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Eel translocation from a conservation perspective: A coupled systematic and narrative review

H. Froehlicher^{a,*}, K. Kaifu^{b,c}, T. Rambonilaza^d, F. Daverat^e

^a UR EABX/ETTIS, INRAE, 50 Avenue de Verdun, 33612 Cestas Cedex, France

^b Faculty of law, Chuo University, 1-4-1 Otsuka, Bunkyo-ku, Tokyo 112-8631, Japan

^c Zoological Society of London, Outer Circle, Regent's Park, London NW1, 4RY, UK

^d UMR CESAER, L'Institut Agro Dijon, INRAE, Univ. Bourgogne Franche-Comté, 26, bd Docteur Petitjean, BP 87999, 21079 Dijon Cedex, France

^e UMR ECOBIOP, 1224, INRAE, UPPA, 173 Route de Saint-Jean-de-Luz, 64310 Saint-Pée-sur-Nivelle, France

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ABSTRACT

Translocation is used as a conservation action on a large panel of species, but efficiency of such a measure is still under investigation. This study reviews and synthesizes the existing research evidence to address how translocation of eels could be efficient from a conservation perspective. *Anguilla* spp. are endangered and translocation has been used to manage their population since the middle of XIXth century. Eels' translocation can follow different approaches, depending on the objectives and context. Assessing the outcome of translocation projects aiming at restoring eel population is complex, mainly because the last part of its lifecycle, reproduction, is unresolved and has never been observed in the wild. We thus combine a systematic and narrative review approach. We first generated a data set of 956 articles published between 1933 and 2021. Based on a thematic analysis, we linked eel life traits with the main concepts identified in the corresponding corpus. This quantitative approach revealed key controversies about the effect of translocation on eel biological processes. The main thematic associated to translocation were survival, migration and selection by environment. These thematic were further analyses within a narrative review on the basis of a selection of recent articles. The review revealed that there is a consensus on the fact that translocation interacts with natural selection processes (phenotype/environment mismatch), and that translocated eels migrate towards the reproduction area as silver eels, but there are still research gaps on the comparative survival of translocated and wild eels. An emerging thematic was the effect of eel translocation at the community level. Based on review findings, the future research have to focus on the direct comparison of the ecology of translocated eels and their wild counterparts in the natural environment as well as the study of the translocation actions' impact at community level.

1. Introduction

The conservation of aquatic ecosystems is a major challenge worldwide, as freshwater ecosystems are disproportionately affected by the global changes underway (Albert et al., 2020; Cooke et al., 2022). Freshwater biodiversity provides key ecosystem services, and management actions are striving to restore a “good level” of freshwater biodiversity (Vörösmarty et al., 2010; Szabolcs et al., 2022).

* Correspondence to: UR EABX/ETTIS, 50 Avenue de Verdun, 33612 Cestas Cedex, France.

E-mail address: hermione.froehlicher@inrae.fr (H. Froehlicher).

The aim of conservation is ecosystem self-maintenance and resilience as well as the population viability of species, concepts that are synthesized as “ecological integrity” (Hansen et al., 2021; Karr et al., 2022). In modern conservation, the preservation of ecosystem functions is based on the assessment of interspecific and intraspecific biodiversity and their interactions (Cabello et al., 2012). Recently, conservation efforts began targeting rare species that provide rare functions (Violle et al., 2017). Rare functions were found to contribute disproportionately to ecosystem integrity (Bracken and Low, 2012). The rarity of species and associated functions is defined not only in terms of the quantitative scarcity or abundance of living organisms, but also according to the uniqueness of the traits and phylogeny (Violle et al., 2017).

Eels of the genus *Anguilla* are phylogenetically and ecologically rare fish species worldwide (Tsukamoto et al., 1998). The *Anguilla* genus encompasses 19 species/subspecies with unique life history traits, spread across tropical and temperate areas (Jellyman, 2022). *Anguilla* species are migratory fish. They reproduce once in their lives (semelparity) in the open ocean, and grow in continental waters. Their larvae travel across the oceans or seas. They metamorphose into glass eels and colonize various continental habitats such as estuaries, lagoons, marshes, rivers and streams before growing into yellow eels. After their growth phase, yellow eel become silver eel and undertake the journey across the ocean to their spawning areas (Tesch, 2003; Takeuchi et al., 2021; Wright et al., 2022). *Anguilla* spp. exhibit great intraspecific diversity with alternative life histories, in other words facultative catadromy (Tsukamoto et al., 1998). Ecologically, eels are generalist predators and sometimes scavengers (Sporta Caputi et al., 2020), and serve as indicator, umbrella and flagship species for the conservation of freshwater biodiversity (Itakura et al., 2020). *Anguilla* spp. are both a biological resource of considerable ecological and socioeconomic importance (Tamario et al., 2019) and a guarantee of good aquatic environmental quality (Plum and Schulte-Wülwer-Leidig, 2014; Itakura et al., 2020).

Overall, the *Anguilla* genus is at risk, mainly because it is subject to multiple anthropic pressures including environmental changes as well as exploitation (Jacoby et al., 2015; Jellyman, 2022). All temperate eel species inhabiting the Northern Hemisphere are considered threatened by the International Union for the Conservation of Nature (IUCN). The three Northern Hemisphere temperate species that have been widely exploited are either critically endangered (*A. anguilla*) or endangered (*A. rostrata*, *A. japonica*). Moreover, temperate eel species inhabiting the Southern Hemisphere are considered threatened or near threatened. Although there is a lack of data on some of the tropical species, seven tropical species fall within Threatened Species categories (Vulnerable, Endangered, Critically Endangered) or the Near Threatened Species category, which places the tropical species at risk of following the same path as temperate species. Altogether, 10 of the 19 Anguillid eel species are evaluated as threatened or near threatened, while two are considered as Data Deficient.

The status of exploited fish with a high economic value explains why eel stocks have been managed with a view to increase biomass availability for fisheries. Eels were managed as a natural resource before being preserved as endangered species within the framework of conservation. The coexistence of exploitation and conservation in this specific case has led to the implementation of actions that ambiguously mix objectives from both spheres. This ambivalence is best exemplified by actions to translocate young eels from a site of capture to a site of release, termed “restocking” or “stocking” (MacGregor et al., 2008; Dekker and Beaulaton, 2016; Wakiya et al., 2022). Eel translocation is carried out with wild juveniles, as the artificial reproduction of eels does not allow for mass production (Masuda et al., 2012). In the last decade, the continued decline of the three Northern Hemisphere temperate eel species has reinforced the attractiveness of translocation projects as a conservation approach to prevent the collapse of eel stocks.

Translocation has been carried out with a large number of taxa, including flora and fauna (Berger-Tal et al., 2020). Yet, the necessity and potential usefulness of existing translocation projects or programs as conservation tools have been largely questioned (Pérez et al., 2012; Resende et al., 2020). From a conservation perspective, translocation is considered successful when full ecological integrity is achieved for the species of interest, including its socio-economic dimensions (IUCN, 2013; Kaifu, 2019). However, identifying characteristics or criteria that distinguish successful from unsuccessful translocation actions remains a complex task for conservation managers. Lack of baseline knowledge (i.e. species’ biology and ecology, suitable habitat, and species migratory and dispersal behavior) is one of the main factors perceived as a barrier to efficient translocation protocols (Berger-Tal et al., 2020).

