Marine Biology (2025) 172:75
https://doi.org/10.1007/s00227-025-04639-y

ORIGINAL PAPER

Lunar synchrony and reproductive strategies of intertidal-breeding fishes

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Received: 6 December 2024 / Accepted: 4 April 2025 / Published online: 21 April 2025

Abstract

When is the best time to breed? This is an important question, especially for fishes that breed in the intertidal zone, a dynamic habitat where conditions change rapidly and cyclically. Many intertidal fishes reproduce during the spring tides (during the new and full moons when tidal fluctuations are strongest). However, we use long-term field data to present a counter example, the toadfish, *Porichthys notatus*, which spawns more often during the neap tides (during the quarter moons when tidal fluctuations are weakest). We hypothesize that if a species' reproduction involves time-consuming tasks, such as courtship, mate selection, nest preparation, and prolonged egg-laying, and if these activities must occur underwater, then such species will align their reproduction with neap tides rather than spring tides. To examine the prevalence of neap tide spawning, we conducted a comprehensive literature review to explore the diversity of reproductive strategies and timings in intertidal fishes. Because some species must leave the intertidal zone or find refuge when the tides recede, whereas others exhibit amphibious lifestyles and can even breathe air, we paid specific attention to different species' requirements for submersion to perform their reproductive behaviours. We gathered data on 131 fish species and ultimately highlight a scarcity in data on reproductive timing in intertidal fishes. Our literature survey provides preliminary support for our hypothesis, and we now call on researchers to directly examine lunar synchrony of reproduction in intertidal fishes to better understand how reproductive strategies are shaped by the tides.

Keywords Reproductive timing · Environmentally set periodicity · Moon phase · Tidal phase · Beach spawning · Circadian rhythm

Introduction

"For no two successive days is the shoreline precisely the same.…[T]he tides advance and retreat in their eternal rhythms.. On the ebb tide it knows the harsh extremes of the land world, being exposed to heat and cold, to wind, to rain and drying sun. On the flood tide it is the water world, returning briefly to the relative stability of the open sea." Rachel Carson, *The Edge of the Sea*, pg. 1.

Marine biologist Rachel Carson wrote these lines in her 1955 book 'The Edge of the Sea' (Carson 1955), inspired by the rich biodiversity found within the ocean's intertidal zones. Despite the extreme abiotic fluctuations in the intertidal, numerous species choose to reproduce in this habitat. Indeed many species specifically come to the intertidal zone to deposit their eggs in areas where developing young can experience warmer temperatures and/or rich oxygen conditions as well as improved safety from aquatic predators (Demartini 1999; Taylor 1999; Takemura et al. 2004; Martin

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Communicated by Filipe Martinho.

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2014; Brown et al. 2023). However, choosing precisely *when* to reproduce in the intertidal zone is not straightforward because a confluence of seasonal, lunar, and diel cycles generate conflicting options (Korringa 1957; Ikegami et al. 2014; Neumann 2014). Tidal heights, durations of egg submersion, and nighttime luminosities all fluctuate as the moon cycles through its phases, causing reproductive conditions to vary across the lunar (synodic) month (Leatherland et al. 1992). The intertidal zone therefore offers an intriguing opportunity to study how reproductive rhythms can follow environmental periodicities, and how timing is incorporated into species' reproductive strategies in such a dynamic environment.

One commonly reported time for intertidal organisms to reproduce is during the spring tides, which occur just after the new and full moons and constitute the strongest diel tidal fluctuations in each month (Ishimatsu et al. 2018). Spring tides occur year-round and are marked by the tide reaching both its highest and lowest point on the shoreline. Intertidal fishes often show a distinct preference for reproducing or laying eggs are particular elevations in the intertidal zone (Yamahira 1996; Brown et al. 2020). Those intertidal species that prefer high oviposition sites often ride the spring tides to reach these elevations, i.e., regions that offer higher average temperatures, increased oxygenation, and strong tidal fluctuations that can initiate hatching and flush larvae out to sea (Taylor 1984; Ishimatsu et al. 2018). Nocturnal luminosity levels are also at their extremes around these spring tides (highest light levels at full moons, lowest at new moons), potentially improving visibility for detecting mates and/or remaining in the darkness to avoid nocturnally active predators (Acosta and Butler IV 1999; Claydon 2004; Shima et al. 2020; Simons et al. 2022). However, spring tides provide relatively short time windows for reproduction, often lasting only a few hours, when the highest tidal elevations are inundated by the sea and accessible to aquatic animals. Alternatively, individuals could choose to reproduce during the neap tides, which occur with the first and third quarter moons and are characterized by the weakest diel tidal fluctuations and intermediate nocturnal luminosity levels. Water levels do not rise as high during neap tides, and so do not offer animals access to as many oviposition sites, but relative to spring tides, neap tides provide more time for reproduction before the ebb tide interrupts reproductive activities, and perhaps also more stable conditions lessening the chances that broadcast eggs or sperm become washed away before fertilization or attachment to substrates can take place.

