

Chapter 8

Title: Changes in the specific and biogeographic composition of coastal fish assemblages in Patagonia, driven by climate change, fishing, and invasion by alien species.

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Abstract

Climate change, fishing, and invasion by alien species are the drivers of global change that mainly affect Patagonian marine-fish assemblages. In this chapter, we reconstructed the coastal-fish assemblages and their changes in richness and composition in three areas at Northern, Central, and Southern Patagonia between 1970 and 2020. Overall, there was an increase in fish richness (30 species) driven by an influx of species from warmer waters in Northern and Central Patagonia and by the invasion of alien species at Central and Southern Patagonia. Such a trend is consistent with the global pattern of tropicalization in temperate waters described for other regions and recent evidence of change in the sea surface temperature (SST) up to 48°S latitude. We detected only two local extinctions of skates from warm waters that disappeared from the northern area. A large number of fishes (30 species) diminished their frequency of occurrence. A total of twenty species of commercial importance, seven of which were elasmobranchs, were the most affected by partial losses. Future research is needed to understand the functional role of the species arriving or retracting and the consequences of such changes on ecosystem functioning.

Keywords

Southwest Atlantic, Temperate fishes, Range shifts, Climate change, Bottom-trawling effects, Invasive species.

8.1 Anthropogenic causes of global change and fishes

Coastal environments are the marine systems with the most significant interactions between the natural environment and society and the most complex and dynamic. Coastal fish assemblages support and provide a diversity of ecosystem services like food provisioning by commercial fisheries at different scales and recreation by diving, sport angling, and spear-fishing. Although human populations rely on these systems and on their biological resources to survive and maintain economies alive, growing human-induced pressures such as climate change, CO₂ enrichment, fisheries, biological invasions, pollution, and land use have profound and diverse consequences on them, with significant repercussions for society (Marquet et al. 2018, Bezerra et al. 2019, Sage 2020).

Climate change is projected to affect the fitness of organisms during all life stages, thereby impacting the size and structure of their populations, species community composition, and ecosystem functioning (Pörtner and Knust 2007, Bryndum-Buchholz et al. 2019). These impacts on organisms may be direct, through the effect of temperature, hypoxia conditions, ocean acidification, climate-induced shifts in hydrodynamics and sea level, or indirect and mediated through shifts in the structure of food webs or by spatial and temporal fluctuations in food availability (Pörtner et al. 2007: see Figure 8.1). As environmental conditions shift, organisms initially react based on physiological and behavioral responses shaped through their evolutionary history (Somero 2012). Behavioral responses mainly include the avoidance of unfavorable conditions and movement into more suitable areas (McHenry et al. 2019, Fredston-Hermann et al. 2020). New conditions may be physiologically tolerable, allowing acclimatization through several molecular to systemic adjustments of functional capacities (Pörtner 2002), or by promoting adaptation, due to the increased abundance and reproduction of existing heat-tolerant genotypes (Parmesan 2006). Conversely, new conditions may be intolerable, promoting migration of individuals or populations and local extinction if adaptation is impossible (Cheung et al. 2009).

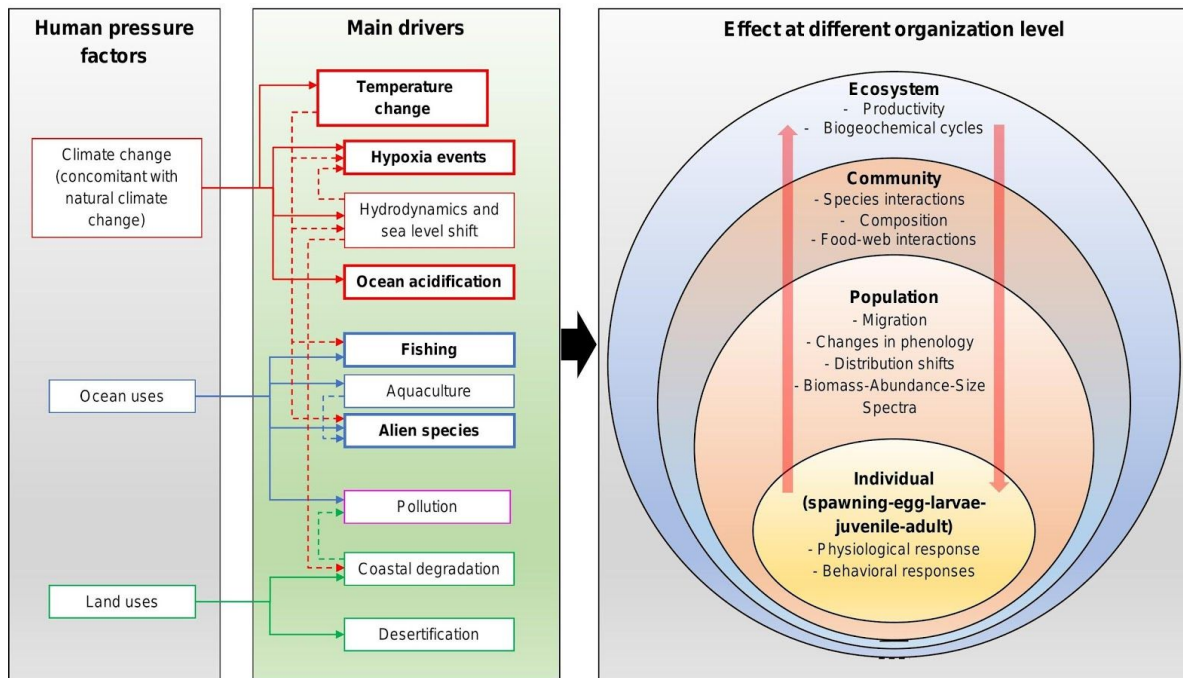


Fig. 8.1. Conceptual map describing drivers of global change affecting marine fishes. Solid lines denote the connection between human factors and main drivers, and dashed lines represent connections among drivers. The big central connector between main drivers and effects includes both direct and indirect effects. Red lines in the third panel indicate indirect bottom-up and top-down effects. Words in bold and thicker arrows indicate the drivers, connections, and organization levels analyzed in particular for Patagonia throughout this chapter. Figure adapted from Pörtner and Peck (2011), Rijnsdorp et al. (2009), and Llopiz et al. (2014).

Temperature is the most pervasive abiotic factor governing an organism's biology (Beitinger and Lutterschmidt 2011). The temperature defines the large-scale geographical distribution of aquatic animals in the oceans, within conditions set by geomorphology, ocean currents, water depth, and stratification or salinity (Pörtner and Peck 2011, McHenry et al. 2019). Thus, the thermal sensitivity of organisms is a fundamental factor resulting in climate-induced changes in marine ecosystems (Pörtner and Farrell 2008). Temperature limitations of aquatic ectotherms are hypothesized to be set mainly by aerobic scope reductions, defined as the difference between standard and maximum metabolic rates. The reduction in aerobic scope is caused by the limited capacity of circulatory and ventilatory systems to satisfy oxygen demand under increased or decreased temperatures (oxygen and capacity-limited thermal tolerance [OCLTT] hypothesis) (Pörtner 2002, Pörtner and Farrell 2008). The difference between upper and lower critical temperatures (which characterizes the onset of the anaerobic metabolism), i.e., the thermal window of marine fishes, might be

very different between life stages, being larvae more sensitive than juveniles and adults (Komoroske et al. 2014, Moyano et al. 2017), and also among species (Beitinger et al. 2000). In general, species with similar, but not necessarily identical, thermal windows will coexist. This fact would explain why climate sensitivity differs among species and would be one of the main reasons for climate-induced changes in community composition and food-web interactions (Pörtner and Peck 2011). The thermal windows also vary with latitude, being narrowest in fishes from high and low latitudes and widest in fishes from intermediate latitudes (Pörtner 2002, Pörtner and Peck 2011). Moreover, in the context of climate change, the difference between the upper thermal limit and the climatological temperature of the organism's habitat (i.e., warming tolerance) represents an essential characteristic of ectotherms because it approximates the amount of environmental warming they can tolerate before their performance drops to fatal levels (Deutsch et al. 2008). In this sense, warming tolerance is higher for temperate fish species than for tropical fishes, thereby confirming that species with the highest thermal limits have the lowest warming tolerance (Vinagre et al. 2016).

In a climate change context, temperature variations co-occur with increasing hypoxia events due to the enhanced stratification of water bodies and elevated O₂ demand of organisms in the warming seas (Breitburg et al. 2018), as well as with progressive CO₂ accumulation leading to scenarios of ocean acidification (Caldeira and Wickett 2005). In waters deeper than the surface mixed layer, hypoxic conditions and elevated CO₂ levels enhance the sensitivity of fishes to thermal extremes by reducing tissue functional capacities, including those involved in oxygen supply (Pörtner et al. 2005). Consequently, their thermal windows narrow, suggesting a considerable sensitivity of their width to warming and CO₂ and O₂ contents (Pörtner 2010). Empirical evidence for different taxa supports this idea. For instance, Dahlke et al. (2017) investigated CO₂-driven ocean acidification effects on embryonic thermal sensitivity and performance in the Atlantic cod, *Gadus morhua*, concluding that increased CO₂ levels constrained the thermal performance window of embryos. Moreover, a reduction of the thermal tolerances of the sea urchin *Loxechinus albus* and the false abalone *Concholepas concholepas* from Chilean waters was observed as a response to the synergistic effects of ocean warming and acidification (Manríquez et al. 2019, 2020).

