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Rapid Communication

Sea slug invasions: the non-native *Archidoris pseudoargus* (Nudibranchia: Dorididae) moves south and the native *Doriopsilla pharpa* (Nudibranchia: Dendrodorididae) moves north on the U.S. Atlantic coast

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Abstract

The European sea lemon nudibranch *Archidoris pseudoargus* was introduced by shipping to the Northwest Atlantic Ocean sometime prior to 2017, the year it was discovered in the Gulf of Maine, USA and in Nova Scotia, Canada. In 2023, it was discovered in Long Island Sound, a large estuary of national significance south of the Gulf of Maine. The native lemon drop nudibranch *Doriopsilla pharpa*, originating in waters south of New England from Maryland to Florida, was first detected in the Sound subtidally in 2019. The two species, both well-known sponge predators, are not known to co-occur as of mid-2025. Sponge population declines in the Gulf of Maine have already been linked to *A. pseudoargus* predation and other bioinvasions, especially non-native colonial ascidians which compete with sponges for space. Here, we report the first discoveries of these nudibranch species in Long Island Sound and consider their potential for deleterious effects on the benthic communities of southern New England.

Key words: species invasion, range expansion, subtidal, benthic, nudibranch, sponge, climate change

Introduction

The spongivorous sea lemon nudibranch *Archidoris pseudoargus* (Rapp, 1827) (= *Doris pseudoargus*) is a common European species (Thompson and Brown 1984) ranging from the Mediterranean Sea to northern Europe. Since 2017, *A. pseudoargus* specimens and egg masses have been discovered in the Northwest Atlantic (Harris et al. 2023), with sightings along the coasts of Nova Scotia, Maine, and Massachusetts (Harris et al. 2023). The lemon drop nudibranch *Doriopsilla pharpa* (Marcus, 1961) (= *Cariopsilla pharpa*), also a sponge predator, is native to the Western Atlantic Ocean, ranging from Maryland to Florida (Marcus 1961, 1972; Marcus and Marcus 1967; Eyster 1980). *Doriopsilla pharpa* was detected in the summer of 1973 in southern New England, when a "large population" was discovered feeding on the sponge *Cliona celata* in Waquoit Bay, on the south shore of Cape Cod,

Massachusetts (Morse 1975; M. Patricia Morse *pers. comm.*, February 2025). This record is misreported as being at Cotuit, Massachusetts in Eyster (1980). Morse (1975) suggested that *D. pharpa* had been introduced by aquaculture practices from "south of New Jersey", and had "established a breeding population". We surmise this population did not survive subsequent winters in New England, as there have been no reports of *D. pharpa* on Cape Cod, or north of Maryland, in the past 50 years.

Here, we report that *A. pseudoargus* has expanded its range south of the Gulf of Maine into Long Island Sound, while *D. pharpa* has moved north into Long Island Sound, setting the stage for potential increased predation on sponge populations of southern New England. Both *A. pseudoargus* and *D. pharpa* were found in subtidal habitats in the eastern and western Long Island Sound, respectively, and are not known to co-occur at the time of publication. Complimentary reports are in preparation on the reproduction, growth, feeding behavior, and population genetics of these species. We follow Fernández-Vilert et al. (2025) and WoRMS in the use of the combination *Archidoris pseudoargus* (WoRMS World Register of Marine Species 2025a, b).

Materials and results

Marine debris recovery and trawl surveys

Archidoris pseudoargus was first collected in eastern Long Island Sound on October 17, 2023, near the New London Ledge Lighthouse, at the mouth of the Thames River near Groton, Connecticut (Figure 1). The benthic environment in this area is primarily composed of clay and silt with a rocky ledge near the lighthouse (University of Connecticut 2025). A single bright yellow specimen, approximately 3.8 cm in length, was found attached to a lobster trap that was recovered during marine debris recovery trawls at approximately 10.88 meters in depth (Supplementary material Table S1; Figure 2A). The lobster trap had multiple sponges attached to it, including *Halichondria bowerbanki*, *Haliclona canaliculata*, *Clathria prolifera*, and *Cliona* sp., although the nudibranch was not actively feeding on sponge during the time of retrieval. Once collected, the nudibranch specimen was photographed and taken to a laboratory of the Williams College – Mystic Seaport Coastal and Ocean Studies program in Mystic, CT. Photographs were sent to Larry Harris (University of New Hampshire) and Terrence Gosliner (California Academy of Sciences) who confirmed the identification through the presence of distinct morphological features (e.g. oval shape, rough texture, yellow or blotchy coloration, large size, and specific mantle, gill, rhinophore, and tubercle arrangement; Thompson and Brown 1984). On October 20, 2023 the nudibranch was transported to The Maritime Aquarium at Norwalk for continued observation in an isolated aquarium, where it was placed with shell substrates and sponges (*Halichondria panicea*,

