Biol Invasions (2024) 26:505–514
https://doi.org/10.1007/s10530-023-03187-0

ORIGINAL PAPER

Testing passive dispersal as the key mechanism for lionfish invasion in the Mediterranean Sea using Lagrangian particle tracking

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Received: 10 July 2023 / Accepted: 6 October 2023 / Published online: 7 November 2023

Abstract The expansion of lionfish *Pterois miles* across the Mediterranean Sea since its introduction via the Suez Canal has been rapid, but the mechanisms by which the expansion occurred have not been fully tested. By using a series of Lagrangian particle tracking simulations and high-resolution hydrodynamic models, we tested the hypothesis that passive dispersal of larvae could explain the east to west expansion of lionfish. By sequentially modelling the annual dispersal of larvae, from the first observation in Lebanon in 2012 and then modelling dispersal of larval from the simulated settlement sites, we showed that passive dispersal driven by ocean currents largely explained the observed expansion of lionfish until 2020. The spread of lionfish was likely restricted by environmental conditions when the population reached the central Mediterranean and the particle tracking simulations diverged from observations. The results emphasize the potential contribution of computational models in understanding the dispersal of non-indigenous and range expanding species in response to changing environmental conditions, identifying high risk areas, and guiding targeted surveillance, early detection, and informing management strategies for such species. Given that many non-indigenous species in the Mediterranean are introduced through a consistent pathway (the Suez Canal), the incorporation of interdisciplinary approaches and high-resolution biophysical models can provide fundamental knowledge for management action prioritization.

Keywords Pterois · Distribution · Invasive species · Larval dispersal · Dispersal mechanisms

Introduction

The Mediterranean Sea is a global hotspot area for the establishment of marine non-indigenous species

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(NIS). Nearly 1000 species have been introduced in the Mediterranean Sea, including species from the Red Sea, the Black Sea and the Atlantic Ocean (Costello et al. 2021; Zenetos et al. 2008, 2022; Zenetos and Galanidi 2020). The rate at which NIS are being introduced into new areas has been accelerating, with an average rate of one new species reported every eight days, and more invasions are evident in the eastern Mediterranean Sea (Costello et al. 2021). The primary pathways for the introduction of NIS are shipping, aquarium trade, and the Suez Canal (Zenetos and Galanidi 2020). Since the opening of the Suez Canal in 1869 and subsequent widening and deepening of the Canal, the coastal ecosystems of the eastern Mediterranean Sea have been facing accelerating biological changes and the increasing establishment of NIS of Indo-Pacific origin (Galil 2023; Kalogirou 2011).

Increased scientific interest, gradual deepening and widening of the Suez Canal, increased sea surface temperature (SST) and gradual equalization of Red Sea salinity with Great Bitter Lakes are among the most important factors that contributed to the increasing rate of reported NIS during the last decades (Galil 2023; Garrabou et al. 2022; Kalogirou 2011; Por 2010; Raitsos et al. 2010). Once a NIS is established in a highly connected ecosystem such as the Mediterranean Sea, it is impossible to eradicate. Impacts of established NIS are dynamic in nature and can reduce ecosystems' resilience, lead to regime shifts and degraded ecosystem states while in some cases it might add redundancy and provide ecosystem services (Chaffin et al. 2016; Kleitou et al. 2021a). These species can impact existing ecological interactions through e.g. competition for resources, habitat to settle, spawning grounds, grazing or predation, trophic cascading effects, or even, filling up empty niches (Azzurro et al. 2007; Bariche et al. 2009; Batjakas et al. 2023; Kalogirou 2011, 2013; Kalogirou et al. 2007, 2012a, b, c; Sala et al. 2011; Savva et al. 2020).

