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Research

The chronology of overfishing in a remote West-African coastal ecosystem

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ABSTRACT. Classic studies of marine overexploitation traditionally analyze cases of "fishing down the food web": turning to smaller species at lower trophic levels after depleting the larger top predators. Much less documented, however, is the preceding phase in which higher trophic level species, previously not exploited or consumed locally, are increasingly added to the catch. Worldwide, this phase happened centuries ago due to technological developments and thus passed before scientific scrutiny and conservation awareness arose, leaving it largely unstudied. Here, we combine a historical reconstruction of fishery with a relatively recent fishing monitoring program to document this early phase in the Parc National du Banc d'Arguin in Mauritania, a marine protected area in Mauritania, West Africa. Long-term trends in mean trophic level of exploited species and total catches provide evidence for an increasing fishing pressure toward the top of the food web, and suggest that the state of "fishing down the food web" is now happening in this ecosystem. This involves the recent intensive targeting of rays and sharks. We show that their contribution to the local economy is marginal compared with the traditionally fished species.

Key Words: *Banc d'Arguin-Mauritania; conservation; elasmobranch; fisheries monitoring; food web; traditional fishing*

INTRODUCTION

For thousands of years, humans have impacted marine fauna by targeting them for food and modifying their supporting ecosystems (Jackson et al. 2001*a*). In the early 1950s, global marine fisheries experienced a rapid growth of fishing intensity, soon leading to the overfishing of fish stocks (Pauly et al. 2002, Pauly 2007). Studies of marine overexploitation show that this can be described as "fishing down marine food webs," where fishing efforts, after first having depleted the large top predators, shift to increasingly smaller sizes at lower trophic levels (Christensen 1996, Pauly et al. 1998, Pauly 2007). This phenomenon can lead to large ecological changes, as marine top- and mesopredators such as sharks and rays exert top-down effects on community structure and ecosystem dynamics (Stevens et al. 2000, Heithaus et al. 2009). Therefore, increased removal of these species at higher trophic levels cascades down the food web, changing the abundance of primary consumers and producers also at lower trophic levels (Myers et al. 2007, Sieben et al. 2011). Similarly, the harvest of high trophic level species also occurs in freshwater systems (Arlinghaus et al. 2002, Welcomme 2011), with indications of fishing down the food webs in these systems (Welcomme 1999).

Much less documented is an earlier phase when fishermen move from a traditional fishery with simple technical means into a well-equipped industrialized fishery, a systematic sequence of increasing the mean trophic levels (mTL) of catches over time (Essington et al. 2006, Stergiou and Tsikliras 2011). This occurs during the transition from fishing for local subsistence based on smaller species low in the food chain to the exploitation of larger species higher in the food chain. Besides the exploitation of higher trophic levels, in this process exploitation moves away from fish that can be caught with little technical means and manual labor (Eide 2009), to more industrialized approaches (motorboats, trawl winches, large nets). In most places of the world, this phase took place before the establishment of systematic monitoring programs (Casteel 1976, Pitcher 2001, Lotze and Milewski 2004, Essington et al. 2006, Bolster 2014), and as a result, is underrepresented in overfishing studies. Furthermore, archeological records suggest that, in many places in the world, coastal overfishing started several centuries ago (Casteel 1976, Wing and Wing 2001, Steadman and Jones 2006). For instance, Casteel (1976) found archeological evidence that the harvest and size of a few fish species, including salmon, beam, rudd, and catfish, declined enormously over the last 5,000 yr. The resulting state of already high levels of exploitation of large top predators in fisheries may even have become the "new normal," a phenomenon more generally known as the "shifting baseline syndrome" (Pauly 1995).

The long-term history of human overexploitation of coastal marine systems in most places makes it difficult to appreciate situations of historically low levels of exploitation (Lotze et al. 2006). Nevertheless, an awareness and better documentation of the drivers of shifting from a traditional subsistence fishery into an industrialized one would enable us to better plan toward a more sustainable fishing practice (Pauly 1995). This is more urgent to address in remote communities that rely on subsistence fishing for living and are often poor, isolated from markets, and have difficulties accessing public services and jobs (Arnason and Kashorte 2006). In many places, rapid changes in these socioeconomic factors have led to accelerated changes from subsistence to commercial fishing, potentially putting the ecological integrity of unique ecosystems they depend on at risk (Erlandson et al. 2009). Human population growth, technological developments, and the pressure from global markets have been postulated as the main drivers of overfishing worldwide (Pitcher 2001, Jackson et al. 2001*a*, Anticamara et al. 2011), but the effect of socioeconomic factors on the overfishing process is less known (Pauly and Chua Thia-Eng 1988, Cinner and McClanahan 2006). Linking fishing practices and socioeconomic conditions will allow us to determine the specific socioeconomic factors that are responsible for overfishing (Cinner and McClanahan 2006).

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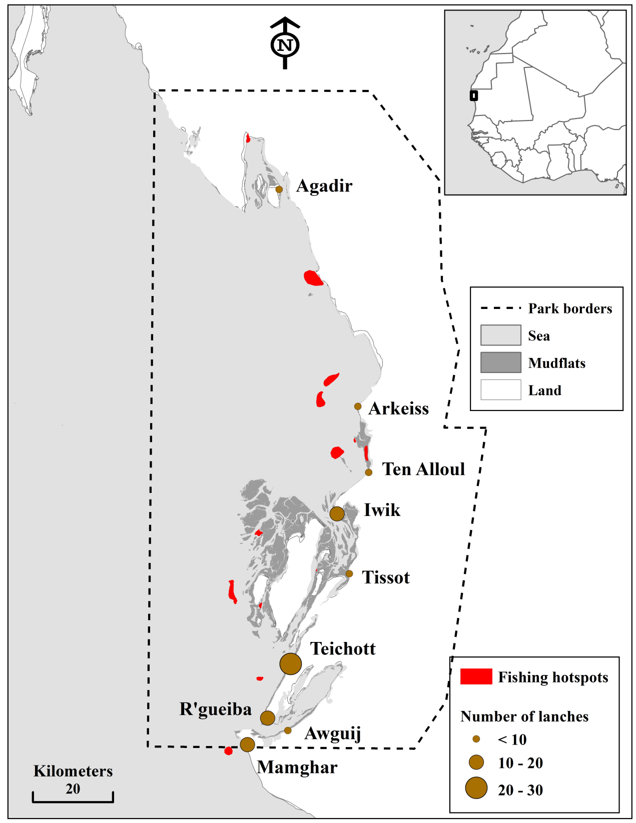
Coastal habitats are among the most vulnerable systems to overfishing (Jackson et al. 2001*a*), yet they are hotspots of biodiversity and often concentration spots for fish (Nagelkerken et al. 2008, Olson et al. 2019). Coastal habitats are major spawning and feeding habitats for many fishes, including iconic species such as rays and sharks (Laegdsgaard and Johnson 2001, Jackson et al. 2001*b*). The worldwide landing data of rays and sharks reported to the Food and Agriculture Organization of the United Nations (FAO) showed an increase of 227% from 1950, peaking in 2003, and subsequently declining by 20% in only 10 yr (Dulvy et al. 2014). This tremendous decline in the catch of elasmobranchs has been attributed mainly to overfishing (Davidson et al. 2016). They are commercially valuable for their fins, meat, liver-oil, and gill rakers (Clarke et al. 2006). The main driver of shark fishing is a global trade to meet Asian demand, coupled sometimes with declines of traditional fisheries (Clarke et al. 2006). Furthermore, deliberate and by-catch in elasmobranch fisheries were subjected to little management till very recently (Davidson et al. 2016).

West African waters are characterized by their richness in fishery resources and have been considered one of five remaining strongholds for elasmobranchs in the world (Stein et al. 2018). The area, however, has been subjected to systematic overfishing by both the international fleet and industrialized artisanal local fisheries over the last couple of decades (Meissa and Gascuel 2015, Belhabib et al. 2018). Beside the Asian market for sharks, an emerging market for the dry-meat of rays and sharks in West Africa has greatly expanded the overfishing of elasmobranchs (Diop and Dossa 2011). This market has led to the collapse of many ray and shark populations in Ghana and the surrounding counties (Diop and Dossa 2011), and is expanding rapidly to West Africa's most important marine protected areas (MPAs), such as the Bijagós Biosphere Reserve in Guinea-Bissau and the Parc National du Banc d'Arguin (PNBA) in Mauritania (Leurs et al. 2021).

The aim of this paper is to study the changes over the last century in fishing practices and its drivers and impacts to biodiversity and local economy in Africa's largest MPA: the Banc d'Arguin (Fig. 1). Our specific objectives were to (1) construct the chronology of fishing in Banc d'Arguin, (2) evaluate the changes in trophic levels over time, and (3) identify the main drivers of these changes and their socioeconomic impact on the local communities. We first used historical reconstruction of catches to analyze how the fishery in Banc d'Arguin has developed from local subsistence fishing on species low in the food web to international market-oriented fishing of top predators. Then, we used 22 yr of continuous quantitative monitoring to analyze changes in catch composition and the mTL of catch over time, as well as changes in total catch per trophic level. Due to the relatively recent expansion of the fishery in this remote area, we expected first an increase in the mTL (targeting apex predators) followed by a drop in the mTL after the reduction of the numbers of the top predators. Finally, we explored how societal changes of the local fishing community and the introduction of new technologies, together with insufficient implementation of regulations and emerging markets, have been driving a fishing transition from subsistence to the exploitation of top predators and how that impacts the socioeconomy of the local population.

Fig. 1. Map showing the position of the nine Imraguen fisher villages along Banc d'Arguin coast where traditional fishing on foot occurs (mainly before the 1970s), especially in front of the southern villages. Diameter of circles is proportional to the present-day number of lanches per village.