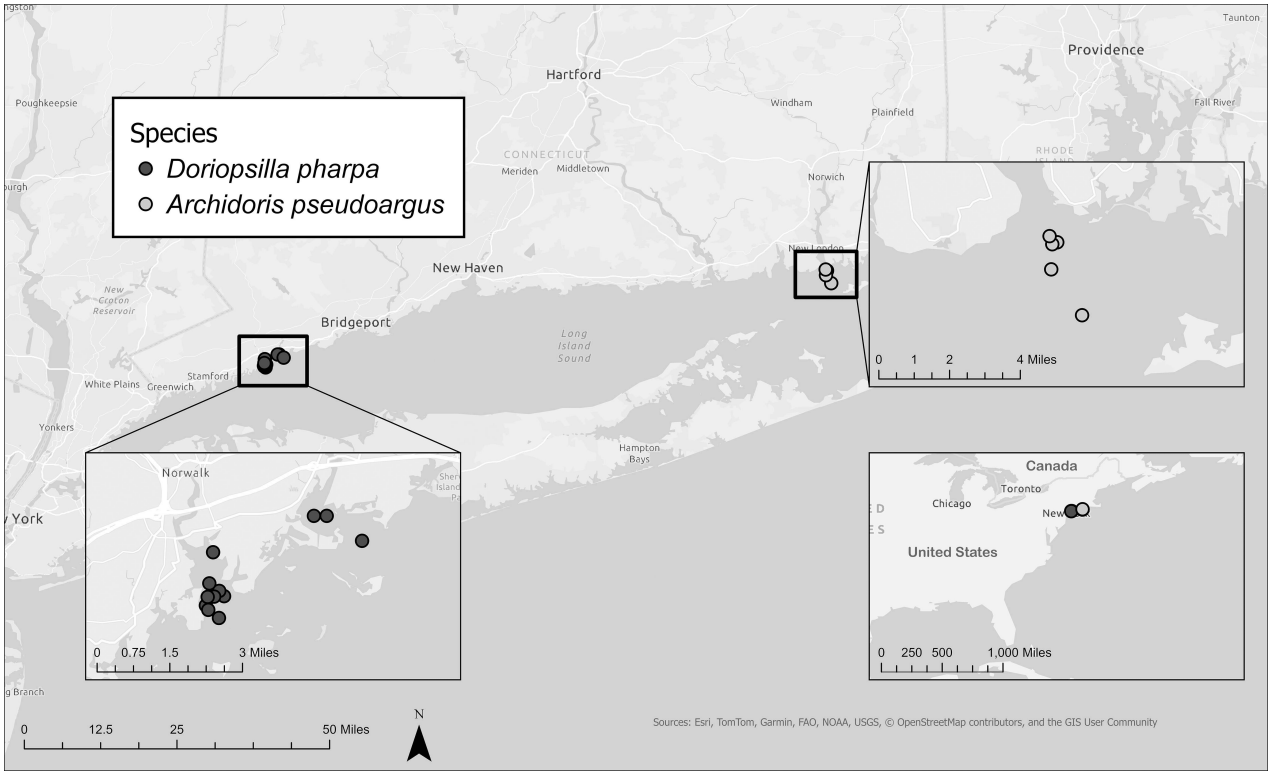

Figure 1. Locations where *Doriopsilla pharpa* and *Archidoris pseudoargus* were found during demersal fish trawls and marine debris recovery boat trawls, respectively (Long Island Sound, United States).

Clathria prolifera, and *Cliona celata*) collected from Long Island Sound. In captivity, *A. pseudoargus* was observed feeding on *H. panicea* and *C. prolifera* (Raviraj et al. *in preparation*). This specimen died on January 7, 2024 at which time it was preserved in 95% ethanol for genetic studies (to be reported upon elsewhere). During its time in captivity, it laid unfertilized eggs that were also preserved.

