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Advances and challenges in modelling the impacts of invasive alien

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species on aquatic ecosystems

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Abstract

Invasive alien species (IAS) have become an important driver of biodiversity change and exert severe pressure on natural ecosystems. The development of modelling approaches to assess and predict their distributions and impacts, and evaluate management options has increased substantially.

We reviewed these modelling approaches, applied in aquatic ecosystems, using a systematic review approach in line with the Preferred Reporting Items for Systematic Reviews and Meta-analyses (PRISMA). According to our results, multispecies/ecosystem models dominated the applications, with dynamic and non-spatial models being the most prevalent. Most of the models included an additional stressor, mainly fisheries, climate change or nutrient loading. The impacts on biota focused on predation, but also on competition and ecosystem functioning, while the impacts on ecosystem services focused on food provision and water purification. At species/population level, most of the studies reported negative impacts; while at multispecies/ecosystem level, negative and both negative and positive impacts were similarly represented.

We reflect on the ability of current models to assess different impacts of IAS populations and highlight the need to advance their capabilities to predict future impacts. Further development of models that allow capturing the arrival, establishment and spread of IAS and assess their impacts in an integrated way is still needed. Spatial-temporal modelling techniques bridging with novel analytical capabilities (such as environmental DNA to investigate the presence of IAS and metabarcoding and machine learning to predict future trophic behavior and distributions) may be the key for future achievement.

Keywords: Invasive alien species; impacts; modelling; marine ecosystems; freshwater ecosystems; PRISMA.

55 **Highlights**

- 56 • We reviewed past and state-of-the-art modelling approaches to assess impacts of
57 invasive alien species (IAS) in aquatic ecosystems.
- 58 • Multispecies/ecosystem models dominated, with dynamic and non-spatial
59 models being the most prevalent.
- 60 • We summarised the main features of available approaches and analysed their
61 capabilities and limitations.
- 62 • We highlighted the need to advance the capabilities of models to predict future
63 impacts of existing, emerging and potential new IAS.
- 64 •

1. Introduction

Biological invasions are currently one of the most important drivers of biodiversity change and exert severe pressure on terrestrial, freshwater and marine ecosystems, with both ecological and economic impacts ([Bax, Williamson et al. 2003](#); [Simberloff, Martin et al. 2013](#); [Gallardo, Clavero et al. 2016](#)). Alien species (also known as exotic, introduced, allochthonous, non-indigenous or non-native species) are any taxa crossing biogeographic barriers that were introduced outside their natural past or present distribution by a human agent, including any part, gamete seeds, eggs, or propagules that might survive and subsequently reproduce ([Essl, Bacher et al. 2018](#)). Invasive alien species (IAS) are defined as those alien species that have negative impacts on biodiversity, ranging from changes in the genetic diversity of native species to species extinction and alterations of an entire ecosystem ([Grosholz 2002](#); [Strayer 2010](#); [Levin and Crooks 2011](#)), and/or on ecosystem services ([Pejchar and Mooney 2009](#); [Katsanevakis, Wallentinus et al. 2014](#); [Vilà and Hulme 2017](#)).

Humans have traded and, intentionally or unintentionally, transported alien species for millennia, but the rapid globalization and increases in trade and transport capacity in recent decades have accelerated biological invasions, despite growing national and international efforts to reduce invasion risk ([Hulme 2009](#); [Katsanevakis, Zenetos et al. 2013](#); [Nunes, Tricarico et al. 2015](#); [Seebens, Blackburn et al. 2017](#)). In addition, biological invasions interact with other stressors, defined as agents (biological, chemical or physical) to which organism and/or ecosystems respond. These agents, such as climate change, habitat degradation and loss, overexploitation and pollution, cause stress and compromise ecosystem integrity ([Dudgeon, Arthington et al. 2006](#); [Halpern, Frazier et al. 2015](#)). In aquatic ecosystems particularly, human stressors have led to high rates of biodiversity loss and ecosystem degradation, which are estimated to be much faster for freshwater systems than for terrestrial or marine ecosystems ([Ricciardi and Rasmussen 1999](#); [Jenkins 2003](#)).

Studying the impacts of IAS in aquatic ecosystems is challenging due to: (1) the dynamic and complex nature of natural ecosystems, and the high connectivity of aquatic ecosystems, with hydrographic barriers occurring at much larger spatial scales than in terrestrial ecosystems; (2) limitations of methodological tools, which include uncertainties in field surveys due to low detectability/catchability ([Katsanevakis, Smit et](#)

[al. 2012](#)) and limitations of models, e.g. due to data availability (distribution of habitats and species is much more difficult to assess in the aquatic than in the terrestrial environment), complexity of models and how processes are represented mathematically ([Fulton, Smith et al. 2003](#); [Evans, Bithell et al. 2013](#)); and (3) a general lack of knowledge about IAS and their invading processes, which include, the factors that affect the introduction and subsequent spread, a time lag between the invasion and discovery of IAS or between the invasion and its impacts, errors in species inventories and alien status, environmental preferences and trophic interactions (potential prey and predators) of IAS in the new environment ([Crooks 2005](#); [McGeoch, Spear et al. 2012](#); [Katsanevakis and Moustakas 2018](#); [Moustakas and Katsanevakis 2018](#)). These have all led to great uncertainties in aquatic invasion science ([Katsanevakis and Moustakas 2018](#)).

Evaluating IAS impacts is essential to developing strategies for prevention and management ([Pyšek and Richardson 2010](#); [Ojaveer, Galil et al. 2015](#)). Approaches range from documenting invaders and examining interactions between invaders and native species to assess the ecological and economic impacts of invasion by using a large variety of modelling techniques ([Wonham and Lewis 2009](#)). Modelling tools can provide a means for increasing understanding of processes, drivers and responses of organisms and ecosystems to human pressures; identifying gaps in available knowledge and allowing the development of predictions about possible future dynamics ([Jørgensen and Fath 2011](#); [Hannon and Ruth 2014](#)).

Although most invasion biologists are familiar with risk and impact assessment and related protocols ([González-Moreno, Lazzaro et al. 2019](#)), very few have applied modelling tools to assess impacts and investigate management options (e.g., [Corrales, Ofir et al. 2017](#); [Michailidis, Corrales et al. 2019](#)). Thus, a comprehensive evaluation of available modelling tools assessing IAS impacts was missing from the literature. The principal aim of this study is to map and review available modelling approaches used to evaluate the impacts of IAS in aquatic systems to date. We summarise the main features of these applications and analyse their capabilities and limitations. Based on the conclusions of this review, we reflect on future directions of development and applications of suitable modelling tools.

2. Methods

We followed a systematic review approach in line with PRISMA (Preferred Reporting Items for Systematic Reviews and Meta-Analyses) ([Moher, Liberati et al. 2010](#)). This approach consists of three steps: (1) systematic article selection using a search engine; (2) article screening; and (3) a review of relevant articles and extraction of the information.

We performed the bibliographic search using Elsevier's Scopus database (www.scopus.com). Eligibility criteria included any article, review, or book chapter published between 1990 (because the focus of the review is recent developments) and the cut-off date, 8th February 2017, with the following search terms in the title, abstract or keywords:

1. "model" or "modelling" or "modeling"; and
2. "impact" or "impacts" or "effect" or "effects"; and
3. "invasive species" or "alien species" or "allochthonous species" or "introduced species" or "non-indigenous species" or "non-native species" or "invasion" or "exotic"; and
4. "marine" or "sea" or "coast" or "coastal" or "estuarine" or "bay" or "freshwater" or "lake" or "river" or "reservoir" or "lagoon".

The search was limited to relevant subject areas (Agricultural and Biological Science, Environmental Science, Earth and Planetary Sciences and multidisciplinary) and to English-language and Spanish-language publications. The search resulted in 1306 publications.

Afterwards, we manually included additional relevant papers from other sources that were not found in the main search as has been done in previous studies ([Mačić, Albano et al. 2018](#)). Additional papers included (1) an available bibliographic search ([Corrales, Gal et al. 2014](#)) of the Ecopath with Ecosim modelling tool that assessed impacts of IAS (e.g., [Kitchell, Cox et al. 2000](#); [Downing, Van Nes et al. 2012](#); [Kao, Adlerstein et al. 2016](#)); (2) papers cited in review papers found in the initial search such as [Wonham and Lewis \(2009\)](#), [Thompson, Giusti et al. \(2013\)](#) and [Piroddi, Teixeira et al. \(2015\)](#); (3) papers from the personal files of the authors (e.g., [Padilla, Adolph et al. 1996](#)); and, (4)

relevant papers found in selected articles during the third step of the systematic review (extraction of the information). With these additional articles, the total number of papers increased to 1382 (Fig. 1 in the Online Supplementary Information A).

