). A monitoring year was arbitrarily defined from Spring to Winter. The first year of monitoring only included autumn and winter in reef A and winter in Type II reefs. (TRL)

The numbers between parentheses indicate the number of levels in each factor.

T, transect counts; R, roaming counts; L, counts along reef ledges.

possible while avoiding repeated counts of the same individual by moving around the reef. Each diver completed at least two, 5-min roams (except for April and July 2002, when one diver roamed only once), starting at randomly selected points while the exit points were free.

In Type-II reefs all fish observed were counted while swimming along the reef ledge. This maximises the sightings of sandperches, which generally do not move more than a few metres from the reefs. The technique is similar to the roaming UVC except that the distance travelled can be measured. Three replicated censuses of the entire reef were completed on each sampling date, one by each diver in random order.

In all three methods, the divers swim continuously and avoid counting fishes that appeared from behind.

Environmental variables registered were horizontal visibility, tidal state, tidal amplitude, hour and duration of the census (Table 2). Underwater visual censuses were conducted during daylight, between 9:00 and 18:00 hour, mostly around noon. Data were recorded on plastic slates.

Demographic data

Chromatic phenotypes of *P. semifasciata* (yellow and grey) were recorded and sizes by 10-cm TL classes were visually estimated (exclusively during *P. semifasciata* censuses) with the aid of a 30-cm ruler attached to the end of a pole.

Size frequency distributions, constructed by averaging the relative frequencies recorded in each replicate, were grouped by reef and by semester (autumn–winter and spring–summer). For the roaming data, the absolute frequencies by size registered in different censuses by the same diver were added because divers roamed in different reef areas during replicates.

Sizes were grouped by < 40 cm TL and ≥ 40 cm TL, using 40 cm TL as a proxy for the size at 50% maturity, estimated at 34–37 cm TL for females (Eliás & Burgos 1988; González 1998). Binomial 95% confidence intervals for the proportion of mature fish were estimated following the method of Clopper & Pearson (1934).

Statistical analyses

Seasonal trends in the abundance of *P. semifasciata* were analysed using generalised linear models (McCullagh & Nelder 1989), with the R software (R Development Core Team 2005).

The three UVC methods resulted in different indices of relative abundance: fish $\times 10 \text{ m}^{-2}$ for transect data, raw counts (fish per 5-min search) for roaming data, and fish per 10 m of reef for censuses along ledges. In Reef A, counts from all transects were pooled to estimate four density values for each date: two replicates from each census type (*P. semifasciata* and Pinguipedidae censuses), except in July 2002 when Pinguipedidae counts were not replicated ($n = 3$), and in February 2003, when they were replicated twice ($n = 6$). When fitting the models, the density values (fish $\times 10 \text{ m}^{-2}$) were weighted in proportion to the total distance surveyed (339.5 m in *P. semifasciata* censuses and 204 m in Pinguipedidae censuses).

Gamma, normal and quasipoisson error models were applied using the identity link for the normal models, and the log link for the gamma and quasipoisson models. Their performance was evaluated by

checking for homoscedasticity in plots of deviance residuals against the fitted values, and by using the regression method proposed by Jiao, Chen, Schneider and Wroblewski (2004). Normality of deviance residuals, although not required for gamma and quasipoisson models, was evaluated using a Kolmogorov–Smirnov (K–S) one-sample test to verify that they were symmetrically distributed around zero.

A minimal adequate model (i.e. a model in which all the terms are significant, *sensu* Crawley 1993) was obtained for each data set by testing the significance of the candidate explanatory variables, added one by one starting from the null model (Hastie & Pregibon 1992), and their interactions. The effects of diver, horizontal visibility, order of census (i.e. disturbance by divers), reef, swimming speed, tidal amplitude, tidal state and type of census were investigated to standardise fish counts (Table 2). Additionally, some *ad hoc* dummy variables were included to reduce the influence of the data collected in a few occasions, which departed from the general trends (see results for details). All the terms in the models were fixed. Model selection was based on the Likelihood ratio test (F tests) and the second-order Akaike Information Criterion, AICc (Burnham & Anderson 1998) for the normal and gamma models, and on the quaslikelihood ratio test for the quasipoisson models.

The temporal autocorrelation between censuses was evaluated for each reef by plotting the autocorrelation coefficients r_k between the data (or between residuals from the minimal model) at time t and $t + k$ against k , the time lag between two sampling dates ($k = 1$ corresponds to about 2 months), up to $k = N/4$, where N is the number of indices (Chatfield 1984). Approximate 95% confidence intervals for r_k were estimated following Legendre & Legendre (1998).

Results

Fish density

A general pattern of seasonal fluctuations in the abundance of *P. semifasciata* was observed and verified for more than two annual cycles in all inshore reefs monitored (Figs 2 & 3). Densities were highest in winter (July to September), lowest in spring and summer (October to March) and generally intermediate in autumn (April to June). The temporal variable *Season* explained 14.6–33.2% of the variability in the three data sets, while *Reef* (used for Type-II reefs) explained 11.7%. Their interactions were not significant, nor were the other factors evaluated after having accounted for the temporal and the dummy factors.