Physiological and behavioral responses to climate change will then be evident at the population level as shifts in biomass, phenology (i.e., the timing of recurring life-history events), and spatial organization of organisms (Doney et al. 2012). Biomass is affected because the productivity of fish populations, in terms of recruitment, growth, and mortality, is

highly influenced by direct and indirect effects of climate change (Rijnsdorp et al. 2009). Under the current climate change scenario, predictions show that marine animal biomass in the South Atlantic will decline between 15% and 30% to 2100 (Bryndum-Buchholz 2019) unless emission mitigation measures are implemented.

Another critical mechanism that allows species to cope with climate change impacts includes altering phenology (Burrows et al. 2011). Marine fish have evolved to align the timing of their seasonal life cycle events with environmental seasonality and other organisms' phenology to maximize survival (Llopiz et al. 2014). Moreover, novel interspecific interactions may occur (i.e., invasive vs. native species), or the strength of pre-existing ones may be intensified (i.e., warm- vs. cold-adapted). Under a warming scenario, local or regional relocations following tolerable conditions and reducing competitive costs are viable solutions for mobile species (Parmesan and Yohe 2003, Parmesan 2006). This process may result in 'winner' (warm-adapted) species dominating the best quality habitat at the expense of 'loser' (cold-adapted) species (Milazzo et al. 2012). An increasing number of studies showed that marine fish geographical ranges are expanding polewards (Perry et al. 2005, Last et al. 2010, Fredston-Hermann et al. 2020) or into deeper depths (Dulvy et al. 2008). Such shifts are generally most evident near the northern or southern boundaries of the geographic range of a species (Pörtner and Peck 2011, Fredston-Hermann et al. 2020). However, these processes' strength will depend on food-webs complexity, environmental conditions, and interaction with other drivers (Fig. 8.1), as the direct and indirect effects of climate change on marine ecosystems do not act isolated.

Commercial fishing is another crucial driver that alters the population structure of both targets and incidentally captured organisms and, consequently, the community structure. The direct effects of fishing at the population level include reductions in total biomass and mean body size; and, as a result, changes in biomass production. The magnitude of these changes in response to the fishing pressure strongly depends on each species' reproduction and growth features. As a general rule, species exhibiting slow-growing, late-maturing, low fecundity, and long-living are profoundly affected and least resilient to exploitation pressure. All these traits are correlated with maximum body-size, and in areas with a history of intensive fishing pressure, fish assemblages have fewer large top-predators (Lotze et al. 2011). Recent studies emphasize the simultaneous importance of both fishing (top-down) and climate- (bottom-up) induced effects in marine ecosystem reorganization (Rijnsdorp et al. 2009), with results showing a dichotomous size-dependent response to both drivers (Genner et al. 2010). For instance, in the North Sea, it has been shown that small species had rapid responses to the prevailing thermal environment, suggesting that fast-growing and

early-maturing populations respond quickly to changing climates (Genner et al. 2010). In contrast, larger species have declined in abundance and size, reflecting expectations from sustained size-selective overharvesting in the area (Genner et al. 2010). In addition to the direct impacts of fishing on fish populations and assemblage structures, there are indirect effects in their functional organization and food web structure. Classic examples of indirect impacts include changes and simplification of food web structures (Frank et al. 2005, Lotze et al. 2011, Coll et al. 2008), and reduction of omnivory (Bascompte et al. 2005) through top-down cascading effects that promote the increase of mesopredators triggered by the overfishing of large predators (Heithaus et al. 2008). Among commercial fisheries, bottom trawling is the dominant gear, responsible for most possible indirect changes in fish community composition and impaired ecosystem functioning (Navia et al. 2012, Amoroso et al. 2018). In some circumstances, and depending on the fish assemblages composition in the fishing grounds, trawl nets remove many non-target species, even producing massive discards (e.g., Bovcon et al. 2013). This gear also scraps bottoms damaging their structural complexity (Martín et al. 2014) and causes changes in the species composition and functional structure of associated benthic invertebrate communities (Tillin et al. 2006, Jiménez et al. 2016, Bolam et al. 2017). Discards and damaged benthic organisms may increase the food supply for scavengers and promote their increase in marine systems (Catchpole et al. 2006). However, intermediate predator fishes can also consume that massive food supply altering their feeding ecology and predator-prey and competitive interactions in a community (Funes et al. 2019). Classic “fishing down the food web” theory indicates that those changes lead to a decrease in the mean trophic level of the fish assemblages (Pauly et al. 1998, Jennings et al. 2002, Pinnegar et al. 2002). However, a review on trophic level changes induced by fishing indicates that effects are case-dependent, and even increases in trophic level may occur (Funes et al. 2019, Funes 2020). Considering that commercial fisheries are increasing the number of species targeted (e.g., Victorero et al. 2018), it is expected that the ecological roles affected increase as well (Trinidade-Santos et al. 2020), enhancing the magnitude of indirect mixed effects in ecosystem functioning.

Although climate change and commercial fishing are the main threats to fish diversity, regional pressures also affect coastal areas (Jackson 2008). The intensive use of fertilizers, coastal degradation, increase in aquaculture production, and invasion by alien species are the most harmful (Halpern et al. 2008, Bezerra et al. 2019). Individualizing the effects of all of these drivers acting together is a difficult task that requires independent data collated under specific designs to test singular hypotheses. Given the absence of such data for fish assemblages of the Patagonian coast, in this chapter, we will focus on changes in their

diversity due to the combined effects of climate change-related drivers, fishing, and colonization by alien species (Fig. 8.1). To achieve this goal, we first provided a summary of the published information for Patagonia, and then we reconstructed three coastal fish assemblages and changes in their composition between 1970 and 2020. The approach relies on range shift published records, expert knowledge, and a stage-based model (Bates et al. 2014). The staged model assumes that range extensions occur as a sequence of arrival, population increase, and persistence. In contrast, range contractions progress as yield and population decline, and local extinctions occur (Bates et al. 2014).

8.2 Global change effects in the fish assemblages off the Patagonian coast

Our bibliographic search conducted through the academic web browsers Scopus and Google Scholar returned a low number of references about global change effects on fish assemblages in the Southwest Atlantic (SWA). References were organized and discussed according to the three drivers of global change here analyzed (climate change, fishing, and invasion by alien species) and their individual effects on fish assemblages of Patagonia.

We did not find studies that addressed climate change's effects on the marine fish assemblages from Patagonia. In the SWA, the first published compilation of gains in range shifts is a technical report for the coastal waters off Buenos Aires province, Argentina (36°S to 38°S). The report collated published and unpublished range expansions towards the south for 34 tropical and subtropical fishes between 2000 and 2017; and related them to an increase of up to 0.5°C in the summer sea surface temperature (SST) during that period (Milessi et al. 2018). Focusing on the relative abundances of the indigenous fishes, rather than on reports of newcomers, Gianelli et al. (2019) and Franco et al. (2020) showed that the mean thermal preference of exploited species weighted by their annual catch increased in Uruguayan landings (34°S - 35°S) between the 1980s and 2017, following an increase in the SST.

Although there is extensive literature on the effects of fishing on the populations of commercial species in Patagonia (see Chap. 13), few studies focused on analyzing the effects of harvesting on the structure and composition of fish assemblages. These studies come mostly from Northern and Central Patagonia. In San Matías Gulf (Northern Patagonia), the industrial bottom trawl and the small longline artisanal fleet that operates in the area seems to have replaced several predators over the food web, even a previously depleted population of the South American sea lion *Otaria flavescens* that prey over hake and other species (Ocampo Reinaldo et al. 2016). Those fisheries mainly target the Argentine hake *Merluccius hubbsi* but affect 32 cartilaginous and 45 bony fishes, and have shown increasing

trawling discards rates over the years (Romero et al. 2010). The landings composition and the spatial distribution of the fishing effort of the industrial fleet are mostly related to the environmental driven fish distribution and temporary market opportunities for new target species (e.g., silver warehou *Seriolella porosa* or Patagonian shrimp *Pleoticus muelleri*; Ocampo Reinaldo et al. 2013, Romero et al. 2013). In Central Patagonia, the shrimp trawl fleet, one of the most important fisheries in the area, caught 101 incidental species comprised of three jawless fishes (Agnatha), 29 cartilaginous, and 69 bony fishes (Góngora 2011, Ruibal Nuñez 2020, Gongora et al. 2020). Based on the life history, abundance, and conservation status of the bycatch species, nine were identified as potentially threatened by the shrimp fishery, and 31 as not impacted due to their low frequency in the catch. The level of impact caused by the incidental capture of the remaining species is unknown (Góngora 2011). The same fish assemblage also had evidence of a decrease in the proportional biomass of cartilaginous to bony fishes that correlated positively with the shrimp trawl fleet's fishing effort between 1998 and 2018 (Funes 2020). These studies identified threats and some changes in the fish assemblages structure caused by incidental fishing of the shrimp fleet in Patagonia; however, the effects of other fisheries in the area are still unknown.