In the case of eels, translocation can follow different approaches, depending on the objectives and context; in particular, “reintroduction” aims at introducing eels in eel-free habitats or at least in habitats where eels have not been observed recently, while “reinforcement” seeks to increase the number of eels in a habitat they already occupy (Lee, Aminur Rahman, 2018; Smith et al., 2018; Kitada, 2020; Cárcamo et al., 2021). Previous review papers have tried to discuss the efficiency of eels’ translocation techniques on the basis of selective studies (Dekker and Beaulaton, 2016) or by collecting and combining expert knowledge and opinions (ICES, 2016). But to date, there is no complete overview of the benefits and risks associated with eel translocation and their implications for conservation, based on a global and systematic review of evidence from the academic literature.

This study provides the first endeavor to conduct a systematic review of the academic literature associated with eel translocation, to describe and discuss key issues related to species conservation. The objective is to provide a comprehensive and synthetic description of what is known about the evolutionary and ecological processes underlying translocation of eel. In addition to facilitate the grasp of the restocking impact as a conservation action, understanding these processes may be more important than ever in the face of intense anthropogenic impacts, such as climate change (Olden et al., 2011; Thomas, 2011) and habitat fragmentation (Germano et al., 2015).

Compared to meta-analyses, which have been used in ecology and evolutionary biology for several years, systematic reviews are rare and are now becoming an established method to aggregate research results (O’Dea et al., 2021). A systematic review can use qualitative or quantitative methods for synthesizing studies (Gough et al., 2012). This review uses a combination of (quantitative) literature synthesis techniques and (qualitative) narrative review. More specifically, we first performed a systematic review based on an automated content analysis (ACA) of all the selected articles (Nunez-Mir et al., 2016). We use the Leximancer software to address the extent and the nature of the research activity. We also use it to identify key concepts and dominant themes in order to give an overview of main research interests and findings. As such, the synthetic review of the literature developed in this article should be

understood as an exploratory approach. It does not necessarily assess the quality of the studies that meet the inclusion criteria. However, in comparison with previous reviews, it demonstrates the value of undertaking a full systematic review to take into account the evolution of the field toward conservation issues. We complete our analysis with a comprehensive narrative review based on a subset of articles that would be representative of the major themes and sub-themes that emerged from the full systematic review. The narrative review method enables us to capture and generalize the main theoretical foundations, methodological approaches and results that have been achieved from the identified themes and sub-themes.

2. Material and method

2.1. Conceptual background and review framework

Assessing the outcome of translocation projects aiming at restoring eel population is complex, mainly because the last part of its lifecycle, reproduction, is unresolved and has never been observed in the wild. Therefore, reproductive success cannot be evaluated, making it difficult to assess eel fitness, defined as the ability to survive and produce viable offspring (ICES, 2016). Translocation practices can therefore only be evaluated based on the fitness gain of eels during their continental growth and the onset of their maturation phase. This aspect has fueled a fierce debate over the pros and cons of eels' translocation. In addition, the ecology of the translocated species across their life cycle must be considered as a whole. The displacement of young eels from their habitat of collection to a recipient water area interacts with their life history path. Translocation might, for example, affect the individual eel's ability to survive (Ovidio et al., 2015; Félix et al., 2021; Newhard et al., 2021; Nzau Matondo et al., 2022) and adapt to a new environment (De Meyer et al., 2020), as well as the maturation of gonads (Marohn et al., 2013; Couillard et al., 2014) and the eel's ability to migrate to the spawning areas (Prigge et al., 2013; Westerberg et al., 2014; Sjöberg et al., 2017; Béguier-Pon et al., 2018). At the population level, translocation can interfere with intraspecific social interactions and density-dependent processes that regulate resource allocation and sex determination (Geffroy and Bardonnet, 2012; Côté et al., 2015; Stacey et al., 2015;). At the ecosystem level, the introduction of eels in eel-free habitats might change the community composition and functioning (Félix et al., 2020; Nzau Matondo et al., 2021).

Despite limited information about the marine phase of eel reproduction, the efficiency of translocation may be assessed using the existing knowledge on the biology and ecology of eel in continental areas. Evolutionary and functional ecology can provide valuable frameworks to analyze and compare studies on the basis of key concepts relevant to conservation: individual eel fitness, population

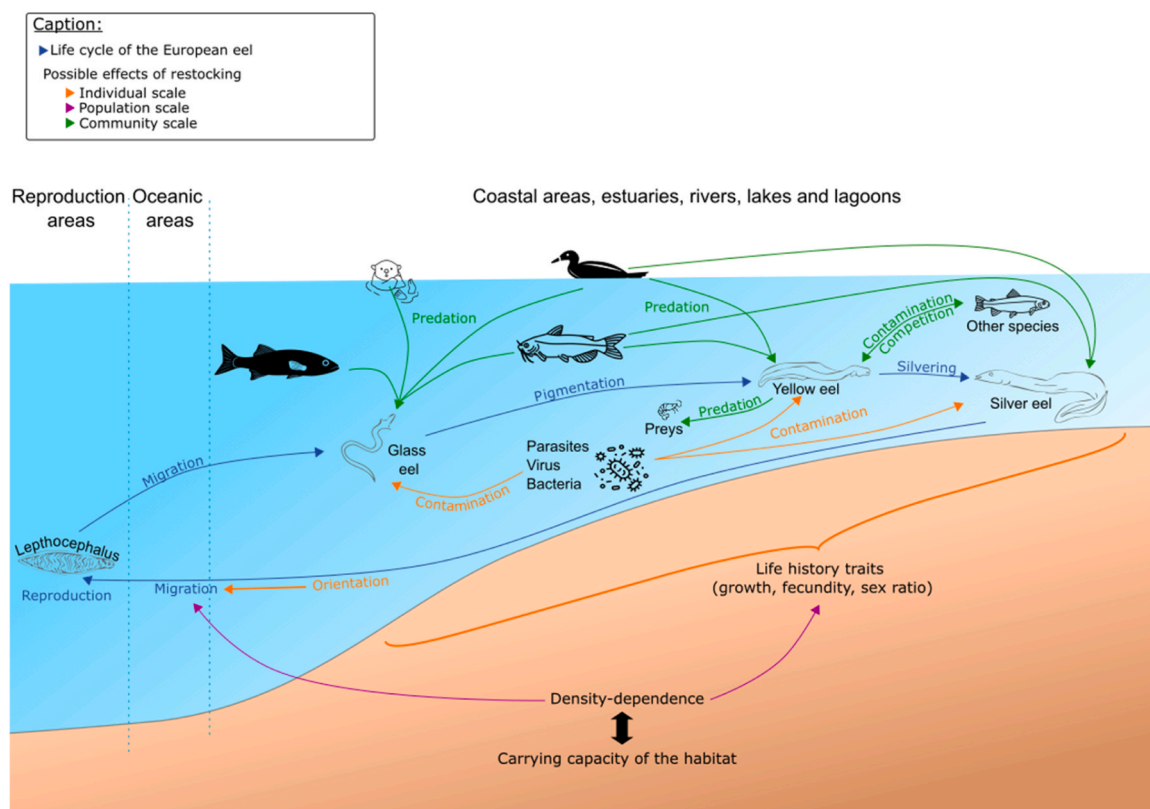


Fig. 1. Illustration of the interactions between translocation and ecological processes in the eel's lifecycle. Warning: the proportions of the different areas and species are not realistically represented.

viability and ecological integrity afforded by eel translocation. Specifically, investigating the ways in which translocation practices interact with life history traits (growth, survival, behavior), demography (sex ratio, abundance), and ecosystems (trophic interactions, community composition) is critical to determine how effective eel translocations are at different scales. A summary of these interactions is provided in Fig. 1.