Since the initial discovery, six additional *A. pseudoargus* were found on lobster traps recovered by staff members of Project Oceanology (Groton, Connecticut) in 2024 (Figure 2B–F), all exhibiting different color morphs, specifically shades of yellow or mottled in brown, green, red, or a combination of colors. One individual was recovered on February 20, 2024 and another on October 28, 2024, both within the vicinity of Ledge Lighthouse at approximately 10.36 meters and 9.60 meters in depth, respectively (Table S1). These individuals were retained for educational purposes. Prior to the spotting in October, two individuals were recovered on September 30, 2024 directly east of the Eastern Long Island Sound dumping grounds (an area of sea bottom reserved for the dumping of waste, such as dredge spoils). On the same sampling trip in September, two additional individuals were recovered at the 1 and 2 channel markers approaching the Thames River. All four individuals were found at depths of 12.95 and 24.99 meters (Table S1). Of these four, one specimen was retained at Project Oceanology while three were transported to The Maritime Aquarium. The three individuals at The Maritime Aquarium were placed in separate tanks and underwent a series

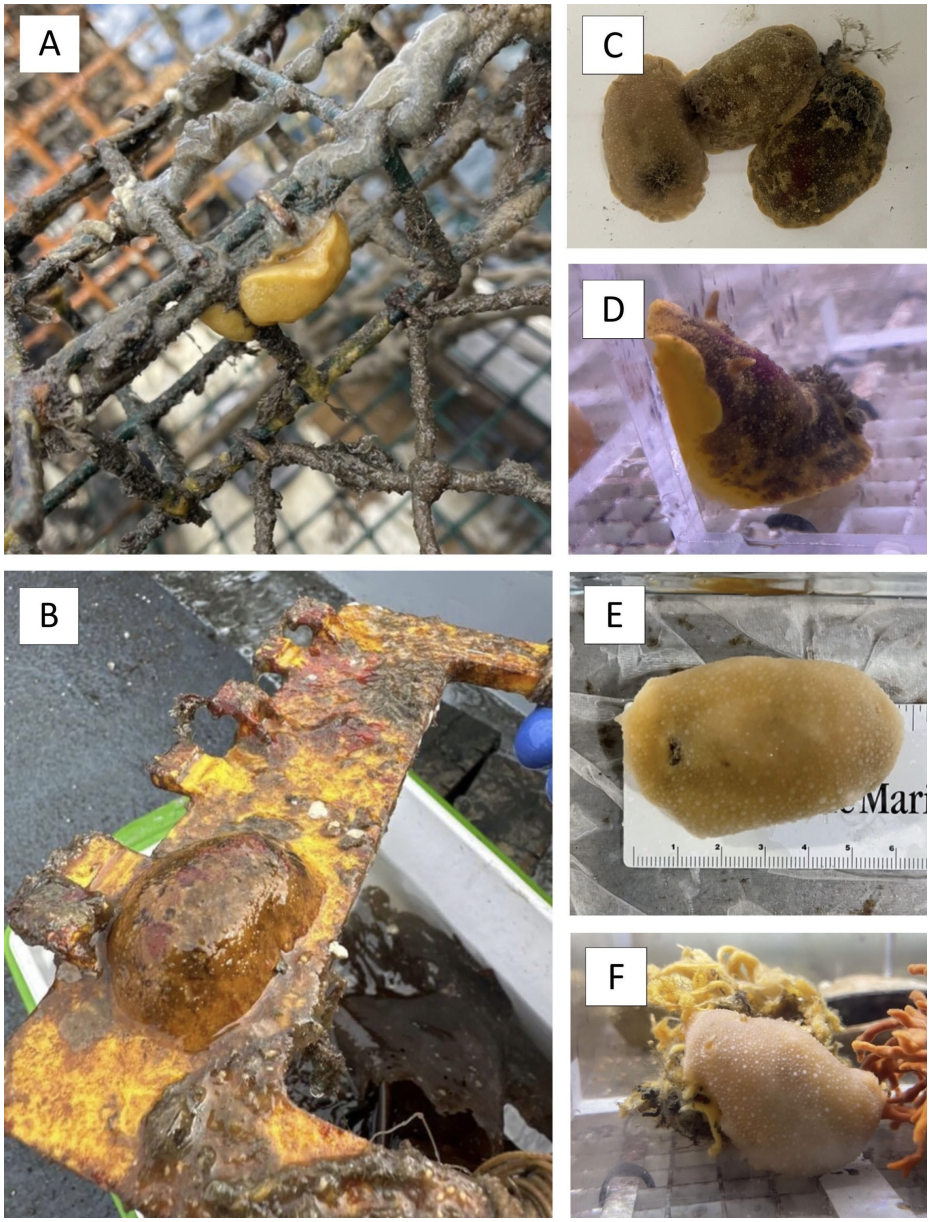

Figure 2. *Archidoris pseudoargus* recovered during marine debris recovery boat trawls in Groton, CT. Nudibranchs are shown in an old, abandoned lobster trap (A), on a detached trap vent (B), in a cooler with a portable aerator (C), in a housing tank at The Maritime Aquarium (D), with a ruler during growth measurements (E), and on the sponges *Halichondria panicea* (yellow) and *Clathria prolifera* (red) (F). Photographs by The Maritime Aquarium at Norwalk and Project Oceanology.