Article screening started with these 1382 articles and consisted of a two-stage process: the first screening of articles was based on the title and the abstract, and the second on the full article. During this process, articles were excluded if they: (1) did not apply or develop a model to evaluate the impact of IAS, or (2) were related only to terrestrial habitat/species. After the first selection process, 389 articles (28.3% of the original papers) were selected. After the second selection process, 189 articles (all in English language, see Online Supplementary Information A for the final list of articles and their full references) were included in the analysis (13.8% of the original papers). Species distribution models (SDMs) and studies based on stable isotope analysis passed the first screening process but were excluded in the second if they did not include, qualitatively or quantitatively, the study of IAS impacts.

The following information was extracted from each selected article (see Online Supplementary Information section B):

(1) Year of publication;

(2) Realm of the study (freshwater, estuarine or marine);

(3) Biogeographic region, based on [Olson, Dinerstein et al. \(2001\)](#) (freshwater) and [Spalding, Fox et al. \(2007\)](#) (marine);

(3) Ecosystem type (e.g., lake, river, bay);

(4) Information related to the IAS included in the model: number of IAS, scientific and common name/s, type of organism/s (the groups were defined based on the taxonomic detail of the studies and the ecology of the organism) (e.g., fish, invertebrates), habitat/s (demersal or pelagic) and trophic level/s (TL). The TL concept identifies the position of organisms within food webs by identifying the source of energy of each organism, with TL 1 for primary producers and higher values for consumers ([Lindeman 1942](#)). We classified TL as low ($TL < 3$), medium ($3 \leq TL \leq 3.5$) and high ($TL > 3.5$) based on outputs from models or databases such as FishBase ([Froese and Pauly 2017](#)) and SeaLifeBase ([Palomares and Pauly 2017](#));

(5) Information related to the model: modelling level (species/population or multispecies/ecosystem level) ([Hollowed, Bax et al. 2000](#); [Jørgensen and Fath 2011](#)), type of model (statistical, i.e. models seeking patterns in the observed data regardless of causative processes involved, versus mechanistic, i.e. models specifying relationships among variables in terms of biological processes) ([Levins 1966](#); [Jørgensen 2008](#)), model category (e.g., bioenergetics and biogeochemical model), data type (time and spatial scales) ([Jørgensen and Fath 2011](#); [Hannon and Ruth 2014](#)), if other external stressors were included aside from IAS (for example, fisheries, climate change and nutrient loading), if the model was validated (defined as an objective test to reflect how well model outputs fit observed data through the comparison of model results with independent data) and how it was validated, if uncertainty was evaluated, and if the model was used to provide management recommendations; and

(6) Information related to the impacts of alien species: number and types of impacts on ecosystem services (based on the classification by [Liquete, Piroddi et al. \(2013\)](#)) and/or on biota (for example, predation, competition and ecosystem processes/function); if the impact was positive (e.g. by providing a new food source for humans or other species or by providing increased biofiltration) or negative (e.g. by causing the decline of native populations due to predation, competition for resources or degradation of important habitats) or both (positive and negative) (see [Katsanevakis, Wallentinus et al. \(2014\)](#) for full classification of positive and negative impacts); and which indicators were used to evaluate the impact (number of indicators, type and units).

To summarise categorical variables and test pair-wise potential dependencies, we applied a crosstabulation analysis and Chi-square test of independence ([Zar 2013](#)), using the statistical software Statgraphics ([Statgraphics-Centurion 2009](#)). We tested the hypothesis that the frequencies of occurrence in the various categories of one variable are independent of the frequencies in the second variable.

3. Results

3.1. Temporal development, ecosystem coverage and species included

Since 1992, there has been an increase in the number of publications of models that assessed the impacts of IAS in aquatic ecosystems (Fig. 1). From 1992 to 2004 the average rate of publications was 3.1 papers per year, while from 2005 to 2016 the rate increased to 12.2 papers per year. Such temporal trends in the number of related published articles were compared to the corresponding trends of published articles (within the same subject areas) in the wider themes of: (i) “aquatic” studies in general, (ii) studies of biological invasions in the aquatic environment, and (iii) studies on the impacts of biological invasions in the aquatic environment (see Online Supplementary Information section C). The number of publications of models that assessed the impacts of IAS in aquatic ecosystems increased at: (i) a faster rate, (ii) the same rate, and (iii) a lower rate, respectively. These trends indicate that although modelling studies of the impacts of biological invasions in the aquatic environment have followed the general trend of studies of aquatic biological invasions, which is much faster than general aquatic-related papers, their relative importance in impact assessments of aquatic biological invasions has been reduced with time. This reduction could be due to the considerable research that has been conducted on the impacts of biological invasions in recent decades ([Ricciardi, Hoopes et al. 2013](#); [Chan and Briski 2017](#)), of which only a small percentage is based on modelling. Most papers studied freshwater ecosystems (75%), especially lakes, followed by marine (22%) and estuarine (3%) ecosystems (Fig. 1).

The studies covered several of the marine and freshwater biogeographic regions (Fig. 2). In the freshwater realm, most of the models were developed in the Nearctic biogeographic region (75%), followed by the Palearctic (10%) and Afrotropical (8%). We did not find studies in the Oceanian and Antarctic biogeographic regions. In the marine realm, the Temperate Northern Atlantic (64%), the Tropical Atlantic (11%) and the Temperate Northern Pacific (9%) biogeographic regions represented most of the studies, while no studies were conducted in the Western and Central Indo-Pacific, Tropical Eastern Indo-Pacific, Arctic and Southern Ocean biogeographic regions.

In freshwater and marine ecosystems, fishes (58 % and 31%, respectively) and molluscs (mainly bivalves) (29% and 20%, respectively) were the most frequently studied groups

in the selected models, while in estuarine ecosystems, zooplankton (50%) and molluscs (31%) were the main groups (Table 1). The frequency of occurrence of the three categories of trophic level (low, medium and high) differed significantly among the three environments (marine, freshwater and estuarine) (Chi-square test, $p < 0.005$). Most of the studies focused on low trophic level species, especially in estuarine (71.4% of the species) and freshwater (54.5% of the species) ecosystems, while in the marine environment low and medium trophic level were equally represented (Fig. 3a). Pelagic and demersal species were equally represented (48 and 52% respectively) (Fig 3b) and did not differ significantly among the three environments (Chi-square test, $p = 0.16$) (Fig. 3b).

3.2. Overview of the main modelling approaches

Multispecies/ecosystem level models (77%) were more prevalent than species/population level models (23%) in all ecosystem types (Fig. 4a). We found no statistically significant difference in the frequencies of occurrence of the two modelling levels among the three types of environment (Chi-square test, $p = 0.1$). The frequencies of statistical or mechanistic models significantly differed between the two modelling levels (species/population or multispecies/ecosystem) (Chi square test, $p < 0.005$). At the species/population modelling level, we did not find large differences between the number of studies that developed statistical ($n=18$) and mechanistic ($n=26$) models, while at the multispecies/ecosystem level, most studies (129 out of 156) used mechanistic models (Fig. 4b). Of the statistical models, we found a similar diversity of models at the species/population and multispecies/ecosystem levels (Table 2). On the contrary, we found a higher diversity of mechanistic models at the multispecies/ecosystem level (Table 2).

The average number of IAS included in the species/population level models was significantly smaller (1.2 ± 0.4 SD), than the average number of IAS in multispecies/ecosystem level models (2.9 ± 6.7 SD) (Mann-Whitney U test, $p = 0.03$) (Fig. 4c). Some species/population level models encompassed two alien species but their impacts were assessed together as they played the same ecological role, for example, zebra mussels (*Dreissena polymorpha* and *D. rostriformis bugensis*) filtering phytoplankton (e.g., [Cha, Stow et al. 2013](#); [Rowe, Obenour et al. 2015](#)).

We found static studies that included a model representing a specific time period (variables and parameters defining the system are time independent), static models comparing different periods (comparative static), and dynamic models, which attempt to capture the change in a simulated time period (variables and parameters defining the system are time dependent). Dynamic models were more frequent than static models and comparison between periods both at the single species and multispecies level (Fig. 5a), but we did not find significant differences in the frequencies of the model types (static, dynamic and comparisons between periods) between the modelling levels (Chi-square test, $p = 0.20$). Non-spatial models were more frequent than model comparisons between study sites and fully spatial models (Fig. 5b) although differences were not significant in the frequencies of non-spatial, fully spatial models or comparisons between sites, between the two modelling levels (Chi-square test, $p = 0.47$).