The history of the fishery in Banc d'Arguin

Traditional fishing of mullet

Flathead gray mullet (*Mugil cephalus*) is a diadromous and schooling fish that migrates between marine, brackish, and freshwater habitats during its life cycle (Chang et al. 2004, Whitfield et al. 2012). In Mauritania, mullet is mainly encountered in the sheltered coastal waters of Banc d'Arguin (Whitfield et al. 2012). It has been reported to perform seasonal migration patterns between its spawning area in the Senegal river and its feeding area at Banc d'Arguin (Bernardon and Mohamed Vall 2004). The Portuguese explorer Valentim Fernandez (1505, cited in Picon 2002) was the first to report the ancient way of Imraguen fishing on foot, targeting schools of mullet. To fish mullet, the Imraguen traditionally used a single net carried on their shoulders, locally known as "Chibkit el Atik" (Fig. 2B; Table 1). This net was also named "filet d'épaule" and it is made from local woodfiber, wrapped around a wooden stick (Maigret and Abdallahi 1976, Bernardon and Mohamed Vall 2004). In addition, Imraguen used a traditional fishing tool, locally called "azalla" (Boulay 2013), shown in Fig. 2C, which consists of an iron barbed spear used for hunting mullet driven toward the net.

Fig. 2. (A) Wooden sailing boat (lanche), origin of Canary Islands, introduced at the end of the 1960s and modified by Imraguen, suitable for navigation in shallow water and through the gullies of Banc d'Arguin. Their number is capped by Banc d'Arguin authorities at 114 units spread over 9 villages. This photo was taken at Nair (Iwik region) on January 2015 by E.M. El-Hacen. (B) Traditional shoulder nets "Chibkit el Atik" (filet d'épaule). The wire with floats and the weights of the net are made from local tree material and baked clay, respectively. The net is wrapped on wooden stick that serves as a support to transport it on the shoulders. Photo by Pierre Campredon. (C) Traditional harpoon "azalla," which consists of iron-teeth fixed on wooden stick. This spear is used alone or combined with filet "Chibkit el Atik" for mullet fishing. Photo by Mohamed Camara.

Fig. 3. The ancestral fishing of mullet performed on foot by Imraguen while walking or swimming a short distance at the shore. This is a type of sustainable artisanal fishing that was practiced for centuries and has disappeared now. (A) From the moment the mullet shoal is detected passing near the shore, the fishermen carry the nets on their shoulders and walk into the sea to encircle the school by the nets. (B) Fishermen closing the nets around the shoal of mullet, while some of them beat the water to chase the mullet into the net. (C) A fishing scene showing how mullets try to escape the encircled net. (D) Wrapping up the catch and get rid of unwanted species. Photos (A) & (D) by P. Campredon. Photo (B) by Jan van de Kam, and photo (C) was taken by T. Piersma, February 1980.

This tool is used especially in combination with "filet d'épaule," in fixed position, when fishing is practiced in the gullies. Women did not participate in the catching activities, but helped to remove mullet from the net and with the transport to the village. Afterwards, fish were processed in traditional ways into sun-dried meat (so-called "tichtar") and the so-called poutargue (mature ovaries, sun-dried) and heads of mullet were used to produce mullet oil.

On some occasions, fishing mullet on foot was done with the help of dolphins, especially in the southern settlements (Fig. 3). This practice has been documented in a film made by Jacques-Yves Cousteau in late 1970s (Boulay and Lecoquierre 2011). Both bottlenose dolphins (*Tursiops truncatus*) and Atlantic humpback dolphins (also called Cameroun River dolphins, *Sousa teuszii*) were shown to be "called in" by Imraguen to engage in fishing cooperation. Imraguen hit the water with sticks, and dolphins chase the schools of mullet toward the coast and into the nets of waiting Imraguen. In turn, dolphins are able to intercept the mullet schools on their way out to sea (Maigret and Abdallahi 1976, Picon 2002). However, the extent and importance of this practice to the people remains unclear.

Foreign fishery in Banc d'Arguin

Portugal was the first colonial power to settle in Banc d'Arguin and build a fort at Arguin Island that was occupied between the 15th and 18th centuries (Revol 1937 cited in Boulay 2013, Monod 1983). Others European settlers (Dutch and French) successively occupied and seized control of the island (Monod 1983, Picon 2002). Fishing attempts by all these settlers failed, with the exception of Canarian fishermen who practiced fishing on meagre (*Argyrosomus regius*) at Banc d'Arguin. They used wooden sailing boats (lanches) originating from the Canary Islands, locally called "E'Tmani" (Fig. 2A). Around the end of the 19th century, Canarian fishing was developed and fish were exported to the Canary Islands and even to Havana in Cuba. From the early 20th century, France colonized Mauritania. Following this, many French fishing projects were attempted, among them the "Société Industrielle de Grande Pêche (SIGP)" established in Nouadhibou city north of Banc d'Arguin, the only successful enterprise. This company produced salted and sun-dried fish for export and trade throughout African countries (Picon 2002). The SIGP was able to maintain their fish trade through barter trade deals with the Canarian and Imraguen fishermen. Imraguen learned from Canarian fishermen how to handle lanches, and some families even acquired such vessels in the 1930s, but these were used only for transport (Picon 2002). The SIGP introduced the method of processing fish using salt (Bernardon and Mohamed Vall 2004).

Introduction of lanches, new tools, and the fishing of top predators

The departure of Canarian fishermen in the late 1960s enabled the Imraguen to collect the abandoned lanches and buy active ones, reaching a total of ~70 boats in the mid-1970s (Maigret and Abdallahi 1976). Lanches are artisanal wooden boats measuring

Table 1. Inventory of fishing gear involved in the Imraguen fishery in the Parc National du Banc d'Arguin, Mauritania, and their characteristics.

Name	Net type	Mesh size (mm)	Length (m)	Fishing method	Target species	Depth (m)	Transport	Year of introduction	Impact
Filet d'épaule	Floating gillnet	100	18-20	Encircling	Mullet	1-1.5	Foot & lanches	Ancestral	Low impact
Filet el kasra	Fixed gillnet	120	50-100	Fixed	Various species	1-1.5	Foot	Ancestral	Low impact
Filet mulet	Floating gillnet	120	100	Encircling & fixed	Mullet	1-1.5	Lanches	1980s	High catch of mullet; deployment in the gullies causes catch of elasmobranchs
Filet courbine	Floating gillnet	200-240	200	Encircling	Meagre	6-10	Lanches	1968	High catch of elasmobranchs, especially large individuals of rays and hammerhead sharks
Filet tollo	Floating gillnet	140-160	100-150	Encircling/ stationary	Milk shark	4-6	Lanches	1968	High impact on sharks
Filet dorade	Floating gillnet	110-120	150	Encircling	Sea bream	1-5	Lanches	1970s	Causing catches of cownose ray and milk shark
Longline	NA	NA	NA	NA	NA	NA	Lanche	1970s	Low impacts on the elasmobranchs
Filet sole	Floating gillnet	100-110	50	Stationary	Flatfish species	4-5	Lanches	1980s	Causing catches of cownose ray and milk shark
Filet raies et requins	Floating gillnet	300-360	100	Stationary	Sharks and rays	1.5-6	Lanches	1986	Targeting guitarfishes and large sharks; causing catches of turtles
Filet courbine Balize aynou	Floating gillnet	240 and larger	300	Encircling/ stationary	Cownose ray	6-8	Lanches	2009	High impact on rays

7–11 m in length and 3–4 m in width and are dependent on the wind for their displacement (Fig. 2A). Usually, one "unit" of lanche-fishery is an association between the lanche owner and Imraguen fishermen who represent the captain and three to four sailors, but some Imraguen fishermen have their own lanches. The possession of lanches motivated Imraguen to exploit further zones and relatively deeper water for meagre fishing in 1969–1970 (Maigret and Abdallahi 1976) and to reach the far away mudflats never visited on foot. Since then, the habit of fishing on foot has progressively declined and is now rarely, if ever, practiced. In addition, Imraguen also acquired new fishing nets from Canarian fishermen locally called "filet courbine" and "filet tollo" used for meagre and small shark fishing (e.g., smooth hound shark, *Mustelus mustelus*) (Table 1). Meagre is a migratory species, and Banc d'Arguin is one of their most important spawning grounds in West Africa (Tixerant 1974). Like mullet, meagre move in schools, and Imraguen fish them by encirclement with two or more lanches. This resulted in a new fishing season for meagre, from February to June (Boulay 2013). Meagre fishing launched a new fishing practice targeting mainly large elasmobranchs, which attracted new international markets.

METHODS

Study system

The Parc National du Banc d'Arguin, Mauritania (Fig. 1) along the West African Atlantic coast is a large MPA since 1976, covering 20% of the whole Mauritanian shelf (i.e., 12,000 km²), equally divided into marine and terrestrial parts (Campredon 2000). The terrestrial part is mostly a dry desert with little human use except by nomadic herders (camels, sheep, and goats). Thus, the park is not affected by any agriculture runoffs or sewage contamination. The northwestern part of Banc d'Arguin borders the open sea and is connected with the nearby upwelling system. The southeastern part, or Banc d'Arguin proper, is a large intertidal area with shallow water (<20 m deep) (Sevrin-Reyssac 1993, El-Hacen et al. 2019). At low tide, a vast area of tidal flats, crossed by many gullies and covering about 453 km² (El-Hacen et al. 2020), is exposed, of which a variable but major portion is covered by dense seagrass meadows (El-Hacen et al. 2020). The area is a home to a rich marine fauna, including endemic species (Kide et al. 2016, Séret and Naylor 2016), as well as iconic species such as turtles (Hama et al. 2019), dolphins (Araujo and Campredon 2016), and large elasmobranchs (Valadou et al. 2006, Séret and Naylor 2016). Banc d'Arguin is also a major nursery and breeding ground for many endangered shark and ray populations (Valadou et al. 2006) and supports important bony-fish stocks in the region (Jager 1993, Schaffmeister et al. 2006, Guénette et al. 2014, Correia et al. 2020). The park is mostly famous for its wealth and richness in avian biodiversity (Altenburg et al. 1982, Wolff and Smit 1990), including two endemic species (Oudman et al. 2020) and the largest seabird colonies in West Africa (Campredon 2000, Araujo and Campredon 2016).