of feeding trials to observe sponge preference. Consumption of *H. panicea* was commonly witnessed, with occasional sightings of *A. pseudoargus* feeding on *C. prolifera* (Raviraj et al. *in preparation*). Once all retained nudibranchs died, two individuals at Project Oceanology were preserved in 70% ethanol while three individuals at The Maritime Aquarium were preserved in 95% ethanol for genetic analyses. Before expiring, most individuals laid eggs (Figure 3) that were later preserved.

From May through October of 2023, demersal fish trawl surveys were conducted by Harbor Watch in Norwalk Harbor and Saugatuck Harbor, Connecticut, in Long Island Sound, during which time multiple bright yellow

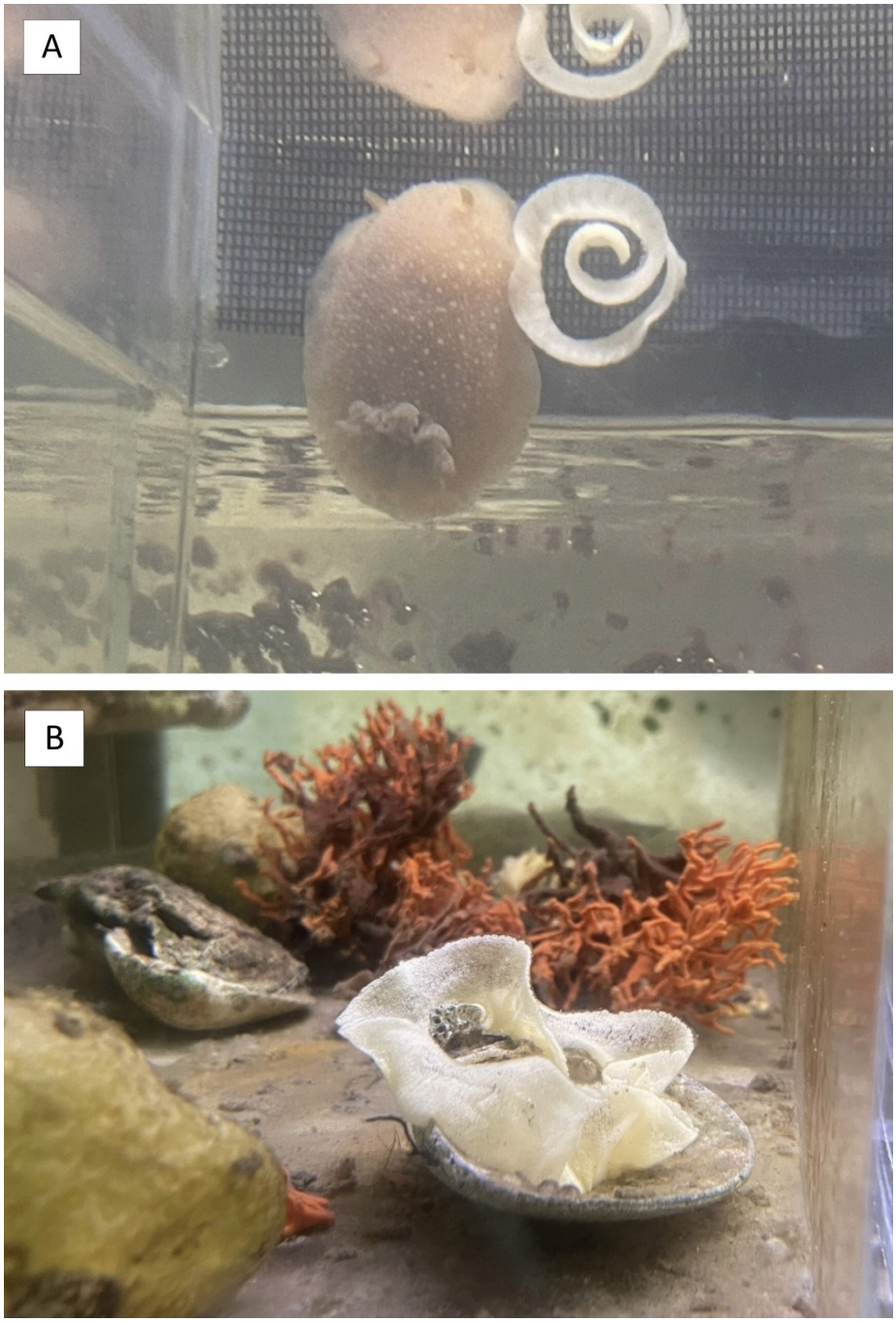

Figure 3. *Archidoris pseudoargus* egg masses laid in observation tanks at The Maritime Aquarium. A nudibranch is resting next to eggs in one tank (A) while one large egg mass is seen attached to a shell in another tank (B). Photographs by The Maritime Aquarium at Norwalk.