According to Martin (1995) there are different ecophysiological 'styles of living' among intertidal fishes that vary in their reliance on tidal submersion. These include 'visitors' who swim into the intertidal zone during high tide and then leave when the tide goes out. There are also 'remainers' who find shelter in humid microclimates such as under rocks or algae when the tide goes out, and 'tidepool emergers' who remain in tidepools at low tide. Finally, there are 'skippers' who are well adapted to life on land and can emerge at all tidal phases and routinely engage in terrestrial activity. A species' lifestyle will therefore dictate the degree to which its activities in the intertidal zone are restricted by the tidal cycle because of constraints on movement, fertilization, or physiology when air exposed. For example, visitors must complete all their reproductive behaviours while the intertidal zone is submerged, but skippers are not so constrained. Remainers will also be moderately constrained by tidal fluctuations, and tidepool emergers may in theory still interact with conspecifics at low tide but must do so within the confines of their tidepools. Ultimately, the tides should constrain visitors the most, followed by remainers, then tidepool emergers, and finally skippers would be the least constrained. This diversity of ecophysiological lifestyles described by Martin (1995) is mirrored by a tremendous diversity of reproductive strategies in the intertidal zone that ought to coevolve with each lifestyle (Ishimatsu et al. 2018). We argue that the reproductive strategies employed by intertidal species should reflect the levels of constraints the tides impose on each species as a result of their lifestyle.

Species vary in the amount of time they require to successfully reproduce, which can include (depending on the species) performing the following consecutive tasks– mate searching, courtship and/or mate choice, preparing an oviposition site, mating and oviposition. Some species require very little time for these activities. For example, the grass puffer, *Takifugu niphobles*, aggregates along the shoreline and broadcast spawns large quantities of gametes relatively quickly (Yamahira 1996). In some intertidal sculpins, like the Fluffy Sculpin, *Oligocottus snyderi*, females may also be able to find mates and copulate ahead of their time in the intertidal zone, storing sperm and delaying oviposition until later (internal gametic association, e.g., Ito et al. 2024). This delay in oviposition allows females to wait until a favorable tidal height that will maximize the probability of embryo survival, and shortens the time they must spend in the intertidal zone relative to if mate choice and copulation also had to occur within the same tidal cycle. In contrast, other species may require relatively long periods of time to reproduce because they must progress through mate search, courtship, mate choice, and egg oviposition stages consecutively (e.g., dusky frillgoby, *Bathygobius fuscus*, Taru et al. 2002), which may be cumulatively time consuming.

We hypothesized that the timing of a species' reproduction will be determined by two major factors in the intertidal zone: (1) the degree to which their activities are constrained by the tides and (2) the duration of time required for them to reproduce (i.e., time it takes to find, court, and mate with partners). We test this hypothesis using several proxy variables that are detailed below. We predicted that tidally constrained species (e.g., visitors, remainers, or tidepool emergers) with time consuming reproductive activities will breed primarily during neap tides, whereas tidally unconstrained species (e.g., skippers) will be free to reproduce across the lunar month. Furthermore, tidally constrained species with rapid modes of reproduction (e.g., broadcast spawners without the need to search for, or choose among, mates) would similarly be free to reproduce across the lunar month. We provide support for our idea and predictions in two ways.

First, we present long-term field data on the reproductive timings of an intertidal-breeding toadfish, the plainfin midshipman, *Porichthys notatus.* This species is classified as an intertidal remainer, since males excavate nests beneath intertidal rocks and remain there during low tides. Males attract searching females to their nests by emitting vocalizations via swim bladder vibrations (Bass and Marchaterre 1989). Females come to densely clustered nesting grounds to select a mate among many courting males. Once they have made their choice females will slowly deposit their eggs in this male's nest (Brantley and Bass 1994; Bose et al. 2018; Brown et al. 2020). Spawning and oviposition occurs underwater and requires multiple hours to complete (longest recorded was 20 h, Brantley and Bass 1994), after which the males provide extended care (for up to 2 months) to the offspring (Cogliati et al. 2013). Because courtship, mate choice, and oviposition in *P. notatus* can cumulatively exceed the duration of a spring tide (*c.* 6 h), we predicted that peak reproduction would align with the neap tides as these tides offer longer inundation periods for these activities. Second, we conducted a comprehensive literature survey to characterize the variation in lunar synchronicity of reproductive timings in intertidal fishes. We summarize the surprising scarcity of information on this topic in the literature, discuss different species examples in relation to our hypothesis, and then provide a guide for future work to help study how reproductive strategies have been shaped by the predictable rhythm of the tides.

Methods

Spawning periodicity in an intertidal-breeding toadfish

We investigated the timing of reproduction in relation to the lunar cycle in the plainfin midshipman, a toadfish found along the west coast of North America. Following spawning, females return to deeper parts of the ocean and leave their male mating partners behind to care for their eggs over a two-month period (Cogliati et al. 2013; Bose et al. 2016). However, males can spawn with multiple females who contribute their eggs to the males' existing broods that they care for even as the tides repeatedly emerge and submerge them (Bose et al. 2018). Between April - July of 2009–2011, 2013–2015, and 2017–2019, we located a total of 702 plainfin midshipman nests across 12 field sites in Canada and the USA (see Table S1 for breakdown of sample sizes by site and year). Since nests are most easily accessible at low tide, our sampling typically took place during the five days leading up to and the five days following the new and full moons, when nests are above the water long enough to be surveyed. Sampling generally did not take place on days of the quarter moons (neap tides) as this is when nests remain submerged and are inaccessible by land. However, in 2019, nests were visually inspected during the neap tides by snorkelers throughout the lunar cycle.