2.2. Literature search and selection

Literature search is a key step in systematic review. Our corpus consisted of all scientific articles we could find online, written in English and published before 2022. We included articles that dealt with either of the three Northern hemisphere temperate eel species, as these are the most studied in the scientific literature in the context of translocation, because of their commercial importance. We used the Web of Science (WoS) citation indexing service, Google Scholar, Springer, and ScienceDirect to obtain an exhaustive list of peer-reviewed articles. We performed a search query combining (i) keywords for proxies to “eel translocation” such as “translocation” or “restocking”, (ii) keywords for the denomination of eel species at their different life stages, (iii) keywords for biological or ecological processes, (iv) proxies for the concept of effectiveness, and (v) habitats. We thus established a list of 39 keywords ([supplementary material S1](#)). The ScienceDirect and Google Scholar search engines could not process more than 15 keywords simultaneously for the present study. We therefore proceeded to an iterative selection of 15 of the 39 keywords. We obtained a shortlist of 15 keywords (Fig. 2) by comparing the top articles for each query output. The full PDF text of these articles was collected from the publishers’ websites and Google Scholar, with the help of 25 people to speed up the process (Fig. 2).

2.3. Synthetic review with automated content analysis

Most systematic review studies perform automated content analysis (ACA), to synthesize and analyze the titles, keywords, and abstracts of articles (Westergaard and al., 2018; McCallen et al., 2019). We analyzed the entire article text, since the word or synonyms for translocation may only have been located in the discussion section. Various tools can be used to carry out automatic content analysis (Nunez-Mir et al., 2016). Since we had a large number of articles in PDF format, we used the Leximancer software (see details in Appendix 3). We performed an ACA to identify the main themes (hereafter referred to as concepts), the relationship between themes, and their frequency (Heberling et al., 2019). Concepts are defined in ACAs as collections of correlated words that encompass a central theme (Nunez-Mir et al., 2016). A length of two sentences per statistical individual (block) has been set up. We targeted concepts related to the translocation of eels, as well as the relationships between translocation, eel traits, and ecological processes. The ACA returned conceptual clouds or maps of related concepts. We calculated the probability of association between concepts in the same text segment (likelihood).

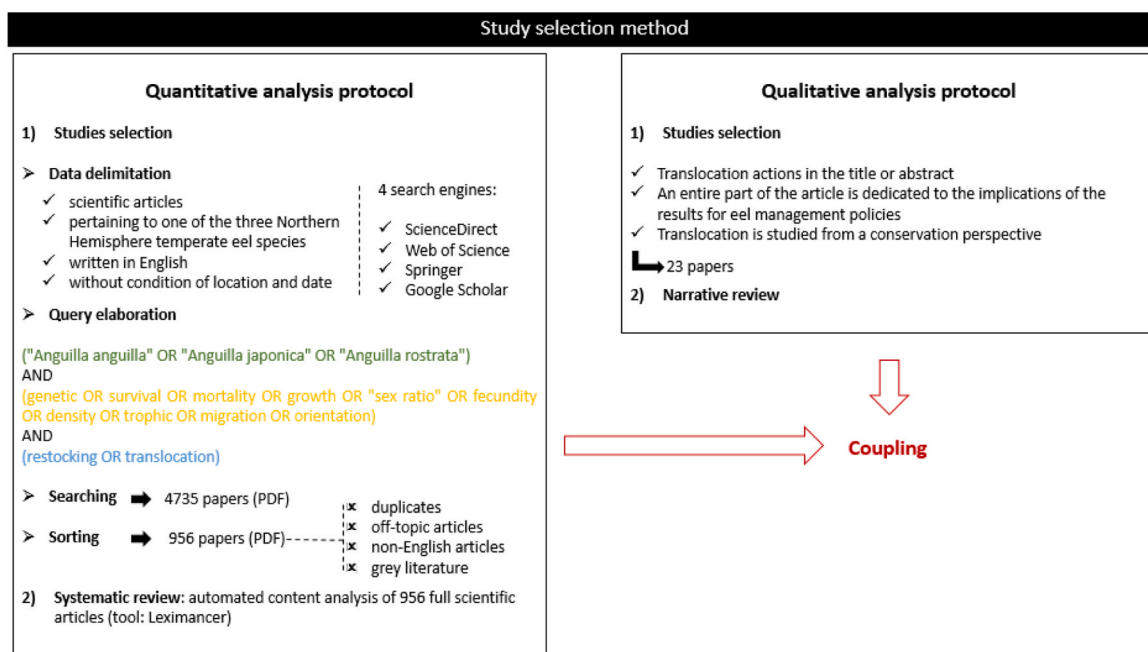


Fig. 2. Coupled quantitative and qualitative methodology.

2.4. A comprehensive narrative review method

The quantitative approach to the literature review helps demonstrate the nature and diversity of research topics amenable to provide essential evidence for those concerned with the internal and external validity and likely effects of eel translocation in different settings. However, it provides little information on how available research approaches, their theoretical perspective, empirical protocols and results can support the evaluation of the efficiency of complex translocation interventions. We complemented the quantitative analysis with a qualitative analysis focused on the main themes or sub-themes identified from the literature most studied ecological processes (ACA concepts) related to translocation (see details in Fig. 2). To this aim, we compiled a smaller corpus of 23 articles drawn from the large corpus (Appendix 4), based on the following criteria:

1. translocation actions such as “restock*”, “translocate*” or “stock*” are mentioned in the title or abstract
2. a whole section of the article is dedicated to the implications of the results for eel management policies
3. the article addresses translocation from a conservation perspective

3. Results

3.1. Content analysis

3.1.1. Bibliometric

The corpus initially counted a total of 4735 research articles. After removing duplicates, off-topic articles, non-English articles and grey literature, it was reduced to 956 articles published between 1933 and 2021 (supplementary material S2). The publication numbers increased over time, in line with the general trend in the overall scientific literature.