individuals of *Doriopsilla pharpa* were recovered from encrusted and decayed bivalve shells. While some *D. pharpa* were found on shells that had multiple fouling organisms and *Cliona celata* attached to them, most *D. pharpa* were found on substrate without sponge or other visible fauna. These nudibranch specimens were identified by Terrence Gosliner through morphological confirmation from photographs taken in situ (Figure 4), with individuals displaying a bright yellow-orange coloration, small size, flattened and oval-shaped body, and distinct gill and rhinophore arrangement (Marcus 1961, 1972; Eyster and Stancyk 1981). Most individuals were returned

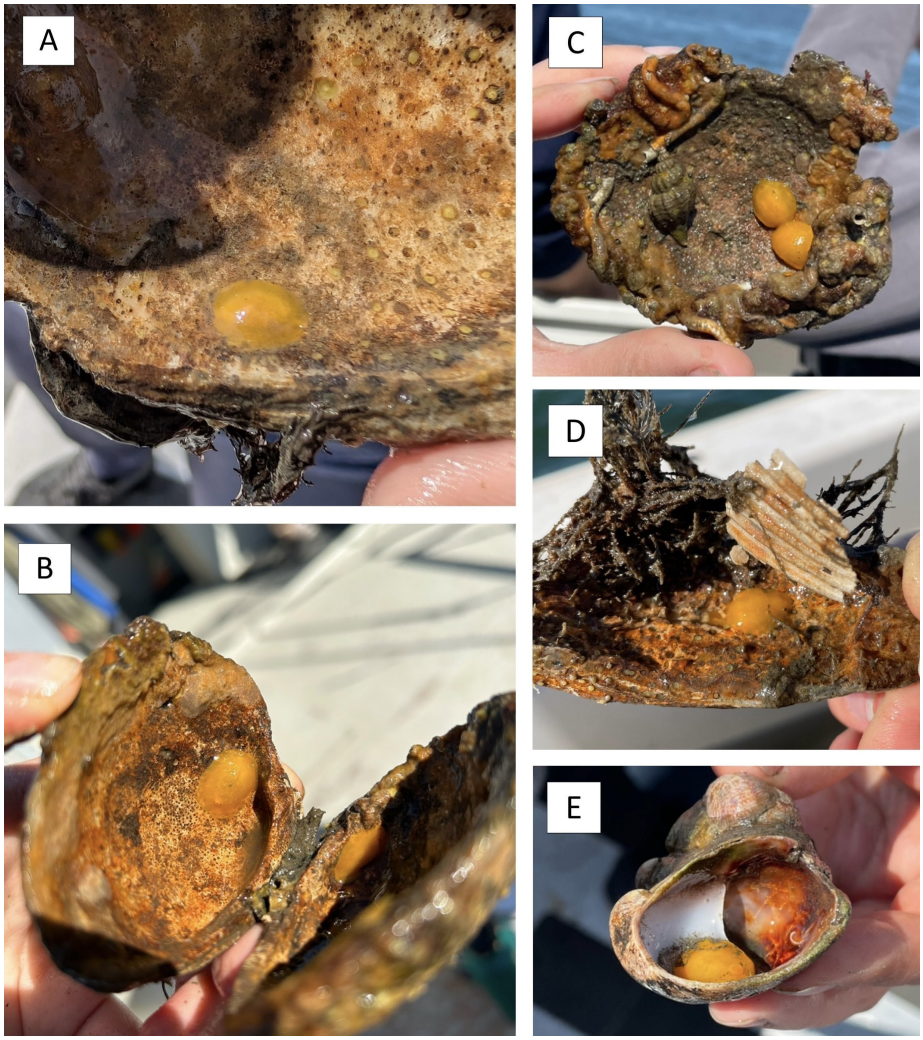

Figure 4. *Doriopsilla pharpa* in Norwalk Harbor resting on decaying *Mercenaria mercenaria* clam shell edge (A), shell hinges (B), encrusted shell (C), and a decayed bivalve shell (D). *Doriopsilla pharpa* in a slipper limpet (*Crepidula fornicata*) stack in Saugatuck Harbor (E). Photographs by Harbor Watch.

to the water, while three individuals were preserved in 95% ethanol upon their natural death for genetic studies. Additional *D. pharpa* caught between April 2024 and July 2024 were kept at The Maritime Aquarium for observation, where they were also held with local sponges and appeared to be primarily consuming *C. celata* (Raviraj et al. *in preparation*). On September 4, 2024, Brian Penney (Saint Anselm College) visited The Maritime Aquarium and a trawling survey was conducted in Norwalk Harbor to collect additional sponge samples and *D. pharpa* for research into their morphology and DNA structure.