For each nest that contained a male with offspring, we photographed the brood in the nest. We then used these photographs to age offspring. Ages can be estimated based on the presence of visually distinct developmental milestones (Cogliati et al. 2013; Brown et al. 2020). Eggs take about 30 days to hatch and then hatched young typically remain attached to the roof of the nest for another 4 weeks, continuing their development and using energy stores from a large yolk sac (Cogliati et al. 2013; Brown et al. 2020, 2023). For this study, we recorded which nests contained newly laid eggs (eggs deposited within the previous 24 h), which could be identified by the presence of white blastodiscs (see Table 1 in Brown et al. 2020) (Fig. 1A). We then assessed how the proportion of nests containing newly laid eggs varied over time and tested for any periodicity that aligned with the lunar cycle.

We conducted all statistical analyses in 'R' (version 4.1.3; R Core Team 2022). We tested for temporal periodicity in spawning by fitting binomial generalized linear mixed effects models (GLMMs) to the nest inspection data. The response variable was the proportion of nests inspected at a field site on a particular date that had new eggs. We included 'sampling day' as a predictor variable and we set it to be relative to the first new moon of the breeding season (day 0), which we defined as the new moon falling within the last two weeks of April or the first two weeks of May. The models also included random intercepts of 'Field site' nested within 'Year' to reflect replication of the sampling design across sites and years, respectively. We also included two periodic functions as additional predictor variables given by the following equations:

$$\sin\left(\frac{2\pi}{period \times sampling\ day}\right) \tag{1}$$

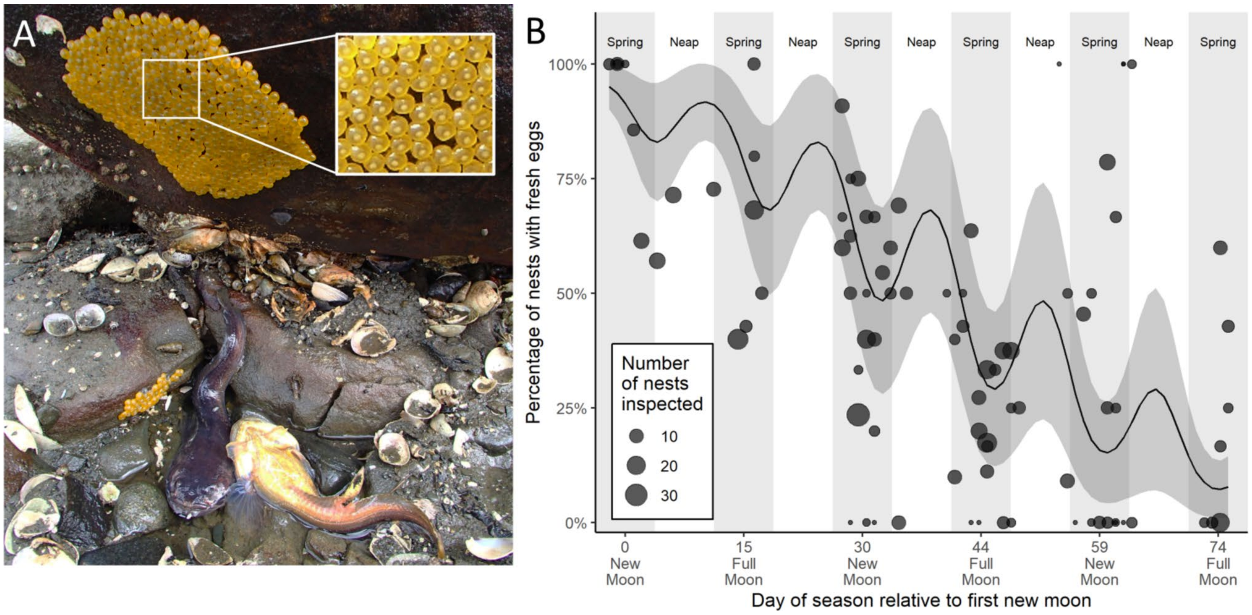

Fig. 1 (**A**) Photograph of a plainfin midshipman spawning pair (a nesting male and a yellow bellied female in the upside down spawning position) within an intertidal nest containing newly laid eggs, still bearing white blastodiscs (Brown et al. 2020). (**B**) Model predictions (black line with grey shaded area depicting 95% CI) from analysis that considers a 14-day periodicity in the data. Observed data (black dots) show the proportion of nests with recent spawning activity (as evidenced by new eggs in the nest) across the plainfin midshipman breeding season. Area of the data points/dots are scaled according to the number of nests inspected at a particular study site and day. Panel backgrounds are shaded to show neap and spring tidal periods.

$$\cos\left(\frac{2\pi}{period \times sampling\ day}\right) \tag{2}$$

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These sine and cosine functions test for periodicity in the data. We tested periodicities ranging from 3 to 30 days (fitting 28 models in total). We then examined the best fitting model(s) based on Akaike's Information Criterion, corrected for small sample sizes (AICc, Hurvich and Tsai 1989).

Literature survey on lunar synchrony in intertidal fish reproduction

We conducted a literature review of reproductive timing in intertidal fishes by searching the *Web of Science* Core Collection on June 18, 2024 using the search query (reproduc* OR mating OR breed* OR Nest* OR Spawn* OR egg* OR Ovar* OR courtship OR brood OR Copulat* OR Pair) AND (*fish OR *fishes OR fish*) AND (synchron* OR phas* OR Cycl*OR Rhythm* OR periodicity OR timing OR pattern*) AND (moon* OR lunar OR semilunar OR intertidal OR inter-tidal OR spring tide* OR neap tide*) in the topic ("TS") field, which searches all titles, abstracts, and key words. See Supplementary Materials for more details on the inclusion/exclusion criteria for our literature search. This search yielded 1083 primary and secondary scientific articles, 159 of which focused on fish in the intertidal zone. This was supplemented by searching all the references of 12 relevant review articles (see Supplementary Materials). Together, this search process produced a list of 182 fishes that reproduced, or potentially reproduced, within the intertidal zone. We then examined these 182 species in greater detail as described below.

