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Research

Multi-secular and regional trends of aquatic biodiversity in European Early Modern paintings: toward an ecological and historical significance

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ABSTRACT. Works of art are testimonies to past civilizations and biodiversity, and provide fundamental information for guiding current conservation programs. The success of such programs requires an understanding of the reference state of ecosystems, which is rarely known because current references are in perpetual slippage toward the acceptance of degraded states. For this reason, international organizations are regularly alerted to the fact that fish and aquatic resources are threatened, signaling a major challenge for our societies. In this article we aim to enrich the historical and ecological knowledge of aquatic resources in Western Europe (Atlantic, North Sea, and Mediterranean Sea) by analyzing the taxonomic composition of aquatic biodiversity as represented in Early Modern paintings, using the statistical tools of numerical ecology. The geographic and temporal variations of the biodiversity represented in these paintings are interpreted according to environmental and human pressures, which we differentiate between using technical and socio-cultural "sieves." Our results highlight the natural and anthropic factors that shape the spatial and temporal variations of the aquatic species depicted. These species belong to significantly different periods and regions, with a convergence between the origin of the paintings and the biogeographic area of the species. We show an overall decrease over time of represented taxa, and particularly of continental and freshwater species. We discuss the results in the light of previous works of historical ecology, archeology, history, and biology. Finally, we discuss the relevance and potential future contributions of the method developed herein to better understand the past reference state of aquatic socio-ecosystems.

Key Words: *art; biodiversity; freshwater; historical ecology; marine; painting*

INTRODUCTION

Biodiversity has been depicted in art by humans for the past 35,000 years, thus constituting a major source of inspiration for mankind. Art works and historical legacy are testimonies of past biodiversity and civilizations, and provide crucial information for the orientation of current conservation and restoration programs. Indeed, the implementation of such programs requires sufficient knowledge of the reference state, or baseline, of an ecosystem. When this baseline needs to be more accurately informed, art works from the past, reviewed from a historical point of view, can provide valuable clues (Guidetti and Micheli 2011). This is especially true for aquatic socio-ecosystems that are particularly affected by the biodiversity crisis (Worm et al. 2006), and in which the preservation of resources represents a major human and societal issue (Liquete et al. 2013, Schwerdtner Máñez et al. 2014). Indeed, previous studies have shown strong evidence of the existence of shifting baseline syndrome specific to exploited marine ecosystems (Papworth et al. 2009), meaning a generational amnesia leading to the loss of the reference state (Pauly 1995). Further to this, Jackson et al. (2001) used an innovative method involving paleoecological, archaeological, and historical data to study the long-term impact of overfishing on ecological communities. Numerous marine biologists have since engaged in historical approaches applied to exploited marine ecosystems (e.g., Schwerdtner Máñez et al. 2014), usually using trophic models to validate and interpret past variations of marine biodiversity (e.g., Lotze et al. 2011). More recently, a few freshwater ecosystems have been studied to permit the reconstruction of long-term historical changes of exploited fish populations in rivers (e.g., Lenders 2017, Haidvogl 2018) and lakes (e.g., Schmidt et al. 2011). In his review of historical ecology, Szabó (2015) classified this field as a mainly ecosystem-centered approach (in contrast to human-centered approaches), aware that the overall research trend combines ecology and anthropology. The present article clearly belongs to these last categories because it treats a typical human production: art.

We propose in this article to investigate artistic representations of aquatic biodiversity using a transdisciplinary approach corresponding to the main author's specialties: ecology and history. As undertaken by Begossi and Caires (2015), we will use the occurrence of artistic representations of aquatic species as temporal and geographical indicators to better inform the past composition of these species and their abundances.

Aquatic biodiversity in art: an overview in Europe

Aquatic biodiversity in art is an infrequent but constant motif. In their introduction to 80 examples of fish imagery in art, Moyle and Moyle (1991) summarized the depiction of fishes in this way, and their notion was corroborated by the similar approach that Charmantier (2014) applied to crustaceans. The European cave art bestiary dating from prehistoric times consists essentially of large mammals. Depictions of aquatic biodiversity are rare, and even the fishes are difficult to identify (Cleyet-Merle 1990), with the notable exception of the salmon figuring in "l'Abri du poisson" (Eyzies de Tayac), which dates back 25,000 years and shows the typical morphology of a spawning specimen. Only a few aquatic species can be dated back to the Bronze and Iron Age Scandinavian civilizations, and they are poorly recognizable (e.g., the fish of the Kivik royal grave, Sweden, 600 years BCE). With a history of earlier artistic traditions, many Mediterranean civilizations represented aquatic biodiversity in a more realistic way: the open sea fauna of the Minoans (Crete, between 2700 and

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1200 BCE), coastal fishes, crustaceans and mollusks in Greek, Sicilian, Campanian, Paestan, and Apulien pottery (between 800 and 100 BCE, see Delorme [1987], McPhee and Trendall [1987] and Metzger [1990] for more details), the representations of live aquatic organisms in Roman mosaics (from 500 to 100 BCE, as reported by Guidetti and Micheli in 2011), or the still lifes featuring sea food in Xenia style mosaics. Later, during the Middle Ages, fish took on Christian symbolism, and the realism of their representation was no longer of concern. It was not until the Renaissance that the depiction of aquatic biodiversity became recognizable again. The Early Modern period in Europe started with the Renaissance and ended with the Industrial Revolution, spanning approximately the years 1500 to 1800. These three centuries saw an increase of artistic productions in all fields, with painting persisting as the major medium in figurative art until the invention of photography (Gombrich et al. 1997).

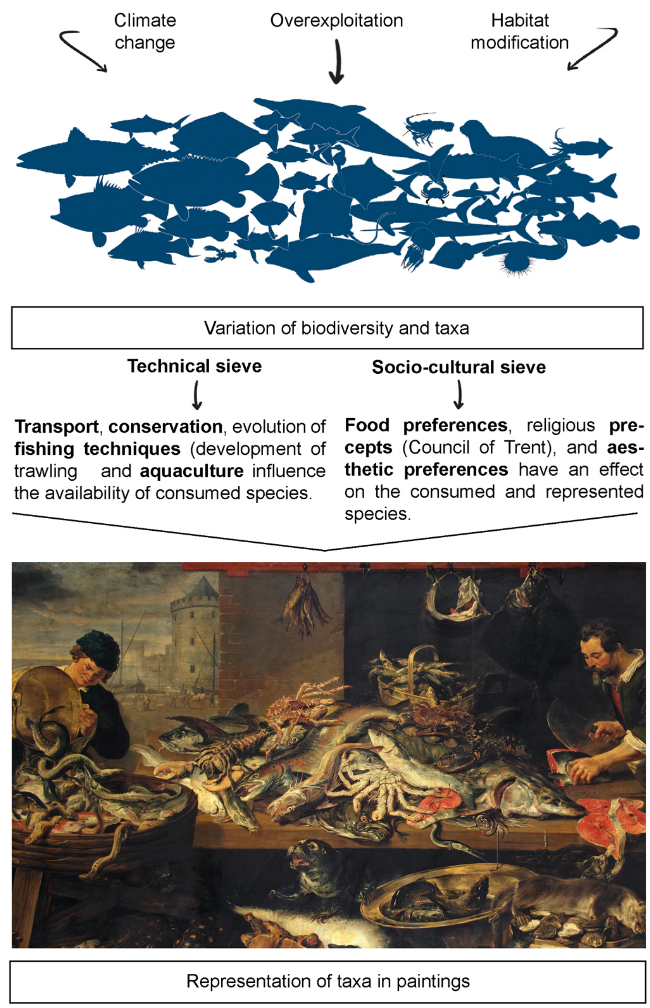
Purposes of the present study

The objective of the present study is to analyze the taxonomic composition of aquatic biodiversity represented in European Early Modern paintings, using the statistical tools of numerical ecology. First, we undertake a set of explanatory analyses to identify the main variations in the pictorial representation of aquatic biodiversity across space and time. Second, statistical tests and representations are used to analyze these variations more precisely, according to the biological and biogeographical characteristics of the species. Finally, we endeavor to interpret these variations in the light of historical hypotheses related to technical and socio-cultural factors that may influence the representation of species in painting. To address ecological significance, we took into account ecosystem variations in relation with the biogeography of the species and trends in population changes.

Surprisingly, such a transdisciplinary study has never been done before. A search in the Web of Science revealed only one similar study on paintings (Goddeeris et al. 2002), which concerned a single artist, Frans Snyders, and which was limited to the depiction of birds seen from a single socio-cultural angle, that of gastronomy. To our knowledge, there are only two publications that carry out statistical analyses of the frequency of fish images: the first explores archival photographs of fishing competitions (McClenachan 2009), and the second examines naturalistic drawings that do not pre-date the 19th century (Fortibuoni et al. 2010).

Before a given species can be represented in a painting, many different conditions must align. Large-scale spatial and temporal variations in the depiction of aquatic biodiversity may reflect changes in climate, overexploitation, and habitat modification (Fig. 1). For this reason, we have applied two main "sieves" to sort the representations of aquatic taxa in paintings. First, a technical sieve that determines the availability of the specimen: Has it been caught with a specific fishing technique, or raised by aquaculture before being transported to the place where the artist worked? This knowledge is often made possible thanks to the depiction of special conservation techniques in the paintings. Second, a socio-cultural sieve that sorts primarily according to food preferences, interrelated with fishing, aquaculture, and conservation techniques. The aesthetic choices of the artist are also related to this last category.

Fig. 1. Main selection sieves of species represented in paintings. Painting: Snyders, Frans. Fish Market. Flanders, between 1618 and 1621. Oil on canvas. Image is used from https://www.hermitagemuseum.org, courtesy of The State Hermitage Museum, St. Petersburg, Russia.



Our approach involves four steps: the collection of a sufficient number of paintings to enable statistical analysis, the identification of species or taxa, the study of their spatial and temporal variations, and finally, the interpretation of these variations through the identification of ecosystem variations (under natural and human pressures) and socio-cultural (or historical) sieves that are involved in the selection of the depicted species. These interpretations are described in the Discussion because they are based primarily on historical assumptions rather than on the statistical analyses performed in this study.