Due to the lack of freshwater and its geographical isolation, the area has been inhabited by only a small local population of fishermen called "Imraguen" (i.e., "those who gather life"), an ancient nomadic community that practiced subsistence fishing of mullet on foot (Fernandes 1506 cited in Lotte 1937, Maigret and Abdallahi 1976, Pelletier 1986, Bernardon and Mohamed Vall 2004, Boulay and Lecoquierre 2011). Imraguen used to live as semi-fishermen and part-time herd keepers, alternating seasons of pastoralism and fishing (Lotte 1937, Trotignon 1981, Dahou and Cheikh 2007). In the early 1930s, Imraguen settled in fixed small villages at the coast of Banc d'Arguin (Fig. 1). They still followed their long-standing traditional practices of fishing along the shorelines. To cross gullies, they used traditional small boats made from local material (called "al-musulmât," Ould Cheikh 2003), but they rarely used these boats for fishing. Furthermore, Imraguen did not have agricultural land or livestock farming as alternative sources unlike similar communities in neighboring countries (Tvedten 1990).

Socioeconomic aspects

Along the coast of Banc d'Arguin, the Imraguen lived semi-nomadic styles, following mullet during the dry season and practicing pastoralism during the wet season (Tvedten 1990), with little contact with other fishing communities in the wider region. Over the past few decades, the arrival of foreign merchants and fishermen who introduced lanches, new ideas, and means, have changed the way Imraguen live in terms of living conditions as well as social setting. However, the effects of the progressive changes in fishing techniques and interaction with outsiders on the socioeconomic conditions and livelihood of Imraguen remain unevaluated. Particularly, the values of the new emerging markets (regional and Asian) and their contribution to the Imraguen's daily income are unknown but merit investigation. Before the 1990s, the fishing practices in Banc d'Arguin hardly involved non-Imraguen. Since then, the crews on lanches have gradually become mixed with outsiders, not only from elsewhere in Mauritania but also from neighboring countries, such as Mali and Senegal. Nowadays, it is not uncommon to see crews dominated by non-Imraguen, including even the captains. Thus, it is important to assess how the inflow of foreign fishermen and merchants have affected the catch composition and the local economy.

Data sources

This study used two sources of information motivated by reliable data availability: (1) historical (before 1997), primarily a literature review combined with interviews with local knowledgeable fishermen and conservationists; (2) relatively recent information (1997–2020), based on an intensive quantitative fishing monitoring program.

Literature review and interviews

Due to the lack of historical quantitative data regarding fishing with primitive methods, we combined two different sources of information to trace back changes in target species, fishing techniques, as well as trading markets. Firstly, we qualitatively summarized published and unpublished information on targeted species, catches, gear, year, season, and fishing zone, mainly internal reports of PNBA, the Institut Mauritanien de Recherches Océanographique et de Pêches (IMROP), and the Fondation Internationale du Banc d'Arguin (FIBA). Secondly, we interviewed knowledgeable local fishermen and traders ($n = 18$), park wardens and managers ($n = 8$), and local fishery scientists ($n = 4$) on questions related to changes over the years in captured species, gear types, seasons as well as fishing zones. All targeted individuals for interviews have been acting in the area and witnessed changes in fishing practices over at least the last three decades.

Landings

A fishery monitoring program in the Parc National du Banc d'Arguin was set up in 1997 and conducted by IMROP. The monitoring program provided data on daily catch and effort at the landing sites (nine villages) in Banc d'Arguin, recorded by IMROP scientists based in these villages. Upon the arrival of each lanche, the name of the boat, species caught, fishing gear, fishing zone, total weight per species, and total fishing effort (days fished) were recorded on forms that were later digitized in a database.

Socioeconomic data

The socioeconomic analyses were based on two different types of data: (1) interviews and a literature review of the available information on fishing socioeconomic indicators in Banc d'Arguin, such as the intermediate consumption (costs) and the distribution of fishing benefits among stakeholders; and (2) quantities and values of landing catches, including prices of captured species per gear from 2006–2020. Only socioeconomic information collected at the landing sites in Banc d'Arguin were available. Thus, although we recognize them as a powerful and driving ecopolitical force, this study does not take into account revenues made at the national and international markets exclusively made by non-Imraguen.

Economic and financial revenues of fishery within Banc d'Arguin were calculated based on landing catches and their values (value of landings) at site per species/gear. The gross value of landings per year/gear is estimated as follows:

Gross value of landings = catch kg * Average price (USD/kg)

The net income benefit (added value) is calculated as the difference between gross value of landings at the landing site and total costs (i.e., food, gear repair). The gross value of landings is calculated per gear, as they can belong to different owners. The distribution of the generated added values (benefit) in our study area is usually as follows: 50% for the owner of the lanche, 17% for the captain, and 33% combined for the sailors (Tarbiya et al. 2012).

Data analyses

All statistical analyses were performed with the free software R (v. 4.0.2) (R Development Core Team, Vienna, Austria) in RStudio environment (v. 1.3.1073) (RStudio Inc., Boston, Massachusetts, USA). Historical fishing activity and practices obtained via literature review and interviews, such as changes in targeted species, fishing techniques, types of the net, fishing zone, and markets, were summarized in chronological order based on presence/absence data grouped at the family level.

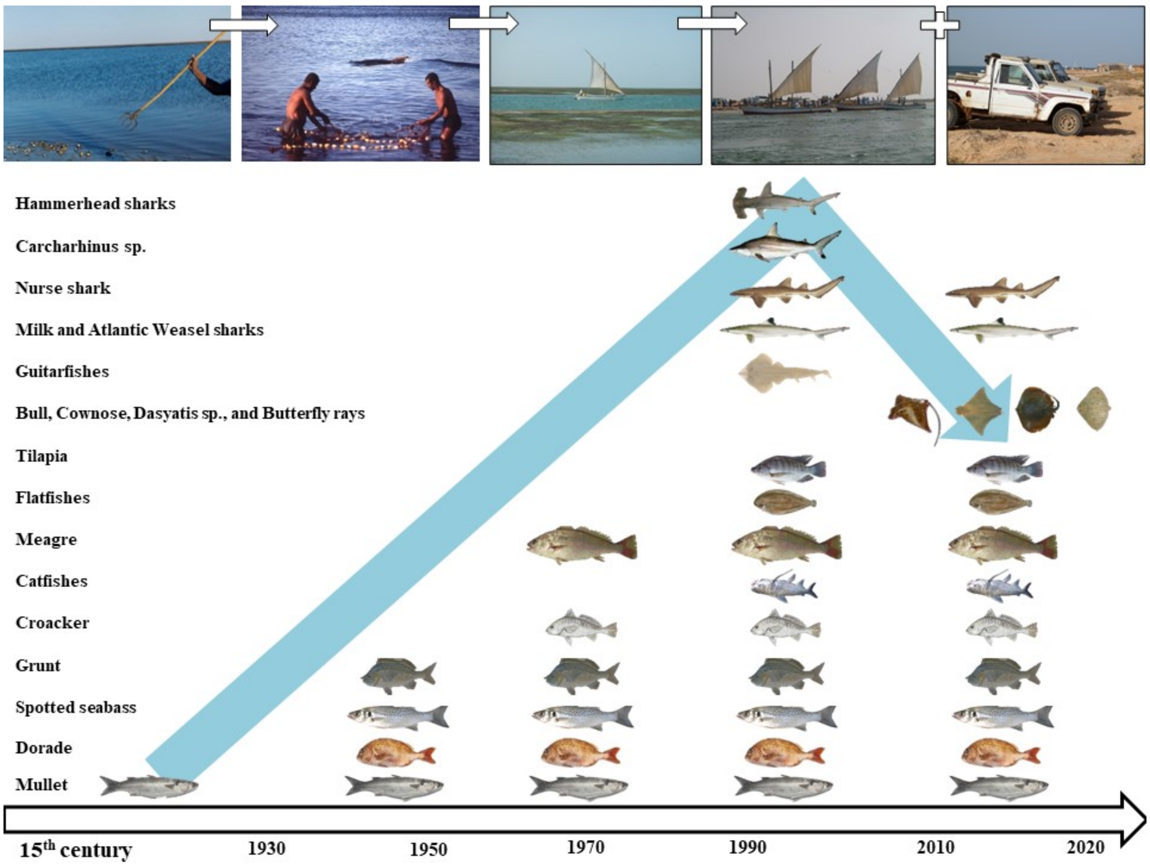
Mean trophic levels of the main targeted species were used to assess changes in catch composition over time. Species trophic levels were obtained from FishBase, a global information system on fishes. Mean trophic level of the total catch per year (kg) was estimated following Pauly et al. (1998):

$$\overline{mTL_k} = \frac{\sum_i TL_i \times Y_{ik}}{\sum_i Y_{ik}} \quad (1)$$

where Y_{ik} are the landings of species i in year k, and TL_i is the trophic level of species i.

Generalized additive models (GAMs), with a log link function and Gamma error distribution, were used to model the changes in mTL over time (yr). GAMs were chosen over linear regression, ARIMA, and LOESS due to their ability to handle uneven spacing of samples in time and to model non-linear trends in time series using powerful non-parametric smoothers (Wood 2017, Simpson 2018). Generalized additive models can estimate non-linear trends, provide estimates of the magnitude of change, identify periods of change, and account for the lack of

Fig. 4. Illustration showing a summary of the chronological changes in the fishing practices of Imraguen at Banc d'Arguin based on presence/absence data grouped at the family level (see Table S1). It indicates the fishing transition from mullet (down in the food web) to sharks and rays (top of the food web) and changes in fishing method. Photos on top show the timeline of changes in fishing practices from individual and small-scale collective fishing of mullet into subtidal fishing with the introduction of lanches, toward commercialization with the arrival of new skilled traders with cars. This illustration was inspired by Erlandson et al. (2009) and was based on a literature review and interviews. The first two photos from the left are by M. Camera and P. Campredon, and the last one by M. E. Feis.



independence (Simpson 2018). The GAM model was fitted by using gamm() function of the "mgcv" package with restricted maximum likelihood (REML) (Wood 2017), and accounted for temporal autocorrelation with CAR(1) process (Simpson 2018).