Since 1992, there has been a progressive increase in the number of models that included an additional stressor, especially since 2001. From 1992 to 2001, the average rate of publications that included additional stressors aside from IAS was 1.1 papers per year, while from 2002 to 2016 the rate increased to 6.3 papers per year (Fig. 6a). Most of the multispecies/ecosystem models included additional stressors, while most of models at the species level did not incorporate an additional stressor aside from the IAS (Fig 6b). The frequencies of the inclusion or non-inclusion of other stressors significantly differed between species/population and multispecies/ecosystem modelling levels (Chi-square test, $p < 0.005$). The most frequently included additional stressors were fisheries (commercial and recreational) (45%), followed by nutrient loading (25%) and climate change (through changes in water temperature and primary production) (21%) (Fig. 6c).

Most studies (70%) did not evaluate uncertainty, with a similar percentage in species/population and multispecies/ecosystem models (see Fig. 1 in the Online Supplementary Information section D) (Chi-square test, $p = 0.37$). From those models that assessed uncertainty we mainly found studies that manually changed different input parameters using literature ranges (e.g., [Jiang, Xia et al. 2015](#)), estimated a degree of increase or decrease based on expected changes ([Johnson, Bunnell et al. 2005](#); [Van Guilder and Seefelt 2013](#)), assessed effects of different initial IAS biomass values ([Zhang, Culver et al. 2008](#); [Schwalb, Bouffard et al. 2014](#)) or used Monte Carlo routines ([Yurista and Schulz 1995](#); [Cha, Stow et al. 2011](#)).

3.3. Modelling impacts of IAS

3.3.1. At the species/population level

Several statistical models that focused on the species/population level were used to assess the impact of IAS (Table 2). For example, [Onikura, Miyake et al. \(2013\)](#) used a generalised linear model to predict potential inter-sub-specific hybridisation and to identify important areas of conservation. To evaluate the impact of competition for a resource, [Van Zuiden, Sharma et al. \(2016\)](#) used multiple regression models to assess the impact of smallmouth bass (*Micropterus dolomeiu*) and climate change on native walleye (*Sander vitreus*). [Olden, Vander Zanden et al. \(2011\)](#) used a SDM to assess impacts of invasive rusty crayfish (*Orconectes rusticus*) on two native congeners (*O. virilis* and *O. propinquus*), while [Woodford, Cochrane et al. \(2011\)](#) used a GIS-based spatial model to predict whether two invasive trout species (*Salmo trutta* and *Oncorhynchus mykiss*) would exclude the native *Galaxias vulgaris* due to predation using a quantile limit function.

In addition, a variety of mechanistic models were used to assess the impact of IAS at the species level. For example, [Liu, Olausson et al. \(2014\)](#) developed a bioeconomic model to capture the effects of invasive farmed fish on native stocks (growth and stock size) and harvest. [Caldow, Stillman et al. \(2007\)](#) developed an individual-based model to evaluate the positive effects of the invasive Manila clam (*Tapes philippinarum*) on the Eurasian oystercatcher (*Haematopus ostralegus*), which provided additional food and therefore reduced winter mortality of the bird.

3.3.2. At the multispecies/ecosystem level

A large variety of statistical models that focused on the multispecies/ecosystem level were used to assess the impact of IAS (Table 2). For example, [Bajer, Beck et al. \(2016\)](#) fitted multivariate linear models to quantify the effects of the invasive common carp (*Cyprinus carpio*) on plant cover and species richness, as well as additional effects of water quality and total phosphorous. [De Amorim, Umetsu et al. \(2015\)](#) assessed the impacts of the invasive African signalgrass (*Urochloa arrecta*) on a macrophyte community using a generalised linear model, while [Knapp \(2005\)](#) used a generalised additive model to assess the effects of invasive trout and habitat characteristics on lentic herpetofauna. [Wenger, Isaak et al. \(2011\)](#) assessed the effect of flow regime,

342 temperature and biotic interactions on the distribution of four trout species (of which
343 three were IAS) under climate change using a SDM.

344 A large variety of mechanistic models were used to assess the impact of IAS at the
345 multispecies/ecosystem level (Table 2). Within these model types, approaches ranged
346 from simple to more complex, including coupled models, where models were integrated
347 (with or without dynamic feedbacks) and outputs of one model provided inputs to the
348 other ([Travers, Shin et al. 2007](#)).

349 A common method for assessing the impacts of IAS at the multispecies/ecosystem level
350 was the development of bioenergetics models (24.8% of the mechanistic
351 multispecies/ecosystem models). For example, [Walrath, Quist et al. \(2015\)](#) used a
352 bioenergetics model to estimate predation of the invasive northern Pike (*Esox lucius*) on
353 westslope cutthroat trout (*Oncorhynchus clarkia lewisi*) and other prey taxa. [Reed-
354 Andersen, Carpenter et al. \(2000\)](#) coupled a zebra mussel bioenergetics model with an
355 empirical phytoplankton growth model to predict the impacts of zebra mussels on water
356 clarity.

357 Some ecological models were coupled with economic models (5.4% of the mechanistic
358 multispecies/ecosystem models). For example, [Knowler \(2005\)](#) assessed the economic
359 consequences of the invasive comb jelly (*Mnemiopsis leidy*) on the Black Sea anchovy
360 (*Engraulis encrasicolus*) fishery using an integrated ecological-economic approach.
361 This model combined a Ricker stock-recruitment model of the anchovy population with
362 a mass balance model of *Mnemiopsis* biomass and an economic model. [Grosholz,
363 Lovell et al. \(2011\)](#) assessed the economic impacts of the invasive European green crab
364 (*Carcinus maenas*) on commercial shell-fisheries along the West Coast of the USA
365 using a combination of ecological and economic models. They first estimated the
366 probability of spread using information of the potential northern and southern
367 boundaries and a multiple logistic regression approach. Then they calculated the
368 impacts on shellfish population due to predation using a regression analysis. Finally, the
369 economic analysis used the losses from the second ecological model to estimate the
370 overall economic consequences of these reductions in commercial shellfish harvest on
371 shellfish producers and consumers, via market demand and supply relationships
372 ([Grosholz, Lovell et al. 2011](#)).

373 Biochemical models, which were mainly developed to represent chemical fluxes
374 (mainly nitrogen and phosphorus) affecting low trophic level groups (e.g.
375 phytoplankton and zooplankton), were also used to assess impacts of IAS (8.5% of the
376 mechanistic multispecies/ecosystem models). For example, [Magnea, Sciascia et al.](#)
377 [\(2013\)](#) developed a dynamic model for 12 alpine lake ecosystems to describe the
378 dynamics of phosphorous (the limiting nutrient), phytoplankton, three zooplankton
379 compartments and fish abundance (in 6 lakes they included the invasive brook trout
380 *Salvelinus fontinalis*). [Bierman, Kaur et al. \(2005\)](#) used an ecosystem model in Saginaw
381 Bay (Lake Huron, US) in which zebra mussel bioenergetics were integrated with an
382 eutrophication model that represented nutrients and multiple functional groups of
383 phytoplankton and zooplankton.

384 The coupling of biogeochemical models with hydrodynamic models (19.4% of the
385 mechanistic multispecies/ecosystem models) allowed the inclusion of spatial and
386 temporal variability of the environment, mainly represented by variables such as
387 temperature, irradiance, salinity and currents. For example, [Schwalb, Bouffard et al.](#)
388 [\(2014\)](#) and [Bocaniov, Smith et al. \(2014\)](#) used a three-dimensional (3D) hydrodynamic
389 model (ELCOM) coupled with a biogeochemical model (CAEDYM). CAEDYM
390 included a mussel sub-model that allowed the authors to assess impacts of invasive
391 dreissenids on phytoplankton. [Isaev, Eremina et al. \(2016\)](#) used a 3D ecosystem model
392 (SPBEM), that coupled a transport module with a biogeochemical module, to assess the
393 impact of bioirrigation activity of the invasive alien polychaetes *Marenzelleria* spp. in
394 the Gulf of Finland. In addition, [Zhang, Culver et al. \(2011\)](#) used a coupled 2D-
395 hydrodynamic model and a water quality model (CE-QUAL-W2) to evaluate effects of
396 invasive dreissenids and zooplankton on phytoplankton in Lake Erie, USA.