This study of paintings representing aquatic biodiversity over three centuries and across the different regions of Europe provides the opportunity to better understand the variation of the taxonomic composition of the different periods and regions through socio-cultural and technical sieves. These elements will constitute relevant keys for an improved understanding of the evolution of aquatic socio-ecosystems during the Early Modern period.

METHODS

Studied regions

The European peninsula is bounded to the north and west by the Atlantic Ocean and to the south by the Mediterranean Sea. Following Longhurst (2007), this region comprises two distinct provinces: the Northeast Atlantic Continental Shelf (NECS) and the Mediterranean Sea (MEDI), which are physically separated by the Straits of Gibraltar. Abundant oceanic precipitations feed numerous inland rivers and lakes of the Atlantic coast, to the contrary of the dry climate surrounding the Mediterranean Sea. This contrasted climate and the common geological history of the Mediterranean region explain the existence of many aquatic marine or continental endemic species (Tortonese 1985, Bianchi and Morri 2000, Boudouresque 2004, Coll et al. 2010, Tierno de Figueroa et al. 2013). The Atlantic region hosts more widely distributed species, some of which have been very important for human consumption since prehistoric times, but that are not adapted to the Mediterranean environment, e.g., Atlantic salmon (*Salmo salar* Linnaeus 1758), Atlantic herring (*Clupea harengus* Linnaeus 1758), and Atlantic cod (*Gadus morhua* Linnaeus 1758).

Period

The Early Modern period in Europe, spanning the years 1500 to 1800, is included within the longer climatic cooling period known as the Little Ice Age that began at the beginning of the 14th century and ended at the end of the 19th century (Lamb 1967, Le Roy Ladurie 1993). The effects of this climate change as represented in art, and especially in painting, have been well documented by several authors (Neuberger 1970, Burroughs 1981, Neuberger and Thornes 2005).

During this 300-year period, the European population doubled (De Vries 1994). This trend was particularly significant in Northern Europe, in countries such as Ireland, Belgium, or England, which are all important fishing countries. Central European countries experienced an average progression. On the contrary, Southern countries increased in population by only two-thirds for many reasons, including the Thirty Years War during the first half of the 17th century, several outbreaks of plague, the emigration of Protestants to the North, and the shift of the main trade routes from the Mediterranean to the Atlantic.

This period is characterized by the intensification of exchanges both within Europe and between Europe and the rest of the world, made possible by the discovery of remote ecosystems and by the development of distant fisheries that were able to return their catches to Europe thanks to very well-controlled conservation processes, e.g., salting and smoking. As a luxury commodity, the trade in fresh seafood acquired structure at the national level with the establishment of special wholesale fishmonger routes. For instance, the "Chasse-marées" vessels were able to supply Paris with fresh seafood, 100 km from the sea (Fontaine-Bayer 1993, Robert 2018). New fishing techniques, such as benthic trawling or pair trawling, became more widespread. Inland fish farming, mostly practiced by monks, was essential for food during the 40 days of Christian Lent before Easter, when no other meat or animal products were eaten. This food ban was renewed at the beginning of this period with the Council of Trent (1545–1563). All these factors provided many opportunities for painters seeking inspiration from subjects of aquatic biodiversity.

Just as portrait artists painted from living subjects, the Renaissance witnessed the advent of still life painting in connection with "Vanitas," symbolizing the ephemeral nature of life and associated with the Protestant religious reforms, the practice of Christian Lent, and the consumption of fish. From the 16th to the 17th centuries, art, science, and techniques progressed simultaneously, carried forward by the same people. In the 18th century, the Age of Enlightenment led to the exploration of scientific approaches, which would finally lead to the separation of art and science, a rupture that goes beyond the scope of our study. At roughly the same time, new artistic movements broke away from realism, leading finally to Impressionism in the 19th century and the production of artworks where the depiction of species as such remained non-recognizable "impressions."

Data sources

Most of the paintings we examined were obtained by searching the web using museum databases or grouped museums databases such as "Joconde" in France (Ministère de la Culture, France, http://www2.culture.gouv.fr/documentation/joconde/fr/pres.htm). The objective was to have the most reliable information on the artist behind each painting, the location, and the period of the work. The paintings (n = 73) were selected for their realism, and a sufficiently good quality image had to be available to enable species identification. Some museums were questioned directly to ensure the traceability of the painting and to obtain quality reproductions and copyrights.

Data treatment

Species selection, identification, and characterization

The depicted species were identified by a panel of more than 10 specialists from three different institutions (see Acknowledgements). A protocol was determined by the panel in order to adopt the level of precision they deemed necessary. For each painting, every specimen or group of specimens of the same species was identified using a figure that corresponded to one line in a data frame that was filled in by each specialist to indicate presence (1)/absence (0). Finally, many of the presumed "species" identified were not determined at the species level and are identified in the text as taxon/taxa. They were all described using the appropriate taxonomic level following TAXREF nomenclature. Any representations of shells without their living organism inside, and any obviously mounted fishes such as pufferfish (Tetraodontidae), were excluded from identification because of their obvious provenance from worldwide collections (e.g., "Cabinet of Curiosities") rather than belonging to the local available aquatic biodiversity. The few algae were also excluded they are not portrayed with the same fidelity as the fauna. The size of specimens was not retained because their relative lengths are not necessarily respected in the paintings.

Every taxon was characterized by its biogeographical status and habitat group using the Ocean Biodiversity Information System (OBIS) database and the French Freshwater fish guide (Keith et al. 2020) with the following nomenclature: Biogeographical Status (European; Atlantic and North Sea; Mediterranean; Introduced);

and Habitat Group (Continental; Migratory and Pelagic Amphihaline; Sea; Sea-Benthic; Sea-Demersal; Sea-Pelagic). When these data were available, trophic level, maximum size, weight, and lifespan were determined for fishes using FishBase (https://www.fishbase.org). Fishing gear was identified following the authors' expertise for the period.

Positioning of paintings in space and time

We assigned each painting to a period and a region according to the artists' attribution currently in use by the museum. The life of each artist (n = 41) was documented using Bénézit (2006) and the website of the Netherlands Institute for Art History (https://rkd.nl/en/explore/artists). The date and places of birth and death were the most consistently known elements of information, alongside the major town of activity. This distribution was determined in order to have a sufficient number of paintings for a statistical analysis of spatial and temporal variations.

General distribution of the taxa across the paintings

For regions and periods alike, we analyzed the distribution of taxa in two steps: (i) first, main distribution trends were highlighted using multivariate analyses and then, (ii) the relationship between these trends and the biological and biogeographical characteristics of the species were analyzed using statistical tests and comparisons of proportions. In order to highlight the distribution of taxa across the paintings, we used the non-normalized principal component analysis (PCA) available in FactoMineR (Lê et al. 2008). PCA is a dimensionality-reduction method that aims to determine the principal components of a data set, based on the variance of combined variables. We used this method herein to visualize how well the principal components fit the variables of interest (region and period), and thus to identify a pattern in the representation of taxa across space and time. Non-normalized PCA was chosen in order to keep the respective variances of each variable (data are centered but not standardized). In order to test the relationship between regions of representation and the distribution of taxa according to their characteristics (Biogeographical Status, Habitat Group, Trophic Level, and Fishing Gear), we performed Pearson's chi-squared tests based on the counts of each taxon across regions. To quantify more precisely the distribution of each taxon, we compared the proportion of their presence in the paintings of each region (in %) and calculated the difference of proportion between the two regions. Thus, if the obtained value is positive, the taxon appears mainly in the Atlantic-North Sea region, whereas a negative value indicates that the taxon is mainly represented in Mediterranean paintings. We used this method to quantify each taxon according to Biogeographical Status, Habitat Group, Trophic Level, and Fishing Gear.

To analyze the relationship between the distribution of taxa and the three periods (16th, 17th, and 18th centuries), we performed the same set of chi-squared tests. We then plotted the residuals of each variable for significant chi-squared tests. To analyze the variations of the representation of each taxon individually during the three periods, we then calculated the standard deviation of the count of each taxon within the three periods.

Focus on selected taxa

In order to identify the most representative species of the geographical and temporal distribution of the different taxa, we selected the taxa that exhibited the most variance in the previous PCA (at least 80% of the explained variance). We then performed a second non-normalized PCA using the selected taxa.

RESULTS

Identified species and taxa

Among the 73 selected paintings (Appendix 1), 126 taxa were identified, including 67 families among 34 different orders (Appendix 2). The most represented classes were Actinopterygii (i.e., ray-finned fishes, 69%) and Malacostraca (i.e., crustaceans, 10%). These taxa are all commercial, and are fished for food. Other represented classes were Mammalia (i.e., mammals, 5.5%), Bivalvia (i.e., mollusks with two shells, 4.5%), Elasmobranchii (i.e., sharks and rays, 3.5%), Cephalopoda (i.e., squids, octopus, and cuttlefish, 2.5%), Reptilia (turtles 2%), Gastropoda (i.e., snails, 1.5%), Petromyzontidae (i.e., lampreys, 1.5%), and Echinoidae (i.e., sea urchins, < 1%). Represented taxa were from both marine environments (80%) and freshwater environments (20%). Note the absence of whales from the corpus. We also identified an introduced taxon: *Cyprinus carpio*, Linnaeus 1758 (i.e., common carp).

General distribution of paintings in space and time

The 73 paintings have been attributed to 41 artists who were active in two regions, the Atlantic Ocean-North Sea and the Mediterranean Sea (Fig. 2a) during three periods (the 16th, 17th, and 18th centuries (Fig. 2b). Further to the distribution of the artists by city within the two regions, we identified two schools of art: the Flemish School (related to the Atlantic and North Sea) and the Italian School (related to the Mediterranean). We partitioned the 73 paintings as follows (Table 1): those representing Atlantic-North Sea species (n = 44), and those depicting Mediterranean species (n = 29). They date from the 16th (n = 23), the 17th (n = 28), and the 18th (n = 22) centuries. Note that the dataset is rather unbalanced regarding the geographic origin of the paintings. However, the Pearson's chi-squared test based on the count of each taxon across the three periods was not significant for Biogeographical Status (p-value = 0.643), showing that the imbalance in the paintings dataset did not affect the distribution of taxa across the three time periods.