The corpus spanned 238 different journals covering a wide range of fields, all generalist journals on ecology, aquaculture, fish biology, or aquatic ecology. The diversity of scientific journals also increased over time. In the early 1980 s, the journal *Aquaculture* became the leading journal for eel research, and it still remains a dominant journal (Fig. 3). In recent years, the cumulative number of publications in environmental sciences and ecology journals has by far exceeded that in aquaculture journals.

3.1.2. Major research streams

A total of 153 concepts were identified in the ACA (supplementary material S3). The “eel” concept was identified as a central concept in the corpus (supplementary material S5 and Fig. 4). Among the most studied themes, eel translocation featured in the concept “restocking” (supplementary material S5) which was very frequent throughout the entire corpus, and appeared 4130 times (5% of concept occurrences in the corpus) (supplementary material S5). This result might seem obvious since “restocking” is part of the list of keywords used to select the articles, but some other keywords of this list, such as “fecundity”, “trophic” or “orientation” do not appear in the list of concepts. The keywords chosen to feed the query do not necessarily drive the conceptual analysis.

At first, the keyword “translocation” didn’t appear in the results as a concept, contradictory to “restocking”. To deepen the analysis, we added 5 concepts related to the keyword “translocation” (“translocation”, “translocated”, “translocate”, “translocates”, “translocating”) and merged them manually with the concept of “restocking” (supplementary material S3).

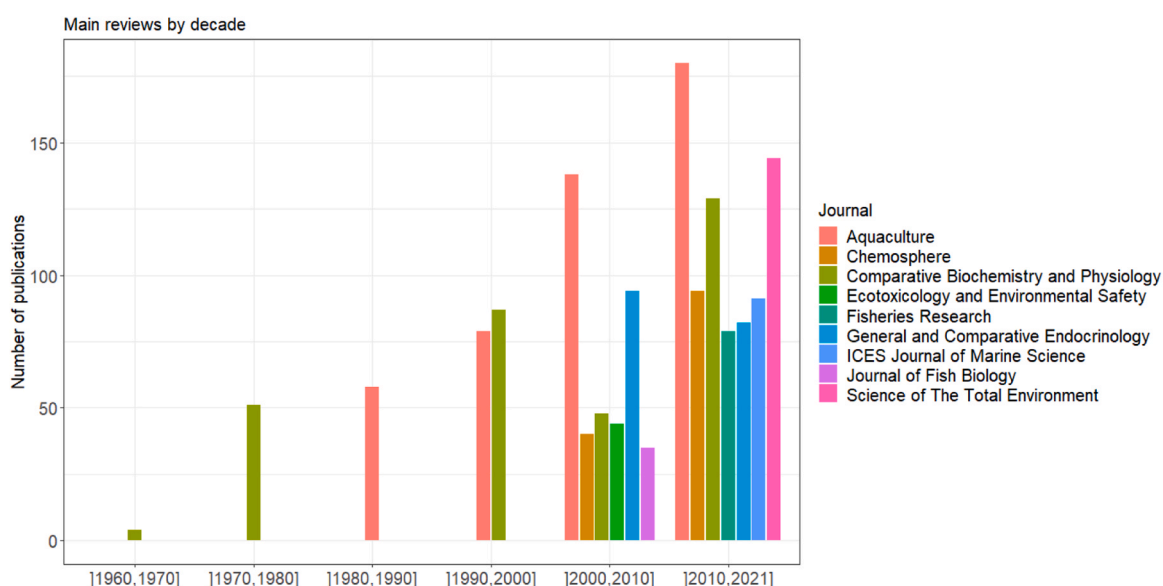


Fig. 3. Main journals by decade (journals in which 95% of the scientific articles included in the literature review were published, per decade).

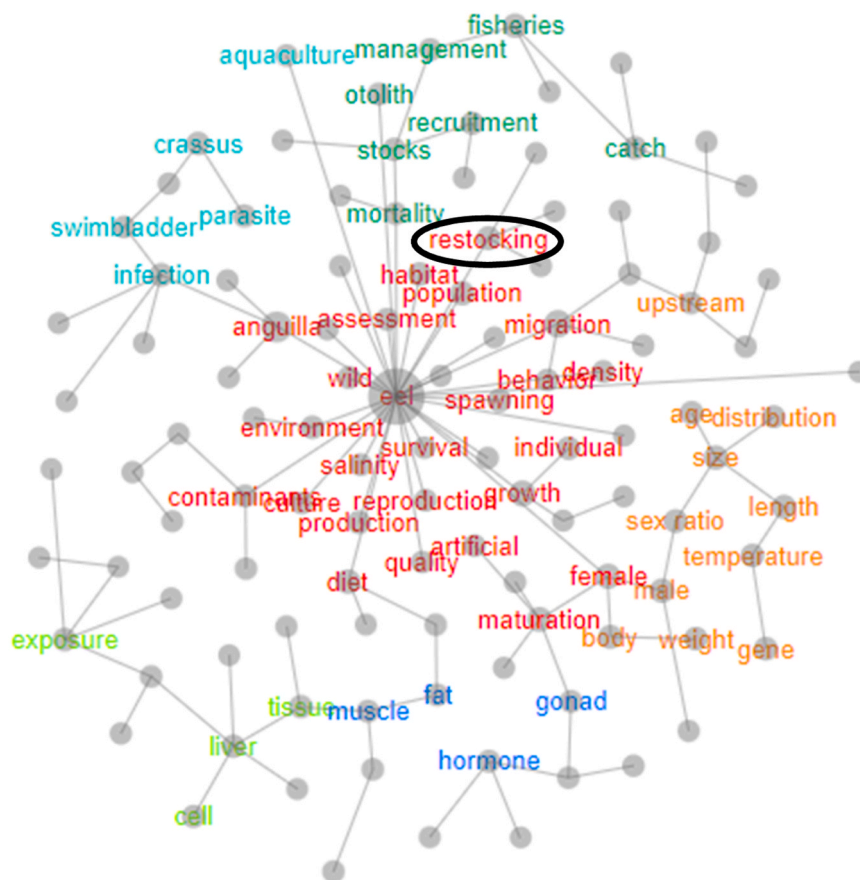


Fig. 4. Concept cloud (Gaussian distribution to facilitate the reading). For the sake of clarity, a list of concepts related to habitats, species and development stages was removed: European; glass; silver; japonica; rostrata; freshwater; larvae; river; yellow; estuary; elver; coast; egg; trout; sea; lake; salmon; marine; juvenile; adult; ocean; lagoon; continental; seawater; brackish; catchment; leptocephali; inland; young; American; European; Japanese; and Sargasso sea. This conceptual map represents 50% of the most relevant concepts over the 120 remaining concepts and how they are related. The themes are heat-mapped, meaning that warm colors (red, orange) denote the most important themes, while cool colors (blue, green) denote less important ones ([Leximancer User Guide](#).).