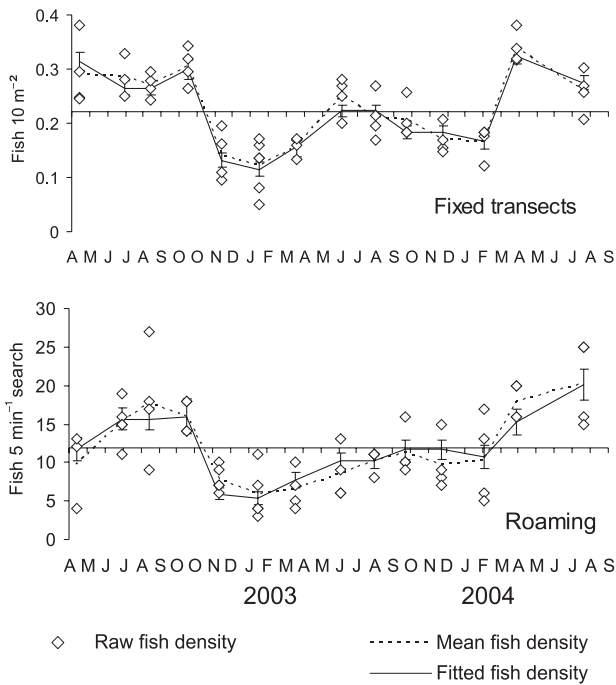


Figure 2. Raw, mean and fitted \pm SE fish density for fixed-strip transect (upper panel) and roaming (lower panel) counts in reef A.

Mean oscillations around the overall mean were $\pm 17\%$ for Type-II reefs (excluding reef C where two sparring events apparently reduced the number of fish, as discussed later) and $\pm 23\text{--}31\%$ for the second and third years in reef A.

Temporal autocorrelations in either the raw data or the residuals were not significant. The error models chosen were normal and quasipoisson for Type-I reef transects and roaming counts, respectively, and gamma for Type-II reefs. In all cases, departures from normality of residuals were not significant according to the K-S test.

Type-I reef: transects counts. The selected model Fish density (fish $\times 10\text{m}^{-2}$) \sim Season + D1 + D2 + Year, where D1 and D2 represent the censuses conducted in April 2003 (autumn) and October 2002 (early spring), respectively, explained 79% of the variability in counts [$F = 26.53$; $P(> F) < 0.0001$]. The density of *P. semifasciata* at reef A was greatest in autumn, intermediate in winter and lowest in spring and summer, being the only case in which autumn density was highest (Tables 3a and 4a). Fitted densities oscillated between ± 26 and 30% around the mean estimated for each year. This seasonal trend was superimposed to an apparent gradual recovery from a sharp (about 56%) drop in abundance during the first spring sampled, between 17 October and 11 December 2002 (Fig. 2 and Table 5). Although density in other reefs also decreased during spring, the drop in reef A was larger, and an undocumented fishing episode or a predation event cannot be ruled out. Densities recovered to pre-drop levels after 18 months and differences between the second and third years were significant (Table 4a).