Table 1. Number of paintings by period and region.

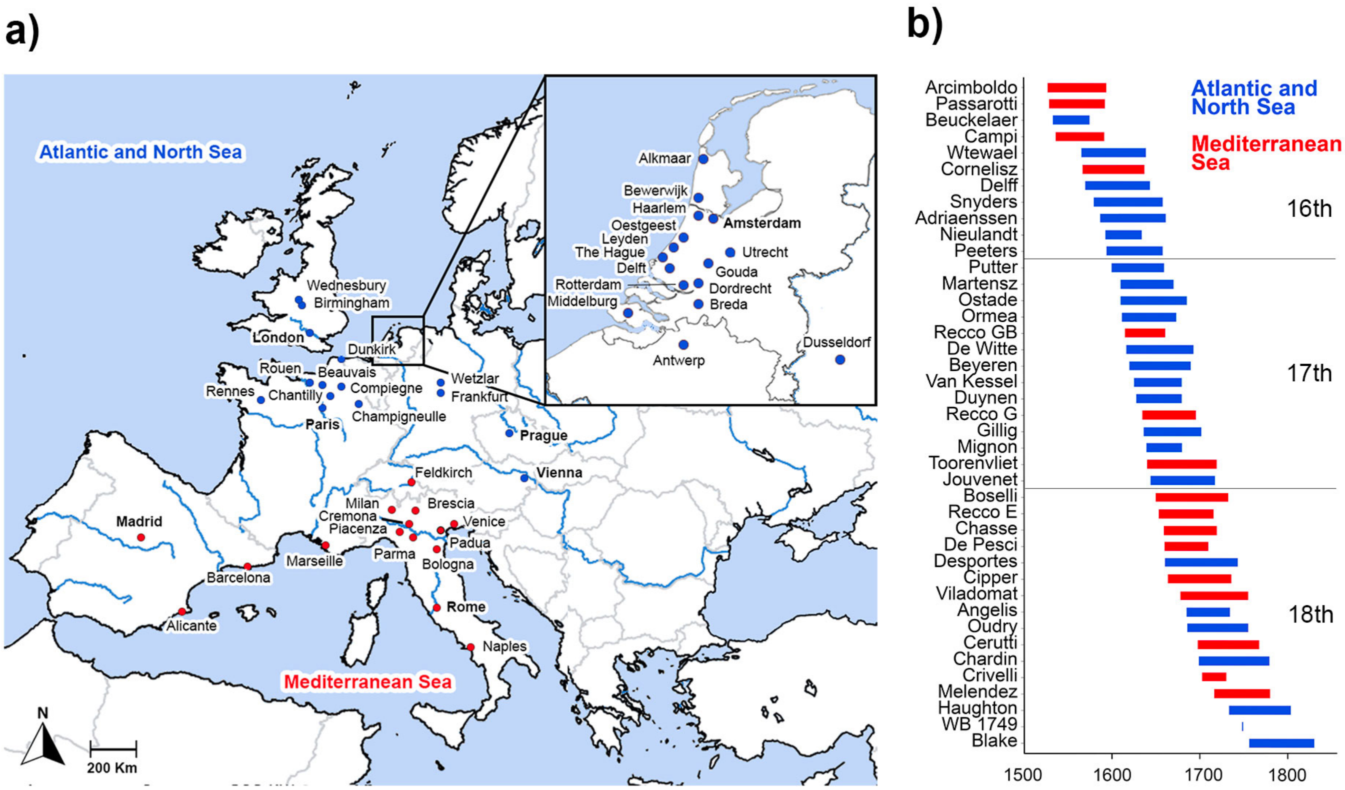
	16th Century	17th Century	18th Century	Total
Atlantic-North Sea	15	19	10	44
Mediterranean	8	9	12	29
Total	23	28	22	73

General distribution of the taxa across the paintings

Distribution of the taxa across regions

The distribution of taxa in the Atlantic-North Sea and Mediterranean paintings was seen to depend on the biogeographical origin and the natural habitat of the taxa. Indeed, Pearson's chi-squared test (based on the count of each taxon across regions according to Biogeographical Status and Habitat Group) showed a significant relationship (respectively, p-value = 9.971 x 10-16 and 1.464 x 10-08), while tests based on

Fig. 2. Locations and dates of birth and death of the artists included in the study. (a) Location of the cities of birth and death, and of the main activity of the artists included in the study with delineation of their zonal belonging. (b) Dates of birth and death of the artists, colored according to their region of origin.



Trophic Level and Fishing Gear were not significant (p-values = 0.021 and 0.285, respectively).

Generally speaking, the region in which a taxon was represented was consistent with the geographical origin of the painting, showing that painters tended to represent the taxa they could observe locally. Regarding the habitat, Mediterranean paintings showed more pelagic taxa, suggesting that these species were probably more targeted by the Mediterranean fisheries. To visualize more precisely the distribution of each taxon according to its Biogeographical Status and Habitat Group across regions, we plotted the proportion of taxa (in %) in the given region for each painting (see Fig. 3b).

Distribution of the taxa across periods

The abundance (in %) of each class of taxa according to the three periods is shown in Fig. 4a. All classes except Malacostraca and Bivalvia showed a decrease between the 17th and 18th centuries. Reptilia, Petromyzontidae, and Mammalia (harbor porpoises, Eurasian otters, seals and dolphins) were depicted in the 16th and/ or 17th centuries, but disappear (except Delphinidae) from the 18th century paintings. Conversely, Gastropoda (snails) and Echinoidea (sea urchins) are present only from the 18th century. The abundance (in %) of each taxon in the three periods is plotted in Fig. 4b. To identify the taxa with the highest shifts during the periods, we performed the standard deviations of abundance across the three periods, and selected the first decile of this distribution (n = 13 taxa).

The Pearson's chi-squared tests based on the count of each taxon across the three periods showed a significant relationship with Habitat Group (p-value = 0.002) and Trophic Level (p-value = $9.427.10^{-7}$), but not for Biogeographical Status (p-value = 0.643) and Fishing Gear (p-value = 0.046). Values of the residuals for chi-squared tests of Habitat Group and Trophic Level are shown in Fig.4c.

Focus on selected taxa

Identified groups

In order to identify the most representative species of the geographical and temporal distribution of the different taxa, we performed a first PCA using all the taxa of the dataset (explained variance: Axis 1 = 10.82 %, Axis 2 = 7.90%). We then selected the 20 taxa with the highest explained variance of the previous PCA (80% of the explained variance) and performed a second non-normalized PCA by using these 20 selected taxa (explained variance: Axis 1 = 20.09 %, Axis 2 = 15.98%, Fig. 5a). Axis 1 was mainly explained by taxa represented in (i) Mediterranean paintings from the 18th century, and (ii) Atlantic-North Sea paintings from the 16th and 17th centuries (99% of the explained variance). This suggests that the abundance of Atlantic-North Sea taxa decreased from the 17th. Axis 2 was mainly explained by freshwater taxa (74% of the explained variance). The PCA was thus composed of three groups: one of freshwater taxa, with the exception of *C. harengus* (Group 1), a second group of taxa mainly represented in Atlantic-North Sea paintings from the 16th and

Fig. 3. Representation in paintings of taxa by region. Differences between the proportions (in %) of paintings (located in the Mediterranean Sea and in the Atlantic-North Sea) where each selected taxon is represented. Left panel: taxa colored according to Biogeography. Right panel: taxa colored according to Habitat Group. Only the taxa with a difference of more than 5% between the Atlantic-North Sea and the Mediterranean Sea are shown.

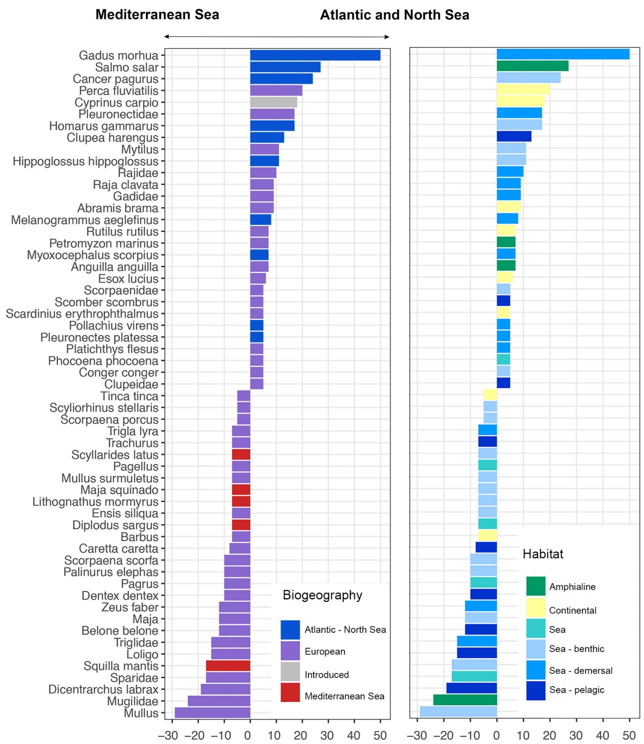
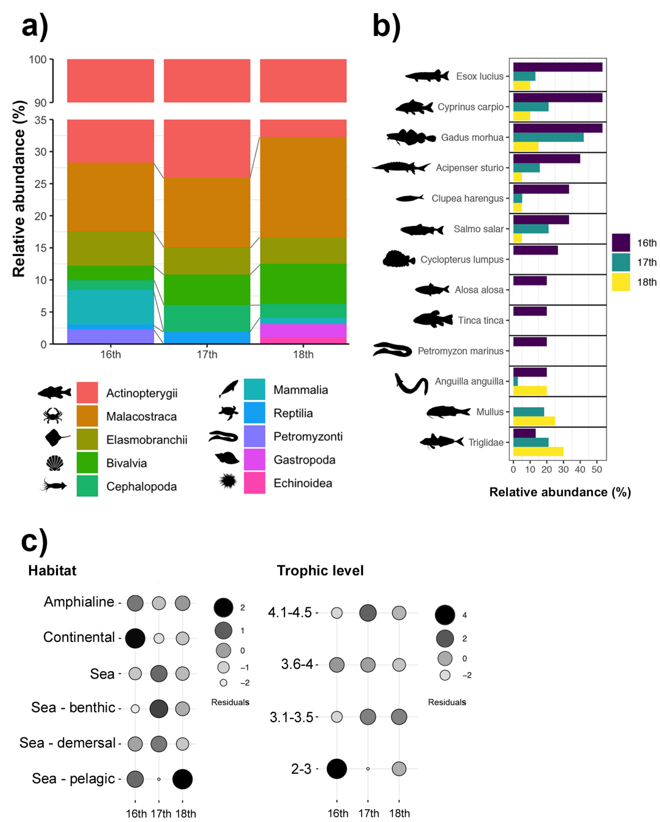