The lionfish *Pterois miles* (Linnaeus, 1758) was among the fastest reported NIS colonizers in the Mediterranean Sea with a rapid geographic expansion from the eastern to the western parts of the Mediterranean Sea (Bariche et al. 2013; Poursanidis et al. 2020). Lionfish (*Pterois miles/Pterois volitans* complex) has also been involved in a major invasion in the Western Atlantic where an unprecedented population expansion across a wide range of natural habitats raised important impacts on marine biodiversity and ecosystem resilience (Azzurro et al. 2017; Kletou et al. 2016; Muñoz et al. 2011; Poursanidis et al. 2020; Whitfield et al. 2007). The Mediterranean lionfish population is of Red Sea origin, founded by individuals immigrating through the Suez Canal (Bariche et al. 2017), likely through multiple introductions (Dimitriou et al. 2019). Even though evidence on the relationship between climate and extended distribution of NIS is limited, climate change (increasing survival) is often suggested as a main contributor for spread of the species (Occhipinti-Ambrogi and Sheppard 2007; Poursanidis et al. 2022). Predicting the potential geographic distribution of *P. miles* in the Mediterranean Sea is of high importance for early warning and mitigation of NIS management (Kleitou et al. 2021c; Poursanidis et al. 2020, 2022). To accurately model and predict future spread of *P. miles*, the mechanism by which it spreads needs to be understood and this can be tested using the recorded expansion of the species since its introduction through the Suez Canal.

Lionfish are known to have a relatively small home range and limited movement as mature fish with estimates ranging from no movement to up to 1.35 km over 15 days (Tamburello and Côté 2015). It is therefore believed that most of the previous distribution expansion has been due to dispersal in the larval phase (Del Río et al. 2023; Johnson et al. 2016; Morris and Whitfield 2009). Female lionfish employ broadcast spawning, releasing a substantial number of eggs in a gelatinous mass (Morris and Whitfield 2009). This reproductive strategy maximizes dispersal through ocean currents while enhancing fertilization by limiting egg predation (Fogg et al. 2017). The eggs and subsequent embryos disintegrate within a short period, leading to the release of free-floating embryos or larvae. These larvae have a pelagic phase, allowing them to disperse over significant distances for approximately 20–35 days before ultimately settling in benthic habitats (Ahrenholz and Morris 2010). It is likely that it is the planktonic larval phase which has enabled *P. miles* to spread rapidly. This also aligns with water currents being identified as the most influential parameter for transport of lionfish in the Western Atlantic (Johnston and Purkis 2011).

This combination of residentiary adults and pelagic dispersal of larvae make it an excellent hypothesis to address via particle tracking simulations. Particle tracking simulations can combine reproductive biology knowledge with hydrodynamic models to simulate dispersal under specified conditions. Lagrangian particle tracking methods have been widely used to investigate dispersal of fish, crustaceans, kelp, sea urchins and plastics (Castro et al. 2020; Durrant et al. 2018; Everett et al. 2017; Hewitt et al. 2022; Kaandorp et al. 2020; Schilling et al. 2020). By using Lagrangian simulations in conjunction with high-resolution hydrodynamic models of the Mediterranean Sea, we aim to test whether the expansion of *P. miles* across the Mediterranean Sea from east to west, up to 2020, can be explained solely by passive dispersal. If so, this may open up the possibility for future predictions of dispersal based upon forecastable ocean currents enabling targeted monitoring and the establishment of strategic surveillance systems.