Our aim was to characterize where and when various species of intertidal fish reproduce, as well as how time-consuming their reproduction is. For each of the 182 species, we conducted additional in-depth searches of all the available peer-reviewed as well as any grey-literature we could uncover (including government reports, MSc and PhD theses, etc.) and extracted any relevant information on each species. In particular we were looking for information about *i*) where the species reproduces (e.g., in the intertidal zone, at the spring tide water mark, above the spring tide water mark, or elsewhere), *ii*) which intertidal lifestyle category the species expresses (i.e., visitor, remainer, tidepool emerger, or skipper, Martin 1995), *iii*) whether the species' reproductive activities show 'peaks' across the lunar cycle—that is, are there certain times of the lunar month (the synodic month, lasting ~29.5 days) where reproduction is significantly more frequent than at other times? *iv*) whether reproductive peaks align with one or more lunar phases (with the new and full moons corresponding to the spring tides and/or the first and third quarter moons corresponding to the neap tides), and *v*) any additional information regarding how time consuming reproduction is likely to be for each fish species. Because precise time durations for the different reproductive phases, such as mate searching, courtship, mating, and spawning, are rarely presented in the literature, we used proxies that are expected to correlate with the duration of the reproduction phases for each species. First, nest construction and parental care are widely acknowledged to have strong sexual selection consequences in fishes with females often choosing males after carefully assessing their nests and paternal care abilities (Coleman and Jones 2011; Svensson and Kvarnemo 2023). We therefore expected nest constructing and care-giving species to be associated with more time-consuming mate searching and mate choice stages than species without nest construction or parental care. Second, modes of reproduction in intertidal fishes range from egg-laying (oviparity) to live-bearing (viviparity, oviviparity), though the vast majority are oviparous and either broadcast spawn into the water, scatter demersal eggs onto the substrata, or carefully oviposition adherent eggs onto hard surfaces (Ishimatsu et al. 2018). In this study, we expected the oviposition of adherent eggs one at a time to be the most time-consuming mode of reproduction particularly compared to the mass release of eggs as in broadcast spawners. If a species had nests, provided care, and oviposited adhesive eggs on hard substrate, we considered that such a species would have relatively lengthy time requirements for reproduction relative to species without these characteristics. Because of the use of proxies, our approach here represents the first steps in investigating reproductive timings and constraints in the intertidal zone, and we hope to inspire future work that can more fully and directly quantify these reproductive timings.

Overall, our literature search resulted in a dataset containing information on 131 intertidal-breeding fish species. We use this cross-species dataset to summarize the current state of knowledge about reproductive timings in relation to the lunar/tidal cycle across intertidal fishes. When reproductive timings were known, we evaluated whether reproduction aligned with spring tides or neap tides in accordance with species' intertidal lifestyle and time requirements for reproduction.

Results

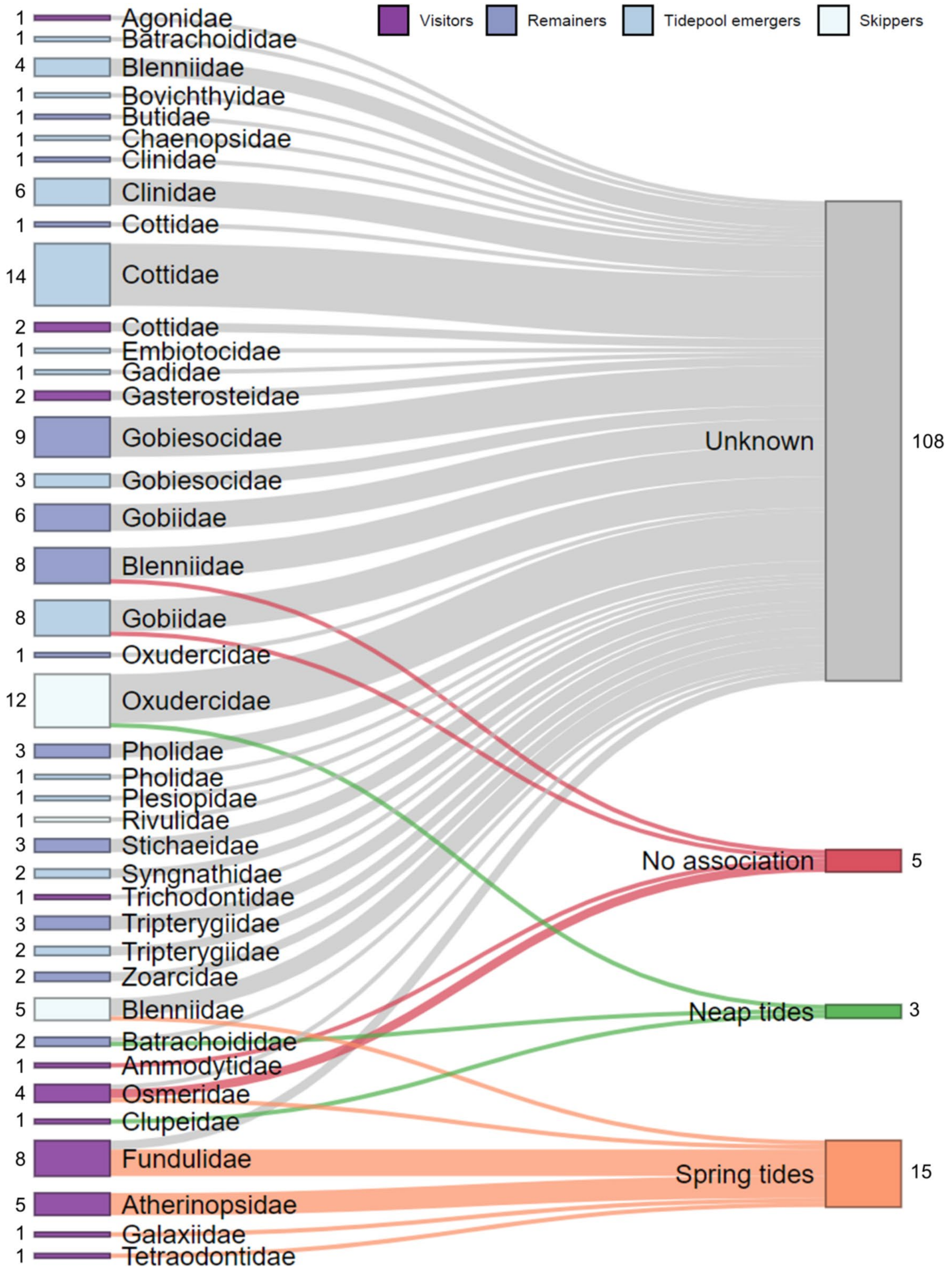
Plainfin midshipman spawning activity peaks during the quarter moons (neap tides)