The Patagonian marine region does not escape from species introductions and invasions. A total of 63 introduced species belonging to different taxa, from 129 reported in the SWA, have appeared in Patagonian waters (Schwint et al. 2020). The salmonids *Salmo trutta*, *Oncorhynchus mykiss*, *Oncorhynchus tshawytscha*, and *Oncorhynchus kisutch* are the four alien fishes identified in Patagonia (Schwint et al. 2020, Chalde et al. 2019, Figueroa 2019). A century ago, *S. trutta* and *O. mykiss* were introduced in rivers and lakes of Patagonia, and later they established anadromous populations (Pascual and Ciancio 2007). Escapements of salmon ranching in Chile facilitated the invasion of *O. tshawytscha* and *O. kisutch*, which actively colonized the Argentinean marine waters (Ciancio et al. 2005, Chalde et al. 2019). The evaluation of these salmonids' potential impact on their prey showed that it would be negligible for the populations of *Sprattus fuegensis*, but instead, they could cause depletions in the abundance of *Odontesthes smitti* (Ciancio et al. 2010).

8.2.1 Reconstruction of the fish assemblages off the Patagonian coast

To evaluate patterns of change properly, a baseline of information on species occurrence is a primary condition to be accomplished (e.g., Lotze et al. 2006, Bates et al. 2014). Despite the good understanding of the Argentinean waters biogeography (see Box 8.1), detailed lists of alien species (Schwindt et al. 2020), and reports on fish range expansions and rare occurrences (see references in the appendix ESM 8.1), we did not identify previously comprehensive lists of the coastal-fish assemblages' composition of Patagonia to test

distribution change patterns. For this review, we first compiled species checklists for three coastal areas (gulfs and continental shelf up to 100 m depth) representative of the Northern (40°S-42°S, San Matías Gulf), Central (43°S-47°S), and Southern Patagonia (50°S-55°S) (Fig. 8.2). Then, we classified fishes according to their occurrence history, biogeographical origin, fishery relevance, and thermal preference. Third, we examined the resulting database in search of trends; and fourth, we postulated correlations with drivers of global change. Also, we suggested future research lines aimed to evaluate how these changes in the composition of the assemblages might impact ecosystem function and structure.

We selected an area-based approach because of its representativeness of a zoogeographical condition and data availability to achieve a good reconstruction of the assemblages and their potential changes. The availability of data on the occurrence of coastal fishes was related to the historical settlement of academic and scientific institutions (Fig. 8.2) and the existence of regular on-board observer programs carried out by the fisheries authorities of Río Negro and Chubut (e.g., Bovcon et al. 2011, Romero et al. 2013). Although the areas chosen have different sizes, relative comparisons of the observed changes in each area can be made. The Northern Area, the San Matías Gulf, is a semi-closed basin with a limited water exchange with the adjacent shelf. The gulf has two depressions of 160 and 216 m depth, one located to the south and the other to the north of the parallel 41°40'S. Primary and secondary productions seem sustained by at least three areas: a tidal front, which extends in a northwest-southwest direction from October to March,; the San Antonio Bay in the north, and the San José Gulf in the south (Svendsen et al. 2020). The Central Patagonia area encompasses the San Jorge Gulf and adjacent northern waters up to 100 meters in depth. The gulf is a shallow basin with the deepest area around 100 m depth in its center and a bank at its eastern limit (60 to 90 m depth) (Matano and Palma 2018). Production in the area is supported by two fronts in the San Jorge Gulf (a southern thermohaline front and a northern tidal front) and the Península Valdés tidal front extending to northern shelf waters (Bogazzi et al. 2005). The Southern Patagonia area encompasses the continental shelf up to 100 m depth between 50°S and 55°S. Primary and secondary production are supported mainly by the Atlantic Patagonia cold estuarine front, close to the Pacific Patagonia cold estuarine front (Acha et al. 2004). In the beagle Channel sector, there is evidence of significant energy input of terrestrial detritus (Ricciardelli et al. 2016). For more details on the oceanography of the Patagonian continental shelf, see Chapters 2 and 5.

The reconstruction of the fish assemblages involved an extensive review of records encompassing the period 1970 – 2020. Sources of data included: published papers and books, unpublished theses, databases from local ichthyological collections, technical reports

from exploratory fishing surveys that partially covered the areas of interest, records from the provincial observer programs that monitor commercial fisheries, landing statistics from commercial, artisanal, and recreational fisheries, and personal observations provided by authors of this chapter ([ESM 8.1](#)).

We classified species occurrences, status (*sensu* Evans et al. 2020), and temporal distributional trends within each selected area for the compiled species records, following the categories proposed in Table 8.1.

To assess the robustness of our reconstructions, we also evaluated the information quality. A score of information quality ranging between 1 and 4 was assigned to each species based on an *ad hoc* criteria (e.g., Bates et al. 2014): (1) general knowledge but uncheckable, (2) unpublished personal observations made by the authors of this chapter, (3) published personal observations, (4) certified data in which the authors captured individuals or studied captured material (e.g., peer-reviewed papers, reports, and museum collections).

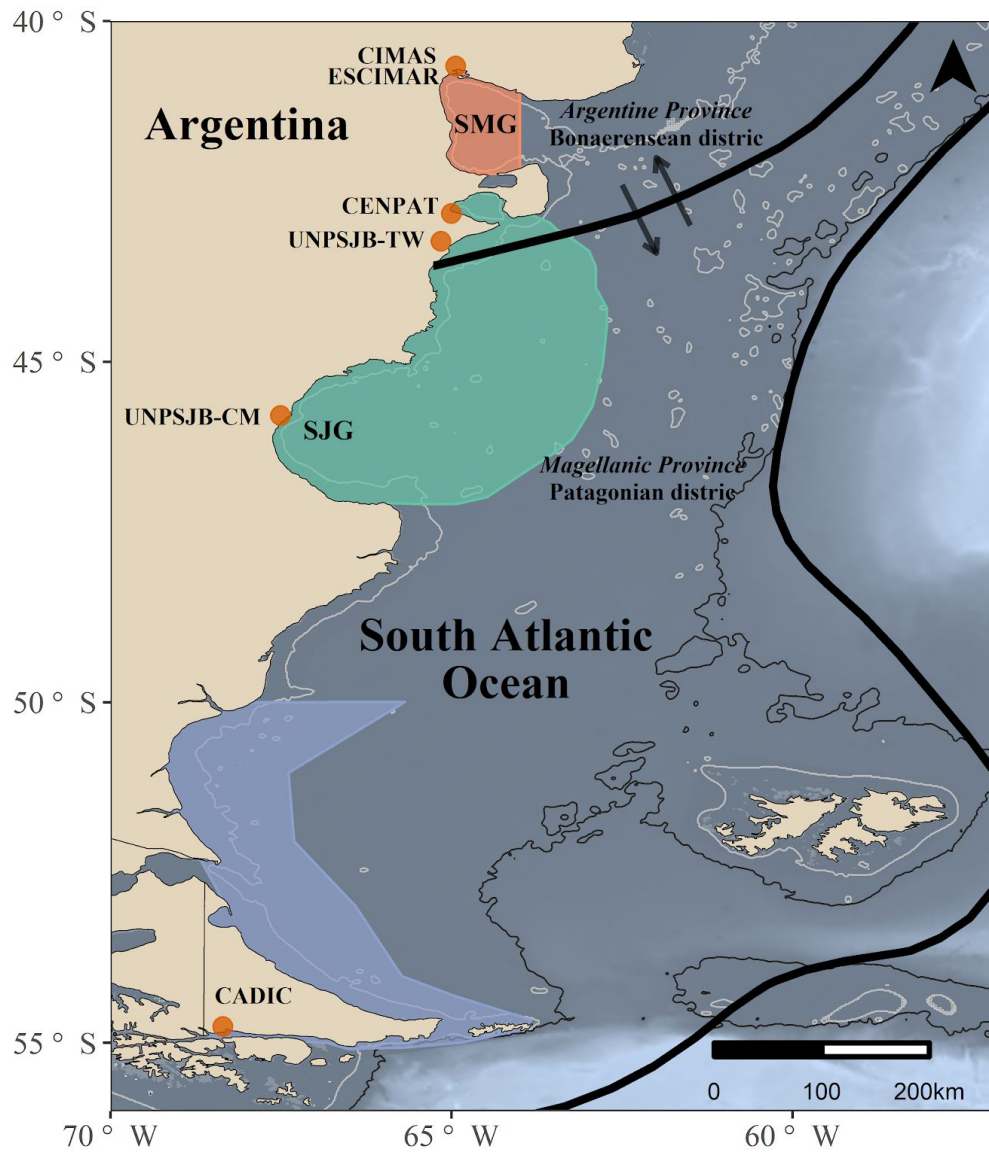


Fig. 8.2. Study areas, location of historical research institutes (orange dots), and biogeographical provinces in Argentine Patagonia. The location of biogeographical provinces follows the scheme by Balech and Ehrlich (2008). CIMAS: Centro de Investigación Aplicada y Transferencia Tecnológica en Recursos Marinos Almirante Storni; ESCIMAR: Escuela Superior de Ciencias Marinas (University of Comahue); CENPAT: Centro Nacional Patagónico; UNPSJB: Universidad Nacional de la Patagonia San Juan Bosco; TW: Trelew; CM: Comodoro Rivadavia; CADIC: Centro Austral de Investigaciones Científicas; SMG: San Matías Gulf and SJG: San Jorge Gulf.