Quantitative data spanning 1997–2018 on daily catch (kg) per species per lanche were used to assess changes in total catch per TL over time. Total catch per trophic level was only estimated for the landing data (1997–2020), but not the historical period due to the lack of total catch per species. Generalized additive models were also used to model changes in total catch per TL over time (yr).

Linear regressions with least square method were used to model changes in landing values between 2006–2020 over time (yr). Furthermore, differences in added values between the different gears were tested with one-way anova.

RESULTS

Fishing activities over time

The chronology of fishing activities obtained via literature review and interviews showed two distinct fishing practices: traditional fishing with low impact on the food webs and a relatively recent commercialized fishing driven by fins and salted-meat markets (summarized in Fig. 4). Before the 20th century, fishing was traditionally practiced on foot and was subsistence based (Fig. 4; Table 1). This concerns only one targeted species, migratory mullet, at low trophic level in the food web (TL = 2). Mullet fishing was usually practiced during two periods: (1) in the warm season, from August to October in the center of Banc d'Arguin, when mullet migrate in to fatten up, and (2) in the cold season from December to February in the southern parts of the Banc d'Arguin, when their gonads have matured and mullet perform spawning migration southward to the breeding area. From the 20th century onward, when Imraguen settled in fixed villages, few coastal fishes were added to the catch using the so called "filet iderane" (Table 1). This new fishery was practiced mainly outside the mullet seasons and includes dorade (e.g., *Sparus* sp., *Dentex* sp., and *Diplodus* sp.), spotted seabass (*Dicentrarchus punctatus*), grunt (*Pomadasys* sp.), croaker (*Pseudotolithus* sp.) and catfish (*Carlarius* sp. and *Arius latiscutatus*) (Fig. 4; Table 1). The commercialization of fishing was restricted to small-scale exchanges of sun-dried mullet meat by barter trade deals for goods from nomadic tribes at the periphery of Banc d'Arguin and even at remote villages in the mainland. Imraguen continued this fishing mode until the 1970s, when they obtained new fishing nets and acquired Canarian lanches (Fig. 4; Table 1). These tools allowed them to move their fishing activities toward deeper zones to catch meagre and then sharks and rays (TL = 4), starting from the end of the 1970s.

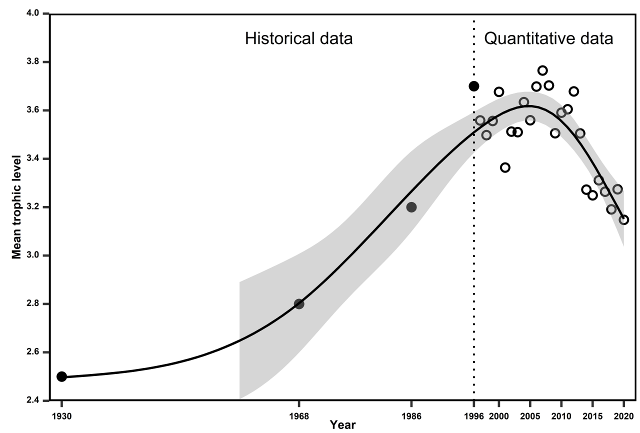
From the start, meagre fishing gave rise to the bycatch of elasmobranchs, especially Carcharhinidae blacktip shark (*Carcharhinus limbatus*), spinner shark (*Carcharhinus brevipinna*), Sphyrnidae hammerhead sharks (*Sphyrna* sp.), Ginglymostomatidae nurse shark (*Ginglymostoma cirratum*), and Myliobatidae lusitanian cownose ray (*Rhinoptera marginata*), all of which were processed also through the bacalhau technique. In the mid-1980s, fishing activities shifted progressively toward higher trophic levels, especially elasmobranchs, which became a major targeted species (Fig. 4; Table 1). The changes in fishing activities and targeted species were motivated by the arrival of skilled traders from neighboring countries (Senegal, Mali, and Ghana) with access to Asian elasmobranch fin markets. Furthermore, elasmobranch fishing was expanded to meet the demands of their salted-dried meat from sub-Saharan markets, especially in Ghana (see Append. 1 for details). The transition from subsistence to commercial fishing was consistent with the addition of top-predatory sharks (*Carcharhinus* sp.), hammerhead sharks, and nurse sharks (TL = 4), starting from the mid-1980s (Fig. 4; Table 1). Overall, elasmobranchs are never consumed by Imraguen fishermen; they are fished only for trade, especially their fins. Although there is no data on the catch during this instalment of commercial fishing, the boom of shark fishing for fins in 1989 in response to international markets in Asia provided the best revenue at the time.

Empirical evidence for the overfishing of Banc d'Arguin

Overall, more than 167 species were recorded in PNBA landing data since 1997, of which 33 are sharks and rays (Table A1). Since 1996, seven elasmobranch species have disappeared from the landings at the nine villages (Table A2). Over the course of time, mTL of Imraguen fishery showed significant non-linear trends (GAM smooth terms; $F_{(1, 28)} = 30.7$, $p < 0.001$, $R^2_{adj} = 0.86$, deviance explained = 89.3%), with first a steady increase that peaked from the mid-1980s to the early 2000s followed by a strong decrease over the last decade (Fig. 5). A doubling of mTL occurred in less than a decade starting from the mid-1980s (Fig. 5).

Analyses of the changes in total catches per trophic level over time showed a continuous increase in species at the base of the food web (TL1 & 2) over time, whereas top predator (TL3 and 4) catches showed an initial increase, followed by a strong decline over the last decade (Fig. 6). Overall, the contribution of TL3 and 4 to the landings has decreased by 18% in the last decade, whereas

Fig. 5. Changes in mean trophic levels (mTL) of fishery catches in Banc d'Arguin from 1930 to 2020. Historical data (closed dots) obtained from a literature review and interviews with artisanal fishermen and conservationists of the park. Quantitave data (open circles) from 1997 to 2018 were obtained from a daily landing monitoring program. Calculation of mTL of the quantitative data took into account the total catch (t) per species, whereas in the historical data, where no such data exist, mTL was just the average of the trophic levels of the reported species. The shaded area represents standard error of the mean.



that of TL1 and 2 increased also by 18%. The total catches of TL1 showed a significant positive trend over time (GAM smooth terms; $F_{(1, 24)} = 49.8$, $p < 0.001$, $R^2_{adj} = 0.92$, deviance explained = 94%). Similarly, the total catches of TL2 showed a significant positive trend over time (GAM smooth terms; $F_{(1, 24)} = 36.2$, $p < 0.001$, $R^2_{adj} = 0.81$, deviance explained = 84%). The trend of the total catches of TL3 was first significantly positive before 2010 and since then negative (GAM smooth terms; $F_{(1, 24)} = 14.4$, $p < 0.001$, $R^2_{adj} = 0.71$, deviance explained = 75%). Finally, the trend of the total catches of TL4 was also first significantly positive before 2008 and since then negative (GAM smooth terms; $F_{(1, 24)} = 9.8$, $p < 0.001$, $R^2_{adj} = 0.58$, deviance explained = 63%).

Socioeconomic aspects

Overall, the annual average fishery gross value of landings in Banc d'Arguin from 2006–2020 was ca. 1.1 million USD (Fig. 7A), of which 90% ended up as added value benefits (difference between total gross value of landings and total costs). The gross value of landings increased significantly over the years ($R^2 = 0.27$, $F_{(1,13)} = 6.2$, $p = 0.02$), although it was stable to a large extent at around 1 million USD/yr until 2014, then increased significantly to double in 2020 (Fig. 7A). Gear types are significantly associated with local revenue ($F_{(2, 222)} = 35.5$, $p < 0.001$; Fig. 7B). Traditionally, bony fish species captured with "filet mullet" contributed the most to the local economy (50% of the overall added values), followed by the mixed fishing on meagre and bycatches of large elasmobranchs captured with "filet courbine" (41%, 300,000 USD/year) (Fig. 7B). Surprisingly, the deliberate elasmobranch fishing (filet tollo) contributed only 9% to the overall added values (Fig. 7B). For the net income benefits, lanche owners earned on average 523,000 USD/year (50%) of the annual

Fig. 6. Changes in yearly landing catches in tonnes grouped per trophic levels (TL) from 1997 and 2020 obtained from the fishing monitoring program of Parc National du Banc d'Arguin (PNBA) conducted by the Institut Mauritanien de Recherches Océanographique et de Pêches (IMROP). Trophc level (TL) 1 includes mostly mullet and tilapia, TL2 catfish, TL3 rays, and TL4 meagre and sharks (see Table S1). Note differences in y axis scales.