Materials and methods

Hydrodynamic model details

To investigate the hypothesis that the spread of *Pterois miles* in the Mediterranean was primarily driven by passive dispersal of larvae following an initial introduction, particle tracking experiments were run using an offline Lagrangian particle tracking model, PARCELS "Probably A Really Computationally Efficient Lagrangian Simulator" (Delandmeter and Van Sebille 2019; Lange and Van Sebille 2017), described below. These simulations used daily velocity fields from the Mediterranean Sea Analysis and Forecast product MEDSEA_MULTIYEAR_PHY_006_004 (Escudier 2020) and MEDSEA_ANALYSIS_FORECAST_PHY_006_013 (Clementi 2019). These products are both high resolution data-assimilating coupled hydrodynamic-wave modelling systems implemented over the whole Mediterranean Basin with horizontal resolution of 1/24° (approximately 4 km) and 141 vertically unevenly spaced levels and have been extensively validated. MEDSEA_MULTIYEAR_PHY_006_004 is a reanalysis spanning 1987–2019 while MEDSEA_ANALYSIS_FORECAST_PHY_006_013 is the analysis and forecast product spanning 2017-present (2021 when we accessed data). We only used MEDSEA_ANALYSIS_FORECAST_PHY_006_013 velocity fields for 2019 and 2020.

Particle characteristics and experimental design

The Lagrangian particle simulations were conducted using PARCELS v2.0.2 which is an open-source framework for simulating Lagrangian particle trajectories, designed to efficiently process large amounts of data (Delandmeter and van Sebille 2019; Lange and van Sebille 2017). Dispersal simulations were conducted using only velocity data from the 29.88 m depth layer of the hydrodynamic models which aligns with the depth which lionfish larvae are most commonly observed ($\approx$30 m) (Mostowy et al. 2020; Sponaugle et al. 2019).

Lionfish are known to have spawning year-round (although limited) with a peak in spawning activity in summer (Mouchlianitis et al. 2022; Savva et al. 2020). To simulate this in our modelling process, we released particles all year round but increased the release rate by 40 times during May–July, compared to the rest of the year. As lionfish larvae are known to have limited horizontal swimming ability, and use their fins mainly to maintain vertical depths (Mostowy et al. 2020), no active behaviour was included in the simulations and all dispersal was driven by ocean currents to truly test passive dispersal. A small amount of Brownian motion (10 m^2 s^{-1}) was used to add variation to particles released on the same day in the same location (to simulate sub-grid scale effects). Larvae were tracked for 26 days post spawning to match the mean settlement date of the closely related lionfish *P. volitans* (Ahrenholz and Morris 2010). Dispersal was assumed to be successful if after 26 days they were in areas with a bathymetry shallower than 350 m, particles which did not settle successfully were defined as dispersal mortalities (Hewitt et al. 2022; Schilling et al. 2020, 2022). As there was no variation in pelagic larval duration in our simulations, there was no need to apply a mortality rate during the simulations beyond the dispersal mortality.

To simulate the maximum potential spread of *P. miles* in the Mediterranean Sea due to larval dispersal we ran simulations of larval dispersal based upon the first confirmed observations of lionfish which became established. These were two observations in Lebanon from 2012, both at 34.49° N, 35.91° E. Particles were released from this location every day from 1st January 2012 to 31st December 2012 with 80 particles released per day during the