Table 8.1 Categories used for classifying species occurrences, status, and temporal distributional trends within each study area.

Major trait	Category	Definition
Species occurrence	Anecdotic	Fishes recorded only once in the area.
	Occasional	Fishes recorded more than once in the area, but their presence is considered rare.
	Resident	Fishes present in the area throughout the year.
	Seasonal	Fishes present in the area only during part of the year.
Status (<i>sensu</i> Evans et al. 2020)	Indigenous	Fishes with their historic native range within the area.
	Alien	Human-introduced fishes that survive in a new area, expanding their historical range.
	Range shift gain	Fishes that expanded their distributional ranges and established populations in a new area without human intervention.
	Vagrant	Fishes that arrived as isolated cases by natural dispersal from a neighboring area without human intervention.
	Cryptogenic	Fishes with an origin that cannot be cataloged as native, vagrant, range-expanding, or introduced.
	Range shift loss	Fishes that showed retractions in their distributional ranges.
Trends in fish distribution	Expansion	Fishes that appeared for the first time in an area.
	Partial expansion	Fishes whose observed frequency or abundance increased in an area.
	Retraction	Fishes that disappeared from an area due to local extinction processes.
	Partial retraction	Fishes whose observed frequency or abundance decreased in an area.
	No change	Fishes whose observed frequency or abundance maintained relatively constant in an area.
	Insufficient data	Lack of or uncheckable data.

Box 8.1 Biogeographic context

Two biogeographic provinces characterize the main distribution patterns of marine fishes in the southern region of the Southwest Atlantic Ocean (SWA): the Magellanic and the Argentine provinces (Balech 1954, López 1963, 1964, Balech and Ehrlich 2008). The Argentine Province (Fig. 8.2) extends over the continental shelf from a northern limit that fluctuates between 30°S and 32°S (Rio Grande do Sul, Brazil) to a southern boundary in Northern Patagonia between 41°S and 44°S (Balech and Ehrlich 2008). The Argentine Province comprises the Southbrazilian and Bonaerensean districts (Fig. 8.2) located to the north and the south of the 34°S latitude, respectively (Menni et al. 1981, Menni and Stehmann 2000). The Magellanic Province includes the Patagonian shelf from Península Valdés (43°S) to Cabo de Hornos (55°S), and it follows a northward path along the edge of the continental shelf (Balech and Ehrlich 2008, Cousseau et al. 2020). This province splits into the Southchilean district in the Pacific Ocean and the Patagonian district in the Atlantic (Menni and Stehmann 2000). The biogeographic differences between the two provinces are mainly associated with lower water temperatures of sub-Antarctic origin in the Magellanic Province and higher water temperatures with a subtropical origin in the Argentine Province (Menni and Stehmann 2000).

The ichthyofauna of these two large provinces is well-documented and consistent for both chondrichthyans and teleosts, and their species lists are based mainly on data from surveys carried out by foreign and national scientific expeditions carried out up to 1990 (Norman 1937, Krefft 1968, Menni 1981, Menni and Gosztanyi 1982, Menni and López 1984, Menni and Stehmann 2000, Menni et al. 2010). Menni and Gosztanyi (1982) demonstrated the spatial and temporal stability in the species composition of fish assemblages in the Argentine Sea during ten years using data from the Kaiyo Maru survey carried out between 1969 and 1970 and from the Orient Maru I survey, carried out between October 1976 and January 1977. Then, Menni and López (1984) recognized the same defined assemblages using data from the Shinkai Maru survey collated in 1978. However, the biogeographic scheme proposed between the 1960s and the 1980s changed since the 1990s, with accentuation in the 2000s, due to temperate-warm fishes from the Argentine Province and subtropical species that moved southwards to Central Patagonia (47°S). Some indicators for these changes include the finding of reproductive populations of sciaenids (*Micropogonias furnieri*, *Cynoscion guatucupa*) and sparids (*Diplodus argenteus*, *Pagrus pagrus*), typical of the Argentine Province, in waters belonging to the Magellanic Province (Galván et al. 2005, Góngora et al. 2009, Bovcon et

al. 2011).

8.3 Coastal-fish assemblages of Northern, Central, and Southern Patagonia

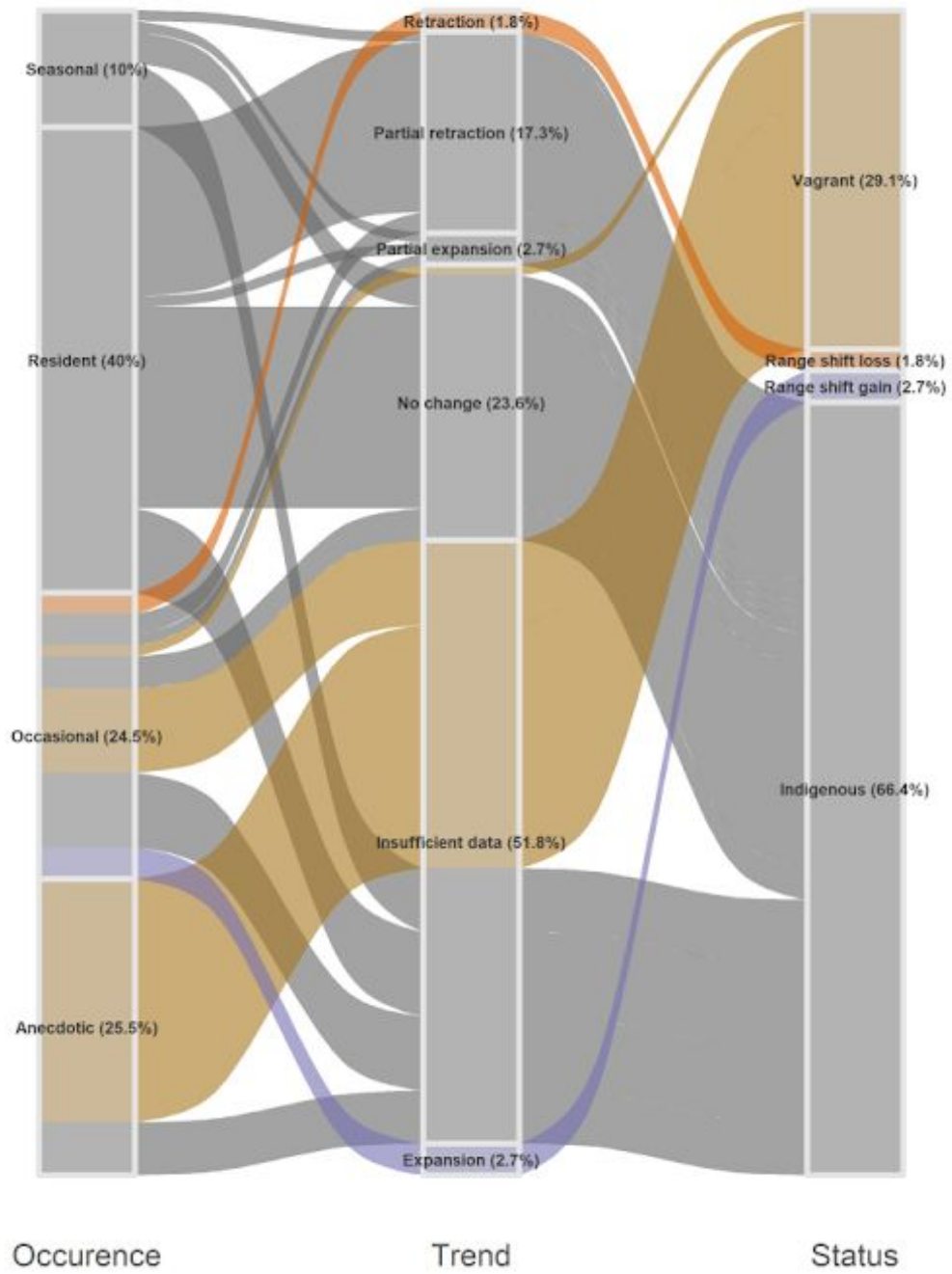
According to the latest update on fish diversity of the Argentine Sea (Figueroa 2019), 601 fish species have been recorded. For the three areas considered in this chapter, we collated records of occurrence for 192 species between the years 1970 and 2020 (Table 8.2 and Fig. 8.3). Those species belong to five classes and 86 families. The three reconstructed assemblages comprised 35% of the Argentine ichthyofauna and showed a decreasing gradient in richness towards higher latitudes. This pattern is consistent with the expected latitudinal trends in overall fish species richness (Macpherson 2002) and studies on particular groups, such as rocky reef fishes in the SWA (Floeter et al. 2004, Galván et al. 2009) or chondrichthyans (Lucifora et al. 2012, Sabadin et al. 2020).