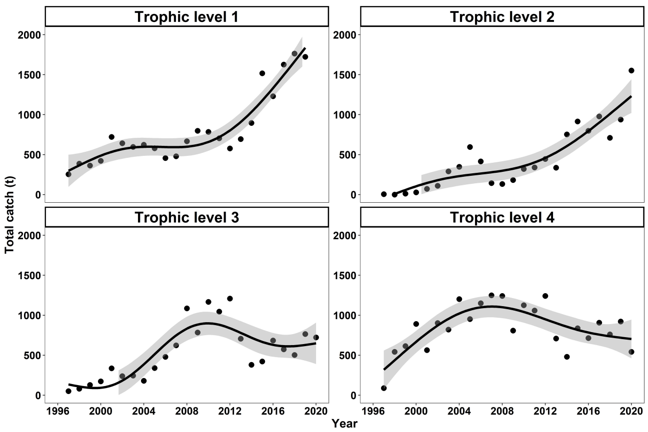
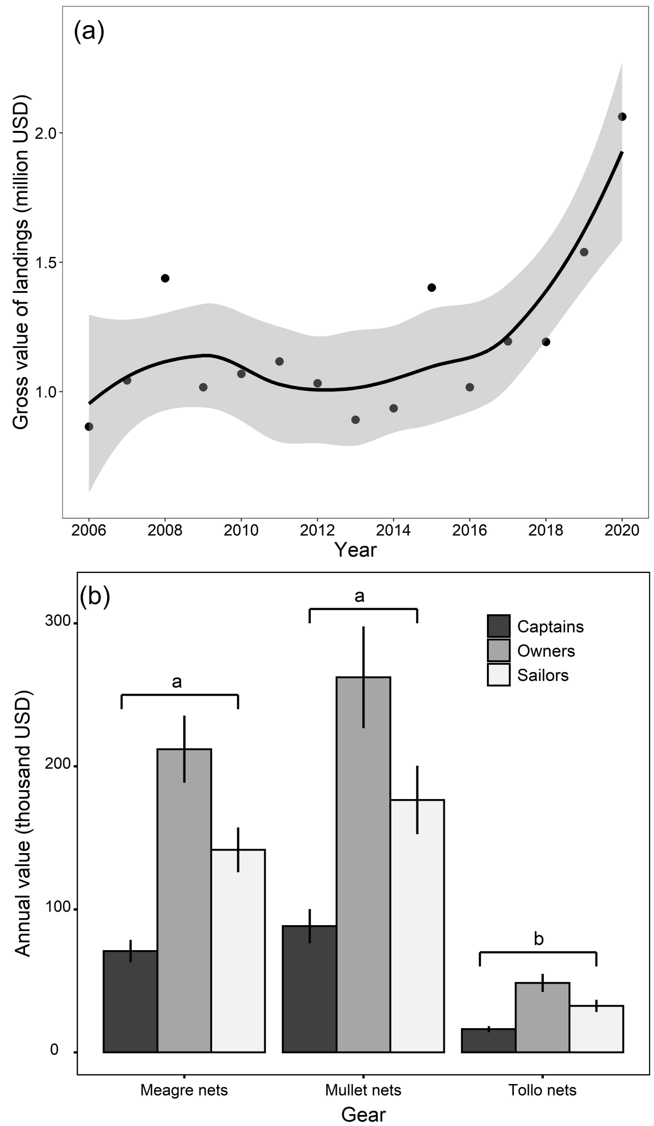


Fig. 7. (a) Changes in fishery gross value of landings (million USD) over time in Banc d'Arguin based on values of the captured species at landing sites. The shaded area shows the 95% CI. (b) Comparisons of the mean (± standard error) annual added values (thousand USD) between the different gear types. Significant differences between gear types are depicted with lower-case letters ($p \leq 0.05$). Different bars represent the share of the different stakeholders involved in the fishing operation. Species caught by each gear type are shown in Table 1.



added value, followed by sailors who earned on average 351,000 USD/year (33%), whereas captains earned on average 175,000 USD/ year (17%) (Fig. 7B).

DISCUSSION

Socioeconomic and technical drivers of the overfishing in Banc d'Arguin

Our results show that Imraguen subsistence fishing on foot had long targeted mainly small coastal bony-fishes until the 1970s, when it suddenly expanded to deeper zones with a focus on top predators such as elasmobranchs (Fig. 4). The acquisition of lanches and the arrival of new traders who invested capital in fishing and made attractive markets available were the two most important factors explaining the transition from subsistence to commercial fishing within Banc d'Arguin. The introduction of lanches in the area has contributed to improve the Imraguen fishing efficiency by expanding potential fishing grounds and increasing catches by expanding fishing on meagre and other small coastal fish (Maigret and Abdallahi 1976). This in turn led to an increased income for fishermen through the transport of artisanal fish products for commercialization at the nearby markets of Nouadhibou and Nouakchott (Boulay 2013). Furthermore, the impact of lanche fishing on the ecosystem and resources was considered light as long as the fishing fulfilled the criteria of subsistence fishing, i.e., only targeting migratory mullet and meagre species for local consumption (Harris et al. 2002). These two species have a high rate of reproduction and thus a good capacity for stock recovery (Abou Shabana et al. 2012, Gil et al. 2013, Espino-Barr et al. 2016). However, lanches were also used to commercialize fishing by their capacity of transport to market. Besides this, the lanches attracted capital invested in targeting elasmobranchs, which were not locally consumed but purely fished for commercial purposes (Maigret and Abdallahi 1976, Boulay 2013).

Similar patterns of change in small-scale fisheries from traditional to globalization happened many decades before in neighboring West African countries (Atta-Mills et al. 2004, Jönsson 2019, Moore et al. 2019). For instance, the use of destructive methods and overexploitation of stocks have destroyed the fishery business in Ghana, which jeopardized the livelihood of many millions of local communities (Danquah et al. 2021). The trade of elasmobranchs that was developed earlier in many neighboring countries led to the overexploitation and subsequent collapse of their local populations in the 1980s (Diop and Dossa 2011), and thus drove these African traders to seek new providers of their products, entering Banc d'Arguin in 1986–1989. In particular, the arrival of Ghanaian shark fin traders marked the onset of a shift in fishing practices within the Banc d'Arguin and the commercialization of targeted fishing on elasmobranchs (Diop and Dossa 2011). Traders provided loans and the new technology, including fishing gear (Table 1), along with opportunities for labor and processing methods of elasmobranch fins and meat. The fishing took a new organization in which capital is provided by traders, the lanches by the owners, and Imraguen do the actual fishing. It seems that the overfishing of rays and sharks and the collapse of their populations is following a serial sequence along the cost of West Africa, starting from Ghana and its surroundings and moving northward (Atta-Mills et al. 2004, Diop and Dossa 2011, Jönsson 2019, Moore et al. 2019). This moving wave of exploitation from areas with large markets after depletion into more remote areas has been documented before in other part of the world (Kirby 2004, Miller et al. 2014, Ellis et al. 2015). Unsustainable fishing practices can also result from indigenous fishers being replaced by international commercial companies. In many African countries, overfishing due to internationalized artisanal fishing is mainly associated with the improvement in both fishing technology and the capacity of boats (Belhabib et al. 2018, Temesgen et al. 2019). Also, the growth of the human population led to increasingly more people available to partake in the fishing activities. Together, these factors have increased fishing effort with artisanal methods to levels that now have exceeded that of industrial fisheries (Belhabib et al. 2018).

Historical changes in fishing practices from targeting low trophic levels in the food web for local use to targeting top predators for export have occurred all over the world (Pitcher 2001, Lotze and Milewski 2004, Dulvy et al. 2014, Belhabib et al. 2018). Archeological and historical studies have shown that many important fish species have been under tremendous exploitation pressure in many parts of the world from medieval times onward (Lajus et al. 2007, Barrett et al. 2011, Orton et al. 2014, Barrett 2019). An analysis of the bones of cod (*Gadus morhua*) from northern Scotland revealed that the catches were initially (9–12th centuries) local but were replaced by cod transported long distances in the 13th century (Barrett et al. 2011). A similar discovery also showed that the ancient DNA of stored cod recovered from a British wreck that sank in southern England in 1545 had been caught in Iceland and Newfoundland (Hutchinson et al. 2015). The cod fishery in Newfoundland was initially a low impact subsistence practice by a local population, the Beothuk indigenous people, and an important source of social and cultural identity; the later collapse of this fishery in the 1990s led to a major loss of jobs (Hutchings and Myers 1994, Lear 1998). In the Caribbean islands, an archeological study showed that many populations of reef fishes, including top predators, became heavily exploited only after the arrival and establishment of Europeans (Wing and Wing 2001). Sharks have also suffered severe losses in the Mediterranean Sea since the early 19th century from both commercial and recreational fisheries (Ferretti et al. 2008). Quantitative fishery data worldwide usually begin in the 1950s (Anticamara et al. 2011, Dulvy et al. 2014), and thus often lack the historical perspective. Most of these data miss the onset, and in many cases, the entire phenomenon, of overfishing due to globalization and technology advancement (Pauly 1995, Jackson et al. 2001*a*, 2011). Worldwide, the growth of commercial fishing as a result of improving the capacity of boat engines and refrigeration systems, which allowed the use of remote territories, explains overfishing and removal of the large apex species from marine systems.

Consequences on species composition and habitats

Our landing data suggest that, along the West African coast, in serial fishing of elasmobranchs, the Banc d'Arguin populations are currently the main targeted one (Fig. 6), and many species are on the verge of collapsing. Elasmobranchs are vulnerable even to "light" fishing mortality. This is due to their K-selected life history characteristics, such as slow growth, delayed maturity, long gestation, and the production of only a few young per litter (Dulvy et al. 2014). As a consequence, it is harder for elasmobranchs to recover following depletion compared with fast reproducing species. Elasmobranch fishing is not sustainable and exposes these species to high risks of extinction. Already, the common sawfish (*Pristis pristis*) has been declared extinct in Mauritania (Diop and Dossa 2011).

Considering their role in the ecosystem as top predators, overfishing of first sharks and then rays may expose the ecosystem of Banc d'Arguin to changes in the food web structure through trophic cascades and may affect the ecosystem functioning. The current increase of rays and smaller fish in the Imraguen catches is probably the result of the removal of the bigger sharks. Similar increases in smaller sized rays have been documented in the eastern USA following reductions of 11 large-sized shark species (Myers et al. 2007). In addition, the ongoing boom of the large West African Bloody cockle (*Senilia senilis*) population is also expected to be the result of the overfishing of sharks and rays. For instance, in Banc d'Arguin, bull/eagle rays (*Aetomylaeus bovinus*) and Lusitanian cownose rays (*Rhinoptera marginata*) appear responsible for episodic predation events on *Senilia*, a heavy-shelled mollusc that rays crack with their muscled jaws (Sasko et al. 2006, Serrano-Flores et al. 2019). As a consequence, the increase in the *Senilia* population has led to outcompeting smaller bivalves that occupy the same ecological niche such as *Dosinia* sp., a species that is preferred by shorebirds and has declined tremendously over the last decades (El-Hacen et al. 2020). These observed changes in benthic community contributed perhaps to the decrease of shorebird populations feeding on small benthic species (Oudman et al. 2020).