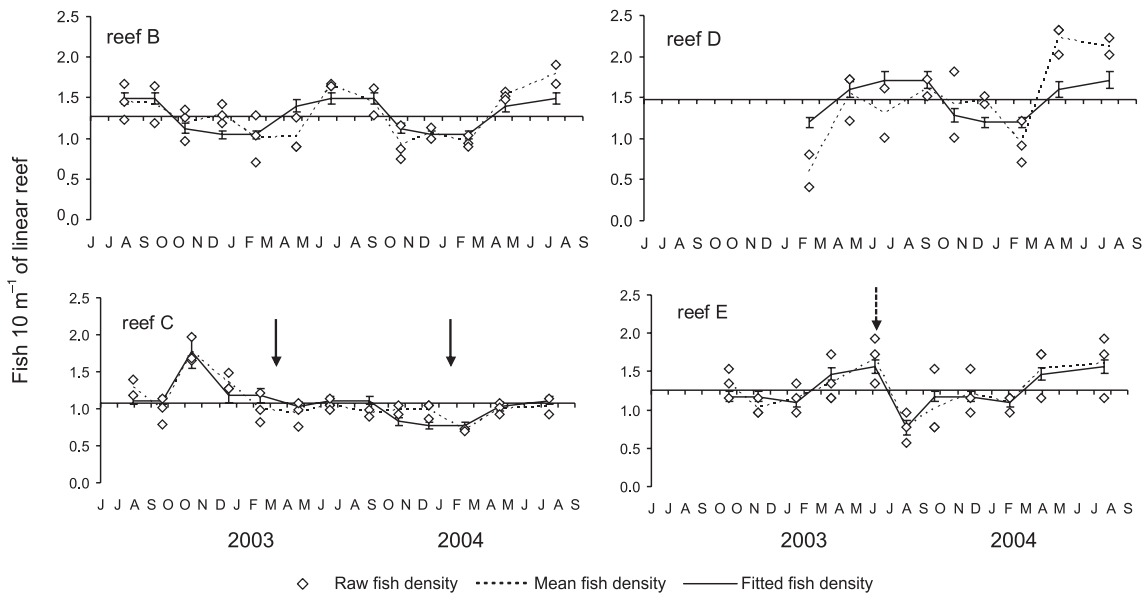


Figure 3. Raw, mean and fitted \pm SE fish density for Type-II reefs. Solid and broken arrows in reefs C and E indicate documented and probable fishing episodes, respectively.

Table 3. Estimated coefficients, standard errors (SE) and confidence intervals (95%) for *Pseudoperca semifasciata* density; (a) normal model for reef A, based on transects-count data; (b) quasipoisson model for reef A, based on roaming counts data and (c) gamma model for Type-II reefs

Level	Coefficient	SE	Confidence intervals (95%)
(a) Normal model: intercept corresponds to winter of year 1			
Intercept	0.265	0.013	0.240; 0.290
Autumn	0.050	0.017	0.016; 0.083
Spring	-0.091	0.015	-0.120; -0.061
Summer	-0.107	0.016	-0.138; -0.077
D1	-0.116	0.026	-0.166; -0.065
D2	0.167	0.023	0.122; 0.212
Year 2	-0.042	0.016	-0.074; -0.010
Year 3	0.010	0.016	-0.022; 0.041
(b) Quasipoisson model: intercept corresponds to winter of year 1			
Intercept	2.749	0.089	2.570; 2.919
Year 2	-0.427	0.128	-0.679; -0.175
Year 3	0.256	0.124	0.012; 0.500
D3	0.997	0.195	0.611; 1.375
Autumn	-0.282	0.122	-0.526; -0.046
Spring	-0.547	0.135	-0.814; -0.284
Summer	-0.632	0.160	-0.953; -0.326
(c) Gamma model: intercept corresponds to reef B in winter			
Intercept	0.4035	0.0469	0.313; 0.496
Autumn	-0.0680	0.0568	-0.179; 0.044
Spring	-0.2877	0.0616	-0.407; -0.167
Summer	-0.3594	0.0538	-0.464; -0.254
D4	-0.7123	0.1358	-0.970; -0.438
Reef C	-0.3001	0.0564	-0.410; -0.190
Reef D	0.1345	0.0600	0.017; 0.253
Reef E	0.0464	0.0549	-0.061; 0.154
D5	0.7536	0.1409	0.485; 1.037
D6	0.4169	0.1043	0.216; 0.624

Type-I reef: roaming counts. The best model for the raw counts was

Fish density (fish \times 5 min⁻¹) \sim Year + D3 + Season, where D3 represents the censuses conducted in October 2002 (early spring). This model explained 57% of the variability in the data [$F = 11.31$; $P(>F) < 0.0001$]. A slight overdispersion (scale parameter $\Phi = 1.29$) justified the use of a quasipoisson model.

The roaming technique produced very similar results to the strip-transects, although the seasonal pattern was smoother (Fig. 2) and predicted counts were higher in winter than in autumn ($t = -2.31$; $P = 0.03$) (Tables 3b and 4b). The fitted values oscillated between 23 and 31% around the predicted mean for each year. Again, counts dropped sharply (by $\sim 63\%$) between October and December 2002,

Table 4. P -value of contrasts between levels for (a) normal model for reef A, based on transects-count data; (b) quasipoisson model for reef A, based on roaming-counts data and (c) gamma model for Type-II reefs based on a Student's- t distribution

(a) Normal model			
Season	Autumn	Winter	Spring
Winter	0.0052		
Spring	< 0.0001	< 0.0001	
Summer	< 0.0001	< 0.0001	0.3062
Year	1	2	
2	0.0128		
3	0.5475	0.0002	
(b) Quasipoisson model			
Season	Autumn	Winter	Spring
Winter	0.0251		
Spring	0.0791	0.0002	
Summer	0.0467	0.0002	0.6176
Year	1	2	
2	0.0016		
3	0.0446	< 0.0001	
(c) Gamma model			
Reef	Reef C	Reef B	Reef D
Reef B	< 0.0001		
Reef D	< 0.0001	0.0268	
Reef E	< 0.0001	0.3994	0.1651
Season	Autumn	Winter	Spring
Winter	0.2334		
Spring	0.0010	< 0.0001	
Summer	< 0.0001	< 0.0001	0.2566

followed by a gradual recovery to pre-drop levels reached in April 2004. Differences in density among the three years were again significant (Tables 3b & 4b). Counts per 5-min search ranged between seven and 27 fish (Table 5).