“Restocking” is directly connected to the concepts of “yield”, “biomass” and “commercial” on the concept cloud ([supplementary material S6](#)) which featured on the map of related concepts, in a pool of concepts associated with “exploitation” and “management of eels”, such as “stocks”, “anthropogenic”, “conservation”, “fisheries” and “management” ([Fig. 4, supplementary material S6](#), dark green). Overall, the central “eel” concept was associated with a wide variety of concepts relating to migration and reproduction (artificial or not) ([Fig. 4, supplementary material S6](#), red, orange and dark blue), to life history traits such as growth or sex ratio ([Fig. 4, supplementary material S6](#), orange), and to the quality of the eel’s living environment, especially in terms of contamination ([Fig. 4, supplementary material S6](#), turquoise).

Within the corpus, the most studied developmental stage was glass eel, followed by silver eel ([supplementary material S5](#)).

The three species of interest for the present study emerged from the ACA output as distinct concepts (“European”, “rostrata”, “japonica”) with a relevance greater than 5% (supplementary material S5). This finding demonstrated the value of focusing the assessment of eel translocation efficiency on this list of species. Yet the three species did not receive the same attention in the research. Concepts associated with the European eel were the most diverse, ranging from reproduction to life history traits, habitats and their degradation, aquaculture, and restocking. The concepts associated with the other two eel species were less varied. The American eel was mostly associated with concepts relating to life history traits, and the Japanese eel was mostly related to the concept of artificial reproduction (supplementary material S7).

The concepts most frequently associated (over 5% likelihood) with “restocking”, were “yield” (23%) and “farm” (19%) (Fig. 5). The association with the concepts “wild” and “conservation” ranked 11th and 12th (11% likelihood) (Fig. 5).

3.1.3. Key themes and representative articles

Based on the concepts most closely associated with eel translocation in the ACA (concept of “restocking”) (Fig. 5), we decided to focus the narrative review on four main associations which captured four key scientific debates surrounding the ecological efficiency of

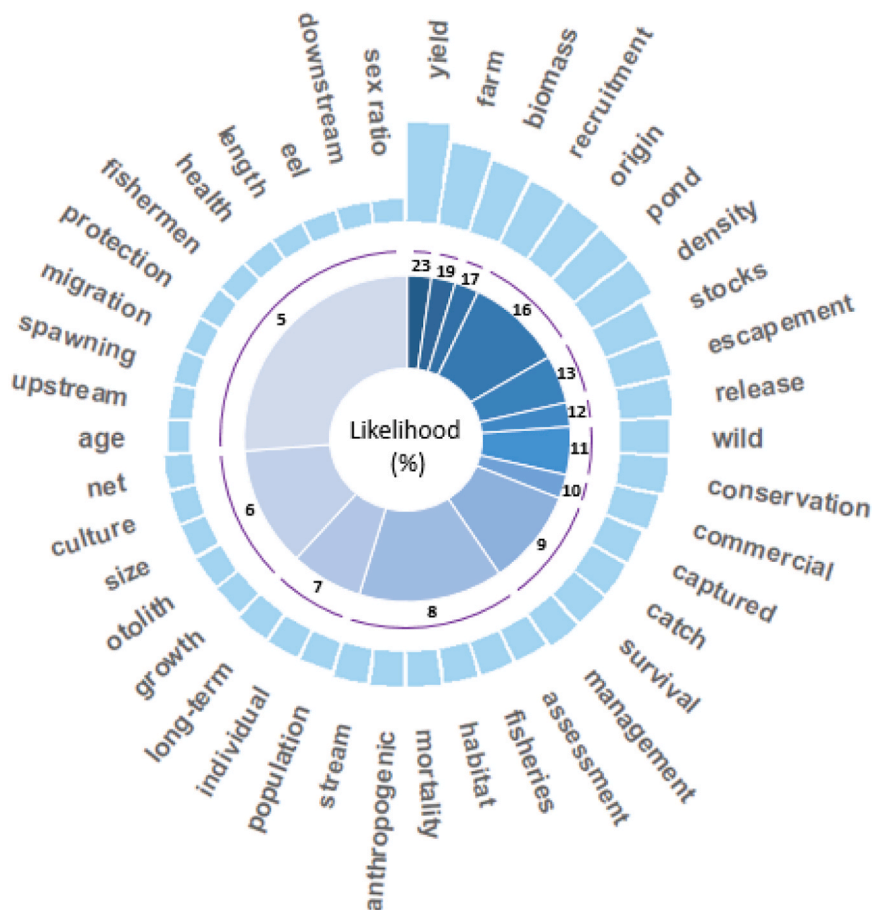


Fig. 5. Main concepts associated with the concept of “restocking” (with a likelihood $\geq 5\%$) revealed by the ACA.

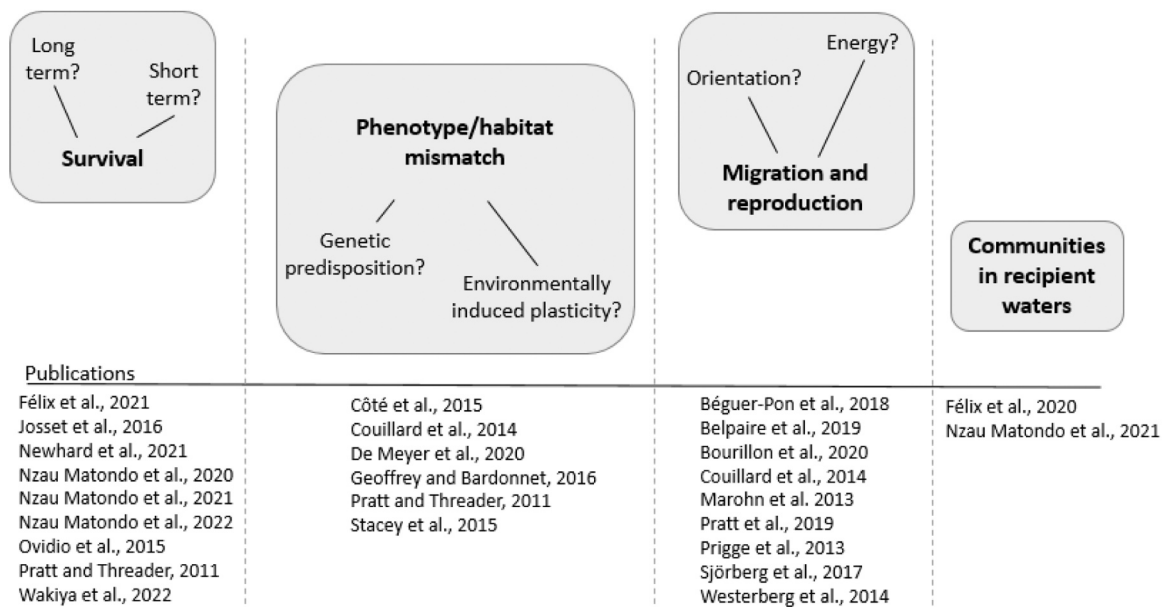


Fig. 6. This figure summarizes the main research issues associated with each ecological process that have been intensely debated in the literature. For each theme, it associates the reference works on which we based ourselves to determine the state of the debate.

eel translocation (Fig. 6). The association of “restocking” with the concepts of “survival” (9% likelihood), “mortality” (8% likelihood), “growth” (6% likelihood), “size” (6% likelihood) and “length” (5% likelihood) (Fig. 5) captured the debate surrounding the relative survival of translocated eels compared to wild eels. The association of “restocking” with the concepts of “health” (5% likelihood), “habitat” (8% likelihood), “density” (16% likelihood) and “sex ratio” (5% likelihood) (Fig. 5) captured the debate surrounding the mismatch between phenotype and habitat. The association of “restocking” with the concepts of “migration” (5% likelihood), “escapement” (13% likelihood) and “downstream” (5% likelihood) (Fig. 5) captured the debate surrounding the migration success of translocated eels. The last scientific debate included in the narrative synthesis was the emerging research issue surrounding translocated eels’ interaction with the aquatic habitat community, even though it was not prominent in the ACA.