Fig. 4. Representation in paintings of taxa by period. (a) Relative abundance (in %) of class of taxa in the paintings according to the three periods: 16th, 17th, and 18th centuries. (b) Abundance (in %) of taxa in the paintings according to the three periods: 16th, 17th, and 18th centuries. Only the species with the highest variations are shown (based on the first decile of the distribution of standard deviation between the three periods). (c) Residual values of chi squared tests performed according to Habitat Group (p-value = 0.002) and Trophic Level (p-value = 9.427 x 10-7). Only the residuals of significant tests are shown.



17th centuries (Group 2), and a third group composed of taxa mainly represented in 18th century Mediterranean paintings (Group 3). To test if the distribution of selected taxa was dependent on region and period, we performed a Pearson's chi-squared test based on a presence/absence matrix of each taxon in each painting, according to the three periods and the two regions. For both the periods and the regions, the tests were significant (p-values = 0.013 and $1.395.10^{-7}$, respectively), showing that distributions of the taxa were statistically dependent across periods and regions

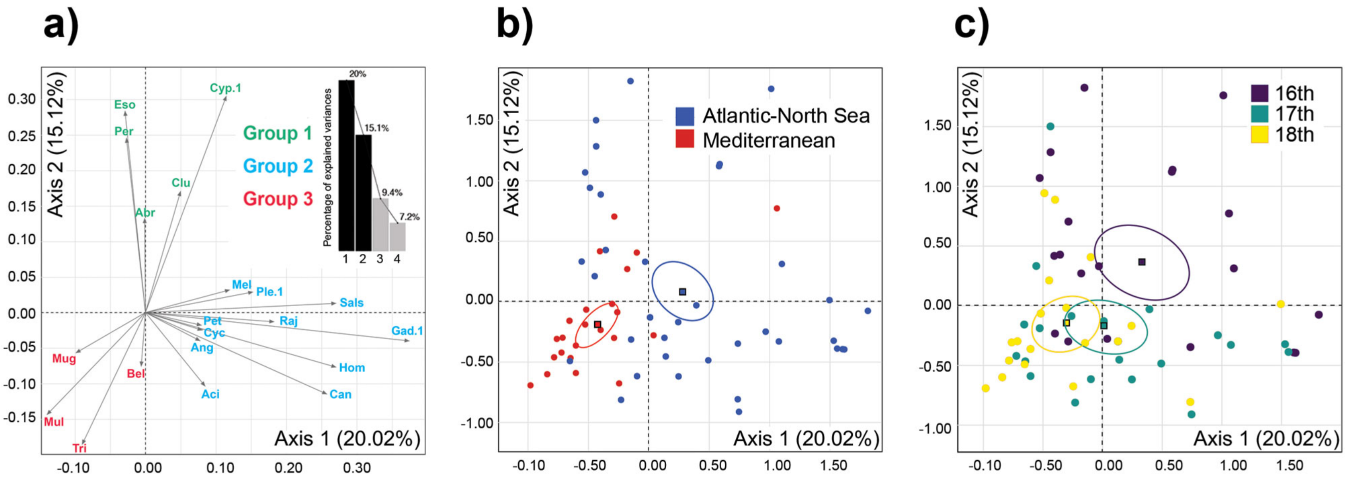
Main paintings

The paintings belonged to three periods and two regions (as shown by the PCAs in Fig.5b and Fig.5c). Note that the Mediterranean paintings tend to date from the 18th century, whereas the Atlantic paintings correspond in general to the 16th and 17th centuries. Regarding the distribution of the paintings, those that contributed the most to the variance of the distribution were P15 (Frans Snyders, Fish Stall, 1618-1621), P14 (Frans Snyders, The Fishmongers, 16th c.), and P45 (Jacob Van Nieulandt, Fishmongers, 17th c.) for axis 1 (23.02% of explained variance), and P3 (Joachim Beuckelear, The Fishmongers, 16th c.), P2 (Joachim Beuckelear, The Fishmongers, 16th c.), and P47 (Jacob Van Toorenvliet, A Fish Seller, 17th c.) for axis 2 (31.01% of explained variance).

DISCUSSION

The paintings selected for our study belong to two regions and three periods. The Mediterranean paintings date mainly from the 18th century, whereas the Atlantic-North Sea paintings tend to date from the 16th and 17th centuries. Despite this unbalanced sample, the bias did not influence the homogeneity of taxa distribution across periods. However, taxa distribution across regions was significantly related to their Biogeographical Status and Habitat Group. This may mean that the places where taxa were painted are consistent with their natural ranges, suggesting that these works of art may provide reliable clues to inform about reference states of the past.

Fig. 5. Distribution of selected taxa. (a) Principal component analysis (PCA) of the selected taxa represented in the paintings, showing that taxa are distributed in the paintings according to three distinct groups. Mul = *Mullus*, Mug = Mugilidae, Tri = Triglidae, Bel = *Belone belone*, Aci = *Acipenser sturio*, Ang = *Anguilla anguilla*, Raj = Rajidae, Ple.1 = Pleuronectidae, Cyc = *Cyclopterus lumpus*, Can = *Cancer pagurus*, Hom = *Homarus gammarus*, Pet = *Petromyzon marinus*, Gad.1 = *Gadus morhua*, Sals = *Salmo salar*, Mel = *Melanogrammus aeglefinus*, Clu = *Clupea harengus*, Abr = *Abramis brama*, Eso = *Esox lucius*, Per = *Perca fluviatilis*, Cyp.1 = *Cyprinus carpio*. (b) PCA across the two regions: each point corresponds to a painting, colored according to its geographical origin. (c) PCA across the three periods: each point corresponds to a painting, colored according to its period. For each PCA, only the first two dimensions are shown. The segmentation in space and time was given by confidence ellipses around barycenters at the 95% level.



Following the purpose of this article, we investigated the significance of aquatic biodiversity representations from ecological and historical points of view. To determine historical significance, we divided the interpretations of variations using two "sieves": a technical one (determined by fishing techniques, aquaculture and transport), and a socio-cultural one (derived from food preferences and aesthetic choices). To address ecological significance, we took into account ecosystem variations in relation with the biogeography of the species and trends in population changes.

Sorting taxa using technical sieves

Transport and conservation

We have identified three types of containers used for the transport of fish: wooden barrels, wicker baskets, and tanks. Conditioned fish was transported in wooden barrels after being salted, smoked, or dried (Hoffman 2000). Barrels had been used since the Middle Ages and were primarily dedicated to salted salmon, dried cod, and brine herring. Thanks to this method, these species were widely transported and were consumed inland despite having been caught at sea (Hoffman 2005, Barrett et al. 2008). Such a barrel is visible in Appendix 3b ("Nature morte aux poissons", Unknown artist, Musée maritime de l'île Tatihou, Conseil départemental de la Manche). The fresh and live fish were transported in tanks, as can be seen in the painting at the bottom of Fig. 1. Tanks had also been used for this purpose since the Middle Ages, and were generally dedicated to the transport of freshwater species inland (Hoffman 2005), as is visible in the painting in Fig. 1. Note that these tanks are represented in 30% of the selected paintings. Wicker baskets were also used to transport fresh fish from the coasts to inland areas, as is visible in Appendix 3a ("Still life with fish", Abraham van Beyeren 1655, RISD museum). The baskets were lined with straw to improve the conservation of the fish during transport by horse or donkey (Robert 2018).

In our results, the depicted taxa whose biogeography did not converge with the region in which they were painted provide a clue for the identification of transported species. This is the case for herring, whose representation is related to freshwater species (Group 1). Because herring was widely consumed inland from the Middle Ages on (Robert 2018), we find it depicted as being transported as fresh fish in tanks or baskets (Duhamel du Monceau and La Marre 1772), and as traveling at the same time as freshwater fish.

In the Mediterranean, the transport of oysters and shellfish started in the 17th century, in particular, oysters from Tuscany (Italy), which were renowned for their quality. Oyster spat was also transported from Corsica, and from Livorno (Italy) where it was cultivated for the Grand Duchy of Tuscany. The transport of shellfish and oysters developed further during the 18th century with design improvements to the "Chasse-marées" vessels (Faget 2017).

Regardless of region, we observed that the representation of Malacostracans (i.e., crustaceans) increased sharply beginning in the 18th c. We believe that this phenomenon is linked to the improvement of transport conditions that facilitated the trade, and therefore the consumption, of crustaceans throughout Europe.