Type-II reefs. The model selected was

$$\text{Fish density (fish} \times 10 \text{ m}^{-1}\text{)} \\ \sim \text{Season} + D4 + \text{Reef} + D5 + D6,$$

where D4 represents the censuses conducted in August 2003 (winter) in reef E, and D5 and D6 those conducted in November 2002 (spring) and January and March 2003 (summer) in reef C. The variability explained by the gamma model was 49% ($F = 13.68$; $P < 0.0001$).

Table 5. Mean density of sandperch in shallow rocky reefs within San José Gulf, by year

	Type-I reef		Type-II reefs			
	Strip-transects (fish × 10 m ⁻²)	Roaming (fish per 5-min search)		Swimming along reef ledges (fish × 10 m ⁻¹)		
	A		B	C	D	E
Year 1						
Period	April 2002 to August 2002	April 2002 to August 2002	July 2002 to September 2002	July 2002 to September 2002		
Mean	0.28	14.67	1.44	1.10		
SE	0.04	5.71	0.23	0.22		
Range	0.24–0.38	4–27	1.19–1.68	0.79–1.40		
Year 2						
Period	October 2002 to August 2003	October 2002 to August 2003	November 2002 to September 2003	November 2002 to September 2003	March 2003 to September 2003	October 2002 to August 2003
Mean	0.19	8.96	1.26	1.19	1.30	1.22
SE	0.08	4.08	0.29	0.33	0.47	0.34
Range	0.05–0.34	3–18	0.71–1.68	0.76–1.97	0.40–1.72	0.58–1.92
Year 3						
Period	October 2003 to August 2004	October 2003 to August 2004	November 2003 to August 2004	November 2003 to August 2004	November 2003 to August 2004	October 2003 to August 2004
Mean	0.23	13.90	1.23	0.94	1.62	1.29
SE	0.07	5.87	0.36	0.15	0.58	0.37
Range	0.12–0.38	5–25	0.74–1.90	0.70–1.14	0.70–2.32	0.77–1.92

Again, fish density was greatest in winter, intermediate in autumn and lowest in spring and summer (Tables 3c & 4c). Although drops in density around summer varied between 30 and 32%, the oscillations around the mean density, excluding reef C, were on average $\pm 17\%$ (Fig. 3). This indicates that fish density in these reefs was rather stable over the sampling period. A slight increasing trend was apparent in reef D (Fig. 3 and Table 5).

Reef C had an unexpected significant increase in density of about 39% in excess of the overall mean in November 2002, followed by a monotonic decrease towards the end of summer (Fig. 3). Two dummy variables (*D2* and *D3*) were added to avoid an undue influence of these counts on the estimated model coefficients. This reef was discovered by two spearfishers who indicated catching 10 fish > 3 kg in April 2003 and other five in February 2004. Given the low number of fish at reef C (mean *n* approx. 34), the speared fish could have caused a large reduction in counts. The last dummy variable (*D4*) was included to account for a large drop in density (39%) observed in August 2003 in reef E.

Size distribution of fish

No Argentine sandperches < 20 cm TL were recorded at the reefs. The SFDs of *P. semifasciata* from different

reefs were similar, mostly with a single mode around 30–40 cm TL and skewed to the right (Figs 4–6). In reef B, the SFD had a second mode around 90–100 cm TL (Fig. 5).

In general, no clear differences in SDF were observed between autumn–winter and spring–summer. The largest shift in size structure was observed at reef C, where fish > 80 cm TL disappeared after the fishing episodes (Fig. 6) and no large fish reappeared for the next 6 months, in both years.

The number of mature and immature fish fluctuated irregularly over the annual cycle (Fig. 7). The median proportion of immature individuals was 0.33 (range = 0.27 to 0.44) in Type-II reefs (Figs 5 & 6). In reef A, the proportion of mature fish increased from ~ 0.50 to 0.70 after the winter of 2003, coincidentally with the recovery of the abundance (Fig. 4).

Chromatic phenotypes

Only a few grey Argentine sandperches, all larger than 40 cm TL, were present in the reefs, relative to the number of yellow individuals. Their density was 1.08 ± 0.55 per 100 m of lineal reef at reef B, 0.35 ± 0.31 at reef C, 0.96 ± 1.01 at reef D and 2.49 ± 1.21 at reef E. In reef A, the mean densities of grey males estimated from transects and roaming data