3.2. Insights from narrative review

3.2.1. The growth and survival of translocated eels compared to wild eels

Only recent articles (>2020) addressed the survival of translocated eels throughout their growth phase up to the silver stage within a reintroduction context (Newhard et al., 2021; Nzau Matondo et al., 2022). Looking at the short term, translocated eels’ survival and growth rate varied and mostly depended on the translocation protocol, whether for reintroduction or for reinforcement (Pratt and Threader, 2011; Ovidio et al., 2015; Josset et al., 2016; Nzau Matondo et al., 2020; Félix et al., 2021; Nzau Matondo et al., 2021). The survival rate can be as high as 95% (Nzau Matondo et al., 2020). The death of translocated eels occurs during fishing, stalling, tagging, transport and release (Josset et al., 2016). With the exception of Josset et al. (2016), none of the authors took into account fishing mortality. Overall, studies found a high short-term survival for translocated eels in the case of tailored protocols. Only one article focused on an experimental setting, comparing natural mortality with the mortality of translocated eels in a context of reinforcement. This showed that wild eels performed better than translocated eels in terms of survival and growth (Wakiya et al., 2022). Due to a lack of information, our literature review on survival could not conclusively determine whether translocated eels had a higher survival rate than their naturally recruited counterparts until they reached their reproductive stage. However, the results shown in this group of papers suggested that translocation carried out for reintroduction achieves better survival and growth rates among the translocated eels than translocation carried out for reinforcement.

3.2.2. A mismatch between phenotype and habitat

The interaction between the eel genome and the environment shapes phenotypic diversity in eels, including sex (Geffroy, Bardonnet, 2016), growth rate, and ultimately age and length at maturity (Couillard et al., 2014; Côté et al., 2015; Stacey et al., 2015). The consensus in the reviewed literature was that early-stage environment-genome interaction, including local density dependence effects, was a significant driver of phenotype induction (Geffroy, Bardonnet, 2016). Many empirical observations and experimental studies supported the hypothesis that sex is determined at an early life stage by the local eel density (Geffroy, Bardonnet, 2016). High densities were found to induce a higher proportion of males and the clustering of translocated eels before release could trigger a male sex induction (Geffroy, Bardonnet, 2016). At the silver stage, eels translocated from coastal habitats to distant upstream habitats exhibited the phenotype observed in their habitat of collection (i.e. small size at maturity, male-biased sex ratio) rather than the phenotype observed in their habitat of release (Couillard et al., 2014; Stacey et al., 2015). Studies concerned with the spatial selection of phenotypes and the environmental sex determination of temperate eels all warned about the interaction between translocation and eel phenotype induction (Geffroy and Bardonnet, 2012; Côté et al., 2015; Stacey et al., 2015). The observation of male eels in distant upstream freshwater habitats after eel reintroduction supports the hypothesis of a sex ratio biased by translocation (Pratt and Threader, 2011). Apart from sex, the bias in other morphological traits – such as head shape and body size – induced by translocation place restocked eels at risk of maladaptation (De Meyer et al., 2020). To avoid this, some authors further recommended a precautionary approach restricting the use of translocation to a trap and transportation process to help eels cross aquatic obstacles within the same river basin (Côté et al., 2015; Stacey and al, 2015).

3.2.3. Translocated eels’ migration capacity compared to wild eels

Temperate eels require sufficient energy stores and adequate navigation abilities to complete their journey to the spawning areas. Whether translocated eels have these assets at the silver stage has long been debated. Studies using tagging methods observed the successful migration of translocated silver eels towards their spawning areas, showing that at least part of the translocated individuals were able to adopt a regular migration behavior within the framework of reinforcement actions (Westerberg et al., 2014; Sjöberg et al., 2017; Béguer-Pon et al., 2018). These studies did not estimate the proportion of translocated eels effectively contributing to reproduction. Compared to wild eels, translocated eels exhibited a delayed migration behavior, which depended on the release location (Prigge et al., 2013; Sjöberg et al., 2017). This delay raises questions regarding the ability of restocked eels to reach their spawning areas in time for the spawning event (Prigge et al., 2013).

Moreover, the physiological capacity of translocated eels to complete the migration journey was called into question. When translocation protocols involved the release of eels into freshwater habitats, results suggested that translocated eels did not store sufficient energy to migrate (Marohn et al., 2013; Couillard et al., 2014). Moreover, they produced smaller females due to maladaptation, and were more prone to infection by a parasite that would impair their migration (Pratt et al., 2019) and to being adversely affected by contaminants (Belpaire et al., 2019; Bourillon et al., 2020).

3.2.4. The impact of translocation on recipient ecosystems

The question of the ecological effectiveness of eel translocation from a community ecology perspective was the last research issue

we identified as an emerging debate in eel conservation. Only recent studies investigated the role of translocated eels as an interactive component of the aquatic community of their habitat of release (Félix et al., 2020; Nzau Matondo et al., 2021). These studies compared the composition of the aquatic community in a tributary of Mondego River before and after the release of translocated glass eels (Félix et al., 2020) and in several tributaries of Meuse River for three years after the release of translocated glass eels (Nzau Matondo et al., 2021). The results showed that the fish community was unchanged after release and that the invertebrate community became more diverse. However, these two localised case studies alone cannot produce conclusive evidence regarding the benefits of eel translocation for aquatic biodiversity or aquatic community functioning. Moreover, the Belgian study suggested interspecific competition between translocated eels and brown trout (*Salmo trutta*).

4. Discussion and conclusion

The present review showed that there is still considerable room for improvement in the evaluation of the effectiveness of eel restocking for conservation purposes. There is a lack of documented comparative studies on the survival, reproduction, and offspring survival of restocked and wild eels (Table 1). This is partly due to the impossibility of accessing the field to evaluate the reproduction success of eels in the open ocean. The efficiency of eel translocation as a conservation measure can therefore only be evaluated based on biological and ecological processes observed during the eels' continental phase. Thus, in order to improve our knowledge on how, when, where, and to what extent the translocation of eels could be implemented, we have highlighted a number of knowledge gaps regarding the effectiveness of eel restocking that warrant further study to support eel conservation (Table 1). Moreover, we have provided a valuable body of evidence for decision making in a conservation policy-making or resource-management context.