397 Food-web models, which include a description of species interactions within the
398 ecosystem, were also frequently used (37.9% of the mechanistic multispecies/ecosystem
399 models). These models ranged from those that included only some species or functional
400 groups to the inclusion of the entire food web. For example, [Blamey, Plagányi et al.](#)
401 [\(2014\)](#) used a Model of Intermediate Complexity for Ecosystem assessments (MICE)
402 (also called Minimally Realistic Model or MRM), to evaluate if overfishing of
403 predatory fish may have caused a regime shift following the invasion of West Coast
404 rock lobster (*Jasus lalandii*). [Miehls, Mason et al. \(2009\)](#) used an Ecological Network
405 Analysis (ENA) to assess the effects of the invasive zebra mussel within and between

two invaded ecosystems and compare food web characteristics before and after the invasion. The Ecopath with Ecosim (EwE) approach ([Christensen and Walters 2004](#); [Heymans, Coll et al. 2016](#)) was frequently used to assess impacts of IAS. For example, [Lercari and Bergamino \(2011\)](#) quantified the impacts of two IAS (the gastropod, *Rapana venosa*, and the bivalve, *Corbicula fluminea*) in Río de la Plata estuary (Argentina and Uruguay) during a specific time period by developing an Ecopath model, while [Downing, Van Nes et al. \(2012\)](#) assessed impacts of IAS and fishing in Lake Victoria through three Ecopath models representing the before, during and after periods of the Nile perch bloom. In addition, [Kao, Adlerstein et al. \(2014\)](#) developed a time dynamic (Ecosim) model to evaluate relative impacts of changes in nutrient loads, fishing and two invasive groups (dreissenids and the alewife *Alosa pseudoharengus*).

Other types of multispecies models were employed to assess impacts of IAS. For example, [Cook, Fletcher et al. \(2014\)](#) used an integrated conceptual ecosystem model (Driver-Pressure-State-Ecosystem Service-Response or DPSE) to explore the direct and indirect relative impact of 12 ecosystem pressures on 11 ecosystem state variables and 11 ecosystem services in southern Florida. [Ortiz and Stotz \(2007\)](#) used qualitative (loop) models of ecological and socio-economic systems to analyse and predict the impact of a possible accidental introduction of the abalone (*Haliotis discus hannai*) into the benthic community of north-central Chile. A conservative additive model was developed to assess the spatial cumulative impacts of IAS on marine habitats in the Mediterranean Sea ([Katsanevakis, Tempera et al. 2016](#)).

Finally, we found a growing interest in recent years to develop models that attempt to represent an entire ecosystem. These models are called end-to-end (E2E) or whole-of-system models and represent ecosystem components from nutrients, biogeochemical cycling and primary producers to top predators (including human and socio-economic components) linked through trophic interactions and the associated abiotic environment (e.g., currents and water column properties such as temperature and salinity) ([Travers, Shin et al. 2007](#); [Fulton 2010](#)). However, only one example of end-to-end models dealing with IAS was found (0.8% of the mechanistic multispecies/ecosystem models). [Nyamweya, Sturludottir et al. \(2016\)](#) developed an Atlantis model for Lake Victoria to assess impacts of overfishing, IAS such as Nile perch and Nile tilapia (*Oreochromis niloticus*), eutrophication and climate change.

3.4. Predicted impacts of IAS at species and ecosystem levels and the utility of models in impact management

The frequency of the types of impacts reported (positive, negative or both) differed significantly between the type of model used (Chi-square test, $p < 0.005$) (Fig. 7a). At the species/population level, 84.1% of the studies reported negative impacts of the IAS on ecosystem compartments and/or ecosystem services, while at the multispecies/ecosystem level, negative (51.4% of the studies) and both negative and positive (47.1% of the studies) impacts were similarly represented (Fig. 7a). We found only a limited number of cases of positive impacts in the results of single species and multispecies models (Fig. 7a).

Most studies reported impacts on biota rather than on ecosystem services, and on multiple-species than single-species (Fig. 7b and c). Most of these impacts (single and multispecies) were due to ecological interactions of IAS involving predation and/or competition for resources. In addition, some models were used to assess impacts on ecosystem processes and function (Fig. 7b), such as biodiversity, biogeochemical fluxes, energy flows and ecosystem stability, and impacts on other ecosystem services (Fig. 7c). Water purification (39%) and food provision (from fisheries or aquaculture) (36%) were the most assessed ecosystem services, followed by recreation and tourism (for example, recreational fisheries) (15.8%) (Fig. 7c).

Most of the studies (90.4%) did not provide management recommendations based on their findings. No significant differences were found in the frequencies of occurrence of studies that reported management recommendations between single and multispecies models (Chi-square test, $p = 0.64$) (see Fig. 2 in the Online Supplementary Information section D) or among the three types of environment (Chi-square test, $p = 0.72$) (see Fig. 2 in the Online Supplementary Information section D). In studies that provided management recommendations, these were mostly of a general nature and no specific management actions were listed (Online Supplementary Information B). However, some studies provided management advice. For example, [Stapp and Hayward \(2002\)](#), based on a stage-structured matrix model, suggested the development of control programs to reduce survival of all age classes of lake trout (*Salvelinus namaycush*). Using an EwE model, [Arias-González, González-Gándara et al. \(2011\)](#) and [Pine, Kwak](#)

469 [et al. \(2007\)](#) assessed, through different scenarios of fishing exploitation, how to
470 eradicate invasive alien top predators.

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4. Discussion

4.1. General patterns in modelling the impacts of IAS on aquatic ecosystems

Our results highlight geographic differences in IAS modelling efforts. While models have been developed for most biogeographic regions (freshwater and marine realms) they have mainly focused on particular areas, such as North America and Europe, in agreement with [Lowry, Rollinson et al. \(2013\)](#), [Pyšek, Richardson et al. \(2008\)](#) and [Buchadas, Vaz et al. \(2017\)](#). This geographic distribution of models can be largely explained by different availability of data and funding opportunities for research ([UNESCO 2017](#)), although there may have been some bias in our findings due to the exclusion of non-English and non-Spanish publications in our review.

Most available studies focused on species occupying low trophic levels. [Lowry, Rollinson et al. \(2013\)](#) and [Pyšek, Richardson et al. \(2008\)](#) also found that most of the research on biological invasions focused on low trophic levels. However, in their reviews most of the species were primary producers (mainly terrestrial plants), while most of the species we identified were fishes and molluscs (mainly bivalves). It is likely that this taxonomic composition indicates research priorities over the last few decades and, in some regions, also reflects the proportion of IAS in the studied ecosystems. In fact, impacts have been assessed for a small proportion of IAS, which tend to be those with the greatest impact on organisms and ecosystems and their services ([Vilà, Basnou et al. 2009](#); [Pyšek and Richardson 2010](#)). For example, dreissenids (freshwater mussels) have been largely studied and modelled due to their wide distribution and dramatic ecological and economic impacts, especially in North America ([Pyšek, Richardson et al. 2008](#); [Higgins and Vander Zanden 2010](#)).

Most models were used to assess the detrimental effects of IAS ([Pyšek, Richardson et al. 2008](#); [Katsanevakis, Wallentinus et al. 2014](#)). However, IAS can also have positive effects on native species and ecosystems (e.g., [Caldow, Stillman et al. 2007](#); [Norkko, Reed et al. 2012](#)). This is highlighted in multispecies/ecosystem level models, which incorporate interactions among many species, and therefore indirect effects can cause both positive and negative impacts. Most of the reported impacts are related to the effect of an invasive alien predator on native preys, but research has also focused on competition for resources and ecosystem processes and function. Effects of invasive alien prey on native predators have been less studied ([Carlsson, Sarnelle et al. 2009](#)),

and according to the trophic position hypothesis, we could expect negative impacts of IAS on biodiversity within a trophic level but positive effects on the biodiversity of higher trophic levels through community-wide antagonism (competition and consumption) and facilitation (habitat and food provisioning) interactions, respectively (Thomsen, Byers et al. 2014).

Ecological processes operate at a wide range of spatial and temporal scales, and thus the choice of these scales in model development is very important (Jørgensen and Fath 2011). These choices affect model complexity, as finer temporal and spatial resolution need more detailed data and require increased computation power and effort, which increase the difficulty of implementation and exacerbate uncertainty (Rose, Allen et al. 2010; Plagányi, Punt et al. 2014). In the context of modelling the impacts of IAS in highly invaded aquatic ecosystems and within an ecosystem-based management, suitable modelling frameworks may need to allow the incorporation of several IAS with different ecological and trophic roles and, therefore, with different temporal and spatial requirements. Connecting these parts of the model or even “sub-models” is a challenging task (Rose, Allen et al. 2010), but is imperative if we want to model the full end-to-end spectrum of these invasions (Heymans, Skogen et al. 2018). Outside the field of biological invasions, models such as OSMOSE and EwE has been coupled satisfactorily with physical and/or biogeochemical models (e.g., Steenbeek, Coll et al. 2013; Akoglu, Libralato et al. 2015; Moullec, Velez et al. 2019) to attempt to represent the whole ecosystem (including humans) and the environment (end-to-end models) (Fulton 2010).