Table 8.2 Number of species and families (between brackets), by class, collated for the three assemblages and Argentina. The numbers for Argentina were extracted from Figueroa (2019).

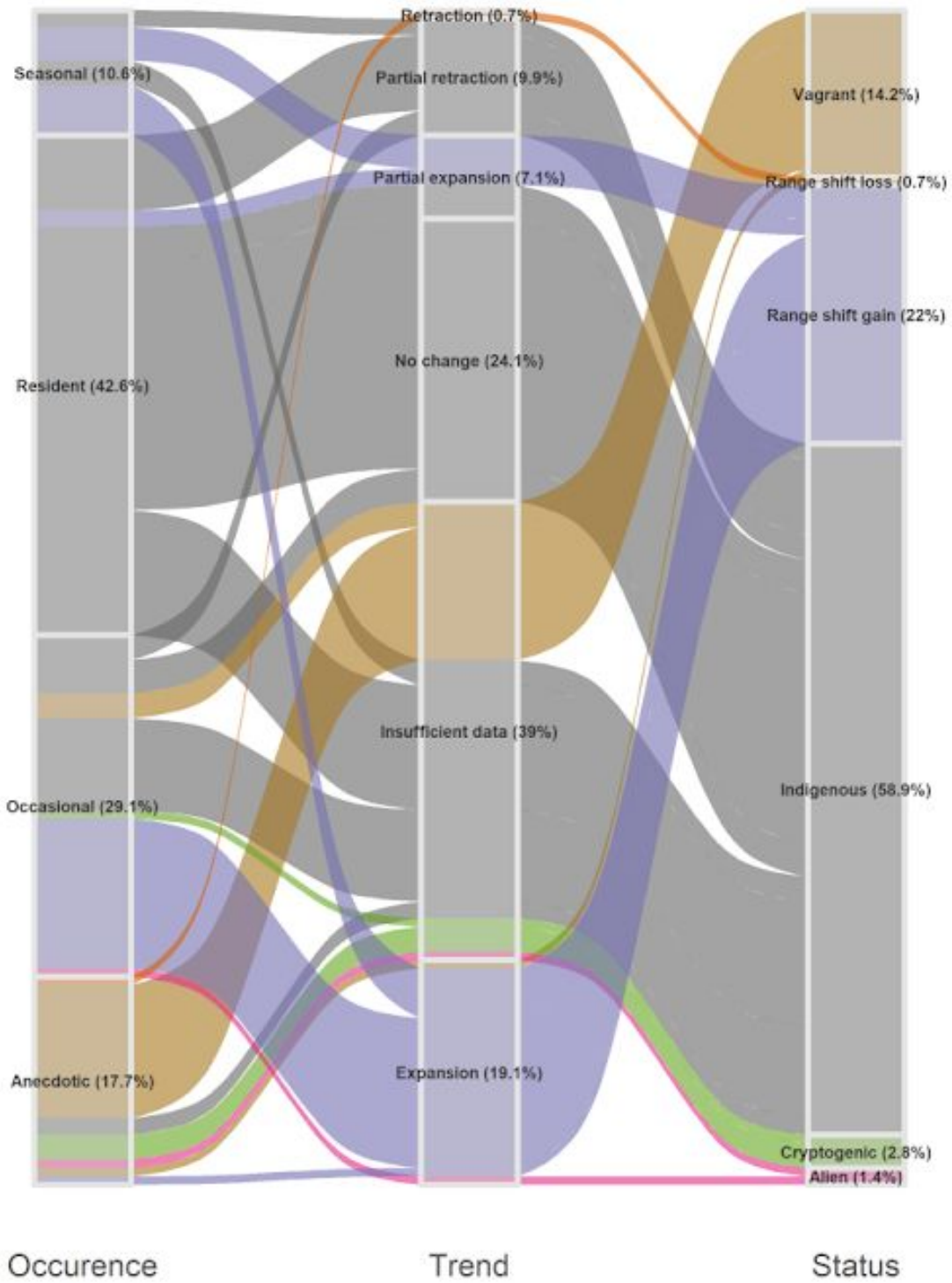
Class	Northern Patagonia	Central Patagonia	Southern Patagonia	Argentina
Myxini	-	-	(1)	(1)
Cephalaspidomorphi	1 (1)	1 (1)	1 (1)	1 (1)
Holocephali	1 (1)	1 (1)	1 (1)	2 (2)
Elasmobranchii	34 (16)	33 (14)	17 (5)	110 (24)
Actinopterygii	75 (48)	106 (54)	65 (33)	481(154)
Total	111 (65)	143 (71)	85 (41)	601 (182)

The reconstructions of fish species occurrence and their status in the studied assemblages are robust because they relied primarily on certified scientific data; the numbers of species with an information quality score equal to 4 were 106 (96.3%) in Northern Patagonia, 138 (96.5%) in Central Patagonia, and 83 (97.6%) in Southern Patagonia (see ESM 8.1 for details). On the other hand, trends in fish distribution have a majority of species classified as data deficiency. The numbers of species with insufficient data were 56 (51.4%) in Northern Patagonia, 57 (39.9%) in Central Patagonia, and 61 (71.8%) in Southern Patagonia (Fig 8.3).