Socioeconomic and management aspects

Although the fishing at Banc d'Arguin is legally allowed only for Imraguen and for subsistence reasons, we found that most of the fishery revenues end up somewhere else (Fig. 7). For instance, benefits from the fishing of elasmobranchs, which is meant for international markets, are very marginal for the Imraguen; it represents only a small fraction of the final values estimated at the regional and international markets. Thus, our analyses suggest that fishing of elasmobranchs did not benefit Imraguen fishermen, nor contribute to improving their living conditions. In fact, most Imraguen work for a handful of families that own the largest number of lanches. Furthermore, the traders, as creditors and buyers, have control over fishing activities and product marketing. Through their monopoly, they can manipulate the prices in their favor. For this reason, fishing of sharks and rays currently does not contribute to the economic and social well-being of Imraguen fishermen, although it does benefit empowered traders and lanche owners (Kinadjian et al. 2012). In other words, the benefits from elasmobranch fishing are mostly transferred outside Banc d'Arguin and outside Mauritania, to the detriment of Imraguen fishermen and impairing the health of the ecosystem.

In addition, the economic projects of the donors proposed as alternatives to sharks and ray fishing have benefited only the minority engaged in the fishing of these resources, whereas most Imraguen remain on the margin (Boulay and Lecoquierre 2011). These are mainly the most active groups with local influence and relationships that have been involved in the projects. The lanche restoration project undertaken to restore old and broken lanches had a large consequence for sharks and rays. By the mid-1980s, most of the lanches that were left behind by the Canarian fishermen were in bad shape and needed restoration. Aimed at promoting sustainable fishing and alleviating poverty, this restoration project has constituted a lucrative investment for a minority and turned against conservation. These projects were not based on socioeconomic evidence regarding Imraguen historical fishing, nor on thorough past fishing histories elsewhere; the proposed techniques opened the door for more harmful fishing practices, such as elasmobranch bycatch and later deliberate targeting. The "filet courbine" that was supposed to form an alternative to "sharks and rays net" was misused in a way that harms conservation, and the lanches attracted investment to the fishery. This led to an increase in fishing effort through increasing the number of trips at sea, involving crews from outside Banc d'Arguin in the fishery, and directing fishing toward sharks and rays for commercial purposes (Boulay and Lecoquierre 2011). Nonetheless, these generous projects were supposed to be accompanied by strict surveillance and monitoring of the activities of fishermen and how they used the offered fishing means. Surveillance, however, was not always implemented and depended strongly on the willingness of the managers of the park, which showed quite some turnover during the last decade.

In order to properly manage the fishery of Banc d'Arguin and stop the overfishing of elasmobranchs, a holistic view and the engagement of all the national and international stakeholders are mandatory. We showed that the main technological and socioeconomic drivers of the fishery of Banc d'Arguin lay outside its borders (i.e., external markets), aside from that Banc d'Arguin is too large to control by patrolling, which is often very costly and suffers from the lack of continuous funding. The co-management approach that includes Imraguen provides a strong ground to implement conservation measures, but can hinder the ban on some fishing practices that Imraguen find important to support their livelihood, including a few elasmobranch species. The co-management approach marked some positive results with the short shark and ray fishing moratorium in 2003, which provided Imraguen with alternative livelihood means in order to cease elasmobranch fishing. One of the main challenges in the management of the elasmobranch fishery in Banc d'Arguin is the absence of a national policy. Whenever the PNBA actively bans elasmobranch catches and processing, foreign fishermen and merchants operating in the system simply move and establish themselves outside its borders, which stimulates an illegal and uncontrolled fishery. Nowadays, the Bellewakh site, which is located just south of Banc d'Arguin, is a major shark and ray processing site, including many endangered species (see Append. 1). Thus, a co-management approach with a focus on improving the livelihood of Imraguen by mitigating the loss of the added values of their fishery to foreigners, together with nationally coordinated conservation measures, is the way to go to stop the ongoing overfishing of Banc d'Arguin.

CONCLUSION AND RECOMMENDATIONS

Historically, Imraguen fishing in Banc d'Arguin was for subsistence and was seasonal, but over the last 40 yr, fishing became commercial. This transition occurred in two phases: (1) before 1986, Imraguen fishing was seasonal and focused on migratory mullet and to a lesser extent meagre—with some effort spent on small fish in the off seasons; all fish was used locally; (2) from 1986 onward, with the two fishing seasons still respected, the fishing added new species of sharks and rays for their fins and salt-dried meat for export to markets in Asia and the West Africa sub-Sahara, respectively.

Although the catch of elasmobranchs is now decreasing, the species are still caught with an even greater effort, but smaller catches (per unit effort) (S.C. Lemrabott et al., *unpublished manuscript*). This suggests that the Imraguen now harvest the top predators in the Banc d'Arguin marine food web. Nevertheless, the story of fishing at the Banc d'Arguin provides an ecological history rarely documented, as most marine ecosystems already experienced the removal of top predators before documentation began (Lotze et al. 2006).

The observed overfishing in Banc d'Arguin is driven by both regional and international factors including: (1) the acquisition of wooden boats (lanches) from the Canarian fishermen in 1970s, which allowed Imraguen to expand their fishery into deeper zones and to add pelagic species to their catches; and (2) the arrival of new experienced fishermen and merchants from neighboring countries, especially Ghana, who brought new advanced techniques and regional (elasmobranch dried meat) as well as international (shark fins) markets.

We recommend that the decision makers of Banc d'Arguin take stronger steps toward ending elasmobranch fishing using a co-management approach with the Imraguen. This could be achieved by placing all species of sharks and rays under a capture moratorium just as in 2003–2004 (see Append. 1) and by raising awareness and enabling communication for effective implementation of management rules and conservation. The above actions must all be translated into material understandable by the unschooled Imraguen and should create pilot projects for village development. We also recommend mitigating the loss to foreign fishermen and merchants of added benefit values of the fishery. It is especially important to ban all possession and trade of ray and shark products as well as their export at a national level in Mauritania. This ban will prevent the products that are sold as by-catch, whereas in reality it is resulting from targeted catches, which will destroy the market for these products, reduce demand, and cascade down to reduced captures.

Author Contributions:

HO, SYCL, TP, EME, and AA conceived the ideas and designed methodology; SYCL CBB, and ACB collected the data; EME and SYCL analyzed the data; SYCL, EME, and AL led the writing of the manuscript with significant input from TP and HO. All authors contributed critically to the drafts and gave final approval for publication.

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Data Availability:

Data supporting the findings of this study are available from the authors and will be archived and made publicly available in the University of Groningen Research Data Repository (http://www.rug.nl/research/gelifes/research/data-management/repository?lang=en)

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Appendix 1

The chronology of overfishing in a remote West-African coastal ecosystem

Changes in Imraguen fishing activities over time

Historically, Imraguen fished mostly Flathead grey mullet *Mugil cephalus* (Bernardon and Mohamed Vall 2004, Maigret and Abdallahi 1976). This fishing practice has changed progressively with the introduction of Canarian sailing wooden boats, new nets and means, and access to new markets. First, the introduction of the wooden boats motivated Imraguen to target meagre (*Argyrosomus regius*) and exploit new fishing grounds (Picon 2002). The bycatch of meagre fishery attracted new traders and fishermen from the region, which rapidly changed Imraguen traditional and subsistence way of fishing (see below for details).

At the end of the 1970s, artisanal motorboats were introduced in Mauritania for fishing outside Banc d'Arguin on meagre (Boulay 2013). At the same time, the arrival of motorized trucks and cars opened Banc d'Arguin for new arrivals of fishermen and traders from other regions of Mauritania, but also from African countries, such as Senegal, Mali and Ghana. The period of these new arrivals was characterised by the overfishing of sharks and rays, a fishery now accessible to the long operating fishing markets in the other African countries. This contributed to the introduction of elasmobranch fishing at Banc d'Arguin around 1986-87, especially through Senegalese traders seeking elasmobranch-fins for Asian market (Diop and Dossa 2011). The Senegalese traders provided some Imraguen fishers with new fishing nets called "filet raies-requins" (Table 1) to target the yet-unexploited large populations of elasmobranchs. Firstly, fishing was directed towards Carcharhindae species (such as blacktip shark and spinner shark), hammerhead sharks (*Sphyrna* sp) and nurse sharks, with important bycatch of guitarfishes (*Rhinobatos* sp.) and largetooth sawfish (*Pristis pristis*). These species were targeted as response to the demand for elasmobranchs' fins from Hong-Kong and Taiwan markets (Diop and Dossa 2011). From then on, elasmobranch fishing nourished finning (cutting off the fins) activities for trade, while the carcasses (bodies without fins) were thrown out.

From 1989, shark fishing and the associated finning activities were expanded with involvement of new fishers motivated by the high revenue of fins. As a result, the catches of large sharks decreased by 1995 (Ducrocq et al. 2004). In the meantime, the elasmobranchs trade attracted new foreign people, mainly from Mali and Ghana as fishing now added guitarfish species with the allocation of a special fishing season from February to August (Boulay 2013, Ducrocq et al. 2004). Catches of guitarfish were large to the point that carcasses were disposed of board immediately after cutting off the fins, so that their mass and volume did no longer hinder the lanches during their sailing. Meanwhile, “filet tollo” was used to especially target small shark species such as milk shark (*Rhizoprionodon acutus*) and smooth-hound shark (Fig. S1). Along with these changes, a new synthetic thread was introduced for the netting of "filet mulet" (Table 1) which had close characteristics of the traditional "filet d'épaule".