Dynamic models, which are based on non-stationary or time-varying differential or difference equations (Jørgensen, Fath et al. 2011), were the most frequently used. This is likely due to the fact that assessing the impact of IAS in aquatic ecosystems requires a dynamic view of the process, which is time-dependent. It may also be due to the need for tools to manage aquatic ecosystems (Cuddington, Fortin et al. 2013; Buchadas, Vaz et al. 2017). Model comparison between periods presents some advantages over developing a single static model, especially if comparison includes models before and after invasion, as it allows the assessment of the overall impact of IAS on the invaded ecosystem with a temporal baseline (the ecosystem before the invasion). Non-spatial models (defined as those models that processes were not modelled in space) were more frequent than spatial ones. This is due to the challenges of spatial modelling of IAS and

associated data requirements ([Fulton, Smith et al. 2004](#); [Jørgensen 2008](#)). In non-spatial models, comparisons between invaded and non-invaded ecosystems have provided insights into the impacts of IAS (e.g., [Rowe 2007](#); [Blamey, Plagányi et al. 2013](#)) while fully spatial models incorporate the representation of important dynamics observed in nature such as distribution, movement, and dispersal ([Jørgensen and Fath 2011](#)). Spatial-temporal models allow a more realistic representations of the ecosystem, especially if they are fitted to observed data, and provide advantages in modelling impacts of IAS (e.g., [Zhang, Culver et al. 2011](#); [Norkko, Reed et al. 2012](#)).

4.2. Advantages and disadvantages of existing modelling approaches

Statistical models have been widely used to study the impacts of IAS in aquatic ecosystems. These models have been shown to be useful to assess impacts of IAS on native species (e.g., [Stapanian, Kocovsky et al. 2009](#); [De Amorim, Umetsu et al. 2015](#)) and also to predict potential spatial exclusion (e.g., [Sharma, Vander Zanden et al. 2011](#); [Wenger, Isaak et al. 2011](#)). In addition, they are used to disentangle the relative importance of IAS and other stressors in native species declines (e.g., [Light and Marchetti 2007](#); [Hermoso, Clavero et al. 2011](#); [Bajer, Beck et al. 2016](#)), as well as changes in abiotic factors (e.g., [Macdonald, Tonkin et al. 2012](#); [Pagnucco and Ricciardi 2015](#)). Such analyses can improve our understanding of broad patterns in biodiversity changes and provide insight into processes that may be responsible for the patterns observed in the data ([Whipple, Link et al. 2000](#); [Light and Marchetti 2007](#)). However, statistical models incorporate low levels of realism (defined as the capability of model to represent the processes ([Levins 1966](#))) as they indirectly capture the ecological processes that generate them ([Levins 1966](#); [Jørgensen and Fath 2011](#)).

A large number of mechanistic models have been used to study the impacts of IAS, ranging from simple to very complex. At the species level, models assessed impacts of IAS on populations. These impacts included effects on growth ([Liu, Olausson et al. 2014](#); [Crane and Einhouse 2016](#)), catchability (effectiveness of fishing gear) ([Kateregga and Sterner 2009](#)), mortality ([Caldow, Stillman et al. 2007](#)), predation ([Green, Dulvy et al. 2014](#); [Rowe, Obenour et al. 2015](#)) and competition ([Liu, Olausson et al. 2014](#)), as well as economic impacts ([Olden and Tamayo 2014](#)) and fisheries ([Liu, Olausson et al. 2014](#)). However, aquatic ecosystems are dynamic and complex, with interactions between species , and interactions with the environment and human stressors ([Garcia,](#)

[Zerbi et al. 2003](#); [Thoms 2006](#)). An understanding of the functional interactions and processes in aquatic ecosystems, as well as the cumulative impacts of human activities, requires a more comprehensive analysis ([EMB 2019](#)), as is emphasized by ecosystem-based management ([Rosenberg and McLeod 2005](#)). This has been achieved in mechanistic multispecies/ecosystem level models, which complement single-species models by taking into account the influence of trophic interactions and the impacts of human activities and abiotic factors on species dynamics ([Hollowed, Bax et al. 2000](#)). Our study has highlighted them as the most applied modelling approaches, in line with the growing perception of the need for more integrated or holistic approaches ([EMB 2019](#)). Therefore, we discussed below a subset of these methodologies that were more used and we consider to have the greatest potential for improving our knowledge of the impacts of IAS and inform management decisions.

Most of the mechanistic models at the multispecies/ecosystem level that we found were quantitative, with only one qualitative model (loop analysis) applied to the study of the impacts of IAS on aquatic ecosystems ([Ortiz and Stotz 2007](#)). Within the context of modelling impacts of IAS, and with the known data limitations, loop analysis could become a valuable tool ([Metcalf 2010](#)). This is because precise model predictions and estimates of the magnitude of the impacts are not always necessary to inform management ([Ramsey and Veltman 2005](#)), and managers need to make decisions regardless of data availability.

In invasion ecology, the development and application of bioenergetics models are particularly useful because they provide a means of evaluating the trophic impacts (e.g., the amount of prey eaten) of IAS (mainly fish species) and assessing the suitability of an ecosystem for invasion considering their energy requirements and food availability (e.g., [Anderson, Chapman et al. 2015](#); [Foley, Andree et al. 2017](#)). In reality, accurate consumption estimates are difficult to obtain and alternative approaches have important limitations. For example, the development of gastric evacuation rate models through stomach content analysis maybe complex, time-consuming and expensive to collect ([Link 2004](#); [Albouy, Guilhaumon et al. 2011](#)). The use of bioenergetics models presents some disadvantages, including the requirement of good data (i.e., consumption, egestion and excretion rates that depend on size and temperature, which usually is based on laboratory experiments or taken from similar species), associated with intense sampling,

601 and the difficulties in calibrating the models ([Chipps and Wahl 2008](#); [Hartman and](#)
602 [Kitchell 2008](#); [Jørgensen 2008](#)).

603 In invasion ecology, biogeochemical models (which may or may not be coupled with
604 hydrodynamic models) have proven to be a useful tool to assess: (1) the role of top-
605 down (grazing by native species, i.e. zooplankton, and IAS, i.e. dreissenids) and
606 bottom-up (nutrient availability) forces on primary productivity and changes to energy
607 pathways due to IAS ([Higgins, Althouse et al. 2014](#)), (2) the competition between
608 native and invasive alien grazers ([Zhang, Culver et al. 2011](#)), (3) the role of IAS (i.e.
609 dreissenids) on nutrients (i.e. phosphorous) and on the native community (i.e.
610 macrophytes) dynamics ([Gudimov, Kim et al. 2015](#)), (4) the role of IAS in the
611 proliferation of toxic algae blooms ([Bierman, Kaur et al. 2005](#)), and (5) the role of IAS
612 in the recovery of hypoxic regions due to the impacts of bioirrigation on
613 biogeochemical cycles within sediments ([Norkko, Reed et al. 2012](#)). Despite these
614 advantages and applications, constructing, calibrating and testing hydrodynamic-
615 biogeochemical models is time-consuming, and can be difficult to calibrate and validate
616 with independent data due to the large amount of data needed and processes included
617 ([Fulton, Smith et al. 2003](#); [Arhonditsis and Brett 2004](#); [Jørgensen and Fath 2011](#)). For
618 all these reasons, some key processes are excluded or are represented with a weak
619 mechanistic basis ([Doney 1999](#); [Robson 2014](#); [Ganju, Brush et al. 2016](#)).

620 From a food web modeling perspective, assessing the impacts of IAS on a food web,
621 including the temporal dynamic context, is challenging, especially for species that
622 invaded the ecosystem after the baseline model ([Langseth, Rogers et al. 2012](#)).
623 Therefore, some applications have addressed this challenge by developing two Ecopath
624 models, one representing the food web before the invasion and one after the invasion
625 (e.g., [Downing, Van Nes et al. 2012](#); [Corrales, Ofir et al. 2017](#)). However, this approach
626 impedes the study of the expansion process and their impact over time. Several
627 strategies have been successfully applied to simulate IAS and their temporal impacts
628 using the temporal dynamic model of EwE, Ecosim (e.g., [Langseth, Rogers et al. 2012](#);
629 [Kao, Adlerstein et al. 2016](#); [Corrales, Coll et al. 2017](#)). In addition, Ecosim has been
630 used to evaluate the eradication and resilience of IAS and the potential effects of its
631 removal on the ecosystem within a management context (e.g., [Pine, Kwak et al. 2007](#);
632 [Arias-González, González-Gándara et al. 2011](#)), as well as the possible impacts that a
633 new IAS might have on the ecosystem ([Pinnegar, Tomczak et al. 2014](#)). At the same

634 time, there has been a growing interest in MICE ([Plagányi, Punt et al. 2014](#)), which,
635 unlike whole food-web models (e.g., EwE), represents a limited number of species
636 believed to have the most important interactions with target species. MICE can be an
637 especially valuable tool for areas where available data for the whole ecosystem are
638 lacking.