This review highlights several key points for both conservation policy making and research on the translocation of temperate eel species. Coupling a systematic review with a narrative review allowed for an exhaustive, reproducible and rigorous analysis of the scientific literature on the efficiency of eel translocation. While the systematic review identified the research topics associated with translocation, the narrative review provided an in-depth analysis of the main debates surrounding the research issues relating to the efficiency of translocation as a conservation measure. The consensus and research gaps revealed in this analysis were summarized (Table 1). A potential publication bias cannot be excluded, which is the under-representation of negative results in the literature, namely eel restocking failures in our case (Cochran-Biederman et al., 2015; Resende et al., 2020). However, the large number of articles reviewed (956) should limit the importance of this bias for the analysis. The choice to focus on the efficiency of translocation for the three Northern Hemisphere temperate species did not restrict the analysis of translocation efficiency, as the literature on other eel temperate species (*A. reinhardtii*, *A. australis*, and *A. dieffenbachii*) is very scarce and is mostly concerned with fisheries issues (Beentjes et al., 2006).

4.1. Implications for research

From a conservation perspective, the long-term monitoring of translocated eels' survival and growth provided a valuable contribution to the research (Pratt and Threader, 2011; Ovidio et al., 2015; Josset et al., 2016; Nzau Matondo et al., 2020; Félix et al., 2021; Newhard et al., 2021; Nzau Matondo et al., 2021; Nzau Matondo et al., 2022; Wakiya et al., 2022). However, the studies were mostly focused on translocated eels exclusively, rather than on the comparison of naturally recruited eels and translocated eels. The evaluation of translocation efficiency from a species conservation perspective was more effectively measured when looking at the outcomes of studies on silver eel migration. The emerging issue of the role of translocated eels in the aquatic community of their habitat of release evidenced a shift in perspective in research on the efficiency of eel translocation. The issue of eel as an umbrella species is also implemented in an ecosystemic conservation framework (Itakura et al., 2020).

A strict evaluation of the ecological efficiency of translocation should directly compare translocated eels with their wild counterparts at the fishing site and the release site (in the case of reinforcement action). Comparisons of wild and translocated eels in a production objective address only partial measure of the fitness (Bisgaard and Pedersen, 1991; Pedersen, 2000; Lin et al., 2007) but these studies do not allow to address the comparison in a conservation perspective since it has been carried out in closed habitats. The

Table 1
Main consensus and research gaps.

Consensus	Research gap
Individual scale <ul style="list-style-type: none"> • Short- and medium-term monitoring • Restocking interferes with natural selection processes • Migration behavior 	<ul style="list-style-type: none"> • Long-term monitoring • Comparison of survival and growth with those of wild eels • Oceanic migration • Impact of delayed migration on reproduction • Fecundity of restocked females
Population scale <ul style="list-style-type: none"> • No depletion of the gene pool (panmixia) • Random dispersal of larvae • Influence of density on traits, including sex ratio 	
Community scale (emerging debate)	<ul style="list-style-type: none"> • Predation of restocked glass eels • Effect on communities after restocking

identification of translocated eels among migrating silver eels suggested that translocated eels were indeed able to survive until the pre-maturation silver stage. Short-term studies found highly variable survival rates of translocated eels, reaching up to 95% (Nzau Matondo et al., 2020). Other older studies reported much lower survival rates, with less than 80% survival in the Commachio lagoon (Rossi et al., 1988). The natural mortality of eels is quite low, most likely due to the eel's exceptionally low energy-consuming metabolism (Lin and Sun, 2013). Compared to naturally recruited eels, translocated eels would have to survive fishing, handling, marking, transport and release in a habitat they did not choose (Josset et al., 2016). Whether the addition of such anthropogenic stresses led to a lower mortality of the restocked eels than that of the naturally recruited individuals is quite doubtful. Altogether, the literature offered little demonstration that translocation provided a survival advantage for eels in wild habitat contexts.

Translocation was found to interfere with the genome-environment relationship in eel, resulting in phenotype inconsistencies in the habitat of release, bias in sex ratios, or mortality. At population level, the consequences of phenotype manipulation through translocation remained unclear, but placed translocated eels at risk of a lower fitness than wild eels, as many authors noted.

Although we did not discuss the different translocation scenarios, from an ecology/evolutionary biology perspective, the more advanced the translocation stage, the more disruption there will be to selection processes. For example, the scenarios involving long storing in artificial environments or yellow eel translocations resulted in strong phenotype/habitat mismatches (Verreault et al., 2009).

Where somatic growth, infection, and contamination load were determined by the ambient environment, the habitat of release seemed to be a significant factor influencing the fitness of translocated eels (Belpaire et al., 2019; Bernotas et al., 2020; Nzau Matondo et al., 2021). Moreover, there is a direct correlation between fat content, body length and fecundity in female eels (Durif et al., 2006). One proxy of fitness in eels is somatic size and fat reserve amounts, two key drivers of success in oceanic reproductive migration (migration and maturation processes). In the present review, available results on translocated silver eels showed that they had a shorter body size and a lower fat content than their naturally recruited counterparts, suggesting that they had attained a lower fitness level at the silver stage.

In the present review, the migration behavior of translocated eels was found to be similar to that of wild eels. However, we did not find any estimate of the proportion of translocated eels that migrated successfully with their wild counterparts. Several studies suggested that eels used their magnetic sense to imprint the orientation of their return migration journey (Durif et al., 2013; Cresci et al., 2019), which would entail that translocated eels lacking this imprinting are at risk of unsuccessfully mapping their migration path. The schooling behavior of silver eels (Burgerhout et al., 2013), whereby silver eels of different origins mix, could foster the migration behavior of translocated eels. Social cues were already found to promote upstream migration behavior in eels (Podgorniak et al., 2016). These social cues could compensate for the lack of magnetic imprinting in translocated eels. In turn, this suggests that translocated eels have to mix with wild eels in order to develop a suitable behavior. Research gaps still remain in the evaluation of the relative reproductive success of translocated eels in the spawning area and the subsequent survival of their offspring. The study of eel biology in the marine environment remains incomplete. The only potentially useful information available on migration journeys comes from a satellite tagging study, where silver eels with the lowest fitness levels (size and fat) leaving continental waters were found to be most prone to predation in the open ocean (Wahlberg et al., 2014).