Fishing techniques

Fishing gear is an important sieve that probably influenced the abundance of depictions of specific taxa. This is particularly true for Mediterranean Sea Mullidae (red mullets) and Triglidae (gurnards), which were specifically targeted as benthic species using the first trawling methods that appeared in the 15th century (Faget 2017). Indeed, important changes appeared in the Mediterranean beginning in the 15th century, characterized by innovations in fishing gear such as the Sardinal drift net (designed to catch small pelagic fishes), the Tartane trawlers (adapted to high seas fishing), longlines beginning in the late 15th century, and trawls towed by two vessels ("au boeuf" fishing) from the 18th century on (De Nicolò 2012, Faget 2015, 2017). This could explain the increasing frequency of depiction of these species during the studied period. In our study we highlight a tendency toward pelagic fishing in the Mediterranean. This may be related to the development of tuna traps in the 17th c. and Sardinal drift nets in the 15th c., both of which targeted pelagic fishes. During this period, the consumption of pelagic fish was characteristic of the diet of Mediterranean peoples (Faget 2017). Finally, the increase in the depiction of oysters (classified among the bivalves in our study) during this period may be related to the development of oyster harvesting in the Mediterranean in the 17th c., when metal dredges replaced hand gathering in shallow water (Faget 2017).

This period is characterized by a general improvement in both Atlantic and North Sea shipping and fishing techniques, such as bottom trawlers, drift nets, and gill nets (Pitcher and Lam 2015), leading to the development and occasional collapse of specific local fisheries. These events were particularly recorded for cod, herring, and sturgeon fisheries, and have been the subject of reviews by Poulsen (2008), Pitcher and Lam (2015), and Lenders (2017).

Aquaculture

Other technical sieves that deserve mention concern the introduction and culture of species. In the Mediterranean, oyster culture began in Livorno (Italy) in the 18th century but remained peripheral. The practice consisted of introducing spat into ponds in order to later harvest the adult oysters (Faget 2017). Further north, the Portuguese oyster (*Crassostrea angulata*, Lamarck 1819) was introduced into the North East Atlantic from Asia in the 16th century (Grade et al. 2016), where it replaced harvests of the indigenous flat oyster (*Ostrea edulis*, Linnaeus 1758). Oyster culture began in the 17th century but remained peripheral until the 19th c (Buestel et al. 2009). Flat oysters appear in the selected 16th century paintings. It must be noted that differentiating between the Portuguese oyster and the flat oyster, as depicted in a painting, is not always possible. For example, in "La Raie" by Pierre-Siméon Chardin (1728, Louvre Museum) the experts we consulted could not identify with certainty the species of oyster represented. Another example of early aquaculture is the case of the common carp, which was raised inland in fishponds as early as the 12th c. (Hoffman 1995), meeting the needs of fresh fish in areas far from sea.

Sorting taxa using socio-cultural sieves

Food preference

Taxa whose natural distribution is European, but whose representation occurs mainly in paintings from a specific region, may indicate a culinary preference. For instance, taxa from Group 3 include European species that are strongly represented in Mediterranean paintings: grey mullet (Mugilidae), red mullet (Mullidae), and garfish (*Belone belone*, Linnaeus 1761). These are emblematic species of the Mediterranean. In particular, grey mullet are directly linked to the regional cultural identity, are consistently present in brackish water, and are easy to catch (De Nicolò 2019). Seabass (*Dicentrarchus labrax*, Linnaeus 1758) and squid (*Loligo* spp.) may also be associated with Mediterranean culinary preferences.

We observed a variation in the trophic levels of represented fishes: they remained low during the 16th c. then increased throughout the 17th and 18th centuries. We hypothesize that this variation is connected to the beginning of standardizations in food preferences, and to an increase in the diversity of depicted species.

Religious precepts

Regarding the effect of religious precepts on fish consumption, a major event was the Council of Trent (1545–1563) in response to the Protestant Reform, for it reaffirmed the dietary rules of the Church: meat consumption was forbidden for roughly 130 days (35%) of the year, during which time only fish could be eaten. This led to an increase in the consumption of freshwater species such as pike (*Esox lucius*), common carp, salmon, and sturgeon (*Acipenser sturio*, Linnaeus 1758). Although these fish were already widely consumed in the Middle Ages (Hoffman 2005), this particular increase occurred in the period corresponding to the beginning of our study.

Aesthetics

The first paintings in our study date from the 16th c. This period corresponds to the European Renaissance, a movement that began in Italy in the 14th century and then spread throughout European art, especially through the Mannerist style. The Italian Renaissance masters greatly influenced the painters of Germany and the Netherlands during the 16th c. (Gombrich et al. 1997). The 17th c. was characterized by Baroque art in Italy, which also influenced Flemish artists who adopted a more demonstrative Baroque style. During the same period, Dutch painters developed the portrait and the landscape, with the objective of faithfully reproducing nature (in particular through still life works of art). We found a predominance of paintings of still lifes, and particularly of fish stalls, in our study. This kind of painting generally depicts an activity, which may be a practice, or even a profession (Blanchard 1981). Here, the activities highlighted are fishing, the preservation and transport of fish, the sale of fishery products at market, and their consumption. This suggests that the species represented are all intended to be eaten. The goal was not to represent the aquatic fauna in a systematic way, but rather to highlight the fish as food, surrounded by all the related activities and protagonists. These paintings therefore provide direct information about these practices. Concerning the other living creatures that figure in the paintings, human beings are predominant (37% of the selected paintings) and are often portrayed as fish sellers or customers. Cats and dogs are also depicted alongside the humans, either through their predatory instinct (cats stealing food) or because they are privileged companions (dogs lying close to humans, or chasing a thieving cat).

A question that arises concerns other species such as whales and other large marine mammals, which are known to have been consumed, but do not appear in the paintings. These species were widely consumed in Europe from the 13th c. (Brito et al. 2019), and yet are not represented in any known painting. Our hypothesis is linked to the large size of these animals, which, because of the constraints of the still life genre, makes them poorly adapted as subjects.

Furthermore, we propose that certain species were depicted in the compositions not only because they were to be consumed, but also for their aesthetic qualities. For instance, salmon is often represented sliced, yet was surely not the only species that was transformed before being sold. We suggest that the orange color of the salmon flesh would have appealed to the painters as a means of bringing color to their compositions, and this regardless of the palatability of the fish. For example, a cock salmon (a male with breeding colors and a long, hooked jaw) is represented in a painting by Frans Snyders (Fig. 1) despite these fish rarely being consumed because of their inferior taste. Its presence in the painting may therefore be explained by the artist's desire to paint a fish with bright colors and an unusual shape. Indeed, painters did not always present market stalls with realism, but often constructed assemblies of different species, which were observed and studied separately by the artist. They sometimes added exotic species to their compositions, perhaps because of their aesthetic attributes. This is particularly true for the "Cabinet of Curiosities." However, because we chose to remove paintings representing species coming from worldwide collections, this type of sieve does not appear in our analyses.

Likewise, some species are not depicted in painting despite being widely consumed, perhaps because of a lack of artistic appreciation. For instance, although the depiction of cod decreased from the 16th to the 18th centuries, it was consumed with increasing regularity (Pitcher and Lam 2015). We suggest that the conservation method for cod transport played a role here, and that thanks to the improvement of transport conditions in the 17th c., the cod arrived to market soon after being salted, dried, and stored in piles. It would therefore have been less recognizable as cod, and therefore less represented by painters. Finally, although this is not the subject of our study, a more in-depth analysis is necessary to better explain the aesthetic choices of the painters and the possible symbolic dimensions of the species represented.

Environmental and human pressures

Climate
The studied period (16th–18th c.) is well documented regarding major climate changes that influenced the geographical distribution of aquatic species. For instance, the Little Ice Age (early 14th to late 19th c.) varied the biomass of certain species fished on European coasts, in particular cod and herring (Øiestad 1994, Holm et al. 2019). This phenomenon, combined with the improvement of fishing techniques and local social and political events, led to stock changes for several taxa. For instance, Ravier-Mailly and Fromentin (2003) found evidence of negative correlations between bluefin tuna (*Thunnus thynnus*, Linnaeus 1758) catches and temperature in the 17th c. Other evidence indicates that episodes of "sterility" (i.e., the temporary weakening of the biomass of certain species fished on the coasts) occurred in the 18th c. in the Gulf of Marseille and coincided with periods of excessively cold winters (Faget 2010). Conversely, the Little Ice Age had positive effects on specific populations such as sturgeon (*Acipenser oxyrinchus*, Mitchill 1815), which is a cold-adapted species that migrated into the Baltic Sea, taking advantage of a weakening of the population of the more cold water-sensitive *A. sturio* (Tiedemann et al. 2007). Further north, cooler periods had a positive impact on herring populations in the Atlantic during the late 17th c. (Southward et al. 1988).

Habitat modifications
Important habitat modifications that occurred in European inland lakes and rivers also led to the decline of many fish populations (Lotze 2007). For instance, the practice of maintaining ponds for harvesting freshwater fish began to be questioned at the end of the 18th c., for these facilities reduced the area available for the cultivation of cereals, and were also considered to be unhealthy (Abad 2006). European countries therefore undertook the draining of these ponds, encouraged by the centralized monarchical states and the declining influence of the monks who had previously maintained a large number of the ponds (Morera 2011). This resulted in a decrease of northern pike (Nilsson et al. 2014) and other pond species such as common carp, perch (*Perca fluviatilis*), and bream (*Abramis brama*). Other pre-industrial societal activities in and along rivers, such as wood rafting or the generation of hydropower using watermills, modified fish habitats and impacted spawning grounds, eggs, larvae, and juvenile fish survival (Haidvogl et al. 2014). The expansion of watermill technology across Europe had a great impact on salmon populations between the Early Middle Ages and Early Modern Times (16th c.; Lenders et al. 2016). In addition, the channeling of European waterways began in the 17th c. in the Netherlands as a remedy for mobility shortcomings (Brolsma et al. 2011).

The pollution of waterways linked to the artisanal or industrial activities of the 18th c. may also have affected freshwater fish populations. Waterways close to cities were seen to be pestilential and dangerous, and the link between artisanal or industrial activities and insalubrity was well established (Le Roux 2011). Pre-industrial mining and metallurgy also had a great impact on lakes and rivers from the 16th to 18th centuries (Bindler et al. 2009, Haidvogl 2018).