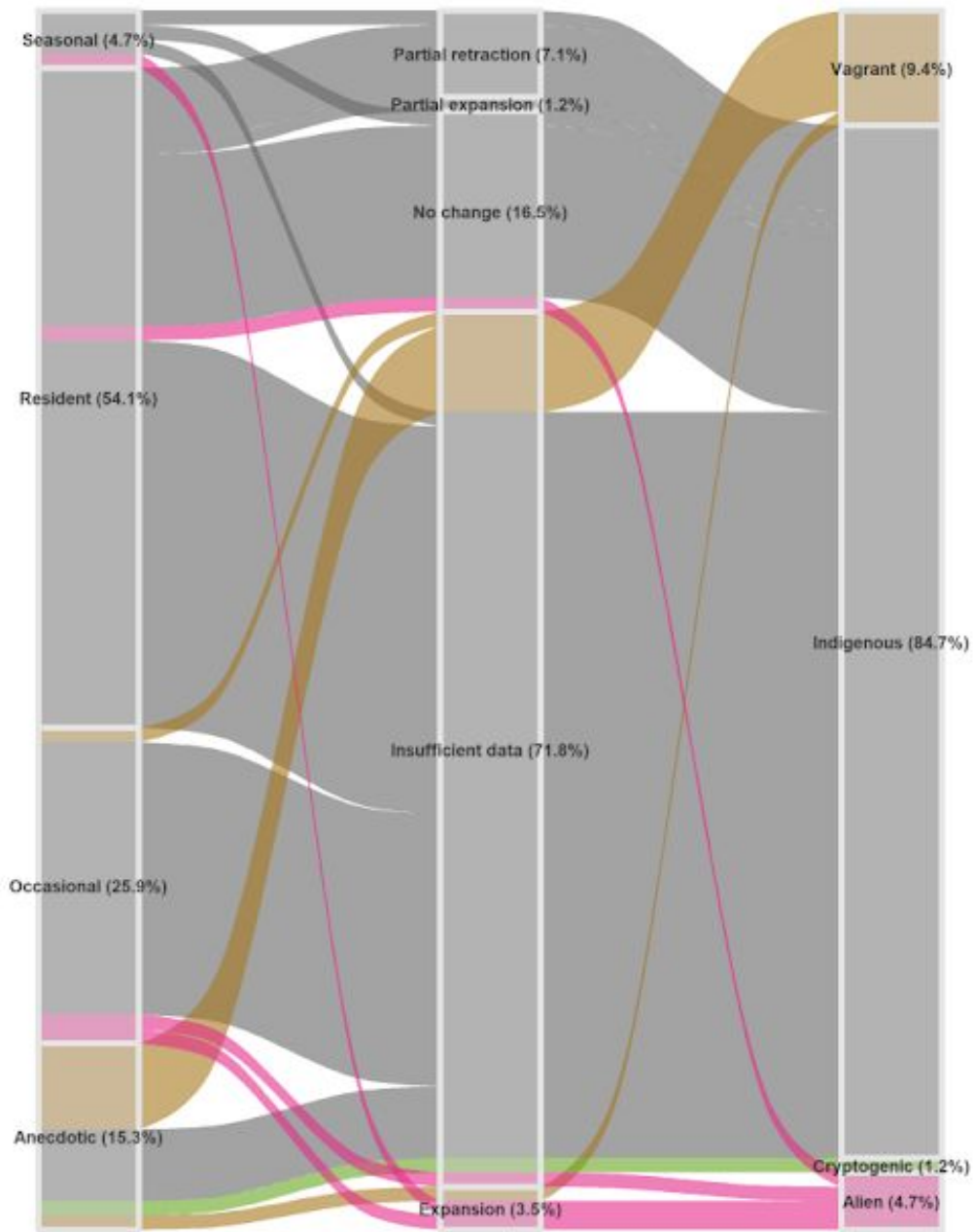
Northern Patagonia



Central Patagonia



Southern Patagonia



Occurrence

Trend

Status

Fig. 8.3. Relationships among the categories of species' occurrence, distribution trend (range shift stage), and distribution status (Evans et al. 2020) for each study area. Categorical classifications for occurrence, trend, and status were divided into blocks in each column. Blocks sizes represent the proportion of species for each level, and stream fields between the alluvial diagrams' blocks represent the proportion of species corresponding to each level through all categories. The stream fields are color-coded according to the distribution status category. Names of levels for each category and their proportion (percentages in brackets) are located in the middle of the corresponding blocks.

8.3.1 Fish-diversity gains and range expansions

Overall, 30 species showed records beyond their indigenous distributional ranges during the time-window analyzed (ESM 8.1). Among these, 27 cases were gains due to range expansions, and three were alien species (Fig. 8.3). Broken down by area, Central Patagonia exhibited more gains, in total and relative numbers, than the other two regions (Fig. 8.3). Around 18% of the species identified for that area correspond to newcomers, against around 3% for Northern and Southern Patagonia. As previously described, the Central area encompasses the confluence between the Argentine and the Magellanic provinces, which makes it an excellent site to detect changes in species distribution driven by temperature or oceanographic conditions. A biogeographical analysis of the newcomers to the Central area showed that the changes mainly consisted of the arrival of species expanding from the north (Table 8.3 and ESM 8.2). The mean thermal preference of the species that expanded their distributional range was higher than the mean thermal preference of the species that previously occurred in the area (Fig. 8.4). Both variables, thermal preference and biogeographical origin, were highly correlated and suggested a process of tropicalization in the area (i.e., an increase in tropical species dominance in temperate assemblages, *sensu* Cheung et al. 2009, 2012). In the northern area, the three newcomers (100% of gains) were from warmer regions (*Epinephelus marginatus*, *Genidens barbatus*, and *Symphurus plagusia*, Table 8.3, ESM 8.2). In the Central area, 86% of newcomers were from warmer areas; 7% were alien species (*O. mykiss* and *S. trutta*), and 7% were species from cold waters (*Mendosoma lineatum* and *Paranotothenia magellanica*) (Table 8.2). The latter seems to be expanding to the north since it was occasionally recorded in coastal waters off Mar del Plata and Necochea, in Buenos Aires province, at 38°S (Figuroa et al. 2005, Venerus Com. Pers.). The complete list of newcomers from warmer waters to the Central area includes *Atlantoraja castelnaui*, *Atlantoraja cyclophora*, *Atlantoraja platana*, *Conger orbignianus*, *Epinephelus marginatus*, *Genidens barbatus*,

Genidens planifrons, *Hyporthodus niveatus*, *Maurolicus stehmanni*, *Micropogonias furnieri*, *Mullus argentinae*, *Myliobatis ridens*, *Pagrus pagrus*, *Prionotus nudigula*, *Psammobatis bergi*, *Selene setapinnis*, *Seriola lalandi*, *Tetronarce puelcha*, *Thyrsopterus lepidoides*, *Trachurus lathami*, *Trichiurus lepturus*, *Urophycis brasiliensis* and *Zenopsis conchifer*. In the southern area, the alien species *O. tshawytscha*, and *O. kisutch*, in addition to the salmonids mentioned for Central Patagonia, represented all the changes recorded in the assemblage composition (Table 8.3). It is remarkable that the white sea catfish *G. barbatus* was identified as a newcomer in the three study areas and that the dusky grouper *E. marginatus* was identified as a newcomer in the Northern and Central areas, and both species come from warm-temperate waters.

Table 8.3 Biogeographical origin of the species listed in each study area. The numbers of species expanding their distributional ranges are informed between brackets. The biogeographical origin follows the classification proposed by Figueroa (2019). Numbers in bold letters highlight the expansions.

	Biogeography	Northern Patagonia	Central Patagonia	Southern Patagonia
Warm-waters	Circum-tropical	21 (1)	21 (10)	1
	Brazilian	5 (1)	4 (1)	0
	Argentine	41 (1)	43 (13)	6 (1)
Cold-waters	Magellanic	25	40 (1)	52
	Circum-antitropical	5	9	5
	Antarctic	0	2	4
	Southern-hemisph ere	9	21 (1)	13
Alien		0	2 (2)	4 (2)

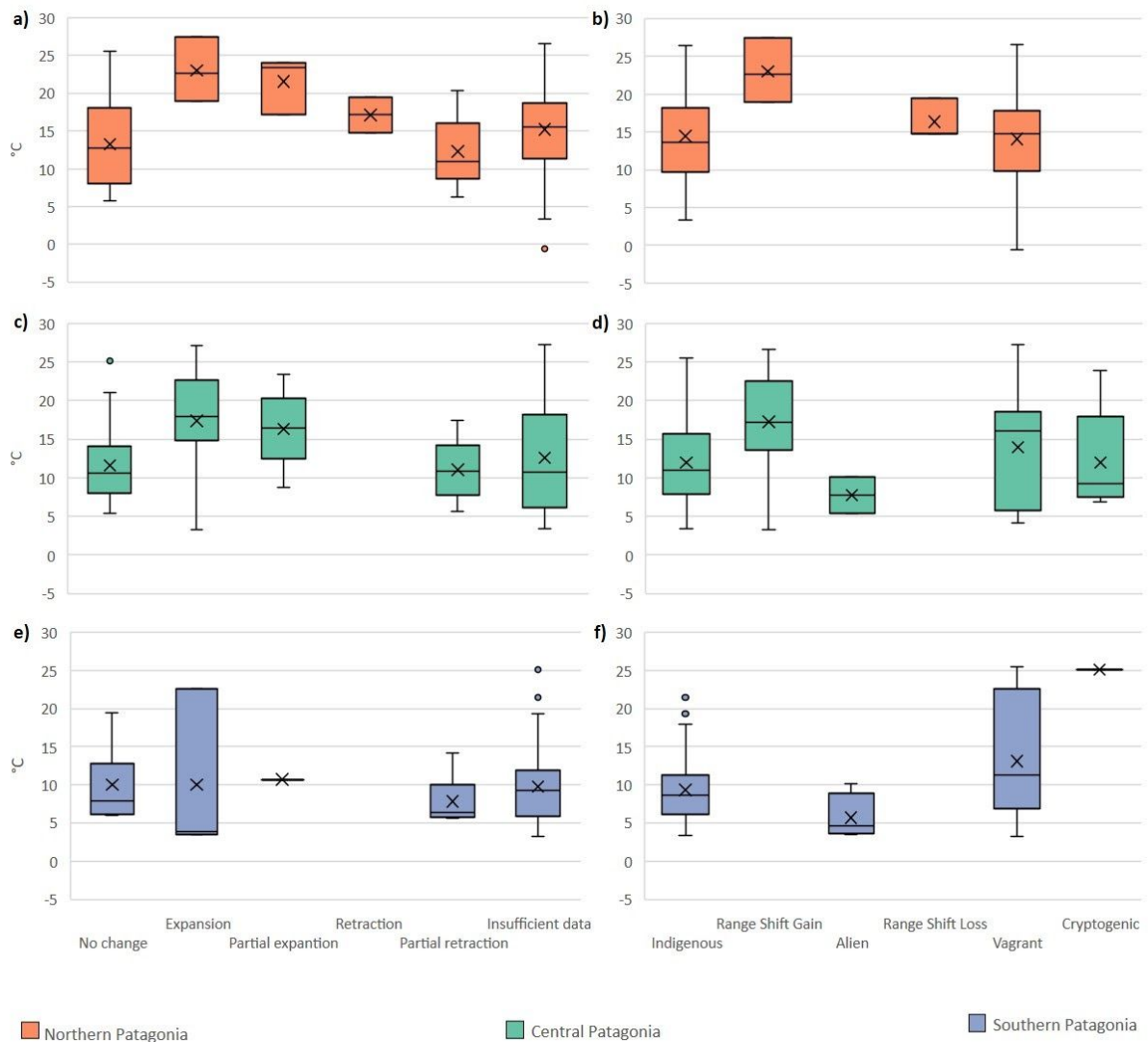


Figure 8.4. Mean temperature preferences for fishes in the three study areas by categories of temporal trends (a,c, and e) and status (b,d, and f). Temperature data were obtained from Fishbase (Froese and Pauly 2019). The boxes comprise the 25th and 75th percentiles for the sample. Whiskers extend between the minimum and maximum values within 1.5 times the box ranges. The horizontal lines within the boxes show the median, x markers represent the mean values and the dots indicate outliers.