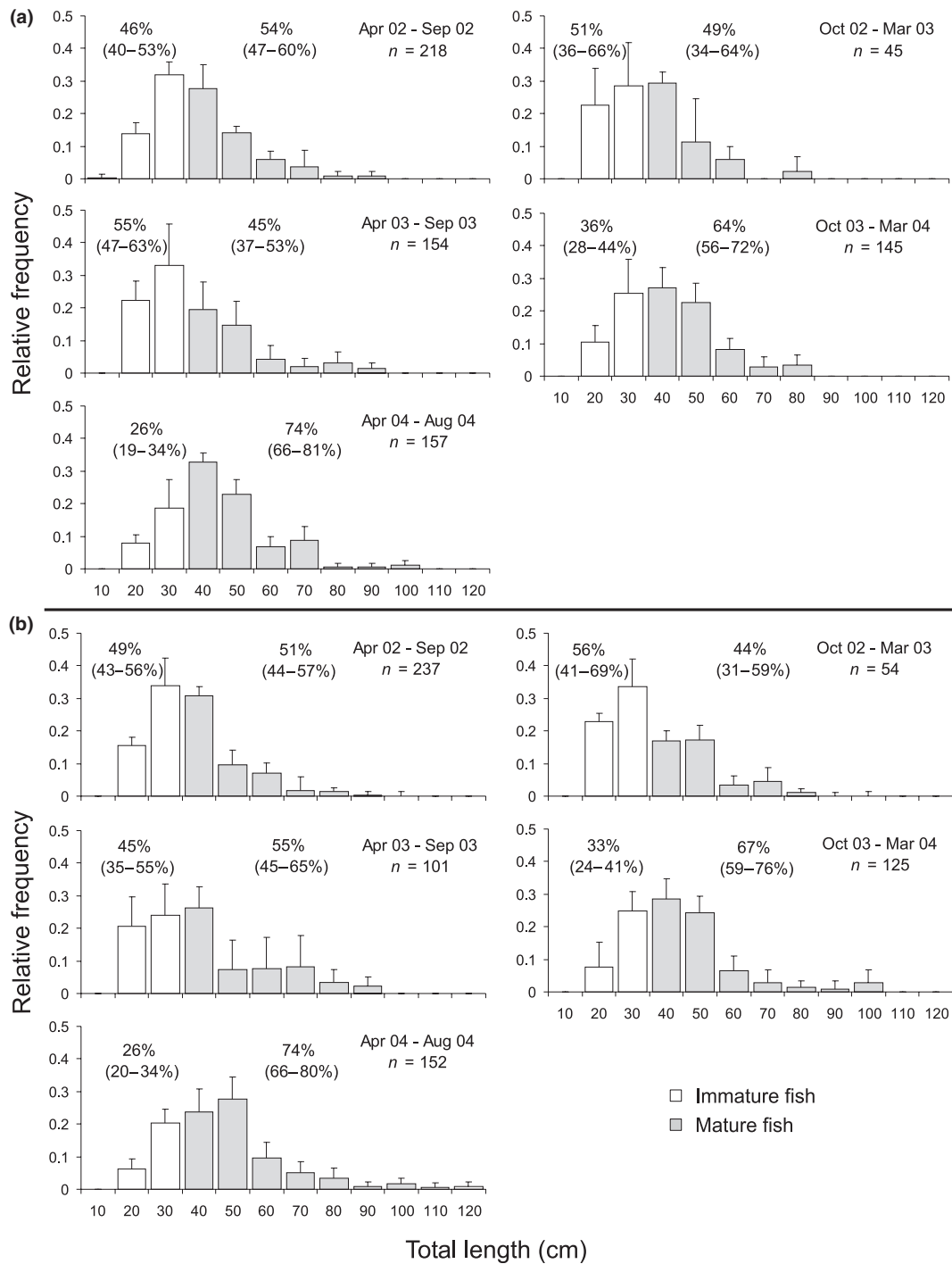


Figure 4. Size frequency distributions of *P. semifasciata*, determined by UVC and grouped by semester for reef A. a) Fixed-strip transect counts and b) roaming counts. Percentage of immature (<40 cm TL) and mature sandperch (≥40 cm TL), and binomial 95% confidence intervals are shown.

were 1.39 ± 1.24 fish $\times 1000$ m⁻² and 0.76 ± 0.75 per 5-min search respectively.

No clear seasonal trend was evident either for the density of grey males or for the ratio of yellow to grey individuals. The average ratio was 13:1 for all reefs. An

increase in the ratio of yellow-to-grey (from 12:1 to 37:1) accompanied the increase in density between November 2002 and March 2003 at reef C. However, no such increase was apparent in the transect counts when the abundance recovered in reef A.