Fish populations
The set of paintings reveals that the natural range of species is mainly convergent with the place they were painted. This is particularly true for the Atlantic-North Sea taxa (Group 2) that are adapted to cold water. For instance, *S. salar*, *G. morhua*, and *C. harengus* are exclusively present in the Atlantic Ocean. Likewise, edible crab (*Cancer pagurus*, Linnaeus 1758) and European lobster (*Homarus gammarus*, Linnaeus 1758) are rarely found in the Mediterranean, and are mainly represented in works painted in the Atlantic-North Sea. In the Mediterranean, we can cite Mantis shrimp (*Squilla mantis*, Linnaeus 1758) whose exclusive representation in the Mediterranean converges with its natural biogeography.

Examples of combined effects on documented species
Although the geographical distribution of species remains constant, the abundance of populations vary over the three centuries. These variations are primarily related to diverse human activities.

The most striking examples are the sturgeon, herring and cod. For example, sturgeon (*A. sturio*) populations were threatened by climate, fishing, and anthropic habitat modification from the 12th

c. and from Italy to the Baltic (Hoffman 2005, Tiedemann et al. 2007). The Danube River sturgeon population, in particular, decreased in the 16th century (Guti 2008). North Sea herring fisheries were shaped by a combination of political, social, economic, and environmental factors between the 16th and 18th centuries (Poulsen 2008), and the expansion in the late 17th c. of the salted barrel herring trade operated by drift net fisheries in the North Sea is thought to have led to the serial collapse of inshore herring stocks (Pitcher and Lam 2015). Thus, complaints by fishers of depleted stocks became more frequent (Thurstan et al. 2014). In addition, the environmental history of Atlantic fisheries exhibits a series of local depletions and shifts in local fish communities (Bolster 2012). The discovery of the Grand Banks off Newfoundland, Canada in the late 15th c. allowed the exploitation of huge cod populations, and the technological improvements of the following century led to a rapid expansion of catches (Pitcher and Lam 2015).

Reductions in the distribution of anadromous fishes such as sturgeon and salmon were also reported in Europe from the Middle Ages to Early Modern times, probably because of the combined effects of fisheries pressure (especially for sturgeons, which are estuarine fish caught at shallow depth with gillnets) and of pollution, habitat modification, and climate (Hoffman 2005, Tiedemann et al. 2007, Guti 2008, Lenders et al. 2016). All of these factors are clearly convergent with the diminishing number of depictions of freshwater and amphihaline migratory species in the paintings in our study.

CONCLUSION

This study highlights both the natural and the anthropic factors that shaped the spatial and temporal variations of aquatic species prior to Modern times in Western Europe. Although it is difficult to fully disentangle what relates to historical or ecological events, significant trends have been identified. The most obvious is that the fish represented in European paintings from the 16th to 18th centuries belong to two regions and three periods, which can be statistically discriminated. All represented taxa were intended for food and thus imply links to fishing and transport techniques. However, we illustrate that there are also environmental and socio-cultural factors that should be taken into account. Regarding spatial variations, our results strongly suggest that there is a convergence between the origin of the paintings and the biogeographic area of the species that are represented. This confirms the objective of the study and the validity of the method used to inform the evolution of aquatic socio-ecosystems. Concerning temporal variations, we found an overall decrease of represented taxa and particularly of continental and freshwater species. Thanks to previous work showing that human impacts on freshwater ecosystems had already begun in the Middle Ages, we conclude that tendencies observed in our study are the result of these earlier changes. This demonstrates the importance of including marine and freshwater species (consumed both on the coast and inland), rather than using a segmenting approach to marine and freshwater environments. On the other hand, we also observed an increase in representations of pelagic species, Malacostraca and Bivalvia, which is probably more closely linked to developments in fishing and transport.

These observations are corroborated by the works cited above, to which we have added a series of hypotheses concerning the effects of mixing environmental variations, technical sieves, and socio-cultural sieves. It is not possible to precisely quantify the effect of any one of these factors on the depicted species, however they do open up interesting fields of investigation. For instance, to our knowledge, no meta-analysis of archaeological data on the Mediterranean aquatic species has been undertaken. There is thus a real need to integrate archeology into Mediterranean historical ecology studies. In terms of aesthetic interpretation, it is necessary to investigate the career and influences of each painter from an art history angle. Increasing the number of paintings studied would also provide more knowledge. Concerning taxa identification, some require more precise specification, e.g., pikes, shads, sturgeons, loligos, octopus, oysters, and urchins, in the search for disappeared, introduced, or recently detected species, e.g., the three species of pikes in France (Denys et al. 2014). In addition, there is a shift between poorly documented species and highly informed commercial species, e.g., sturgeon, herring, and cod, which needs to be rebalanced. This article constitutes an encouraging first step toward the emergence of multidisciplinary methodologies intended to better understand the past reference state of aquatic socio-ecosystems, using an integrative approach.

Responses to this article can be read online at:
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Data Availability:

The data that support the findings of this study are openly available in figshare at https://10.6084/m9.figshare.14035202.

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Appendix 1: Selected paintings

N°	Period	Region	Country	Last name	First name	Title
1	16th	Mediterranean	Italy	Campi	Vincenzo	Christ in the house of Mary and Martha
2	16th	Mediterranean	Italy	Campi	Vincenzo	Fishmongers
3	16th	Mediterranean	Italy	Campi	Vincenzo	Fishmongers
4	16th	Mediterranean	Italy	Bartolomeo	Passarotti	The Fish Stall
5	16th	Mediterranean	Italy	Arcimboldo	Guiseppe	Water
6	16th	Mediterranean	Italy	Bartolomeo	Passarotti	The Fishmongers
7	17th	Mediterranean	Italy	Cornelisz	Pieter	Kitchen scene with the parable of the rich man and Lazarus
8	17th	Mediterranean	Italy	Cornelisz	Pieter	The Kitchen Maid
9	17th	Mediterranean	Italy	Crivelli	Angelo	Nature morte aux poissons
10	17th	Mediterranean	Italy	Recco	Giovanni Battista	Nature morte aux poissons de mer et aux huître orientales
11	17th	Mediterranean	Italy	Recco	Giuseppe	Nature morte aux poissons
12	17th	Mediterranean	Italy	Recco	Elena	Poissons
13	17th	Mediterranean	Italy	Recco	Giuseppe	Poissons de mer et crabes
14	17th	Mediterranean	Italy	Recco	Giuseppe	Poissons de mer et coquillages
15	17th	Mediterranean	Italy	Recco	Giuseppe	Still life with fish and a turtle
16	17th	Mediterranean	Italy	Recco	Giuseppe	A cat stealing fish
17	17th	Mediterranean	Italy	Recco	Giuseppe	Nature morte aux poissons et homard
18	17th	Mediterranean	Italy	De Pesci	Alessandro	Nature morte à la tortue et poissons
19	17th	Mediterranean	Italy	Cipper	Giacomo Francesco	Still life of fish and shellfish
20	17th	Mediterranean	Italy	Toorenvliet	Jacob van	A fish seller
21	18th	Mediterranean	Spain	Viladomat	Antonio	Still life with shellfish, fish and vessels
22	18th	Mediterranean	Marseille	Chasse	Barthélémy	La pêche miraculeuse
23	18th	Mediterranean	Italy	Boselli	Felice	Divers poissons et araignées
24	18th	Mediterranean	Italy	Cerutti	Giacomo	Nature morte avec des poissons et des oignons
25	18th	Mediterranean	Italy	Cerutti	Giacomo	Hummer und Meeresfrüchte
26	18th	Mediterranean	Italy	Cerutti	Giacomo	Garçon au panier de poisson
27	18th	Mediterranean	Italy	Crivelli	Angelo Maria	Pesci e crostacei, con marina lontananza
28	18th	Mediterranean	Italy	Crivelli	Angelo Maria	Nature morte aux poissons
29	18th	Mediterranean	Spain	Melendez	Luis	Nature morte avec rousseaux et oranges
30	16th	Atlantic - North Sea	Antwerp	Beuckelaer	Joachim	Le marché aux poissons; Marchands de poissons
31	16th	Atlantic - North Sea	Antwerp	Beuckelaer	Joachim	Les marchands de poissons
32	16th	Atlantic - North Sea	Antwerp	Beuckelaer	Joachim	The Four Element: Water

