

**REPRODUCTIVE BEHAVIOR OF *GOMPHOSUS VARIUS* (LABRIDAE)  
IN RELATION TO CURRENT PATTERNS AT A SPAWNING  
AGGREGATION SITE: IMPLICATIONS FOR LARVAL DISPERSAL**

**BY**

**KA'OHINANI H. KAWAHIGASHI**

**A thesis submitted in partial fulfillment of the  
requirements for the degree of**

**MASTER OF SCIENCE  
IN  
BIOLOGY**

**SUPERVISORY COMMITTEE  
DR. TERRY DONALDSON, CHAIR  
DR. ATSUSHI FUJIMURA  
DR. PATRICK COLIN**

**UNIVERSITY OF GUAM**

**DECEMBER 2021**

## **Abstract**

A spawning aggregation is an effective and common reproductive strategy among reef fish species, in which conspecific fish congregate for the sole purpose of mating. The bird wrasse, *Gomphosus varius* (Labridae), is a tropical reef fish that forms residential spawning aggregations at specific sites daily if local population densities are relatively high. In this study, the ecological and oceanographic characteristics of *G. varius* was analyzed to further inform reef fish spawning aggregations dynamics. Finger Reef, Apra Harbor, Guam is a multi-species spawning aggregation site for several wrasse species, *G. varius* included. This species utilizes a lek-like mating system while aggregating and a harem mating system when not. The objectives of this study were to understand the social and territorial dynamics of this wrasse's lek-like mating system, determine the optimal oceanographic and environmental conditions at a given site that promote spawning, and determine the dispersal patterns of pelagic *G. varius* eggs from this site. Since October 2018, field observations were conducted at Finger Reef to determine if *G. varius* spawning patterns correlate with tidal, lunar and seasonality patterns, aggression rate and population dynamics. Rates of courtship and aggression were positively correlated, indicating that male fish have higher reproductive success when more effort is put into defense of a mating territory. This species was most reproductively active around times of full moon and high tide. Using surface drifters, pelagic eggs and larvae were initially dispersed away from their natal site, and either self-recruit (rainy season) or drift into the main ocean current (dry season) depending on seasonality. Understanding the structure and function of spawning aggregations at the species level will provide a larger ecological context for mating systems of other fish species that aggregate to spawn and utilize similar reproductive methods

Keywords: *Labridae*, spawning aggregation, larval connectivity, reef fish, lek-like mating system

## **ACKNOWLEDGEMENTS**

To my thesis committee, Dr. Terry Donaldson, Dr. Atsushi Fujimura, and Dr. Patrick Colin for your time, guidance, and support. This material is based upon work supported by the National Science Foundation under Grant Number OIA-1457769. Any opinions, findings, and conclusions or recommendations expressed in this material are those of the author(s) and do not necessarily reflect the views of the National Science Foundation.

## TABLE OF CONTENTS

<i>Acknowledgments</i> .....	4
<i>List of Figures</i> .....	6
<i>List of Tables</i> .....	6
<i>Introduction</i> .....	7
Spawning aggregations and reef fish mating systems.....	7
Oceanographic conditions of spawning aggregations.....	12
Patterns of larvae dispersal.....	15
Aspects of the spawning of the study species <i>Gomphosus varius</i> .....	16
<i>Objectives</i> .....	18
<i>Methods</i> .....	20
Study Site & Species.....	20
Behavioral Observations.....	22
Oceanographic Data.....	23
Statistical Analyses.....	23
<i>Results</i> .....	24
Zero-inflated model for courtship rate.....	32
Non-parametric tests.....	32
Surface drifters.....	37
<i>Discussion</i> .....	39
Timing of spawning.....	39
Tidal and lunar patterns.....	39
Territoriality.....	40
Implications for commercially important fisheries.....	42
Behavioral changes after the onset of the COVID-19 pandemic .....	43
Implications for larval dispersal.....	43
Evidence for self-recruitment.....	44
<i>Conclusions</i> .....	45
<i>References</i> .....	47
<i>Appendix</i> .....	53