Plainfin midshipman spawning activity followed a semi-lunar pattern; egg-laying peaked every ~14 days and the peaks coincided with the first and third quarter moons (i.e., neap tides, Fig. 1B). Of all the periodicities tested (3–30 days), spawning activity aligned most closely with a 14-day periodicity (lowest AICc value) but also aligned well with a 30-day periodicity (Appendix 1; Figure S1). In the 14-day model, egg laying showed a sinusoidal pattern over time. The probability of finding new eggs in a nest was significantly correlated with the model's sine function (Est. ± SE = − 0.61 ± 0.21, z = − 2.88, $P = 0.004$, Fig. 1B). The probability of finding new eggs (Fig. 1A) in a nest also declined by 6% (95% CI: 5–7%) per day in the 14-day model (z = − 9.27, $P < 0.0001$, Fig. 1B), indicating that spawning events become rarer as the summer breeding season progresses.

Literature survey on lunar synchrony in intertidal fish reproduction

Our literature review yielded a total of 131 species from 29 taxonomic families that reproduce in the intertidal zone. The list included examples of all the intertidal lifestyles, including 27 visitors, 40 remainers, 46 tidepool emergers, and 18 skippers. However, only 23 species (18%) had any information regarding reproductive periodicity with respect to the lunar cycle (including 18 visitors, 2 remainers, 1 tidepool emerger, and 2 skippers, Fig. 2). Fifteen species aligned their reproduction with the spring tides (i.e., the new and/or full moons, 14 visitors from 5 families, and 1 skipper), 3 species aligned with the neap tides (i.e., the quarter moons, 1 visitor, 1 remainer, and 1 skipper), and 5 species showed no association with the lunar cycle (3 visitors from 2 families, 1 remainers, and 1 tidepool emerger).

Next, we focused on the species for which reproductive lunar periodicity information could be gleaned and examined their reproductive behaviours in more detail (Table 1). We found 18 species of visitors (from 7 families). The majority of these species (78%) displayed synchrony with the spring tides. These spring tide spawners all displayed relatively rapid reproduction in that none of these species construct nests or provide parental care and most of these species also broadcast spawn or lay non-adhesive eggs across different elevations in the intertidal zone. We also found five species (from 4 families), which were remainers, tidepool emergers, and skippers, and these species all have nest construction, provide parental care to offspring, and oviposit adhesive eggs. These species display a variety of reproductive timings, ranging from synchrony with spring tides, with the neap tides, or no association with the tides.



Discussion

The lunar cycle can dramatically affect animal behaviour and reproduction (Fox 1924; Naylor 1999; Takemura et al. 2004; Ikegami et al. 2014; Mandal 2023) and can have particularly strong effects on organisms living in the intertidal zone due to its influence on the tides (Taylor 1984; Martin 2014, 2015). The reproductive strategies of intertidal fishes show a wide range of adaptations related to how, where, and when a species or population reproduces in the

◂ **Fig. 2** Sankey plot illustrating the results of our literature survey. Species of intertidal reproducing fishes from different taxonomic families are shown on the left and their timings of reproduction within the synodic month in connection with the spring or neap tides are shown on the right (if known). Shades of blue and purple indicate the intertidal lifestyle category of each species (visitor, remainer, tidepool emerger, skipper, Martin 1995) with darker shadings indicating that a species' activity within the intertidal zone is more constrained by narrower time window of the high tides (skippers are least constrained, followed by tidepool emergers, followed by remainers, and finally visitors are the most constrained). Note that some fish families contain species from multiple lifestyle categories and therefore have more than one rectangular node on the left (e.g., Cottidae). Numbers to the left or right of each node represent the number of species. Note that many marine sculpins (traditionally grouped in Cottidae as visualized here), are now considered to be placed in the family Psychrolutidae (Smith and Busby 2014).

intertidal zone. In the present study, we focused on how synchrony with the lunar cycle may be related to the reproductive strategies of intertidal fishes. We found 15 examples of intertidal fishes that reproduce in association with the spring tides (i.e., new and full moons). We also explored the prevalence of neap tide spawning and what traits might predispose fishes to align their reproduction with the neap tides.