33	17th	Atlantic - North Sea	Netherlands	Wtewael	Joachim	Kitchen interior with the parable of the great supper
34	17th	Atlantic - North Sea	Antwerp	Snyders	Frans	Marchands de poissons à leur étal
35	16th	Atlantic - North Sea	Antwerp	Snyders	Frans	The Fishmongers
36	17th	Atlantic - North Sea	Antwerp	Snyders	Frans	Fish Stall
37	17th	Atlantic - North Sea	Antwerp	Adriaenssen	Alexander	Nature morte aux poissons
38	17th	Atlantic - North Sea	Antwerp	Adriaenssen	Alexander	Nature morte aux oiseaux
39	17th	Atlantic - North Sea	Antwerp	Adriaenssen	Alexander	Un marchand de poissons
40	17th	Atlantic - North Sea	Netherlands	Delff	Cornelis Jacobsz	Nature morte de cuisine
41	17th	Atlantic - North Sea	Netherlands	Putter	Pierre de	Tableau de pêche devant un paysage
42	17th	Atlantic - North Sea	Antwerp	Van Kessel 1	Jan	Poissons
43	17th	Atlantic - North Sea	Antwerp	Peeters	Clara	Still life with fish, candle, artichokes, crabs and schrimp
44	17th	Atlantic - North Sea	Germany	Mignon	Abraham	Still life with fruit, fish, and a nest
45	17th	Atlantic - North Sea	Antwerp	Adriaenssen	Alexander	Still life with fish and oysters
46	17th	Atlantic - North Sea	Netherlands	Beyeren	Abraham van	The ray
47	17th	Atlantic - North Sea	Netherlands	Beyeren	Abraham van	Still life with fish
48	17th	Atlantic - North Sea	Netherlands	De Witte	Emanuel	The fish market at evening
49	17th	Atlantic - North Sea	Netherlands	Ostade	Adriaen van	Fishwife
50	17th	Atlantic - North Sea	Netherlands	Ormea	Willem	Still life with fish
51	17th	Atlantic - North Sea	Antwerp	van Kessel 1	Jan	Nature morte de poissons au bord d'un rivage
52	17th	Atlantic - North Sea	Antwerp	van Kessel 1	Jan	The Day's Catch
53	17th	Atlantic - North Sea	Netherlands	Ormea	Willem	Fish Still Life With Stormy Seas
54	17th	Atlantic - North Sea	Netherlands	Martensz	Hendrick	Marché aux poissons
55	17th	Atlantic - North Sea	Netherlands	Nieulandt	Jacob van	Poissonniers
56	17th	Atlantic - North Sea	Netherlands	Beyeren	Abraham Van	Nature morte à la carpe
57	17th	Atlantic - North Sea	Netherlands	Beyeren	Abraham Van	Nature morte aux poissons
58	17th	Atlantic - North Sea	Netherlands	Wijtvelt	JB	Nature morte de poissons sur une plage
59	17th	Atlantic - North Sea	Netherlands	Beyeren	Abraham van	Still life with fishes
60	17th	Atlantic - North Sea	Netherlands	Gillig	Jacob	Poissons sur la plage
61	17th	Atlantic - North Sea	Antwerp	Duynen	Isaac van	Nature morte de poissons
62	17th	Atlantic - North Sea	Antwerp	Kessel	Jan I van	Les quatre éléments
63	18th	Atlantic - North Sea	Paris	Chardin	Jean Siméon	La raie
64	18th	Atlantic - North Sea	France	Oudry	Jean-Baptiste	Canards et poissons
65	18th	Atlantic - North Sea	France	Oudry	Jean-Baptiste	Poissons et oiseaux de mer
66	18th	Atlantic - North Sea	Netherlands	WB		Nature morte aux poissons
67	18th	Atlantic - North Sea	Britain	Blake	Benjamin	Still life with fish
68	18th	Atlantic - North Sea	Britain	Haughton 1	Moses	Fish
69	18th	Atlantic - North Sea	Paris	Jouvenet	Jean-Baptiste	La pêche miraculeuse
70	18th	Atlantic - North Sea	France	Angelis	Peter	The fishmonger
71	18th	Atlantic - North Sea	France	Angelis	Peter	At the marketplace
72	18th	Atlantic - North Sea	Paris	Desportes	Alexandre-François	Breakfast piece with oysters
73	18th	Atlantic - North Sea	France	Oudry	Jean-Baptiste	Poissons oiseaux de mer et perroquets

Appendix 2: Identified taxa

CON= Continental, AMP= Migratory and Pelagic Amphihaline, SEA-D= Sea-Demersal, SEA-P= Sea-Pelagic, SEA-B= Sea-Benthic, SEA= Sea. ANS = Atlantic Ocean and North Sea, EUR= European seas and oceans, INT= Inland waters, MED = Mediterranean Sea. GillNet: Gill nets, BTrawl: Bottom trawling.

Species or taxon	Code	Class	Order	Family	Trop hic level	Habitat	Biogeo graphy	Fishing Gear
Abramis brama	Abr	Actinopterygii	Cypriniformes	Cyprinidae	3,1	CON	EUR	GillNet
Acipenser sturio	Aci	Actinopterygii	Acipenseriformes	Acipenseridae	3,5	AMP	EUR	GillNet
Actinopterygii	Act	Actinopterygii	NA	NA	NA	NA	EUR	NA
Alosa alosa	Alo	Actinopterygii	Clupeiformes	Clupeidae	3	AMP	ANS	GillNet
Anarhichas lupus	Ana	Actinopterygii	Perciformes	Anarhichadidae	3,6	SEA-D	ANS	BTrawl
Anguilla anguilla	Ang	Actinopterygii	Anguilliformes	Anguillidae	3,6	AMP	EUR	Trap
Argyrosomus regius	Arg	Actinopterygii	Perciformes	Sciaenidae	4,3	SEA	EUR	GillNet
Aspitrigla cuculus	Asp	Actinopterygii	Scorpaeniformes	Triglidae	3,8	SEA-B	EUR	Btrawl
Astacus astacus	Ast	Malacostraca	Decapoda	Astacidae	NA	CON	EUR	Trap
Barbus sp	Bar	Actinopterygii	Cypriniformes	Cyprinidae	3,1	CON	EUR	Net
Belone belone	Bel	Actinopterygii	Beloniformes	Belonidae	4,2	SEA-P	EUR	Line
Brachyura sp	Bra	Malacostraca	Decapoda	NA	NA	SEA-B	EUR	Trap
Cancer pagurus	Can	Malacostraca	Decapoda	Cancridae	NA	SEA-B	ANS	Trap
Carcinus sp	Car	Malacostraca	Decapoda	Carcinidae	NA	SEA-B	EUR	NA
Caretta caretta	Car.1	Reptilia	Testudines	Cheloniidae	NA	SEA-P	EUR	GillNet
Caridae	Car.2	Malacostraca	Decapoda	NA	NA	SEA	EUR	NA
Chelidonichthys lucernus	Che	Actinopterygii	Scorpaeniformes	Triglidae	4	SEA-D	EUR	BTrawl
Chelonioidea	Che.1	Reptilia	Testudines	Cheloniidae	NA	SEA-P	EUR	NA
Clupea harengus	Clu	Actinopterygii	Clupeiformes	Clupeidae	3,4	SEA-P	ANS	GillNet
Clupeidae	Clu.1	Actinopterygii	Clupeiformes	Clupeidae	NA	SEA-P	EUR	NA
Conger conger	Con	Actinopterygii	Anguilliformes	Congridae	4,3	SEA-B	EUR	Line
Coregoninae	Cor	Actinopterygii	Salmoniformes	Salmonidae	3,1	CON	EUR	GillNet
Cyclopterus lumpus	Cyc	Actinopterygii	Scorpaeniformes	Cyclopteridae	3,9	SEA-D	ANS	GillNet
Cyprinidae	Cyp	Actinopterygii	Cypriniformes	Cyprinidae	NA	CON	EUR	GillNet
Cyprinus carpio	Cyp.1	Actinopterygii	Cypriniformes	Cyprinidae	3,1	CON	INT	GillNet
Delphinidae	Del	Mammalia	Cetartiodactyla	Delphinidae	NA	SEA	EUR	Spear
Dentex dentex	Den	Actinopterygii	Perciformes	Sparidae	4,5	SEA-P	EUR	Line
Dicentrarchus labrax	Dic	Actinopterygii	Perciformes	Moronidae	3,5	SEA-P	EUR	Line
Diplodus sargus	Dip.1	Actinopterygii	Perciformes	Sparidae	3,4	SEA	MED	GillNet
Diplodus sp	Dip	Actinopterygii	Perciformes	Sparidae	NA	SEA	MED	GillNet
Diplodus vulgaris	Dip.2	Actinopterygii	Perciformes	Sparidae	3,5	SEA	MED	GillNet
Ensis siliqua	Ens	Bivalvia	Adapedonta	Pharidae	NA	SEA-B	EUR	Gather
Epinephelus aeneus	Epi.1	Actinopterygii	Perciformes	Serranidae	4	SEA-B	EUR	GillNet