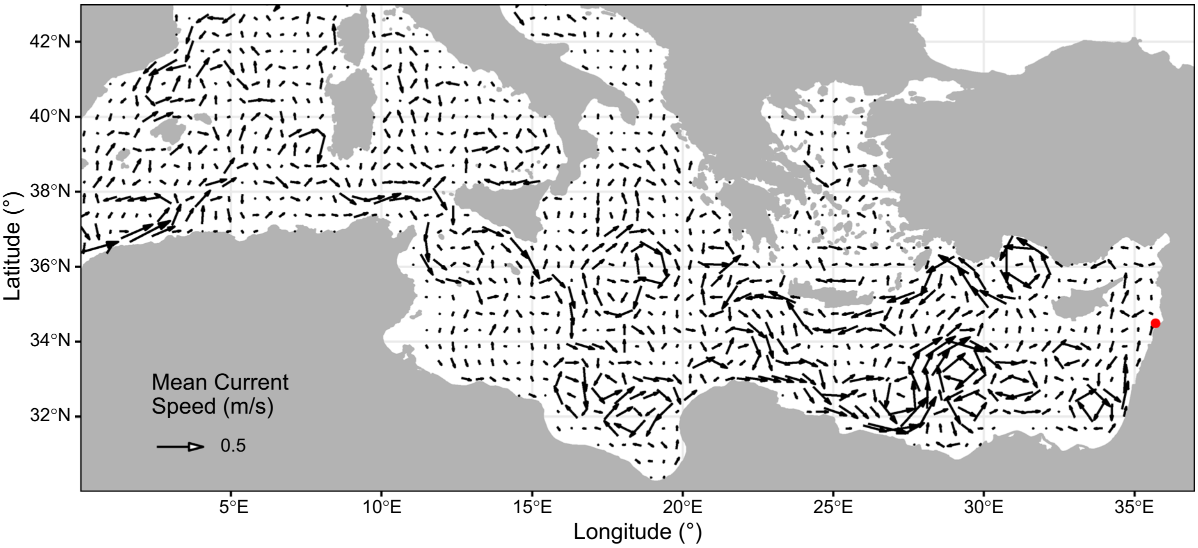

Fig. 1 Mean currents at 29.88 m depth in the Mediterranean Sea during May–July (the main spawning period for lionfish) 2012. The red dot represents the original release location for our dispersal simulations based upon the observed sighting of Bariche et al. (2013)

peak spawning period (May–July) and 2 particles released every other day (Fig. 1). Particles which successfully settled from this dispersal event were then used for similar simulations in following years. Due to computational limitations, in each year in the simulation, the 1000 western-most successful settlement locations were used to release particles. While this will bias the overall larvae settlement distributions in subsequent years, it aligns with our aim of modelling maximum dispersal potential, assuming spawning locations further west will disperse larvae further west. We then visually assessed the dispersal of our simulated population expansion with the recorded observations in the Mediterranean Sea.

Results

Based upon the simulations of larval dispersal from a single introduction in the eastern border of the Mediterranean, the larvae first dispersed north before spreading west. Within the first year, lionfish were estimated to reach the northeast Mediterranean and two years after introduction they began to spread west. The westward expansion slowed through the more hydrodynamically complex area around 25°E. In 2016, our simulations showed a small number of larvae settling on the southern shore which later established into a larger colony between about 22 and 26°E in 2019 and 2020.

There was high agreement between the predicted passive dispersal and observed lionfish dispersal (Figs. 2 and 3). The rate and direction of spread in our simulations was consistent with observed lionfish. There were some differences in our simulations and the observed lionfish particularly after 2018 when our model predicted a larger spread to the north, in the Aegean and Adriatic Seas, which was not seen in the observed data and actual spread may have been restricted by other physicochemical or biological parameters. In addition, lionfish were observed in Italy and Tunisia (10–15°E) earlier than our model predicted.

Discussion

We used Lagrangian particle tracking simulations to successfully recreate the spread of lionfish in the Mediterranean Sea up to 2020 using only passive dispersal. This strongly supports the hypothesis that the main mechanism for the dispersal of lionfish across the Mediterranean has been successive iterations of passive dispersal driven by ocean currents during the pelagic larval phase following an initial introduction through the Suez Canal. In the future, it may be