Among the indigenous species in each assemblage, we detected several cases of fishes whose observation frequency increased. Again, our data showed that Central Patagonia exhibited more increases in total and relative numbers among the evaluated areas. In the northern area, the three species that increased in abundance, *C. guatucupa*, *D. argenteus*, and *P. pagrus*, are all common species from warm-temperate and tropical areas. Even, the

last two species expanded their ranges into the Central area. A total of nine species increased their frequency of occurrence in the Central area. From them, eight had warm-temperate distribution (*Scomber colias*, *Psammobatis extenta*, *Oncopterus darwini*, *D. argenteus*, *Dules auriga*, *Symterygia acuta*, *Squatina guggenheim*, and *Paralichthys patagonicus*), while one (*Cottoperca trigloides*) occurs in cold-temperate waters. The only species for which a partial increase was detected in the southern Patagonian assemblage was *Eleginops maclovinus*, an endemic fish of the Magellanic province (occurring at both Atlantic and Pacific coasts) and typical of Central Patagonia. However, *E. maclovinus* has also been recorded in northern waters, in the coastal lagoon of Mar Chiquita, 37°40'S (Gonzalez Castro et al. 2013), and it seems to be expanding towards the north.

8.3.2 Fish-diversity losses and range retractions

The only two species that have fully retreated are elasmobranchs. Both *Rioraja agassizii* and *S. acuta* occurred in the Northern area, and their distributions extend to warmer waters. There were no species identified as losses at Central and South Patagonia.

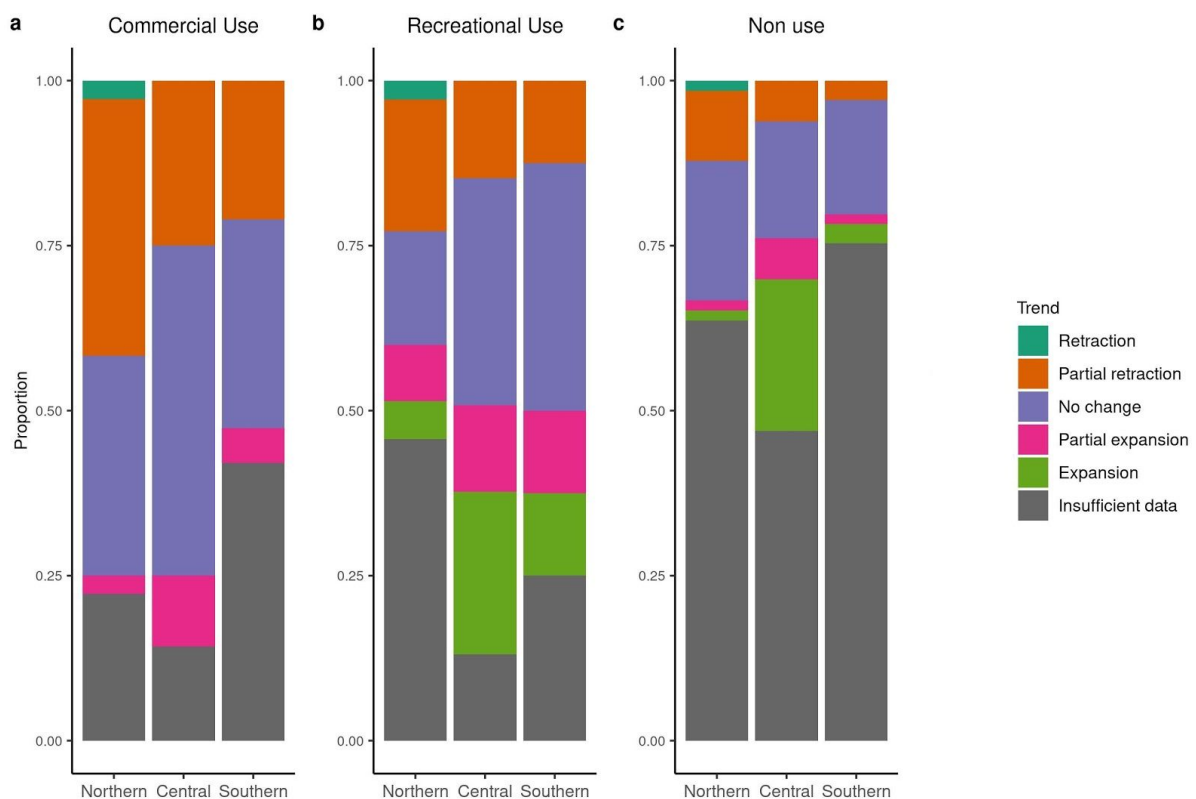


Figure 8.5. Proportions of species classified by use and temporal trends in the studied areas. Commercial use comprises the landings of industrial and artisanal fisheries. Recreational

use covers species targeted by sport anglers and spearfishers. Recreational and commercial use are not mutually exclusive categories. None use comprises the rest of the species.

We identified a total of 30 species in partial retraction. Species exhibiting total or partial retraction did not show a different thermal preference from the species identified as no changing (Fig 8.4 a, c, and e). Seventy-five percent of the species whose observed frequency or abundance decreased are targeted by commercial or recreational fisheries. The species in retraction decreased both in raw and relative numbers from north to south (Fig. 8.3). At Northern Patagonia, 19 species (17%) were identified as in partial retraction, five of which were elasmobranchs (*Galeorhinus galeus*, *Mustelus schmitti*, *Psammobatis bergi*, *Squalus acanthias*, and *S. guggenheim*), and 14 were teleosts (*Acanthistius patachonicus*, *Congiopodus peruvianus*, *Genypterus brasiliensis*, *M. argentinae*, *Nemadactylus bergi*, *Paralichthys isosceles*, *Parona signata*, *Percophis brasiliensis*, *Polyprion americanus*, *P. nudigula*, *Pseudopercis semifasciata*, *Seriolella porosa*, *Stromateus brasiliensis* and *Xystreurus rasile*). Thirteen of those species have a commercial interest, and five are also caught by recreational fishers (Fig. 8.5). In Central Patagonia, 14 species (10%) were identified as in partial retraction, five were elasmobranchs (*S. acanthias*, *Carcharhinus brachyurus*, *M. schmitti*, *G. galeus*, and *Notorynchus cepedianus*), and nine were teleosts (*A. patachonicus*, *P. americanus*, *P. semifasciata*, *P. brasiliensis*, *Brama brama*, *Genypterus blacodes*, *Macruronus magellanicus*, *Salilota australis*, and *Hippocampus patagonicus*). Five of those species are harvested by commercial and recreational fisheries, two have only a commercial interest, and three are targeted exclusively by the recreational sector (Fig. 8.5). In Northern and Central Patagonia, there are well-established on-board observers programs maintained by provincial governments that allowed the reconstruction of the three assemblages and better assignment of the qualitative trends for both targeted and incidentally captured species (Caille et al. 1997, Bovcon et al. 2013, Romero et al. 2013, Gongora et al. 2020). Unfortunately, there is no such detailed information available for the southern assemblage. Therefore, the number of species classified as data insufficient in the Southern Area was higher than for the other two areas, and the species in the other categories were biased towards those commercially targeted. At Southern Patagonia, we identified six species (7%) in partial retraction; one shark captured by recreational anglers (*N. cepedianus*) and five teleosts (*M. magellanicus*, *Merluccius australis*, *Micromesistius australis*, *S. australis*, and *Champscephalus esox*). The first four of those fishes represent important commercial resources.

We identified seven species with partial retractions in two study areas commonly caught by trawling fleets: *A. patachonicus*, *G. galeus*, *M. schmitti*, *P. semifasciata*, and *S. acanthias* in

the Northern and Central areas, and *M. magellanicus* and *N. cepedianus* in the Central and Southern areas. This finding may suggest a population decrease exceeding the Patagonian region, probably due to overfishing.

8.3.3 Drivers of gains and losses in fish biodiversity and resulting assemblage patterns

The observed changes in distributional ranges of fish species documented in this chapter show that, as in other temperate locations where water temperature has increased, species gains outpaced losses (Antao et al. 2020). Then, the observed trend in Patagonia is consistent with the expectation of an increase in local marine richness, as temperate regions undergoing warming will receive an influx of species following suitable temperatures, and increases in the occurrence of warm-affinity generalists, indigenous from those regions (Burrows et al. 2019, Antao et al. 2020). As mentioned earlier in this chapter, these spatial shifts are part of a global biogeographic pattern of change known as tropicalization (Cheung et al. 2009, 2012). Fishes may be expanding their distribution ranges following the warming of temperate waters, but they may also be leaving northern regions to avoid temperatures higher than their physiological tolerance because those regions are experiencing high warming (Franco et al. 2020). At a regional scale, the tropicalization of temperate seas produces a rapid biotic homogenization of the fish assemblages (i.e., the species identity of colder localities increasingly resembled that of warmer localities, Magurran et al. 2015, Bezerra et al. 2019). In Patagonia, the arrival of fish from warmer localities increased the similarity in species composition between the Northern and the Central Area by 8%, and between the Northern and the Southern Area by 1% (these percentages are the differences between Jaccard similarity indexes with and without newcomers). This slight trend may suggest that homogenization of coastal fish assemblages in Patagonia already started.