639 Despite the growing development of a variety of end-to-end models in aquatic
640 ecosystems ([Fulton 2010](#); [Rose, Allen et al. 2010](#)), we only found one published study
641 using end-to-end modelling (within the Atlantis framework ([Fulton, Fuller et al. 2004](#)))
642 to study impacts of IAS on aquatic ecosystems. This may reflect the current challenges
643 of implementing end-to-end modelling within the context of invasion ecology due to the
644 lack of process knowledge, data restrictions and computational limitations.

645 The choice of the modelling approach that should be used would depend on the question
646 that need to be addressed and the data availability (or the feasibility to obtain these data
647 through sampling). For example, if the objective is to assess the impacts of an IAS on a
648 particular species, single species models have been useful as highlighted in this review.
649 However, due to the growing concern about species interactions and cumulative effects
650 between natural and human stressors, there is a need to move towards more holistic
651 approaches, addressed by the development of mechanistic multispecies/ecosystem
652 models, especially if these models are to be used for management. Within this context,
653 biogeochemical models (coupled or not with hydrodynamic models) has been
654 highlighted as a useful tool to assess the impacts of IAS at the base of the food web (i.e.,
655 phytoplankton and zooplankton species but also bivalves) by describing
656 biogeochemistry (mainly nutrients) and the lower trophic levels of the food web.
657 However, their ability to assess the impacts on higher trophic levels and on the entire
658 ecosystem is limited. On the other hand, food web models provide a framework for
659 integrating population dynamics, species interactions and the effects of natural and/or
660 anthropogenic stressors, assessing direct and indirect effects, describe the flow of
661 energy and matter in ecosystems and study patterns in biodiversity and changes in
662 ecosystem structure and functions through food web attributes ([Brose and Dunne 2009](#);
663 [Thompson, Brose et al. 2012](#); [Heymans, Coll et al. 2014](#)). These models have been
664 proven to be useful to assess the impacts of IAS at the whole food web but through are
665 focus on upper trophic levels.

4.3. Moving forward

Some of the main limitations in model development are data availability, accessibility and quality. Within the context of IAS, this is even more important since there is an urgent need to deal with uncertainties in IAS inventories and species information ([McGeoch, Spear et al. 2012](#); [Katsanevakis and Moustakas 2018](#)). For example, there is a general lack of knowledge of IAS population dynamics, biological traits, basic ecology such as trophism and behavior, and environmental affinities. This knowledge is essential for model parameterization and calibration. We found that some taxa, such as bryozoans, barnacles, ascidians and parasites, were not well-represented in the reviewed models despite they often have high impacts ([Katsanevakis, Wallentinus et al. 2014](#)), as they are less studied than taxa such as fish and mollusk, for which the availability of expertise is much higher. For this reason, most of these less studied taxa were generally pooled together with native species in multi-species compartments, making it impossible to assess through modelling their specific role and impacts in aquatic ecosystems. The improvement of data availability and better collaboration among data collectors and modelers is needed to enhance model development validation and interpretation of model results ([EMB 2019](#)).

Calibration (defined as the attempt to find the best agreement between the computed and observed data by changing selected parameters), validation and uncertainty analyses are critical processes for evaluating model performance and testing the validity of the assumptions included in the models ([FAO 2008](#); [Jørgensen and Fath 2011](#); [Grüss, Rose et al. 2017](#)). Our review highlights that most models used to evaluate impacts of IAS on aquatic systems did not assess uncertainties, in line with previous research ([Piroddi, Teixeira et al. 2015](#); [Katsanevakis and Moustakas 2018](#); [Stelzenmüller, Coll et al. 2018](#)) and validation procedures were also scarce. This is an important shortcoming that needs further research and development in the field.

Our study illustrated the capabilities of models to assess the impacts of already established IAS. However, IAS are increasing in aquatic ecosystems and this increase is likely to continue and expand to new ecosystems. Therefore, there is a need for predictive methodologies that allow forecasting of plausible scenarios that include existing, emerging and potential new IAS ([Dick, Alexander et al. 2014](#)). Making predictions about future impacts of IAS presents several obstacles linked to the high

uncertainties of ecological forecasting ([Maris, Huneman et al. 2017](#)). This is in addition to the intrinsic features of IAS and the lack of data and knowledge, especially related to the processes that regulate dispersal and successful establishment of IAS, the unknown population dynamics in current and future invaded ecosystems and how species and ecosystems respond to new species ([Havel, Kovalenko et al. 2015](#)). The invasion process includes the phases of introduction, establishment and spread and, therefore, depends on the combination of dynamic interspecific relationships (with native species or even other IAS), habitats, environmental effects and other anthropogenic activities. We did not find any model that deals with the three phases in an integrative way, which demonstrates a profound gap in IAS modelling. This gap in modelling could be related to the difficulty of implementation and/or the fact that forecasting impacts of potential IAS (horizon scanning) is a new focus of the research community. A modelling approach dealing with these phases fully may require coupling different models that are able to predict the probability of a species to arrive and, once it is established and invades the ecosystem, to model species interactions, its impacts and the effect of multiple environmental factors and human activities.

Several tools are available to predict potential IAS and their spread ([Kolar and Lodge 2001](#); [Wonham and Lewis 2009](#)), such as risk assessments ([Kolar and Lodge 2002](#); [Townhill, Pinnegar et al. 2017](#)), vector-based models ([Seebens, Schwartz et al. 2016](#)), species distribution models (SDMs) ([Jiménez-Valverde, Peterson et al. 2011](#); [Larson, Gallagher et al. 2014](#)), or studies that identify characteristics of species likely to invade, such as environmental affinity and ecological traits ([Belmaker, Parravicini et al. 2013](#)). Within this context, [Romanuk, Zhou et al. \(2009\)](#) simulated invasions by integrating models of network structure and nonlinear population dynamics. In addition, SDMs are increasingly used to forecast potential distributions of species, although the climate niche could be different between the native and invaded ecosystem ([Mainali, Warren et al. 2015](#); [Parravicini, Azzurro et al. 2015](#)). A topical issue in SDM is to ensemble models (create a model based on multiple models) to generate more robust outputs ([Hao, Elith et al. 2019](#)) and how to incorporate the effects of species interactions ([Wis, Pottier et al. 2013](#); [Albouy, Velez et al. 2014](#)). In addition, environmental DNA is a novel method that may be useful to improve SDM (data about presence/absence) and for early detection of IAS and predict their future distribution through SDM ([Muha, Rodríguez-Rey et al. 2017](#); [Bourne, Hudson et al. 2018](#)). This approach is based on

detecting DNA present in the environment ([Valentini, Pompanon et al. 2009](#)). Its high sensitivity and specificity, together with less required effort and lower costs than traditional sampling methods, make this method a valuable tool for detecting and monitoring aquatic species, specially for cryptic species or species (or life stages) hard to detect and populations at very low densities (e.g. earlier stages of biological invasions) ([Ficetola, Miaud et al. 2008](#); [Valentini, Pompanon et al. 2009](#); [Sigsgaard, Carl et al. 2015](#)). Furthermore, [Fournier, Penone et al. \(2019\)](#) provided a new approach by combining generalized linear models and SDM to predict which species would invade (based on species traits and phylogeny) and where they could invade. Within this context, the new habitat foraging capacity (HFC) model and the spatial-temporal module of EwE, Ecospace ([Steenbeek, Coll et al. 2013](#); [Christensen, Coll et al. 2014](#)), provides a step forward for temporal-spatial modelling, as it combines food-web modelling with SDMs and could be a valuable tool for predicting the future spread of IAS within an ecosystem context. Current developments of the HFC model include the integration of Bayesian SDM results within a food web model either using response functions to model species distributions or driving niche preferences directly ([Coll, Pennino et al. 2019](#)).