Epinephelus sp	Epi	Actinopterygii	Perciformes	Serranidae	NA	SEA-B	EUR	GillNet
Esox lucius	Eso	Actinopterygii	Esociformes	Esocidae	4,1	CON	EUR	GillNet
Eutrigla gurnardus	Eut	Actinopterygii	Scorpaeniformes	Triglidae	3,9	SEA-D	EUR	BTrawl
Gadidae	Gad	Actinopterygii	Gadiformes	Gadidae	NA	SEA-D	EUR	Line
Gadus morhua	Gad.1	Actinopterygii	Gadiformes	Gadidae	4,1	SEA-D	ANS	Line
Gobio gobio	Gob	Actinopterygii	Cypriniformes	Cyprinidae	3,1	CON	EUR	GillNet
Gymnocephalus cernua	Gym	Actinopterygii	Perciformes	Percidae	3,3	CON	EUR	GillNet
Haliotis sp	Hal	Gastropoda	Vetigastropoda	Haliotidae	NA	SEA-B	EUR	Gather
Hippocampus guttulatus	Hip	Actinopterygii	Syngnathiformes	Syngnathidae	3,5	SEA-B	EUR	GillNet
Hippoglossus hippoglossus	Hip.1	Actinopterygii	Pleuronectiformes	Pleuronectidae	4	SEA-B	ANS	Line
Homarus gammarus	Hom	Malacostraca	Decapoda	Nephropidae	NA	SEA-B	ANS	Trap
Labrus sp	Lab	Actinopterygii	Perciformes	Labridae	NA	SEA	EUR	GillNet
Lichia amia	Lic	Actinopterygii	Perciformes	Carangidae	4,5	SEA-P	MED	Line
Lithognathus mormyrus	Lit	Actinopterygii	Perciformes	Sparidae	3,4	SEA-B	MED	GillNet
Liza sp	Liz	Actinopterygii	Perciformes	Mugilidae	2,3	AMP	ANS	GillNet
Loligo sp	Lol	Cephalopoda	Myopsida	Loliginidae	NA	SEA-P	ANS	Line
Lotidae	Lot	Actinopterygii	Gadiformes	Lotidae	NA	SEA-B	EUR	BTrawl
Lutra lutra	Lut	Mammalia	Carnivora	Mustelidae	NA	CON	EUR	Spear
Maja brachydactyla	Maj.1	Malacostraca	Decapoda	Majidae	NA	SEA-B	ANS	Trap
Maja sp	Maj	Malacostraca	Decapoda	Majidae	NA	SEA-B	EUR	Trap
Maja squinado	Maj.2	Malacostraca	Decapoda	Majidae	NA	SEA-B	MED	Trap
Melanogrammus aeglefinus	Mel	Actinopterygii	Gadiformes	Gadidae	4	SEA-D	ANS	Btrawl
Merluccius merluccius	Mer	Actinopterygii	Gadiformes	Merlucciidae	4,4	SEA-D	EUR	Btrawl
Mola mola	Mol	Actinopterygii	Tetraodontiformes	Molidae	3,3	SEA-P	EUR	GillNet
Monachus monachus	Mon	Mammalia	Carnivora	Phocidae	NA	SEA	MED	Spear
Mugilidae	Mug	Actinopterygii	Perciformes	Mugilidae	2,6	AMP-P	EUR	GillNet
Mullus sp	Mul	Actinopterygii	Perciformes	Mullidae	3,1	SEA-B	EUR	BTrawl
Mullus surmuletus	Mul.1	Actinopterygii	Perciformes	Mullidae	3,5	SEA-B	EUR	GillNet
Muraena helena	Mur	Actinopterygii	Anguilliformes	Muraenidae	4,2	SEA-B	EUR	Trap
Myoxocephalus scorpius	Myo	Actinopterygii	Scorpaeniformes	Cottidae	3,9	SEA-D	ANS	BTrawl
Mytilus sp	Myt	Bivalvia	Mytilida	Mytilidae	NA	SEA-B	EUR	Gather
Octopus vulgaris	Oct	Cephalopoda	Octopoda	Octopodidae	NA	SEA-B	EUR	Trap
Odobenus rosmarus	Odo	Mammalia	Carnivora	Odobenidae	NA	SEA	ANS	Spear
Ostrea edulis	Ost	Bivalvia	Ostreida	Ostreidae	NA	SEA-B	EUR	Gather
Pagellus sp	Pag	Actinopterygii	Perciformes	Sparidae	3,5	SEA	EUR	GillNet
Pagrus pagrus	Pagp	Actinopterygii	Perciformes	Sparidae	3,9	SEA	EUR	GillNet
Pagrus sp	Pagr	Actinopterygii	Perciformes	Sparidae	3,9	SEA	EUR	GillNet
Palaemon sp	Pal	Malacostraca	Decapoda	Palaemonidae	NA	SEA	EUR	Gather
Palinurus elephas	Pali	Malacostraca	Decapoda	Palinuridae	NA	SEA-B	EUR	Trap
Paracentrotus lividus	Par	Echinoidea	Camarodonta	Parechinidae	NA	SEA-B	EUR	Gather

Patella ferruginea	Pat	Gastropoda	Archaeogastropoda	Patellidae	NA	SEA-B	MED	Gather
Perca fluviatilis	Per	Actinopterygii	Perciformes	Percidae	4,4	CON	EUR	GillNet
Petromyzon marinus	Pet	Petromyzonti	Petromyzontiformes	Petromyzontidae	4,4	AMP	EUR	Trap
Phoca vitulina	Phov	Mammalia	Carnivora	Phocidae	NA	SEA	ANS	Spear
Phocidae	Pho	Mammalia	Carnivora	Phocidae	NA	SEA	EUR	Spear
Phocoena phocoena	Phop	Mammalia	Cetartiodactyla	Phocoenidae	NA	SEA	EUR	Spear
Platichthys flesus	Pla	Actinopterygii	Pleuronectiformes	Pleuronectidae	3,3	SEA-D	EUR	GillNet
Plectorhincus mediterraneus	Ple	Actinopterygii	Perciformes	Haemulidae	3,5	SEA	MED	Line
Pleuronectes platessa	Plep	Actinopterygii	Pleuronectiformes	Pleuronectidae	3,2	SEA-D	ANS	GillNet
Pleuronectidae	Ple.1	Actinopterygii	Pleuronectiformes	Pleuronectidae	NA	SEA-D	EUR	GillNet
Pollachius sp	Pol	Actinopterygii	Gadiformes	Gadidae	NA	SEA-D	ANS	BTrawl
Pollachius virens	Polv	Actinopterygii	Gadiformes	Gadidae	4,3	SEA-D	ANS	BTrawl
Raja clavata	Rajc	Elasmobranchii	Rajiformes	Rajidae	3,8	SEA-D	EUR	Line
Rajidae	Raj	Elasmobranchii	Rajiformes	Rajidae	NA	SEA-D	EUR	Line
Rutilus rutilus	Rut	Actinopterygii	Cypriniformes	Cyprinidae	3	CON	EUR	GillNet
Salmo salar	Sals	Actinopterygii	Salmoniformes	Salmonidae	4,5	AMP	ANS	GillNet
Salmo sp	Sal	Actinopterygii	Salmoniformes	Salmonidae	NA	CON	EUR	GillNet
Salmo trutta	Salt	Actinopterygii	Salmoniformes	Salmonidae	3,4	CON	EUR	Line
Sardina pilchardus	Sarp	Actinopterygii	Clupeiformes	Clupeidae	3,1	SEA-P	EUR	GillNet
Sarpa salpa	Sars	Actinopterygii	Perciformes	Sparidae	2	SEA-BP	MED	GillNet
Scardinius erythrophthalmus	Sca	Actinopterygii	Cypriniformes	Cyprinidae	2,9	CON	EUR	GillNet
Scomber colias	Scoc	Actinopterygii	Perciformes	Scombridae	3,9	SEA-P	MED	GillNet
Scomber scombrus	Scos	Actinopterygii	Perciformes	Scombridae	3,6	SEA-P	EUR	GillNet
Scophtalmidae	Scop	Actinopterygii	Pleuronectiformes	Scophthalmidae	NA	SEA-D	EUR	GillNet
Scorpaena porcus	Scorp	Actinopterygii	Scorpaeniformes	Scorpaenidae	3,9	SEA-B	EUR	GillNet
Scorpaena scorfa	Scors	Actinopterygii	Scorpaeniformes	Scorpaenidae	4,3	SEA-B	EUR	GillNet
Scorpaena sp	Scor	Actinopterygii	Scorpaeniformes	Scorpaenidae	NA	SEA-B	EUR	GillNet
Scorpaenidae	Sco	Actinopterygii	Scorpaeniformes	Scorpaenidae	NA	SEA-B	EUR	GillNet
Scyliorhinus sp	Scy	Elasmobranchii	Carcharhiniformes	Scyliorhinidae	NA	SEA-B	EUR	GillNet
Scyliorhinus stellaris	Scys	Elasmobranchii	Carcharhiniformes	Scyliorhinidae	4	SEA-B	EUR	GillNet
Scyllarides latus	Scyl	Malacostraca	Decapoda	Scyllaridae	NA	SEA-B	MED	Trap
Sebastes sp	Seb	Actinopterygii	Scorpaeniformes	Sebastidae	NA	SEA-D	EUR	BTrawl
Sepia officinalis	Sep	Cephalopoda	Sepiida	Sepiidae	NA	SEA-B	EUR	Trap
Serranus sp	Ser	Actinopterygii	Perciformes	Serranidae	NA	SEA	EUR	GillNet
Siluridae	Sil	Actinopterygii	Siluriformes	Siluridae	NA	CON	EUR	GillNet
Solea solea	Sol	Actinopterygii	Pleuronectiformes	Soleidae	3,2	SEA-B	EUR	GillNet
Sparidae	Spa	Actinopterygii	Perciformes	Sparidae	NA	SEA	EUR	GillNet
Sparus aurata	Spaa	Actinopterygii	Perciformes	Sparidae	3,7	SEA	EUR	GillNet
Spondyliosoma cantharus	Spo	Actinopterygii	Perciformes	Sparidae	3,3	SEA	EUR	GillNet
Squilla mantis	Squ	Malacostraca	Stomatopoda	Squillidae	NA	SEA-B	MED	Trap

Symphodus sp	Sym	Actinopterygii	Perciformes	Labridae	NA	SEA	EUR	GillNet
Thonidae	Tho	Actinopterygii	Perciformes	Scombridae	NA	SEA-P	EUR	GillNet
Thunnus thynnus	Thu	Actinopterygii	Perciformes	Scombridae	4,5	SEA-P	EUR	GillNet
Tinca tinca	Tin	Actinopterygii	Cypriniformes	Cyprinidae	3,7	CON	EUR	GillNet
Trachinidae	Tra	Actinopterygii	Perciformes	Trachinidae	NA	SEA-B	EUR	GillNet
Trachinotus ovatus	Trao	Actinopterygii	Perciformes	Carangidae	3,7	SEA-P	EUR	GillNet
Trachinus radiatus	Trar	Actinopterygii	Perciformes	Trachinidae	4,2	SEA-B	EUR	GillNet
Trachurus sp	Trac	Actinopterygii	Perciformes	Carangidae	3,7	SEA-P	EUR	GillNet
Trigla lyra	Tril	Actinopterygii	Scorpaeniformes	Triglidae	3,7	SEA-D	EUR	BTrawl
Triglidae	Tri	Actinopterygii	Scorpaeniformes	Triglidae	NA	SEA-D	EUR	BTrawl
Trisopterus luscus	Trisl	Actinopterygii	Gadiformes	Gadidae	3,7	SEA	ANS	GillNet
Trisopterus minutus	Trism	Actinopterygii	Gadiformes	Gadidae	3,7	SEA	ANS	GillNet
Veneridae	Ven	Bivalvia	Venerida	Veneridae	NA	SEA-B	EUR	Gather
Zeus faber	Zeu	Actinopterygii	Zeiformes	Zeidae	4,5	SEA-D	EUR	BTrawl

Appendix 3: Example illustrations

a)

Abraham Hendricksz van Beyeren, *Still Life of Fish*, 1655, Netherlands
RISD Musuem, Providence, USA.

b)

W.B., *Nature morte aux poissons*
Musée maritime de l'île Tatihou, Conseil départemental de la Manche.
This work was destroyed during the fire in the museum reserves on July 18, 2017.