Several pieces of evidence point to the occurrence of a warming process in the SWA. Southern Brazil, Uruguay, and the northern Patagonian shelf of Argentina are climate hotspots (i.e., regions where the SST has changed most rapidly in the last 50 years, and it is expected to increase more than 3°C by 2099, Popova et al. 2016). Since the 1980s, the position of the 20°C and 17°C isotherms showed a constant long-term displacement towards the poles (Ortega et al., 2016, Gianelli et al. 2019). The data presented and discussed in Chapter 2 of this book showed that the SST in Patagonia increased to the north of 48° S but diminished southwards. The observed influx of species from warmer waters to the Northern and Central, but not to the Southern Area described in this chapter follows the spatial changes in SST observed for the Patagonian region; and suggests that fishes are good early indicators of regional warming, as it was proposed by Fogarty et al. (2017). In agreement

with the general spatial pattern described for Patagonian fishes, a recent biodiversity analysis on macroinvertebrate assemblages showed the first symptoms of tropicalization in the San Jorge Gulf due to southwards range extensions of warm-temperate species in the area (see Chapter 7).

Even though tropicalization has been evidenced in the ichthyofauna of Patagonia, the dispersion of two species of the suborder Notothenioidei, *P. magellanica*, and *E. maclovinus*, towards lower latitudes, should be highlighted. Both species are typical representatives of the Magellanic province and were recently observed in the province of Buenos Aires, Argentina (Figuroa et al. 2005, González-Castro et al. 2013). Notothenids were suggested as a group in expansion towards temperate waters, a process explained by their origin in moderately warm shallow seas that connected Australia, Antarctica, and South America within the province of Weddell, which existed from the Upper Cretaceous to the Eocene (Balushkin 2000). In fact, *E. maclovinus* is distributed in environments that are widely cooler than their maximum thermal tolerance and preferred temperature range (Lattuca et al. 2018). Therefore, *E. maclovinus* would be expected to be influenced in its current distribution by indirect effects of climate change, such as habitat degradation or changes in trophic structure, rather than by direct effects (Figure 8.1) (Lattuca et al. 2018).

We observed a decrease in the ratio of elasmobranchs to teleosts from north to south in the three assemblages. The ratio was 31% in the Northern Area, 23% in the Central, and 20% in the Southern Area. This finding follows the general pattern described for chondrichthyans in the SWA (Lucifora et al. 2012), which showed the highest richness of elasmobranchs at the continental shelf off Uruguay and southern Brazil, with another small peak at El Rincón, 39°S (Sabadin et al. 2020). Under the current results, a proportional increase of elasmobranchs would be expected if there were an influx of species from the north and both elasmobranchs and teleosts had similar chances of extending their ranges. However, elasmobranchs were proportionally more affected by total or partial losses than gains when the three assemblages were analyzed together. This trend is consistent with the expectation that, as elasmobranchs are slow-growing and late-maturing species, they respond slowly to climate change (Genner et al. 2010) and are more prone to decline by the direct effects of fishing or the cascading indirect effects of global change (Dulvy et al. 2014). In Central Patagonia, 26 of the 34 registered cartilaginous fishes are caught incidentally by the commercial fisheries that target hake and shrimp, and are also discarded on board or landed as by-products (Góngora et al. 2009, Cedrola et al. 2012, Bovcon et al. 2013, Ruibal Nuñez et al. 2016, Gongora et al. 2020, Ruibal Nuñez 2020). In agreement with our results, Funes (2020) reported a decrease in the proportional biomass of elasmobranchs to teleosts and a

decrease in the maximum fish sizes observed at the San Jorge Gulf (Central Patagonia) analyzing independent-fishery data from 1998 to 2018. These two trends described in Central Patagonia are the most anticipated ecosystem alterations caused by the long-lived species' sensitivity and high catchability by trawling (Reynolds et al. 2001).

8.4 General conclusions and future research perspectives

Understanding the temporal stability of fish assemblages composition under changing marine environments is crucial to identify drivers and trajectories of ecosystem function and productivity in marine systems. This stage requires an outstanding effort to compile historical occurrences of fish species at regional levels and evaluate the quality of this evidence (Bates et al. 2014). Our study represents the first approach to reconstruct the species composition of fish assemblages located in three well-studied and productive areas along the Argentine Patagonian continental shelf. We discuss our findings as direct effects of three main drivers, climate change, fishing, and invasion by alien fishes. However, other drivers like pollution or other causes of environmental alteration may also affect fishes (Fig. 8.1, Bezerra et al. 2019). Besides the direct effects of various drivers, there are also indirect effects (Fig. 8.1). For example, the environmental alteration of the shallow bottoms caused by the invasion of the annual kelp *Undaria pinnatifida* has antagonist results in the reef fish fauna of Patagonia. On the one hand, it blocks the access to shelter, crevices, and holes used by reef fishes, having a negative effect (Irigoyen et al. 2010a); but also it increases the abundance of their prey, promoting a positive bottom-up effect (Irigoyen et al. 2010b). Future research should then make efforts to incorporate more drivers than those discussed here and their possible synergies and antagonisms.

We found important information gaps in the trends for the geographic distribution ranges of fishes among the three evaluated areas. More than 40% of the species had insufficient occurrence and abundance data to detect changes in their geographic distributional ranges. This fact represents an information gap in the basic ecological knowledge of marine fish species in the Patagonian region. We hope that other researchers might benefit from our information quality list for the occurrence of fish species (see ESM 8.1) and make efforts to monitor the abundance of fishes with low information quality, such as vagrant species with anecdotal occurrences or non-commercial fishes in coastal areas (Fig. 8.3). Monitoring the abundance of fish species with gaps and low-quality information in trends of distributional ranges would hamper a reliable identification of climatic and anthropogenic drivers of change of the taxonomic composition, functional organization, and productivity of fish communities in the Argentine Patagonian Sea.

Changes in the geographic distributional range of fish species presented in this chapter also constitute a baseline to predict the chances that species have to settle and colonize new areas in the Patagonian marine region. Distributional range shifts in marine fishes correlate with functional traits of morphological (e.g., body size), behavioral (e.g., feeding mode, microhabitat selection), life history (rate of growth) and physiological type (e.g., thermal tolerance) (e.g., Sunday et al. 2015). Such traits determine the species' resistance and adaptability to changing environmental conditions and disturbances (Sunday et al. 2015). As a result, functional traits might facilitate predictions on species composition in novel communities from a functional biodiversity perspective. For example, fish species that have effectively colonized warming areas in the Temperate Northern Atlantic Ocean exhibit high physiological plasticity to colder waters poleward (Dulvy et al. 2008, Wood et al. 2019, Fredston-Hermann et al. 2020) or warmer waters in the Mediterranean region (Moulllet et al. 2019). Many vagrant fishes have broad latitudinal geographic ranges that allow greater environmental adaptability, resource use, and successful colonization in new regions (Frainer et al. 2017). Alternatively, functional traits such as body size and maturity age of marine fishes may account for distributional range shifts caused by the synergy between high fishing intensity and climate change. While highly fished communities shift from the large-body size and late maturity fishes species with commercial importance towards communities dominated by smaller-body size and more fecund species (Barausse et al. 2011); other communities located in areas with low fishing pressure and colder waters shifts by the influx of large species with commercial interest from lower latitudes (Wiedmann et al. 2014). Identifying the functional traits that correlate with species gains and losses is crucial to understanding ecosystem functioning changes and predicting possible indirect effects in food-web functioning and community structure.

Few studies have used a functional-trait approach to describe the distribution range shifts in marine fish species in the Southern Ocean. Existing works mainly focus on describing the thermal responses and tolerance (Lattuca et al. 2018), morphological modifications caused by heat stress (Garofalo et al. 2019), and blood-freezing levels in specific groups of Antarctic fishes (Bilyk 2011). However, studies at the community level in the Patagonian Continental Shelf remain pending in the regional research agenda. Therefore, future work should aim to create databases of functional traits potentially relevant to explain distributional range changes in marine fishes and evaluate those traits as indicators to predict future scenarios of the functional organization of fish communities in the Patagonian Region. Collaborative efforts among researchers working in the region are needed to achieve this goal, whose information is a priority for proposals on biodiversity conservation and fisheries' adaptive management in changing ecosystems.

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