The benefits of eel translocation for the conservation of eel in aquatic communities is an emerging topic in the scientific literature, with research showing that the introduction of eel in eel-free habitats could increase the biodiversity of the invertebrate community and does not induce changes in the fish community (Félix et al., 2020). There is a knowledge gap in the evaluation of the benefits or drawbacks of eel translocation for the aquatic community. At a smaller scale, an earlier study had already evaluated the benefits of American eel reintroduction to enhance the population of freshwater mussel (*Elliptio complanata*) (Galbraith et al., 2018). This study showed that the reintroduction of eel as a host for mussels was beneficial to mussels, thus producing conservation benefits for eel and mussels. Most of the knowledge on the role of eel as a predator comes from studies published between the 1960 s and 1980 s (Dekker and Beaulaton, 2016). Aquatic communities have undergone profound changes since then, which are reshaping aquatic communities' interaction webs (Sommerwerk et al., 2017). Previous studies had focused on eel predation on endangered crayfish (Schulz et al., 2006) and salmonids eggs (Mann and Blackburn, 1991). European eel had been considered as officially harmful (Dekker and Beaulaton, 2016) and was destroyed in salmon streams until the 1980 s. The dominance of invasive species was observed in contemporary aquatic communities (Sousa et al., 2011), invasive species which are either potential predators (*Silurus glanis*) or potential prey for eels (invasive crayfish). Although the translocation of eels was advised to control invasive crayfish species (Aquiloni et al., 2010), the efficiency of the re-introduction of eels into invasive species-dominated habitats was not evaluated. Moreover, the risk of introducing new pathogens in recipient waters should be considered. Even though intraspecific transmissions of pathogens has been studied, as a case study for *A. crassus* infection (Pratt et al., 2019), interspecific infections were not mentioned in the scientific literature.

In order to achieve a broader understanding of the eel's role in ecosystems, more knowledge on the role of translocated eels as prey is also needed, although some studies have already addressed glass eel predation (Miyake et al., 2018) and silver eel predation (Béguier-Pon et al., 2012; Wahlberg et al., 2014). There is an overall lack of evaluation of the consequences of eel introduction in eel-free habitats, or habitats with a low eel density. The introduction of animals or their reintroduction can have unintended consequences that may hinder conservation efforts (Pearson et al., 2022) and call for a careful evaluation of the recipient community's interaction web to identify and mitigate unintended outcomes. The interaction between eel translocation and global warming was not specifically addressed in the literature gathered for the present review, suggesting that there was a knowledge gap on this topic. The fact that eels do not reproduce in recipient waters makes the effect of global warming difficult to assess (Drouineau et al., 2018).

4.2. Implications for conservation policy making

The present review yielded contrasting results: while they showed greater translocation efficiency in the context of reintroduction

in terms of survival, growth and aquatic community, they conversely revealed greater translocation efficiency in a reinforcement context in terms of phenotype/habitat alignment and migration. The phenotype/habitat mismatch tends to show that eel translocation is not an efficient conservation measure at the scale of the eel's continental life stages (from glass eel to silver eel).

Reintroduction of eels where they were absent resulted in better growth and survival. However, eel-free habitats are often located in the freshwater upstream part of river catchments, where obstacles can impede migration. More generally, translocated eels were most often released in landlocked habitats (i.e. lakes with no outlets for silver eel migration), a choice that is irrelevant from a conservation perspective. The choice of landlocked habitats was initially made either for fishing purposes or within the framework of conservation action to facilitate the monitoring and evaluation of restocking (Pedersen, 2000; Kangur et al., 2002; Simon and Dörner, 2014). However, eels restocked in freshwater habitats and/or landlocked habitats may compete resulting in reduced growth rates, lower food production, and subsequent lower habitat carrying capacity, all obstacles to silver eel migration. This disadvantage of landlocked habitats may be offset by the storage of qualitative fatty acids in freshwater habitats (Parzanini et al., 2021). In order to overcome imprinting issues, restricting action to “trapping and transporting” was highlighted as a more valuable practice than translocation. However, releasing eels above manmade obstacles to migration has to be coupled with assistance for downward migration to their spawning areas. Moreover, transferring eels into upstream habitat may bias the sex ratio. The present review did not find that translocated eels had a fitness advantage over wild eels. When translocation actions may allow the optimisation of one part of eel fitness component at a time (i.e. survival, migration, etc.) it is to the detriment of other life traits, which means that fitness cannot be optimised as a whole in the frame of translocations actions.

In the polemics around translocation actions and more specifically for eels, two main arguments arose (emergent). The pros of eel translocation insist on the fact that eels are transported to better quality habitats and avoid mortality but the present study showed that this fitness advantage was not supported in the scientific literature. Another argument is that the translocated eels are taken as a “surplus”, in habitats of limited carrying capacity and hence are saved. The surplus argument is doubtful in a context where glass eel recruitment has dropped dramatically, above 90% from 1980's values for European eel (ICES, 2016). The obstacles inducing local surplus is yet an issue of interest. But translocation action in this case would be restricted to “trap and transport” actions, with the same difficulties previously mentioned.

Beyond the framework of conservation efficiency, eel translocation was initially guided by economic perspectives. The practice of eel translocation is still largely driven by production objectives within the framework of fishery and aquaculture. The ambivalence surrounding eel conservation stems from the fact that eel is still an exploited species with high economic value. Thus, for the three Northern hemisphere temperate species, glass eel fisheries were still allowed within conservation management plans whereas partial or total fishing bans were implemented (Fishery Management Report No. 36 of the Atlantic States Marine Fisheries Commission; Interstate Fishery Management Plan for American Eel, 2000; Décret n°, du 22, 2010–, 1110 relatif à la gestion et à la pêche de l'anguille; The Bureau of Fisheries of People's Republic of China et al., 2014).

In the case of European eel, translocation actions are undertaken by commercial fishery actors. In Japan, where the Fisheries Act has mandated that inland water fishery cooperatives which catch eels in rivers and lakes increase their eel populations, these cooperatives typically restock eels to fulfil this obligation (Kaifu, 2019). As far as we are aware of, there are only few translocation successes reported in the scientific literature for endangered species, either exploited, such as The Golden lion tamarin (*Leontopithecus rosalia*) (Kierulff et al., 2012), or not exploited, such as the threatened Clouded Apollo butterfly (*Parnassius mnemosyne*) (Kuussaari et al., 2015). This tends to show either that translocation efficiency as a conservation action might be underevaluated or that this kind of measure mainly fail considering that failures are less published. However, success was achieved for translocations of several threatened species in the U.S under a conservation framework (Novak et al., 2021). The same study provided evidence that translocation led with economic or recreational frameworks did not fulfil the conservation objectives and failed. This calls for an urgent change of perspective regarding translocations of eels in the objective of conservation.

Eel translocation actions are often designed as mitigation actions (at least for *A. anguilla* and *A. japonica*) to offset fishery activities. “Because mitigation releases are economically motivated, outcomes may be less successful than those of releases designed to serve the biological needs of species” (Germano et al., 2015). The gap in the evaluation of the socio-economic mechanisms underpinning the ambivalence of eel translocation as a conservation measure still remains, and warrants closer study.

To conclude, translocation actions, also known as “restocking” or “stocking”, seems ultimately doubly inefficient. First, they do not increase the catch biomass at the eel population level (Dekker and Beaulaton, 2016). Second, in the present “argumentum absurdum” reasoning, we showed that translocation actions resulted in the fact that fitness of eel cannot be cumulatively optimised along the part of life cycle that was accessible in the scientific literature (mainly continental life stages) and were even sometimes inefficient or harmful (Novak et al., 2021).

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data Availability

Data will be made available on request.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at [doi:10.1016/j.gecco.2023.e02635](https://doi.org/10.1016/j.gecco.2023.e02635).

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