Future scenarios of biological invasions are rarely available in the literature due to the complexity of invasion biology ([Courchamp, Fournier et al. 2017](#)), which, as previously highlighted, include a general lack of knowledge about IAS and invading processes, dynamic relationships between species, dynamic anthropogenic stressors and dynamic abiotic effects. Despite these constraints, there have been attempts to predict impacts of already established IAS, particularly in aquatic ecosystems ([Ricciardi 2003](#)) but also on marine ecosystems ([Corrales, Coll et al. 2018](#)). For example, [Pinnegar, Tomczak et al. \(2014\)](#) used a Rank Proportion Algorithm (RPA) ([Link 2004](#)) to predict the diet composition of a potential new IAS in the Western Mediterranean Sea based on its diet on an already invaded ecosystem in the Eastern Mediterranean Sea. The authors of this study used this new diet information as input to an EwE model representing an ecosystem of the Western Mediterranean Sea. [Pinnegar, Tomczak et al. \(2014\)](#) used the EwE model to assess possible impacts of the IAS on the new ecosystem assuming different expansion rates. The RPA model, or similar approaches, developed using machine learning techniques could be key tools to predict potential new trophic behavior for recent or future invaders. The bridge and integration of novel capabilities

with current spatial-temporal multispecies models may bring new modelling development and applications in the future, and promising future development to enable the inclusion of IAS in future scenarios of global change.

Models, especially multi-species/ecosystem models, have become an essential decision-making tool ([Collie, Botsford et al. 2014](#)). However, they are generally not used to manage ecosystems, mainly due to ecosystem complexity and large uncertainties and the challenge of translating complex results to management decisions ([Fogarty 2013](#); [Collie, Botsford et al. 2014](#); [Lehuta, Girardin et al. 2016](#)). Within IAS management, models are even more rarely used to provide management recommendations. Instead, various impact assessment protocols are commonly used by experts, which suffer from considerable inconsistency as the results can highly depend on the assessor and the specific protocol ([González-Moreno, Lazzaro et al. 2019](#)). A possible reason for rarely using models to inform management decisions is that there is a mismatch between research outputs and decision-makers priorities ([N’Guyen, Hirsch et al. 2016](#); [Piria, Copp et al. 2017](#)). While researcher outputs have focused on IAS impacts, decision-makers have prioritized IAS prevention. In fact, prevention of new introductions through managing vectors and pathways has been a priority for decision-makers in the development of effective policies ([CBD 2002](#)) and as such, risk assessment has been widely used in IAS management ([Pyšek and Richardson 2010](#)). Future collaboration between researchers, decision-makers and other stakeholders is essential to make the use of modelling techniques fully operational within the management context of biological invasions and the likely future use of these tools to test management alternatives of IAS eradication and control ([N’Guyen, Hirsch et al. 2016](#); [Heymans, Skogen et al. 2018](#); [Novoa, Shackleton et al. 2018](#)).

4.4. Concluding remarks

Many modelling techniques have been applied to investigate IAS in aquatic ecosystems, but there are several challenges that need to be addressed in the near future. Due to uncertainties in invasion science, one of the main limitations in model development (data availability, accessibility and quality) is even more considerable in IAS modelling. As new invasions are expected in the future, there is a need for predictive methodologies to forecast existing, emerging and potential IAS and their impacts. Within this context, different tools are available to predict potential new IAS and their

spread. However, models that allow capturing the arrival, establishment and spread of IAS and assess their impacts in an integrated way are still unavailable and highlight a critical gap in IAS modelling despite recent developments. The development of spatial-temporal methodologies that integrate the arrival, establishment and spread of IAS and their impacts within an ecosystem context is needed to inform management advice and contribute to the analyses of future scenarios of global change. Integrating and bridging novel techniques and disciplines such as environmental DNA to investigate the presence of IAS, metabarcoding and machine learning techniques to predict future trophic behavior and distributions with novel spatial-temporal model capabilities may further advance IAS modelling.

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Figures

Figure 1. (a) Cumulative number of publications over time found in the systematic review (the year 2017 covers January 1st to 8th February) per ecosystem type.

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827 **Figure 2.** Distribution of the studies included in the systematic review. Different realms (marine and terrestrial biogeographic regions) are
828 presented with different colours. Realms were based on [Spalding, Fox et al. \(2007\)](#) and [Olson, Dinerstein et al. \(2001\)](#). Numbers in brackets
829 indicate the total number of studies for each biogeographic region.

Figure 3. Number of species included in the models found in the systematic review per (a) trophic level (TL) and (b) habitat in each ecosystem type.

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838 **Figure 4.** (a) Number of studies of each modelling level found in the systematic review
 839 per ecosystem type; (b) number of studies of each type of model per modelling level;
 840 and (c) number of IAS included in multispecies/ecosystem models

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Figure 5. (a) Number of studies found in the systematic review by temporal and (b) spatial scale per modelling level.

Figure 6. (a) Number of models that were driven by additional stressors found in the systematic review; (b) cumulative number of models that included other stressors over time; and (c) number of models that include each stressor.

Figure 7. (a) Number of studies that assessed negative, positive or both negative and positive impacts; and overview of the number of studies that reported impacts on (b) biota and (c) ecosystem services.

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862 **Tables**

863 **Table 1.** Number and percentage of IAS found in the selected models per taxonomic
 864 group and ecosystem type.

	Freshwater		Marine		Estuarine		Total	
	Number	%	Number	%	Number	%	Number	%
Plants	6	2.2	16	9.3	1	7.1	6	5
Parasites	5	1.8	0	0	0	0	5	1.1
Phytoplankton	3	1.1	3	1.7	0	0	6	1.3
Zooplankton	13	4.7	4	2.3	7	50	24	5.2
Bryozoan	0	0	2	1.2	0	0	2	0.4
Polychaetes	0	0	9	5.2	0	0	9	1.9
Barnacles	0	0	3	1.7	0	0	3	0.7
Mollusks	80	28.9	34	19.7	3	21.4	117	25.2
Ascidians	0	0	2	1.2	0	0	2	0.4
Ctenophores	0	0	16	9.3	0	0	16	3.5
Cnidarians	0	0	7	4.1	0	0	7	1.5
Shrimps	0	0	12	6.9	1	7.1	13	2.8
Crabs	3	1.1	11	6.4	0	0	14	3
Other benthic crustaceans	2	0.7	0	0	0	0	2	0.4
Fishes	161	58.1	54	31.2	2	14.29	217	46.8
Birds	4	1.4	0	0	0	0	4	0.9
Total	277	100	173	100	14	100	464	100

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Table 2. Summary table of models found in the systematic review showing the model name, model category, a representative reference and if the modelling approach was coupled with other models (yes or not), temporal scale (ST: static; DY: dynamic; CP: comparative between periods), spatial scale (NS: non-spatial; CS: comparative between study sites; SP: spatial), if the model included other human stressors as drivers and which ones, and if the uncertainty was evaluated (yes or no).

	Model name	Model category	Representative reference	Coupled	Temporal scale	Spatial scale	Other stressor	Which stressor	Uncertainty
Species/population level (17.4% of the total models)									
Statistic (57.6 % of species/population models)									
1	ANCOVA	Single-species	Gribben and Wright (2006)	no	DY	CS	no		no
2	Linear models and structural equation modelling	Single-species	Correa and Hendry (2012)	no	ST	CS	no		no
3	Multiple regression model	Single-species	Van Zuiden, Sharma et al. (2016)	no	DY	NS	yes	Temperature	no
4	Quantile regression models	Single-species	Crane, Farrell et al. (2015)	no	CP	NS	yes	Temperature	no
5	Behavioural choice model	Single-species	Beville, Kerr et al. (2012)	no	ST	NS	yes	Fishing	no
6	Bayesian hierarchical model	Single-species	Cha, Stow et al. (2013)	no	CP	CS	no		yes
7	Poisson model and linear regression model	Single-species	Ricciardi, Rasmussen et al. (1995)	no	DY	CS	no		no
8	Generalised linear model (GLM)	Single-species	Onikura, Miyake et al. (2013)	no	ST	SP	no		no
9	Two-tiered modelling approach	Single-species	Stapanian, Kocovsky et al. (2009)	no	DY	NS	no		no
10	GIS-based spatial model	Single-species	Woodford, Cochrane et al. (2011)	no	ST	SP	no		no
11	Species distribution model	Single-species	Olden, Vander Zanden et al. (2011)	no	DY	SP	yes	Recreational users of lakes	no
12	Geostatistical model	Single-species	Rowe, Obenour et al. (2015)	no	DY	SP	no		yes
Mechanistic (42.4% of species/population models)									
13	Von Bertalanffy growth model	Single-species	Crane and Einhouse (2016)	no	CP	NS	no		no
14	Bioeconomic model	Single-species and economic activity	Liu, Olausson et al. (2014)	no	DY	NS	yes	Fishing	yes
15	Hedonic price	Economic activity	Olden and Tamayo (2014)	no	ST	NS	no		no
16	Schaefer model	Single-species	Kateregga and Sterner (2009)	no	DY	NS	yes	Fishing	no
17	Individuals-based models	Single-species	Caldow, Stillman et al. (2007)	no	DY	NS	no		no