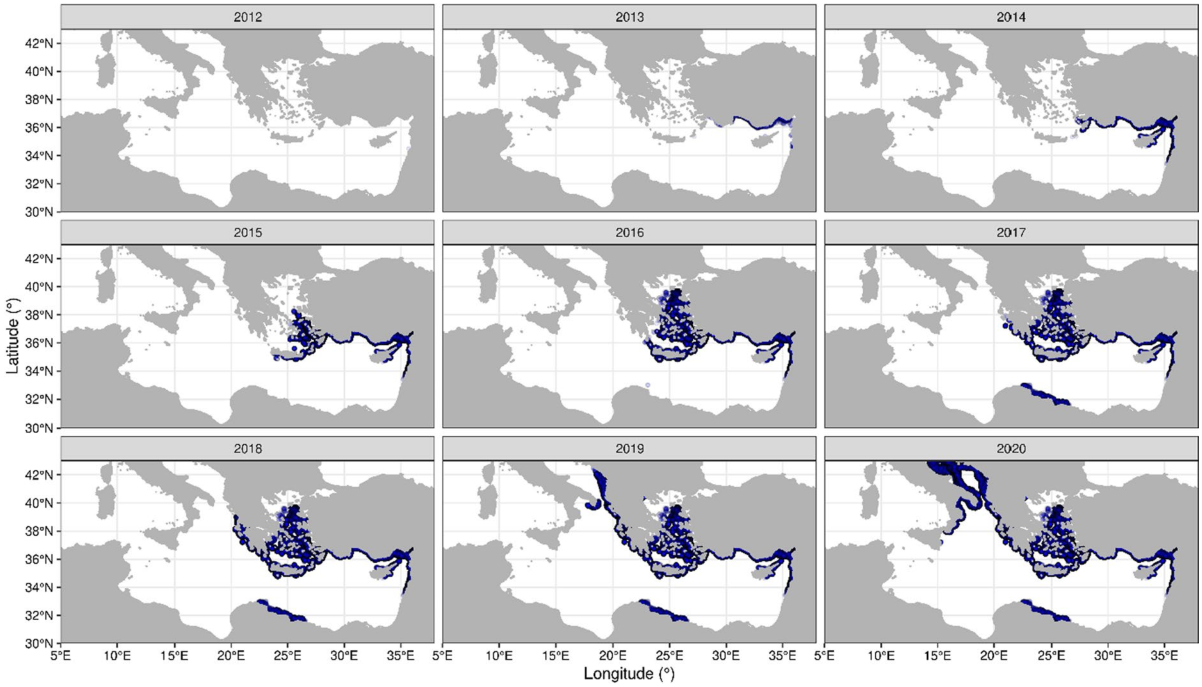

Fig. 2 Simulated predicted lionfish settlement sites based upon passive dispersal

possible to use forecasts of ocean currents and real-time detections of lionfish expansion to forecast probable locations of expansion which could be prioritized for monitoring or management programs aimed at controlling population size, for example targeted removal of lionfish by divers (Ulman et al. 2022).

Most NIS in the Mediterranean Sea arrive through the Suez Canal (Galil 2023; Galil et al. 2015) and recent enlargements of the Suez Canal coupled with climate change are anticipated to facilitate the invasion of more warm water species in the Mediterranean Sea to the detriment of native biological communities (Moullec et al. 2019). The absence of effective surveillance systems has been highlighted as a major bottleneck in lionfish management, and a more strategic and coherent monitoring plan that focuses on hotspot and first detection areas has been recommended (Kleitou et al. 2021b). The development of innovative ways to predict the dispersal of NIS could be fundamental in their effective management (Cowen and Sponaugle 2009; James et al. 2023; Jones 2015; Levin 2006; Lu et al. 2023; Swearer et al. 2019).

The life cycle of many marine species begins with pelagic stages (e.g. larvae, eggs, spores) whose dispersal is largely facilitated by physical transport processes (Simons et al. 2013). Understanding the mechanisms that underline NIS dispersal processes can unveil invasion pathways/routes, high risk areas, and guide effective management actions. In recent decades, several approaches have been used to study and predict the potential dispersal of species (Jones 2015; Levin 2006). Application of empirical methods (i.e., chemical tagging of larvae, genetic analysis, otolith chemical signatures) are often challenging due to logistical and financial constraints (Bode et al. 2019; Cowen and Sponaugle 2009; Swearer et al. 2019). Technological advances, supported by a giant leap in computational resources, have allowed the development of biophysical models that can combine hydrodynamics and larval behaviour to simulate larval movement (James et al. 2023). Such models are cost-effective and can offer high spatial and/or temporal resolution, and are applicable to many types of ecosystem management questions (Swearer et al. 2019).