## LIST OF FIGURES

<i>Figure 1. Map of the study site. Guam, Mariana Islands.....</i>	<i>21</i>
<i>Figure 2. Study species: initial phase female and terminal male.....</i>	<i>22</i>
<i>Figure 3. Courtship rate frequency given as the total rate of courtship bouts per 30-minute observation period. Courtship rate data is right-skewed due to an excess zero-count observations; therefore, a count-data model was used. ....</i>	<i>24</i>
<i>Figure 4. Hanging rootograms of total courtship bouts per 30-minute observation.....</i>	<i>26</i>
<i>Figure 5. The number of 30-minute observations sessions by lunar age. ....</i>	<i>29</i>
<i>Figure 6. Frequency of spawning ascents.....</i>	<i>30</i>
<i>Figure 7. Gomphosus varius courtship bouts observed by time of day, courtship type, and lunar age .....</i>	<i>31</i>
<i>Figure 8. Mean rate of courtship bouts by lunar phase category with standard error .....</i>	<i>33</i>
<i>Figure 9 The number of courtship bouts vs the number of attacks by defending male per 30-minute observation .....</i>	<i>34</i>
<i>Figure 10. The number of courtship bouts vs the number of females present per 30-minute observation .....</i>	<i>35</i>
<i>Figure 11. The number of attacks by defending male vs the number of females present per 30-minute observation .....</i>	<i>36</i>
<i>Figure 12. Released drifter tracks .....</i>	<i>38</i>

## LIST OF TABLES

<i>Table 1. Common count-data models tested using AIC and BIC fitted to number of courtship bouts per 30-minute observation.....</i>	<i>25</i>
<i>Table 2. Study periods, lunar age, number of observation sessions, start time of observation sessions, sunrise and sunset times, and seasonality.....</i>	<i>28</i>

## INTRODUCTION

The reproductive strategies and mating systems of tropical reef fish are driven by a variety of ecological and physical processes. The courtship and spawning behaviors of fish are often defined by their specific mating systems, so studying a spawning aggregation at the species level provides the ecological context for mating systems as a whole. Physical parameters, such as tidal, lunar, and seasonal changes are locality specific drivers of spawning aggregations and uniquely affect reproductive behaviors and larvae dispersion. The successful dispersion of larvae from spawning aggregation sites is responsible for the structure of many reef fish populations. Further, accurate predictions of fish spawning patterns and larval dispersal are both crucial for monitoring fish populations and maintaining sustainable fisheries.

### *Spawning aggregations and reef fish mating systems*

A spawning aggregation is an effective mechanism for facilitating reproduction by many fish species. Domeier and Colin (1997) formally defined a spawning aggregation as “a group of conspecific fish gathered for the purposes of spawning, with fish densities or numbers significantly higher than those found in the area of aggregation during the non-reproductive periods.” So far, 243 reef fish species from 49 families are reported to form spawning aggregations (SCRFA 2020). Domeier and Colin (1997) also defined two types of spawning aggregations: transient and resident. Transient aggregating species tend to be larger-sized fishes, such as groupers (Epinephelidae) and snappers (Lutjanidae), that may travel longer distances to mate depending upon season, moon phase or other variables. Smaller species, such as many surgeonfishes (Acanthuridae), can also form transient spawning aggregations (Kiflawi 1998). Resident aggregating species tend to be smaller herbivores and omnivores, but not exclusively so, and spawning takes place along reefs daily (Domeier 2012). For both types of reproductive

strategies, the spawning aggregation is an important event comprised of intricate ecological and behavioral interactions. The study of spawning aggregation species presents an opportunity for understanding sexual selection, as it shapes a species evolution of life histories and behaviors (Molloy et al. 2012).

Spawning strategies can vary greatly between different locations for fish of the same species (Domeier and Colin 1997, Claydon 2004), further highlighting the need to understand these processes in different ecosystems. Because many commercially important fishes spawning in transient aggregations, often in locations where their numbers are diminished significantly by overfishing, reproducing populations may now be found only in remote areas that may be difficult to access. As a consequence, resident aggregating species are often used as a proxy to more easily examine the dynamics of spawning aggregation behavior. With their frequent and accessible spawning aggregations, they provide greater opportunity for study.