Retrospective search of Harbor Watch data and photograph archives revealed that *D. pharpa* had first been seen on September 25, 2020 in Norwalk Harbor, with additional photographs taken in October 2022. Earlier in May 2022, personnel from The Maritime Aquarium also observed *D. pharpa* in Norwalk Harbor during trawling operations. A search on iNaturalist further revealed that a single *D. pharpa* specimen had been found in Norwalk Harbor as early as July 2019 (McGowan 2019).

While our observations are limited, a single trawl in Norwalk Harbor has been found to contain 10 or more *D. pharpa* individuals, with up to 7 individual *D. pharpa* having been collected during a single trawling survey. *Archidoris pseudoargus* has been more typically found as solitary or paired individuals during the surveys in this study, with up to 2 individual *A. pseudoargus* having been collected during a single marine debris recovery effort (Table S1). The average length of adult *D. pharpa* observed in this study was 11 ± 1.15 mm (n = 9), while the average length of *A. pseudoargus* was 57.25 ± 3.40 mm (n = 4).

Overall, *A. pseudoargus* has been found to date in Long Island Sound from 9.60 to 24.99 meters in depth (above and Table S1), whereas *D. pharpa* has been found consistently in shallower water (2.32 to 4.57 meters in depth; Table S1). *Archidoris pseudoargus* has been found in temperatures (based on NOAA buoy data) ranging from 4.53 to 18.72 °C, whereas *D. pharpa* has been found in temperatures from 10.70 to 20.23 °C (Table S1), the latter perhaps reflecting the lemon drop's more southern, warmer affinities.

Intertidal and marina surveys

To identify other potential areas where *A. pseudoargus* and *D. pharpa* may be found, two intertidal surveys and one marina survey were conducted by The Maritime Aquarium on April 5, June 4, and July 1, 2024 at Avery Point and Groton Long Point in Groton, CT, and Safe Harbor Marina in Mystic, CT. Shallow areas were visually scanned and the undersides of rocks and other hard substrates were examined. A dive survey was also conducted at Avery Point by the University of Connecticut scuba club on September 16, 2024, where divers scanned docks and rocky surfaces in shallow water neighboring previous *A. pseudoargus* sightings. No additional nudibranchs were discovered in these brief surveys.

Discussion

Archidoris pseudoargus may have been introduced to the Atlantic coast of the United States through multiple mechanisms, including transport of planktonic larvae in ballast water (Smith et al. 1999) or on sponges associated with vessel fouling, such as in sea chests, which are known to transport dendrodoridid nudibranchs (Coutts and Dodgshun 2007). Having established itself outside of European waters, Harris et al. (2023) suggested that the broad thermal tolerance of *A. pseudoargus* in its native range might allow it to expand from the Gulf of Maine to the south of Cape Cod, which it now has as of 2023. This expansion is consistent with the expected post-invasion range increases of introduced species to their physiological limits, regardless of latitudinal direction (Carlton and Schwindt 2024). To the north, the *A. pseudoargus* population would be expected to continue expanding in both directions along the U.S. Atlantic coast (Harris et al. 2023). The extent

to which *D. pharpa* will continue to expand further north may depend on the pace and magnitude of warming in New England (Crosby et al. 2018; Snyder et al. 2019), as well as the ability of the species to disperse north of Cape Cod, a common biogeographic break (Hale 2010). Thus, it is possible that both species will overlap as they expand beyond Long Island Sound, with broader implications for the east coast of the United States.