From 1996, Ghanaian traders launched the processing of carcasses of elasmobranchs with salt in processing pits (Fig. S2). This activity rapidly expanded among Banc d'Arguin villages, to respond to the demand of meat from Ghanaian markets and those of neighbouring countries. At this point sharks and rays became the focus of Imraguen fishing. In addition, fishing is directed towards catfishes, which are also processed in pits, to respond to the demand mainly from markets in Mali. Fresh fish such as mullet, meagre, tilapia, flatfish and dorade were traded on the local markets with the growing availability of ice in Banc d’Arguin villages.

Until the mid-1990s, the only fishing rule being implemented was the restriction of fishing to lanches as the only boats authorised to fish within the boundaries of the Parc National du Banc d'Arguin, its number capped to 114 units. Before the 1990s, bycatch prevention and knowledge of the specific biodiversity of exploited marine ecosystems were not of interest to managers. This situation led to such high catches of shark and ray that scientists and conservationist involved with Banc d’Arguin became concerned about the threats on these vulnerable species. Since then, the issue of shark and ray fishing became a central point in the discussions in the scientific council of PNBA.

Furthermore, to mitigate shark and ray fishing, the PNBA, supported by FIBA, in 1998 launched a co-management process including an annual meeting involving PNBA, scientists, donors, and Imraguen. These groups aimed to implement fishing rules, on the one hand, and to create some locally economic projects on the other hand, through restoration of dilapidated lanches therewith increasing the income for and the local development of Banc d’Arguin fishermen community. The minutes of these meetings were issued by the PNBA authorities to act as a consensual regulation of fishing (memo nº 253/03 of 2004, Teichott workshop convention 2017). In addition, annual IMROP-PNBA working group meetings were held to analyse fishery data. The recommendations of this group provided useful tools for decision making and to adjust fishing rules (Braham 2015, 2010). The process resulted in successful agreement with Imraguen fishermen in 2003 to stop targeting sharks and rays, especially guitarfishes and blacktip sharks (Diop and Dossa 2011, Ducrocq et al. 2004). Further, it was agreed to move fishing activities away from intertidal mudflats, where elasmobranchs catch occurred, towards the northern, deeper areas of Banc d'Arguin. There fishermen were converted to meagre fishing. However, meagre fishing entails important bycatch of large rays, especially lusitanian cownose ray. Therefore, fishermen shifted in 2008 towards that species using a special net, locally known as "filet courbine Balize aynou" which is the same as filet courbine, but with a large mesh size (Braham and Taleb Sidi 2014). This led to catches of other large rays as well, including bull ray (*Aetomylaeus bovinus*), stingrays (*Dasyatis* sp), and butterfly rays (*Gymnura* sp).

Fig. A1. (a) One of the first documented illegal catch of sharks in Banc d'Arguin by Senegalese fishermen camping at Kiji island, photo by T. van Spanje in 1989. (b) Ongoing cut of shark fins (finning) at the Bellewakh processing site, just south of Banc d'Arguin. Photo taken by E.M. El-Hacen in May 2016.

Fig. A2. The processing of sharks and rays in ground pits or concrete wells in the Imraguen villages. The carcasses of sharks and rays are put in pits and covered with a layer of salt and with plastic to get a salty fermenting meat in about two weeks. This photo was taken at Ebelq eiznaya beach, north western Iwik village, photo by Han Olff in May 2015.

Table A1: Inventory of species and group of species encountered in the catches of Imraguen fisheries within Banc d'Arguin, over the time. The signs 1 and 0 note that the species was involved or not in fishing, respectively. Historical data (before 1997) are based on literature review and interviews, while the relatively recent (1997-2020) data are based on the daily monitoring of the landings of fishery at Banc d'Arguin.

Scientific name	**Common name**	**Trophic level (TL)**	**TL groups**	**5000 BP - XVII**	**XVII-1930**	**1931-1967**	**1968-1980**	**1981-2018**
Acanthocybium solandri	Wahoo	4.3	TL 4	0	0	0	1	1
Acanthurus monroviae	Monrovia doctorfish	2.5	TL 1	0	0	0	1	1
Aetomylaeus bovinus	Bull ray	3.8	TL 3	0	0	0	0	1
Alectis alexandrina	Alexandria pompano	3.6	TL 3	0	0	0	1	1
Argyrosomus regius	Meagre	4.3	TL 4	0	1	0	1	1
Arius latiscutatus	Rough-head Sea catfish	3.3	TL 3	0	0	1	1	1
Auxis rochei rochei	Bullet tuna	4.4	TL 4	0	0	0	1	1

Auxis thazard thazard	Frigate tuna	4.4	TL 4	0	0	0	1	1
Balistes punctatus	Bluespotted triggerfish	3.4	TL 2	0	0	0	1	1
Boops boops	Bogue	2.8	TL 1	0	0	0	1	1
Bothus podas	Wide-eyed flounder	3.4	TL 2	0	0	0	1	1
Brachydeuterus auritus	Bigeye grunt	3	TL 2	0	0	0	1	1
Campogramma glaycos	Vadigo	4.5	TL 4	0	0	0	1	1
Caranx hippos	Crevalle jack	3.6	TL 3	0	0	0	1	1
Caranx rhonchus	False scad	3.6	TL 3	0	0	0	1	1
Carcharhinus brevipinna	Spinner shark	4.2	TL 4	0	0	0	0	1
Carcharhinus falciformis	Silky shark	4.5	TL 4	0	0	0	0	1
Carcharhinus limbatus	Blacktip shark	4.4	TL 4	0	0	0	0	1
Carcharhinus obscurus	Dusky shark	4.3	TL 4	0	0	0	0	1
Carcharhinus plumbeus	Sandbar shark	4.5	TL 4	0	0	0	0	1
Carcharhinus signatus	Night shark	4.6	TL 4	0	0	0	0	1
Carlarius heudelotii	Smoothmouth sea catfish	3.8	TL 3	0	0	1	1	1
Carlarius parkii	Guinean sea catfish	4.1	TL 4	0	0	1	1	1
Cephalopholis taeniops	Bluespotted seabass	4.4	TL 4	0	0	0	1	1
Chelon auratus	Golden grey mullet	2.8	TL 1	0	0	1	1	1
Chelon dumerili	Grooved mullet	2.7	TL 1	0	0	1	1	1
Chloroscombrus chrysurus	Atlantic bumper	3.5	TL 3	0	0	0	1	1
Citharus linguatula	Spotted flounder	4	TL 4	0	0	0	1	1
Coptodon guineensis	Guinean tilapia	2.8	TL 1	0	0	0	1	1
Coryphaena hippurus	Common dolphinfish	4.4	TL 4	0	0	0	1	1
Cynoglossus cadenati	Ghanian tonguesole	3.4	TL 2	0	0	0	1	1
Cynoglossus monodi	Guinean tonguesole	3.6	TL 3	0	0	0	1	1
Cynoglossus senegalensis	Senegalese tonguesole	3.6	TL 3	0	0	0	1	1
Dactylopterus volitans	Flying gurnard	3.7	TL 3	0	0	0	1	1
Dasyatis centroura	Roughtail stingray	3.8	TL 3	0	0	0	0	1
Dasyatis hastata	Stingray	3.8	TL 3	0	0	0	0	1
Dasyatis marmorata	Marbled stingray	3.6	TL 3	0	0	0	0	1
Dasyatis pastinaca	Common stingray	4.1	TL 4	0	0	0	0	1
Dentex angolensis	Angolan dentex	3.5	TL 3	0	0	1	1	1
Dentex canariensis	Canary dentex	3.6	TL 3	0	0	1	1	1
Dentex gibbosus	Pink dentex	4.1	TL 4	0	0	1	1	1
Dentex macrophthalmus	Large-eye dentex	3.5	TL 3	0	0	1	1	1
Dentex maroccanus	Morocco dentex	3.9	TL 3	0	0	1	1	1
Dicentrarchus punctatus	Spotted seabass	3.9	TL 3	0	0	1	1	1
Dicologlossa cuneata	Wedge sole	3.3	TL 2	0	0	0	1	1
Diplodus bellottii	Senegal seabream	3.6	TL 3	0	0	0	1	1