Our literature search revealed a striking lack of data on the timing of reproduction in relation to the lunar/tidal cycle for intertidal breeding fishes. This is surprising given that lunar synchrony in animal behaviour has been a topic of study for over a century (see Fox 1924). It is even more surprising given how strongly tidal cycles influence the intertidal zone, driving dramatic abiotic fluctuations that affect the animals that spend time there. Yet, we found information on reproductive lunar periodicity for only 23 intertidal fishes (out of 131 total species, or 18%, in our literature search, including our own study species, *P. notatus*), representing 13 families. This scarcity of information is in part because many field studies do not perform repeat sampling of wild populations at regular enough time intervals needed to test for (semi)lunar periodicity. Some species may also have reproductive seasons that are too short to test for periodicity with any statistical power unless multiple years of data are compiled. Furthermore, many intertidal species are highly cryptic and breed under vegetation or rocks, and so are difficult to observe directly in wave-washed, rocky habitats. Because of this data scarcity, we examined the evidence for our hypothesis by drawing on specific examples. We acknowledge that a phylogenetically controlled statistical analysis with more species is now needed to formally test our hypothesis, and we hope that our work will inspire future empirical studies to provide the data needed for such an analysis.

We hypothesized that the timing of peak reproduction for intertidal fishes would be influenced by *i*) the time duration needed for reproduction, which can include nest preparation, courtship, mate choice, and mating itself, and *ii*) the degree to which these species' reproductive behaviours are tidally constrained (Do reproductive activities require submersion during high tide? Does the species prefer to oviposit at high intertidal elevations?), which can in-part be captured by categorizing species as intertidal visitors, remainers, tidepool emergers, or skippers (Martin 1995). We predicted that species that can complete their reproduction within a couple of hours would be free to reproduce at any time in the synodic month, but that species with lengthy time requirements for reproduction (e.g., > 6 h) ought to prefer the neap tides. We also predicted that, all else being equal, species that are not tidally constrained, i.e., skippers, would also be freer to reproduce at any time across the synodic month. Preliminary evidence for our hypothesis, comes from two observations, (1) that the plainfin midshipman fish with its slow reproductive process prefers to spawn during the neap tides, and (2) that species with either quick reproduction or skipper ecophysiological lifestyles show a range of different timings across the lunar cycle (but with a clear bias towards spring tide spawning).

Our main study species, *P. notatus*, is rather unconventional among the intertidal breeders uncovered by our literature review in that it requires many hours (up to 20) to complete courtship, mate choice, and oviposition (Brantley and Bass 1994). Although the plainfin midshipman is considered an intertidal remainer and is well-adapted to the physiological demands of periodic air exposure or aquatic hypoxia during low tides (Craig et al. 2014; Bose et al. 2019; Houpt et al. 2020), if the tides interrupt the reproductive process, this are likely to be costly as females are less hypoxia tolerant than males (Craig et al. 2014). Plainfin midshipman also nest across a range of intertidal elevations, but males prefer to nest in the lower reaches of the intertidal zone where eggs and caregivers are exposed to less extreme abiotic regimes (Bose et al. 2019; Brown et al. 2020). In line with our predictions, the long-term field data revealed that egg-laying in *P. notatus* peaks during the neap tides. Furthermore, *P. notatus* courtship vocalizations, as captured on hydrophone arrays, also peak in intensity during the neap tides (Ogurek et al. 2025). Stronger tests of our hypothesis will require additional sampling of other species with lengthy time requirements for reproduction, and so in the future it would be a valuable to measure reproductive periodicity in other Batrachoidid species that may show similarly slow reproduction relative to the tidal cycles (e.g., *Halobatrachus didactylus*).

Species with relatively quick reproduction—i.e., without elaborate nest construction, parental care, and with either broadcast spawning or mass ovipositing, particularly of non-adhesive eggs—were all intertidal visitors, and these species sometimes reproduced during the spring tides, the neap tides or had no clear reproductive association to the

Table 1 Reproductive behaviours of intertidal-breeding fishes for which lunar synchrony and reproduction data were obtained from the literature survey (see Methods)