In this study, we demonstrated the efficacy of a simple passive dispersal biophysical model in predicting the initial stages of lionfish invasion and its subsequent spread across the Mediterranean. By simulating dispersal patterns using a single introduction point

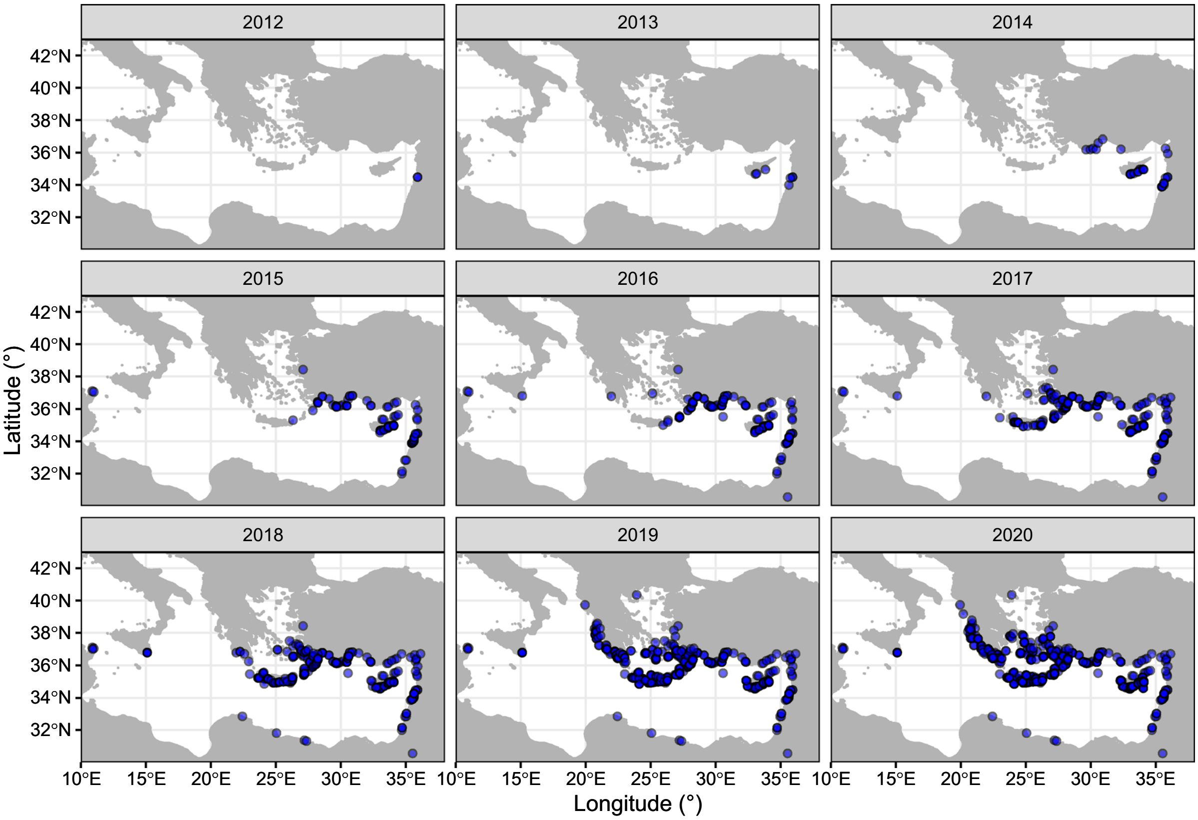

Fig. 3 Observations of lionfish in the Mediterranean as reported by (Kleitou et al. 2021b). Each dot represents an observation from the year it was observed through to 2020

(southeast Mediterranean), we confirmed the dynamics of passive larval dispersal and the significance of ocean currents as the primary driver of lionfish population spread. These findings highlight the potential of Lagrangian particle tracking in predicting the passive dispersal of lionfish larvae and providing a reasonable understanding of invasive species dispersal in the Mediterranean Sea, at least for those species with planktonic life phase(s). Such models could provide several benefits in the field of invasive species management by identifying potential source locations and paths of planktonic NIS, and shedding light on the propagule pressure, helping to assess the risk of invasions. Additionally, understanding the connectivity and the dynamics of species with pelagic planktonic larval phases capable of long-range dispersal via ocean currents may enable the identification of sites suitable for early warning systems (Crivellaro et al. 2022).