Diplodus cervinus	Zebra seabream	3	TL 2	0	0	0	1	1
Diplodus puntazzo	Sharpsnout seabream	3.2	TL 2	0	0	1	1	1
Diplodus sargus	White seabream	3.4	TL 2	0	0	1	1	1
Diplodus vulgaris	Common two-banded seabream	3.5	TL 3	0	0	0	1	1
Drepane africana	African sicklefish	3.1	TL 2	0	0	0	1	1
Echelus myrus	Painted eel	4.3	TL 4	0	0	0	1	1
Elops lacerta	West African ladyfish	4.2	TL 4	0	0	0	1	1
Engraulis encrasicolus	European anchovy	3.1	TL 2	0	0	0	1	1
Ephippion guttifer	Prickly puffer	3.6	TL 3	0	0	0	1	1
Ephippus goreensis	East Atlantic African spadefish	3.5	TL 3	0	0	0	1	1
Epinephelus aeneus	White grouper	4	TL 4	0	0	0	1	1
Epinephelus caninus	Dogtooth grouper	3.8	TL 3	0	0	0	1	1
Epinephelus costae	Goldblotch grouper	3.9	TL 3	0	0	0	1	1
Epinephelus itajara	Atlantic goliath grouper	4.1	TL 4	0	0	0	1	1
Epinephelus marginatus	Dusky grouper	4.4	TL 4	0	0	0	1	1
Ethmalosa fimbriata	Bonga shad	2.5	TL 1	0	0	0	1	1
Eucinostomus melanopterus	Flagfin mojarra	3.4	TL 2	0	0	0	1	1
Euthynnus alletteratus	Little tunny	4.5	TL 4	0	0	0	1	1
Fistularia tabacaria	Cornetfish	3.7	TL 3	0	0	0	1	1
Galeocerdo cuvier	Tiger shark	4.5	TL 4	0	0	0	0	1
Galeoides decadactylus	Lesser African threadfin	3.6	TL 3	0	0	0	1	1
Gerres nigri	Guinean striped mojarra	3.2	TL 2	0	0	0	1	1
Ginglymostoma cirratum	Nurse shark	4.2	TL 4	0	0	0	0	1
Gymnothorax maderensis	Sharktooth moray	4.1	TL 4	0	0	0	1	1
Gymnura altavela	Spiny butterfly ray	4.5	TL 4	0	0	0	0	1
Gymnura micrura	Smooth butterfly ray	3.6	TL 3	0	0	0	0	1
Katsuwonus pelamis	Skipjack tuna	4.4	TL 4	0	0	0	1	1
Lagocephalus laevigatus	Smooth puffer	4	TL 4	0	0	0	1	1
Lagocephalus lagocephalus	Oceanic puffer	3.7	TL 3	0	0	0	1	1
Leptocharias smithii	Barbeled houndshark	3.8	TL 3	0	0	0	1	1
Lichia amia	Leerfish	4.5	TL 4	0	0	0	1	1
Lithognathus mormyrus	Sand steenbras	3.4	TL 2	0	0	0	1	1
Lobotes surinamensis	Tripletail	4	TL 4	0	0	0	1	1
Lutjanus agennes	African red snapper	4	TL 4	0	0	0	1	1
Lutjanus dentatus	African brown snapper	4	TL 4	0	0	0	1	1
Lutjanus goreensis	Gorean snapper	4	TL 4	0	0	0	1	1
Merluccius merluccius	European hake	4.4	TL 4	0	0	0	1	1

Merluccius senegalensis	Senegalese hake	4.5	TL 4	0	0	0	1	1
Mobula birostris	Giant manta	3.5	TL 3	0	0	0	1	1
Mugil capurrii	Leaping African mullet	2	TL 1	0	0	1	1	1
Mugil cephalus	Flathead grey mullet	2.5	TL 1	0	1	1	1	1
Mullus barbatus barbatus	Red mullet	3.1	TL 2	0	0	0	1	1
Muraena helena	Mediterranean moray	4.2	TL 4	0	0	0	1	1
Muraena melanotis	honeycomb moray	3.5	TL 3	0	0	0	1	1
Muraena robusta	Stout moray	4	TL 4	0	0	0	1	1
Mustelus mustelus	Smooth-hound	3.8	TL 3	0	0	0	1	1
Mycteroperca rubra	Mottled grouper	4.1	TL 4	0	0	0	1	1
Myliobatis aquila	Common eagle ray	3.6	TL 3	0	0	0	0	1
Negaprion brevirostris	Lemon shark	4.3	TL 4	0	0	0	0	1
Oblada melanura	Saddled seabream	3.4	TL 2	0	0	0	1	1
Orcynopsis unicolor	Plain bonito	4.5	TL 4	0	0	0	1	1
Pagellus acarne	Axillary seabream	3.8	TL 3	0	0	0	1	1
Pagellus bellottii	Red pandora	3.8	TL 3	0	0	1	1	1
Pagrus auriga	Redbanded seabream	3.8	TL 3	0	0	0	1	1
Pagrus caeruleostictus	Bluespotted seabream	3.7	TL 3	0	0	1	1	1
Pagrus pagrus	Red porgy	3.9	TL 3	0	0	1	1	1
Paragaleus pectoralis	Atlantic weasel shark	4.3	TL 4	0	0	0	0	1
Parapristipoma octolineatum	African striped grunt	3.6	TL 3	0	0	0	1	1
Pegusa lascaris	Sand sole	3.3	TL 2	0	0	0	1	1
Pentanemus quinquarius	Royal threadfin	3.6	TL 3	0	0	0	1	1
Plectorhinchus mediterraneus	Rubberlip grunt	3.5	TL 3	0	0	1	1	1
Pomadasys incisus	Bastard grunt	3.8	TL 3	0	0	1	1	1
Pomadasys jubelini	Sompat grunt	3.3	TL 2	0	0	1	1	1
Pomadasys perotaei	Parrot grunt	3.3	TL 2	0	0	1	1	1
Pomadasys rogerii	Pigsnout grunt	3.6	TL 3	0	0	1	1	1
Pomatomus saltatrix	Bluefish	4.5	TL 4	0	0	0	1	1
Pristis pristis	Largetooth sawfish	4	TL 4	0	0	0	0	1
Psettodes belcheri	Spottail spiny turbot	4.1	TL 4	0	0	1	1	1
Psettodes bennettii	Spiny turbot	4.2	TL 4	0	0	1	1	1
Pseudotolithus senegalensis	Cassava croaker	3.8	TL 3	0	0	1	1	1
Pseudotolithus senegallus	Law croaker	3.9	TL 3	0	0	1	1	1
Pseudotolithus typus	Longneck croaker	3.7	TL 3	0	0	0	1	1
Pseudupeneus prayensis	West African goatfish	3.2	TL 2	0	0	0	1	1
Rachycentron canadum	Cobia	4	TL 4	0	0	0	1	1
Raja miraletus	Brown ray	3.7	TL 3	0	0	0	0	1

Remora australis	Whalesucker	3.5	TL 3	0	0	0	1	1
Remora remora	Shark sucker	3.5	TL 3	0	0	0	1	1
Rhinobatos albomaculatus	Whitespotted guitarfish	4.1	TL 4	0	0	0	0	1
Rhinobatos cemiculus	Blackchin guitarfish	4	TL 4	0	0	0	0	1
Rhinobatos irvinei	Spineback guitarfish	3.8	TL 3	0	0	0	0	1
Rhinobatos rhinobatos	Common guitarfish	4.1	TL 4	0	0	0	0	1
Rhinoptera marginata	Lusitanian cownose ray	3.8	TL 3	0	0	0	0	1
Rhizoprionodon acutus	Milk shark	4.3	TL 4	0	0	0	0	1
Rhynchobatus luebberti	African wedgefish	4.4	TL 4	0	0	0	0	1
Sarda sarda	Atlantic bonito	4.5	TL 4	0	0	0	1	1
Sardina pilchardus	European pilchard	3.1	TL 2	0	0	0	1	1
Sardinella aurita	Round sardinella	3.4	TL 2	0	0	0	1	1
Sardinella maderensis	Madeiran sardinella	3.2	TL 2	0	0	0	1	1
Sarotherodon melanotheron	Blackchin tilapia	2.5	TL 1	0	0	0	1	1
Sarpa salpa	Salema	2	TL 1	0	0	0	1	1
Schedophilus velaini	Violet warehou	4.2	TL 4	0	0	0	1	1
Sciaena umbra	Brown meagre	3.8	TL 3	0	0	0	1	1
Scomber colias	Chub mackerel	3.9	TL 3	0	0	0	1	1
Scomberomorus tritor	West African Spanish mackerel	4.3	TL 4	0	0	0	1	1
Selene dorsalis	African moonfish	4;1	TL 4	0	0	0	1	1
Seriola carpenteri	Guinean amberjack	4.5	TL 4	0	0	0	1	1
Seriola dumerili	Greater amberjack	4.5	TL 4	0	0	0	1	1
Serranus scriba	Painted comber	3.8	TL 3	0	0	0	1	1
Solea senegalensis	Senegalese sole	3.3	TL 2	0	0	0	1	1
Solea solea	Common sole	3.2	TL 2	0	0	0	1	1
Sparus aurata	Gilthead seabream	3.7	TL 3	0	0	1	1	1
Sphyrna lewini	Scalloped hammerhead	4.1	TL 4	0	0	0	0	1
Sphyrna mokarran	Great hammerhead	4.3	TL 4	0	0	0	0	1
Sphyrna zygaena	Smooth hammerhead	4.9	TL 4	0	0	0	0	1
Spondyliosoma cantharus	Black seabream	3.3	TL 2	0	0	0	1	1
Stromateus fiatola	Blue butterfish	4	TL 4	0	0	0	1	1
Syacium guineensis	Papillose flounder	3.3	TL 2	0	0	0	1	1
Synaptura cadenati	Guinean sole	3.5	TL 3	0	0	0	1	1
Taeniura grabata	Round stingray	4	TL 4	0	0	0	0	1
Thunnus alalunga	Albacore	4.3	TL 4	0	0	0	1	1
Thunnus albacares	Yellowfin tuna	4.4	TL 4	0	0	0	1	1
Thunnus obesus	Bigeye tuna	4.5	TL 4	0	0	0	1	1
Thunnus thynnus	Atlantic bluefin tuna	4.5	TL 4	0	0	0	1	1

Trachinotus ovatus	Pompano	3.7	TL 3	0	0	0	1	1
Trachurus trachurus	Atlantic horse mackerel	3.7	TL 3	0	0	0	1	1
Trachurus trecae	Cunene horse mackerel	3.5	TL 3	0	0	0	1	1
Triaenodon obesus	Whitetip reef shark	4.2	TL 4	0	0	0	0	1
Trichiurus lepturus	Largehead hairtail	4.4	TL 4	0	0	0	1	1
Umbrina canariensis	Canary drum	3.4	TL 2	0	0	0	1	1
Umbrina cirrosa	Shi drum	3.4	TL 2	0	0	0	1	1
Zeus faber	John dory	4.5	TL 4	0	0	0	1	1

Table A2. Shark and ray species, which have disappeared from the landings in Banc d'Arguin. The disappearance of these species at the top the food web points out an overfishing of top-predators.

Species	**Last record**
Pristis pristis	1996
Carcharhinus signatus	2007
Mobula birostris	2008
Carcharhinus plumbeus	2008
Carcharhinus obscurus	2009
Rhinobatos irvinei	2009
Rhynchobatus luebberti	2009