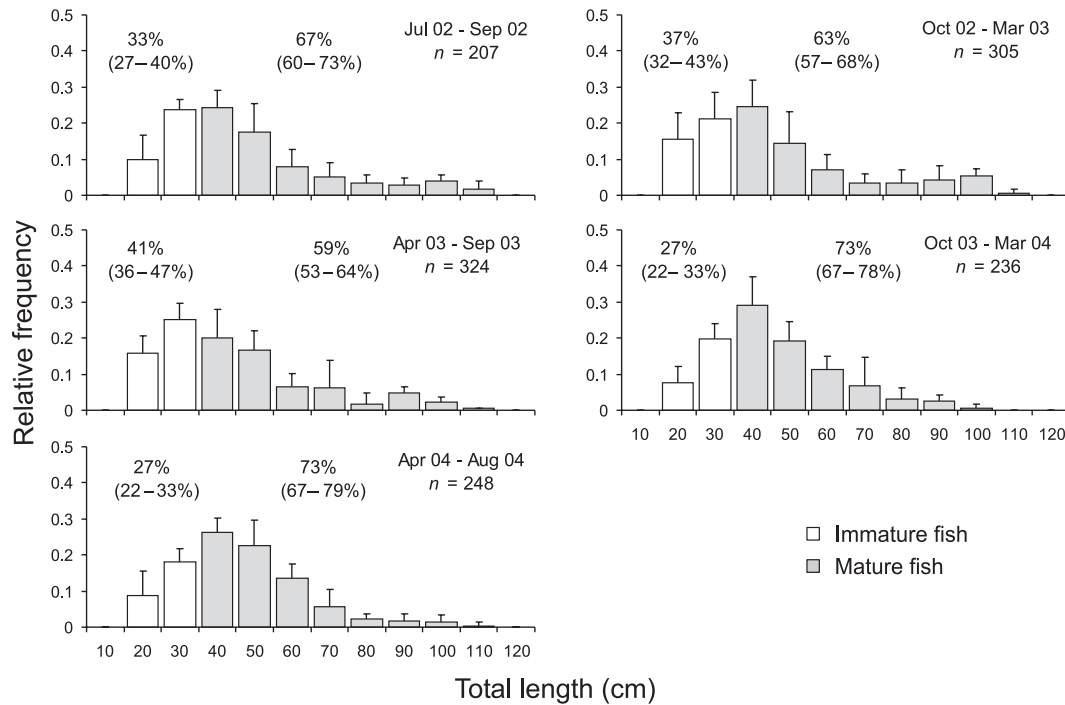


Figure 5. Size frequency distributions of *P. semifasciata*, determined by UVC and grouped by semester for reef B. Percentage of immature (<40 cm TL) and mature sandperch (≥40 cm TL), and binomial 95% confidence intervals are shown.

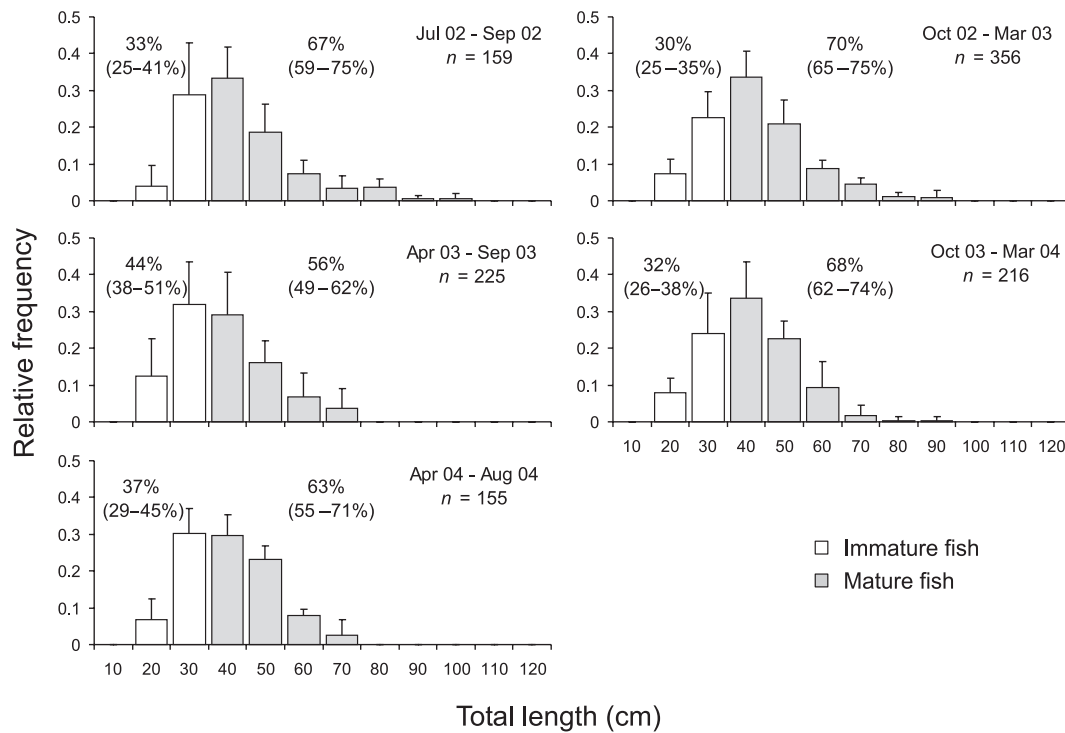


Figure 6. Size frequency distributions of *P. semifasciata*, determined by UVC and grouped by semester for reef C. Percentage of immature (<40 cm TL) and mature sandperch (≥40 cm TL), and binomial 95% confidence intervals are shown.