18	Stage and age-structured models	Single-species	Ferguson, Taper et al. (2012)	no	ST	NS	no		no
Multispecies/ecosystem level (82.6% of the total models)									
Statistic (17.3% of multispecies/ecosystem models)									
19	Linear model	Community	Bajer, Beck et al. (2016)	no	ST	CS	no		no
20	Least-squares regression	Community	Ricciardi (2003)	no	CP	CS	no		no
21	Multiple regression model	Community	Clavero, Hermoso et al. (2013)	no	ST	NS	yes	Footprint	no
22	Hierarchical Bayesian model	Community	Nilsson, Solomon et al. (2012)	no	ST	CS	no		yes
23	Generalised linear model (GLM)	Community	De Amorim, Umetsu et al. (2015)	no	ST	CS	no		no
24	Generalised additive model (GAM)	Community	Knapp (2005)	no	CP	CS	no		no
25	Species occupancy models, boosted regression trees and linear and logistic regression models	Community	Macdonald, Tonkin et al. (2012)	no	ST	CS	no		no
26	Partial least square path model	Community	Jellyman and Harding (2016)	no	ST	NS	no		no
27	MARSS model	Community	Kratina, Mac Nally et al. (2014)	no	CP	CS	yes	Temperature	no
28	Intervention time series model	Community	Pace, Findlay et al. (1998)	no	DY	CS	no		yes
29	Structural equation modelling	Community	Pagnucco and Ricciardi (2015)	no	ST	CS	no		no
30	Transfer function (TF) models	Community	Aravena, Villate et al. (2009)	no	DY	CS	yes	River discharge and temperature	no
31	Species distribution model	Community	Wenger, Isaak et al. (2011)	no	DY	SP	yes	Temperature	no
Mechanistic (82.7% of multispecies/ecosystem models)									
32	Size-structured model	Community	Green, Dulvy et al. (2014)	no	DY	NS	yes	Fishing	yes
33	Bioenergetic model	Bioenergetics model	Walrath, Quist et al. (2015)	no	DY	NS	no		no
34	Age-structured model with bioenergetic model	Bioenergetics model	Stewart, O'Gorman et al. (2010)	yes	DY	NS	yes	Temperature	no
35	Bioenergetic model coupled with phytoplankton growth model	Bioenergetics model	Reed-Andersen, Carpenter et al. (2000)	yes	DY	NS	no		yes
36	Integrated ecological-economic model for the Black Sea anchovy fishery	Bioeconomic model	Knowler (2005)	yes	DY	NS	yes	Fishing and nutrients	no
37	Integrated economic-biological model	Bioeconomic model	Settle and Shogren (2002)	yes	DY	NS	yes	Fishing	no
38	Ecological and economic model	Bioeconomic model	Grosholz, Lovell et al. (2011)	yes	DY	CS	yes	Fishing	yes
39	Social-ecological model	Bioeconomic model	Roy, Martin et al. (2011)	yes	DY	NS	yes	Temperature and nutrient loading	yes

40	Mathematical model of the food web	Biogeochemical model	Fontaine and Stewart (1992)	yes	DY	NS	yes	Nutrient loading and pollution	no
41	Lake autotrophic model	Biogeochemical model	Higgins, Althouse et al. (2014)	no	DY	NS	yes	Nutrient loading	no
42	Bioenergetic model coupled with eutrophication model	Biogeochemical model	Bierman, Kaur et al. (2005)	yes	DY	SP	yes	Temperature and nutrient loading	yes
43	Coupled model of bioenergetic-based anchovy population dynamics and lower trophic food web structure	Biogeochemical model	Oguz, Salihoglu et al. (2008)	yes	DY	NS	yes	Fishing and nutrient loading	no
44	Reactive-transport model	Biogeochemical model	Norkko, Reed et al. (2012)	no	DY	NS	no		no
45	Total phosphorous mass model	Biogeochemical model	Gudimov, Kim et al. (2015)	no	DY	SP	yes	Nutrient loading	yes
46	Simplified lake ecosystem mathematical model	Biogeochemical model	Magnea, Sciascia et al. (2013)	no	DY	NS	yes	Nutrient loading	no
47	Biophysical model	Biophysical model	Rowe, Anderson et al. (2015)	yes	DY	SP	no		yes
48	Ecosystem model developed for the Port Phillip Bay Environmental Study	Hydrodynamic-biogeochemical model	Murray and Parslow (1999)	yes	DY	SP	yes	Nutrient loading	no
49	Hydrodynamic model	Hydrodynamic-biogeochemical model	Macisaac, Johannsson et al. (1999)	yes	DY	SP	no		yes
50	ELCOM-CAEDYM	Hydrodynamic-biogeochemical model	Schwalb, Bouffard et al. (2014)	yes	DY	SP	yes	Temperature and nutrient loading	yes
51	3D SPBEM	Hydrodynamic-biogeochemical model	Isaev, Eremina et al. (2016)	yes	DY	SP	yes	Temperature and nutrient loading	no
52	Lake Michigan ecosystem model (LM-Eco)	Hydrodynamic-biogeochemical model	Miller, Kreis Jr et al. (2010)	yes	DY	SP	yes	Temperature and nutrient loading	no
53	Two-dimensional hydrodynamic and water quality model (CE-QUAL-W2)	Hydrodynamic-biogeochemical model	Zhang, Culver et al. (2011)	yes	DY	SP	yes	Nutrient loading	no
54	2-dimensional physical and biological/reactive-transport model	Hydrodynamic-biogeochemical model	Laruelle, Regnier et al. (2009)	yes	DY	SP	yes	Nutrient loading	no
55	PEGASE with POTAMON model	Hydrodynamic-biogeochemical model	Pigneur, Falisse et al. (2014)	yes	DY	SP	yes	Temperature, nutrient loading and hydrodynamic	no
56	Dynamic ecosystem model of the lower trophic levels	Hydrodynamic-biogeochemical model	Fishman, Adlerstein et al. (2009)	yes	DY	SP	yes	Temperature and nutrient loading	no
57	Ecological model BIOGEN	Hydrodynamic-biogeochemical model	Lancelot, Staneva et al. (2002)	yes	DY	SP	yes	Temperature and nutrient loading	yes
58	Dynamic water quality model	Hydrodynamic-biogeochemical model	Glaser, Rhea et al. (2009)	yes	DY	SP	yes	Nutrient loading	no
59	One-dimensional physical-biological ecosystem model	Hydrodynamic-biogeochemical model	Oguz, Ducklow et al. (2001)	yes	DY	SP	yes	Nutrient loading	no
60	Ecological-mathematical model	Hydrodynamic-biogeochemical model	Volovik, Volovik et al. (1995)	no	DY	SP	yes	Temperature	no
61	CIMPAL	Conservative additive model	Katsanevakis, Tempera et al. (2016)	no	ST	SP	no		

62	DPSER	Conceptual integrated model	Cook, Fletcher et al. (2014)	no	ST	NS	yes	Fisheries and temperature	
63	Loop models of ecological and socio-economic systems	Qualitative model	Ortiz and Stotz (2007)	no	DY	NS	yes	Fisheries	
64	Mathematical model of trophic interactions	Food-web model	Padilla, Adolph et al. (1996)	no	DY	CS	no		yes
65	Pelagic food web	Food-web model	Amundsen, Lafferty et al. (2013)	no	CP	NS	no		no
66	Intermediate complexity for ecosystem assessments (MICE)	Food-web model	Blamey, Plagányi et al. (2014)	no	DY	NS	yes	Fishing	yes
67	Ecological Network Analysis	Food-web model	Miehls, Mason et al. (2009)	no	CP	CS	no		no
68	Ecopath with Ecosim (static)	Food-web model	Downing, Van Nes et al. (2012)	no	CP	NS	yes	Fishing	no
69	Ecopath with Ecosim (dynamic)	Food-web model	Kao, Adlerstein et al. (2014)	no	DY	NS	yes	Fisheries and nutrient loading	no
70	Atlantis	End to end model	Nyamweya, Sturludottir et al. (2016)	no	DY	SP	yes	Fisheries, nutrient loading and temperature	no

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