Lifestyle	Species name	Common name	Family	Lunar/tidal synchrony	Nest construction	Parental care[1]	Reproductive mode[2]	Spawning location	Example references
Visitors	*Ammodytes hexapterus*	Pacific sand lance	Ammodytidae	No association	No	No	Broadcast	Intertidal	(Robards et al. 1999)
	Atherinops affinis	Topsmelt silverside	Atherinopsidae	Spring tides	No	No	Oviposit adherent eggs	Intertidal	(Baumann and Conover 2011)[3]
	Clupea pallasii	Pacific herring	Clupeidae	Neap tides	No	No	Oviposit adherent eggs	Intertidal[4]	(Hay 1990)
	Colpichthys regis	False grunion	Atherinopsidae	Spring tides	No	No	Oviposit non-adherent eggs	Intertidal	(Russell et al. 1987)
	Fundulus grandis	Gulf killifish	Fundulidae	Spring tides	No	No	Oviposit non-adherent eggs	Intertidal	(Greeley and MacGregor III 1983; Able and Hata 1984)
	Fundulus heteroclitus	Mummichog	Fundulidae	Spring tides	No	No	Oviposit non-adherent eggs	Intertidal	(Taylor et al. 1979; Able and Hata 1984)
	Fundulus jenkinsi	Saltmarsh topminnow	Fundulidae	Spring tides	No	No	Oviposit non-adherent eggs	Intertidal	(Lang et al. 2012)
	Fundulus pulvereus	Bayou topminnow	Fundulidae	Spring tides	No	No	Oviposit adherent eggs	Intertidal	(Greeley 1984)
	Fundulus similis	Longnose killifish	Fundulidae	Spring tides	No	No	Oviposit non-adherent eggs	Spring tide water mark	(Greeley et al. 1986)
	Fundulus xenicus	Diamond killifish	Fundulidae	Spring tides	No	No	Oviposit adherent eggs	Intertidal	(Hastings and Yerger 1971)
	Galaxias maculatus	Common galaxias	Galaxiidae	Spring tides	No	No	Broadcast	Spring tide water mark[5]	(McDowall and Charteris 2006)
	Hypomesus pretiosus	Surf smelt	Osmeridae	No association	No	No	Broadcast	Intertidal	(Thompson 1936)
	Hypomesus pretiosus japonicus	Japanese surf smelt	Osmeridae	Spring tides	No	No	Broadcast	Spring tide water mark	(Hirose and Kawaguchi 1998)
	Leuresthes sardina	Gulf grunion	Atherinopsidae	Spring tides	yes[6]	No	Oviposit non-adherent eggs	Intertidal	(Thomson and Muench 1976)
	Leuresthes tenuis	California grunion	Atherinopsidae	Spring tides	Yes[6]	No	Oviposit non-adherent eggs	Intertidal	(Smyder and Martin 2002)
	Mallotus villosus	Capelin	Osmeridae	No association	No	No	Oviposit adherent eggs[7]	Intertidal	(Nakashima and Wheeler 2002; Martin et al. 2004)
	Menidia menidia	Atlantic silverside	Atherinopsidae	Spring tides	No	No	Oviposit adherent eggs	Intertidal	(Middaugh 1981)

Table 1 (continued)

Lifestyle	Species name	Common name	Family	Lunar/tidal synchrony	Nest construction	Parental care[1]	Reproductive mode[2]	Spawning location	Example references
	Takifugu niphobles	Grass puffer	Tetraodontidae	Spring tides	No	No	Oviposit adherent eggs	Intertidal	(Yamahira 1994)
Remainers	*Lipophrys pholis*	Shanny	Blenniidae	No association	Yes	Yes	Oviposit adherent eggs	Intertidal	(Carvalho 2017)
	Porichthys notatus	Plainfin midshipman	Batrachoididae	Neap tides	Yes	Yes	Oviposit adherent eggs	Intertidal	Present study
Tidepool emergers	*Bathygobius fuscus*	Dusky frillgoby	Gobiidae	No association	Yes	Yes	Oviposit adherent eggs	Intertidal	(Taru et al. 2002)
Skippers	*Alticus monochrus*	Combtooth blenny	Blenniidae	Spring tides	Yes	Yes	Oviposit adherent eggs	Supratidal	(Bhikajee et al. 2006)
	Boleophthalmus pectinirostris	Great blue spotted mudskipper	Oxudercidae	Neap tides[8]	Yes	Yes	Oviposit adherent eggs	Intertidal	(Wanshu et al. 2007; Wang et al. 2008; Hong et al. 2014)

[1] Parental care is only seen in the non-visitor species in this table. Parental care in the intertidal zone tends to be seen primarily in air-breathing species (Ishimatsu et al. 2018). Though, in some species like *Enophrys bison*, males guard their nests when submerged, but then leave to forage during low tide, before returning to their nests again (Demartini 1978).

[2] Broadcast spawning and non-adhesive eggs are only seen in species that do not provide parental care in this table.

[3] Baumann and Conover (2011) state that the reproductive behaviours of *A. affinis* are similar to those of *M. menidia*, but more directed studies of *A. affinis* intertidal reproduction would be valuable.

[4] Pacific herring spawn mostly in the subtidal zone, but a portion of eggs get laid in the intertidal zone during neap tides when wave action may be more amenable to laying eggs onto vegetation (Hay 1990).

[5] *G. maculatus* reproduces along the water line of tidal rivers as opposed to in the marine intertidal zone.

[6] Grunion females will bury their eggs in the sand in discrete balls. They dig a spot in the sand with their tails as a simple and rapidly formed nest that protects the young from predators and desiccation (Smyder and Martin 2002).

[7] Capelin may enter the intertidal zone in male-female duos or male-male-female trios, suggesting that some form of mate selection can occur ahead of time (Orbach et al. 2019). Such pre-spawning mate sorting behaviour ought to help relax any temporal constraints the species may experience while reproducing in the intertidal zone.