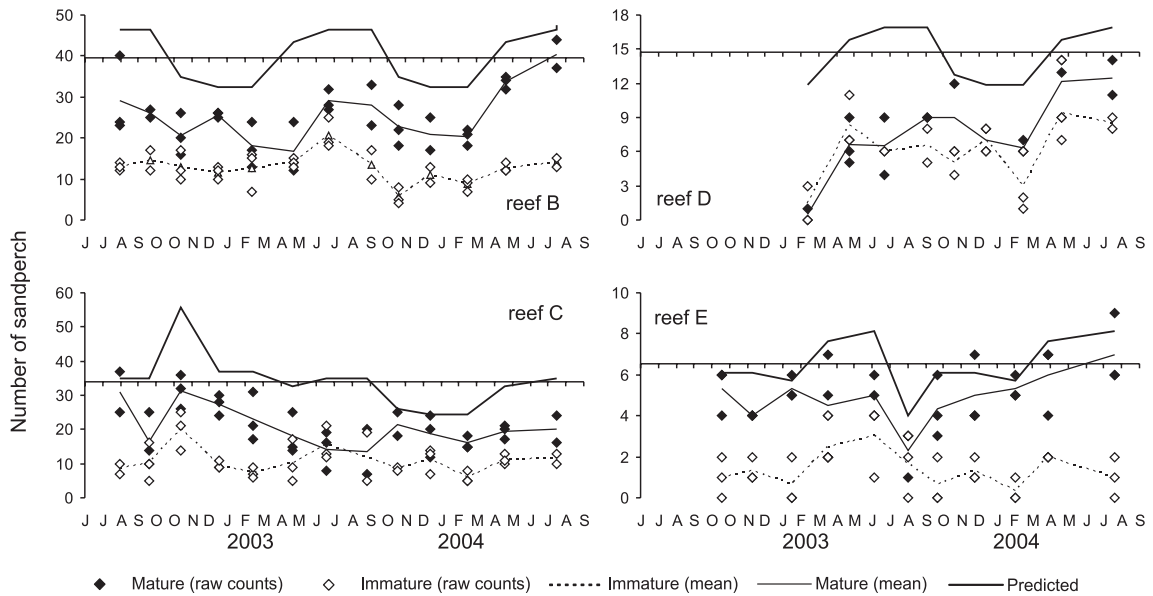


Figure 7. Raw and mean numbers of immature (<40 cm TL) and mature sandperch (≥40 cm TL) in Type-II reefs (B, C, D and E). The thick solid line indicates the number of fish predicted by the best minimal gamma model for each reef.

Discussion

Density, size structure and chromatic phenotypes of sandperch

The decrease in fish abundance observed in spring and summer coincided with the reproductive season of *P. semifasciata*. However, if large spawning migrations occurred, only mature fish would be expected to disappear from the reefs. Instead, the abundance of both mature and immature fish fluctuated erratically over the annual cycle (Fig. 7). It is possible that some individuals move to adjacent soft bottom areas during the reproductive season either to spawn or to feed, disappearing from the reefs even if only for brief periods.

Despite the observed seasonal changes in density, no regular changes in the size distribution of fish indicative of recruitment pulses by season and size groups were evident. Furthermore, no fish <20 cm TL (~1 year old, see González 2006) were recorded during the visual censuses. Thus, it is concluded that *P. semifasciata* recruits to the reefs when fish are at least 1 year old; the habitat of the younger fish remains unknown. The spatial segregation of young and adult *P. semifasciata* could be an adaptation to avoid cannibalism, as *P. semifasciata* is a piscivorous predator exceptionally found to prey on its own kind (Elías & Rajoy 1992; González 2002; Venerus 2006).

The similarity of fish sizes all year round in reefs that suffered nil to light extractive pressures, and the slow recovery of abundance following removal or disappearance of big fish (e.g. at reefs A and C), are consistent with *P. semifasciata* having high reef fidelity and relatively long residence times. The lack of seasonal changes in the ratio of yellow to grey fish, together with the stability in their size distribution, confirm the absence of seasonal demographic changes such as might be expected if spawning migrations had taken place.