The movement of *A. pseudoargus* from the Gulf of Maine into Long Island Sound mirrors a long history of other marine invasions moving south and west in New England. As early as the 1870s, the European periwinkle *Littorina littorea*, in the Gulf of Maine since the 1860s, crossed around Cape Cod into southern New England (Carlton 2014). The Asian ascidian *Styela clava*, first detected in the Gulf of Maine in 1970, subsequently appeared south of Cape Cod several years later in 1973, and continued south into Long Island Sound (Carlton 1989; Berman et al. 1992; Brunetti and Cuomo 2014). The European kelp bryozoan *Membranipora membranacea* first appeared in the Gulf of Maine in 1987, with arrival in Long Island Sound by 1990 (Berman et al. 1992; Carlton 2014). The Asian ascidian *Didemnum vexillum* similarly first colonized the Gulf of Maine in the 1980s, followed by its appearance south of Cape Cod and into Long Island Sound by 2000 (Bullard et al. 2007; Mercer et al. 2009; Auker 2019).

In parallel, the arrival of the southern *D. pharpa* in Long Island Sound is consistent with a well-known pattern of warmer-water, lower latitude species moving poleward around the world due to climate change (Sorte et al. 2010), including into New England (Pederson et al. 2021). A relatively recent example of the latter is the southern sea anemone *Aiptasiogeton eruptaurantia*, first appearing in New England waters in 2010 (Pederson et al. 2021). In concert with the post-invasion movements noted above, the recently introduced Indo-West Pacific shrimp *Lysmata vittata*, first documented in 2013 in Chesapeake Bay (Aguilar et al. 2022), was found commonly in recovered lobster traps in southern Long Island Sound from late 2022 to date (authors' *personal observations*).

While only a small number of *A. pseudoargus* and *D. pharpa* have been observed in Long Island Sound thus far, the observation of multiple individuals across years despite limited sampling effort of the benthos suggests that continued investigation is warranted to fully understand their spatiotemporal coverage, feeding behavior, interspecific relationships, and resulting ecosystem implications. For example, the combined arrival of these two sponge-eating nudibranchs raises questions about both the potential interactions of these two species as they get closer to each other, and about potential impacts on sponge populations in southern New England. There are diverse sponge populations in Long Island Sound, including *Clathria prolifera* (red beard sponge), *Cliona celata* (boring sponge), *Halichondria panicea* (breadcrumb sponge), *Halichondria bowerbanki* (yellow

sun sponge), *Chalinula loosanoffi* (erect sponge), *Haliclona oculata* (mermaid's glove), *Isodictya palmata* (finger sponge), and *Polymastia boletiformis* (= *P. robusta*) (papillate sponge) (Hartman 1958). The dietary range of *A. pseudoargus* is similar to that of other dorids as a specialist sponge predator (Penney 2013), and it has been previously documented to prefer certain sponge species over others, prioritizing the consumption of *H. panicea* and *Hymeniacidon perlevis* (Krings et al. 2023). *Halichondria panicea* is abundantly found along coastal areas in the North Atlantic and is widely present in Long Island Sound (Diaz et al. 1993; Erpenbeck et al. 2004). Thus, this region is a viable hunting ground for *A. pseudoargus*. In contrast, *D. pharpa* appears to have a narrower dietary range, typically consuming the boring sponge *Cliona celata* (Morse 1975; Guida 1976; Eyster and Stancyk 1981) which is dispersed throughout the Sound and plentiful in both the Norwalk and Saugatuck Harbors, in Connecticut (authors' *personal observations*).

Considering the feeding preferences of these nudibranchs, their impact on the marine benthic ecosystem may be felt through the loss of sponges, given that sponges are an important source of habitat heterogeneity and food (Hartman 1958). Increased sponge predation may alter carbon and nutrient cycles (Maggioni et al. 2023) and the existing trophic patterns in the Sound, directly affecting animals such as fish, turtles, and invertebrates, and indirectly affecting animals in higher trophic levels (Wulff 2006). Differences in the size of both nudibranchs may also result in differential impacts on Long Island Sound benthic communities, given that *D. pharpa*'s adult size is smaller than that of *A. pseudoargus*. Furthermore, their differences in size, color, and potential chemical defense systems may dictate which predators may prey upon them, and thus to what extent their populations may be controlled locally by predation (Long and Hay 2006).

Conclusions

Ultimately, the limited study of benthic habitats in Long Island Sound may have allowed these invasions, and others yet to be discovered, to go undetected for prolonged periods of time. General biodiversity surveys are unlikely to capture an exhaustive list of species present in an area, making it difficult to inventory all non-native species, especially those in dynamic habitats such as the intertidal and subtidal (Morisette et al. 2020; Roesch et al. 2024). Therefore, increasing the frequency and area of targeted surveillance measures may serve to detect future invasions and range expansions in a timely manner (Morisette et al. 2020). Early detection and monitoring techniques are also particularly useful, especially in ports, marinas, harbors, and boat launches. Periodic watercraft inspection stations may also be an effective way to check for non-native species in ballast water or attached to water-related equipment (Fisheries and Oceans Canada 2024).