The observed dispersal of lionfish aligned with our simulation of their maximum dispersal capacity. This simulation assumed that spawning locations located farther west consistently contributed to the lionfish dispersal in each simulation cycle. Therefore, additional factors might have also assisted the lionfish dispersal (e.g. swimming of larvae or adults, longer larval/egg drifting phase, opportunistic use of extreme currents) (Leis 2021). In 2020, the prediction of passive dispersal in lionfish larvae indicated an extension to the north beyond their established range, indicating that other environmental conditions likely restricted the further population expansion of lionfish. This finding agrees with species distribution modelling studies which found that suitability of areas with minimum surface temperature of 10–15 °C will be low (Loya-Cancino et al. 2023; Poursanidis et al. 2022). Indeed, the performance of our model started decreasing (predicting larger population expansion/spread) when lionfish reached the 15 °C minimum thermal boundary, highlighting the importance of combining multiple models to account for physical, environmental, biological, and ecological processes and provide a more comprehensive understanding of species movement dynamics.

While biophysical models have shown promise in predicting invasion areas and understanding the dynamics of NIS, there are still some limitations and areas for future development to optimize their predictions. The accuracy of such models requires the incorporation of ocean (tide, current velocity and direction, wave) and environmental data (temperature, salinity, nutrients) at high spatial and temporal resolution, The availability of such data has not kept pace with the dramatic increases in computer processor speed (Swearer et al. 2019). In addition, the need for further empirical research is crucial to improve the precision and dependability of marine larval dispersal models (Bode et al. 2018, 2019). The scarcity of field-based estimates presents a challenge. Factors such as the timing and duration of propagule release, larval abundance, onset and duration of settlement competency, and the magnitude and variability of mortality contribute to the complexity of dispersal dynamics, can lead to highly variable dispersal outcomes (Bode et al. 2018; Swearer et al. 2019), which if not properly validated may provide inaccurate or erroneous results. For example, in the case of lionfish in the Mediterranean there is a need to understand if the invasive population is adapting its physiology to new habitats, it may be that there could be variations in aspects such as larval duration compared to their native habitats. Priority for collection of field based estimates could be given to species of high concern for the region such as those listed in the European Union List (EC/2016/1141) (Kleitou et al. 2021b) or species identified as high risk through horizon scanning exercises (Peyton et al. 2019, 2020; Tsiamis et al. 2020). By combining high resolution data with empirical evidence, we can proactively improve our ability to prevent and manage invasive species invasions, preserving the integrity of ecosystems and minimize their ecological and economic impacts.

Acknowledgements This research includes computations using the computational cluster Katana supported by Research Technology Services at UNSW Sydney (Katana 2010). We thank the reviewers of this paper for their helpful comments.

Author contributions HTS and PK contributed to the study design and conception. Simulation analyses were undertaken by HTS. All authors contributed equally to the writing of the manuscript. All authors commented on previous versions of the manuscript. All authors read and approved the final manuscript.

Funding Open Access funding enabled and organized by CAUL and its Member Institutions. The authors declare that no funds, grants, or other support were received during the preparation of this manuscript.

Data availability No new data was collected as part of this study. The code for the particle tracking simulations is available at: https://github.com/HaydenSchilling/Lionfish-Dispersal. The lionfish observations are available in Kleitou et al. (2021b).

Declarations

Conflict of interest The authors have no relevant financial or non-financial interests to disclose.

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