Some of the life-history traits are also consistent with the absence of spawning migrations. The small size of the testes in relation to total body mass in *P. semifasciata*, giving a male gonadosomatic index (GSI) between 0.02 and 0.14% (González 1998), suggests that male and female would need to be in close proximity at the time of spawning or that the eggs are laid in an enclosed space, e.g. inside crevices. Comparative studies across different fish families have shown that the size of testes and the GSI in ripe males are associated with the mating system and spawning behaviour (Suquet, Billard, Cosson, Dorange, Chauvaud, Mugnier & Fauvel 1994; Stockley et al. 1997; Taborsky 1998; Erisman & Allen 2006). High male GSI values (e.g. ≥4% for serranids: Erisman & Allen 2006) are common in group-spawning fishes under intense sperm competition, while low GSI values (e.g. <2% for serranids, Petersen & Warner 1998) are typical of pair-spawning fishes, where sperm competition is less important. In general, pinguipedids have low maximum

GSI values (2.7% in *Pinguipes chilensis* Valenciennes; González & Oyarzún 2002; 0.8% in *Parapercis colias* (Forster); Pankhurst & Conroy 1987; 0.31% in *Parapercis cylindrica* (Bloch); Walker & McCormick 2004). Some hermaphrodite pinguipedid species belonging to the genera *Parapercis* show harem mating systems in which males defend a territory (Nakazono, Nakatani & Tsukahara 1985; Sano 1990; Ohnishi, Yanagisawa & Kohda 1997; Walker & McCormick 2004). In this context, the hypothesis that spawning in *P. semifasciata* occurs either in the reefs or in nearby soft bottom areas through resource- and/or female-defence mechanisms appears more likely than the occurrence of long-range spawning migrations and the formation of spawning aggregations. However, mating displays were never observed in the reefs during this or other studies conducted during daylight (Venerus 2006; D.E. Galván, unpublished data).

Departures from the general pattern of seasonal occurrence

The seasonal pattern in the abundance of *P. semifasciata* over two annual cycles was more evident and regular for reefs B and D, which are the deepest: 18 and 20.5 m at flow tide respectively (Table 1). Some occasional large deviations from the general pattern in fish counts were recorded at the shallower reefs A, C and E, which could not be explained by the factors examined. The impact of these deviations on the estimated seasonal coefficients was removed by including dummy variables to account for them. Although some subjectivity is introduced, these variables resulted in a highly significant reduction in the residual deviance. A limitation of the models used in this study is that they do not have the flexibility to accommodate the variability in the time at which some seasonal phenomena may occur. For example, in reef A, the 2002 spring drop in abundance was delayed, resulting in unusually high counts in October 2002, similar to the previous winter counts (Fig. 2).

At reef C, an increase of ~39% in excess of the overall mean density was observed in the spring of 2002, followed by a gradual decrease through the summer, according to the general pattern. Persistence of an above-average density during the summer suggests that the high spring counts reflected a strong recruitment pulse. Alternatively, the high counts could be related to some behavioural difference associated with the early time of day at which the census was conducted. However, time of day did not have a consistent effect across reefs (e.g. the only morning census done at reef E in August 2003 resulted in lower-than-expected densi-

ties), although the design did not provide the needed contrasts to test for its effect. When investigating the diurnal variability in fish counts in the Great Barrier Reef, Australia, Thompson & Mapstone (2002) concluded that diurnal differences were largely stochastic for the majority of taxa, and recommended sampling during the middle of the day, between 2 to 3 h after sunrise and 2 to 3 h before sunset, to minimise possible time-of-day effects. Only the UVCs of July 2003 at reef E were conducted outside that window.

The third dummy variable in the model for Type-II reefs (*D6*) was included to account for an unexpected drop in counts recorded at reef E in August 2003. This drop could have been caused by fishing, as a boat was observed in the vicinity of the reef after the previous census.

Annual differences in *P. semifasciata* abundance were only detected at reef A. The sharp drop in density observed at this reef during the first monitored spring could be caused by fishing, predation or emigration.

Implications for management

The strong association of *P. semifasciata* with the reefs increases the potential for locally depleting them from fish. The spatial proximity of fish to the reef ledges, their preference for certain types of refuges/crevices, and the permanence of fish in the reefs over the entire annual cycle increase the predictability of fish locations and hence their susceptibility to fishing. These characteristics make the Argentine sandperch a very vulnerable target even for recreational extractive activities like spear, hand-line, and rod-and-reel fishing, a feature that is common to other large reef species (e.g. Jouvenel & Pollard 2001; Westera, Lavery & Hyndes 2003; Coll, Linde, García-Rubies, Riera & Grau 2004). At the same time, the potentially long residence times in the reefs imply that reserves may be an effective tool for the conservation of this species, as has been recommended for other long-lived, large-bodied, sedentary reef fish species (Coleman, Koenig, Huntsman, Musick, Eklund, McGovern, Chapman, Sedberry & Grimes 2000; Heppell, Heppell, Read & Crowder 2005). A network of permanent (no-take) reserves may be the most promising management strategy for *P. semifasciata*. Other management measures such as size limits are less effective given the high post-release mortality of sandperch angled in deep reefs. Daily bag limits, on the other hand, have limitations because the overall effort is not capped and they may induce high-grading. Yet, they would help control the occurrence of alleged sport fishers actually involved in small-scale commercial operations.

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