[8] Great blue spotted mudskippers have shown reproduction around the quarter moons in several studies, though peaks typically occur several days after the quarter moons (Wanshu et al. 2007; Wang et al. 2008; Hong et al. 2014).

lunar cycle. However, the majority of these species demonstrated strong associations with spring tides. By completing reproduction quickly, individuals can take advantage of certain times within the lunar cycle, such as spring tides, that provide unique benefits to the adults and/or their offspring. For example, the grunion, *L. tenuis*, is an intertidal visitor that conducts spawning runs during spring tides in which they emerge onto sandy beaches in the upper intertidal zone to bury and incubate their eggs in the sand (Smyder and Martin 2002). Spawning is relatively quick with individuals remaining out of the water for only a few minutes to release gametes, and with no apparent mate choice (Byrne and Avise 2009). Spawning of *L. tenuis* is strongly aligned with the spring tides presumably due to the benefits offspring receive from being deposited in warm, air-exposed locations, where they are protected from aquatic predators and are eventually dispersed out to sea by strong currents of subsequent spring tides (Ishimatsu et al. 2018). The grass puffer, *T. niphobles*, also rapidly spawns by broadcasting gametes during spring tides, but carefully chooses to spawn on days just before or just after the new or full moons to maximize the survival of embryos left at their preferred (upper) intertidal elevation (Yamahira 1996, 1997; Motohashi et al. 2010). On the other hand, the Pacific sand lance, *Ammodytes hexapterus*, is an intertidal visitor but does not show any strong reproductive association to the lunar cycle; large schools of fish aggregate together and deposit eggs in the sandy sediment with little opportunity for mate choice and not in any clear association with the spring or neap tides (Robards et al. 1999). It is possible that species such as the sand lance use some other cues such as temperature or wave action to coordinate their spawning. Indeed, some intertidal breeders, like the surf smelt, *Hypomesus pretiosus*, use certain non-lunar related cues to coordinate their reproduction, such as spawning at particular times of the day and on beach locations with specific physical characteristics (e.g., Hirose and Kawaguchi 1998; Quinn et al. 2012). Furthermore, it is possible that some populations/species will show weak or negligible associations with the lunar cycle simply if they spawn in narrow intertidal zones with very weak tidal excursions, where differences in oviposition elevation are not associated with meaningful changes in fitness. Interestingly, in the two species of skippers for which we found lunar periodicity data, *Alticus monochrus* showed reproductive peaks during spring tides while *Boleophthalmus pectinirostris* showed reproductive peaks during the neap tides. The data on *B. pectinirostris* reproduction show semilunar alignment with the quarter moons, but peaks tend to occur several days following the quarter moons (Wanshu et al. 2007; Wang et al. 2008; Hong et al. 2014). Since skippers are relatively unconstrained by the tidal cycle, we predicted that they would be more flexible in terms of reproductive timings across the lunar cycle. Skippers make for a particularly interesting group of fishes with which to investigate lunar synchrony because their air-breathing abilities render them far less reliant on submersion than other fishes as they progress through the stages of reproduction (mate searching, courtship, mate choice, mating, and oviposition), and so they are expected to face much weaker temporal constraints from the tidal cycle. In fact, the rockhopper blenny, *Andamia tetradactyla*, a skipper, not only spawns and lays eggs while nests are emergent from the water, but males also actively care for their eggs above the water line (Shimizu et al. 2006). Also, the Japanese mudskipper, *Periophthalmus modestus*, maintains air-filled nesting burrows within the intertidal zone so that their eggs develop in air even when the tide is high (Ishimatsu et al. 2007).

We urge researchers studying intertidal-breeding fishes to better characterize the relationship between reproduction and the lunar/tidal cycle in their focal species, across all categories of intertidal lifestyles (visitors, remainers, tidepool emergers, and skippers). We also acknowledge that the current preponderance of intertidal fish species found to spawn during the spring tides could be biased by the fact that it is easier for scientists to sample fish during the spring tides. Another bias probably emerges from our tendency to publish results only when there is a clear pattern of lunar synchrony in relation to conspicuous tidal events such as spring tides. This would necessarily exclude a great deal of information on species whose reproduction is not synchronous with the tides or remains overlooked during the neap tides. We call for researchers to assess the time durations needed for their species to successfully find, court, and choose partners, and then mate with them in comparison to the time windows afforded by the tidal cycle at their species' preferred spawning elevations. This information will help clarify whether there are limitations on when in the lunar month (i.e., spring tide vs. neap tide) intertidal reproduction can take place. Overall, we highlight how intertidal-breeding fishes are an understudied but informative group for understanding how fluctuating environmental conditions can shape biological rhythms and reproductive strategies.

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s00227-025-04639-y.

Acknowledgements We thank the Stz'uminus, Semiahmoo, and Skokomish First Nations for allowing our work to be conducted on their lands. We also thank many past and present members of the Aquatic Behavioural Ecology Lab at McMaster University and the Juanes Lab at the University of Victoria that helped with the data collection between 2009 and 2019. We thank Karen Martin and another anonymous reviewer for comments on the manuscript. Finally we are grateful to Dr. Rick Harbo for his continued support of our research and to Fisheries and Oceans Canada (DFO) for collection permits.

Author contributions AB and SB conceived of and designed the study. AB, KC, NB, and SB conducted the field sampling. RH conducted the literature survey. AB and NB conducted the statistical analyses. AB wrote the first draft of the manuscript with input from all co-authors.

Funding Open access funding provided by Swedish University of Agricultural Sciences.
This work was funded by Natural Sciences and Engineering Research Council of Canada (NSERC) Discovery and Accelerator grants to SB. Additional funding was provided to AB, KC, and NB in the form of scholarships from NSERC and from the Department of Psychology, Neuroscience, & Behaviour at McMaster University. AB is support by the Swedish Research Council (Vetenskapsrådet, DNR 2023–03866).

Data Availability Data and R scripts have been provided as Supplementary Material.

Declarations

Competing interests We declare no conflicting interests.

Ethical approval Our methods were reviewed and approved by the McMaster University Research Ethics Committee (AUPs 10 - 11 - 70, 18 - 01 - 02). This work conformed to the Canadian Council on Animal Care guidelines and was sanctioned by Fisheries and Oceans Canada.

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