Alternatively, environmental DNA (eDNA) surveys may be of value since this non-invasive method allows for species identification without physically capturing or observing them, making it a viable tool for detecting rare, elusive, or inaccessible species (Holman et al. 2019). Other DNA-based tools, such as High Throughput Sequencing technologies, also have the potential to be highly sensitive, precise, and inexpensive techniques for identifying the presence of non-native species soon after introduction (United States Environmental Protection Agency 2025). Ultimately, a variety of approaches exist to track the range expansions of non-native species; however, many are not currently well suited to detect small subtidal species like nudibranchs, hindering our ability to identify these invasions in real time. Therefore, comprehensive benthic surveys and a tailored approach to the observation of *A. pseudoargus* and *D. pharpa* populations will be necessary.

In essence, due to the double invasion of these non-native nudibranchs, essential sponge populations and the species that depend on them are potentially at risk. Invasions like these may be going undetected due to the lack of regular survey data regarding the benthos and cryptic species. *Archidoris pseudoargus* and *D. pharpa* ecology and behavioral patterns are particularly understudied, meaning that the full impact of their novel presence in Long Island Sound may remain unknown unless additional research is conducted to assess their habitat use, feeding preferences, and other ecological relationships. With the rapid pace of climate change and changing species assemblages worldwide, bioinvasions will only continue to exacerbate the threats to vulnerable intertidal and subtidal ecosystems. We must strategically address these overarching concerns to protect vital ecosystems like Long Island Sound.

Authors' contribution

R.R., C.S., J.T.C., S.C.C., research conceptualization; R.R., C.S., J.T.C., K.T.B., S.C.C., K.C., M.K.D., M.F., I.M., M.O., D.R., H.S., N.C.S., J.P.S., sample design and methodology; R.R., C.S., J.T.C., K.T.B., S.C.C., K.C., M.K.D., M.F., I.M., M.O., D.R., H.S., N.C.S., J.P.S., investigation and data collection; R.R., C.S., J.T.C., S.C.C., J.P.S., data analysis and interpretation; R.R., S.C.C., N.C.S., ethics approval; R.R., S.C.C., M.F., D.R., J.P.S., writing – original draft; R.R., C.S., J.T.C., K.T.B., S.C.C., M.F., D.R., H.S., N.C.S., J.P.S., writing – review and editing. All individuals listed as authors have: (1) agreed to be listed; (2) approve the submitted version of the manuscript. The discovery of *A. pseudoargus* resulted from the observations of the sampling team in October 2023 (Raviraj, Scheetz, Cuzco, Morrison). The determination of its species identity and potential importance resulted from the contributions of Raviraj and Scheetz. *D. pharpa* was first reported by Spiller, Burns, Donato, and Olavarria to Carlton and Crosby. Carlton assisted with identification of both species and participated in surveys for additional individuals. Susarchick was responsible for overall coordination of the marine debris recovery sampling program and review of the datasets that led to identification of additional individuals. Raviraj, Crosby, Fajardo, and Susarchick assisted with intertidal and fouling surface field surveys in search of additional individuals of *A. pseudoargus*. Raviraj, Scheetz, Crosby, and Spiller coordinated the integration of the field datasets and general coordination among all involved parties. The first draft of the manuscript was written by Raviraj, Crosby, Fajardo, Romanello, and Susarchick. All authors contributed to the development of the location dataset presented. All authors contributed to further development of the manuscript, revision of manuscript draft, and preparation of the final manuscript draft.

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Ethics and permits

The authors have complied with the institutional and/or national policies governing the humane and ethical treatment of the experimental subjects, and we are willing to share the original data and materials if so requested. To ensure the ethical and safe use of animals in research and teaching settings in line with federal law and guidelines, we follow the protocol of The Maritime Aquarium at Norwalk's Institutional Animal Care and Use Committee (IACUC). Our animal protocol was approved by the IACUC, and the animal project number is TMA2021-001. Animals were collected under Connecticut Department of Energy and Environmental Protection permit number SC-23035a and SC-23026 for The Maritime Aquarium and Harbor Watch, respectively.

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Supplementary material

The following supplementary material is available for this article:

Table S1. *Archidoris pseudoargus* and *Doriopsilla pharpa* collection locations and water temperatures (NOAA Tides and Currents 2025; USGS 2025).

This material is available as part of online article from:
http://www.reabic.net/journals/bir/2025/Supplements/BIR_2025_Raviraj_etal_SupplementaryMaterial.xlsx