Current literature suggests that healthy aggregations are associated with healthy fisheries, therefore it is crucial to proactively manage spawning aggregations and their sites as they are useful indicators of ecosystem health (Sadovy de Mitcheson & Erisman 2012). Although fishing communities have known and relied upon the historical presence of spawning aggregations, the first scientific study of them was not reported until when Randall and Randall (1963) described a spawning aggregation of parrotfishes (Labridae: Scarinae) in the Virgin Islands. Many papers have been published since then, however fundamental questions still remain unanswered. Though fish spawning aggregations sites (FSAS) are disappearing in many areas globally due to overfishing, extirpated sites have the potential to recover after effective management implementation and rebuild existing fisheries (Chollett et al. 2020). FSAS, especially multi-species sites, are productivity hotspots and are disproportionately of ecological and



conservational importance because many fish species depend on these sites to produce the next generation (Erisman et al. 2015). High biodiversity helps regulate the size of local fish populations within coral reef communities (Carr et al. 2002), so conservation and proper management of these FSAS are beneficial both economically and ecologically.

Within spawning aggregations, increasingly complex mating systems, such as those that are promiscuous or in groups, harem, and lek-like, exist for many fish species. Strictly harem systems, such as that of *Chaetodon trifascialis* (Yabuta & Kawashima 1997), are characterized by the presence of a dominant male that defends a territory and up to several females within that territory (Colin & Bell 1991, Gladstone 1994). Robertson and Hoffman (1977) first hypothesized that harem systems resulted from continuing attachment of a female to a fixed and limiting resource (such as a foraging site), that enables a larger male to aggressively dominate her. Harem mating systems occur primarily in many species that do not form spawning aggregations, such as razorfish (Labridae; Victor 1987), hawkfish (Cirrhitidae; Donaldson 1999), and flounders (Bothidae; Carvalho et al. 2003). Alternatively, a lek-like mating system occurs in a number of species and it may be derived from a harem mating system. Loiselle & Barlow (1978) defined a lek, as applied to fishes, as a “temporary aggregation of sexually active males for reproduction.” There are four criteria for a lek mating system: (1) a spawning ground that is visited by females for the purpose of mating, (2) females choose a male amongst those gathered at the spawning ground, (3) the display sites occupied by males contain no resources required by the females, and (4) males have no role in parental care. Coral reef fishes that share some of these features have been described as “lek-like” (Moyer and Yogo 1982, Donaldson 1990, Gladstone 1994). In a lek-like system, as applied to fish in spawning aggregations, the limiting resource is a favorable spawning aggregation site that is defended temporarily by a male as he

attempts to attract and court females. A lek or lek-like mating system has reproductive benefits, as females can select their potential mate from up to several different males while males may have the opportunity to mate with several females (e.g., Gill et al. 2021). Lek-like mating has thus far been documented in nine families of teleost fishes including the Balistidae (Gladstone 1994), Cichlidae (McKaye 1983), Gadidae (Windle & Rose 2007), Labridae (Warner & Robertson 1978), Salmonidae (Figenschou et al. 2004), Sciaenidae (Saucier & Baltz 1993), Serranidae (Thresher 1984), Syngnathidae (Monteiro et al. 2017), and Synodontidae (Donaldson 1990).

There are three hypotheses that explain why males aggregate to form leks: the female-preference model, the hotshot model, and the hotspot model. Tests of each have been supported in some species but not others. The female-preference model states that males aggregate because females prefer to choose mates from clusters and this may reduce predation risks, reduce the costs of comparing mates, or because more fit males form successful leks (Bradbury 1981). In this model, males participate in leks when the costs of holding territories are outweighed by being preferred by females. The hotshot model states that females prefer a particular male, and in response, inferior males form mating territories around the competitively dominant “hot shot” male for the chance to intercept with a female intending to mate (Beehler and Foster 1988). A variation of that, in which the female accepts a dominant male but also group spawns with secondary males, was found in the lizardfish *Synodus dermatogenys* (Synodontidae) (Donaldson 1990). The hotspot model states that males form leks in areas that already have high concentrations of females (Bradbury and Gibson 1983), although in practice “high concentrations” is a relative term (see Donaldson 1990). Sherman (1999) hypothesized that males who lek together are kin (unlikely in marine fishes with pelagic larvae), or that there is a

hierarchical system. Males have higher probabilities of reproductive success in leks because group displays attract more females (Petrie et al. 1999).

Studying the mating systems of lekking species, as well as other mating systems in spawning aggregations, is important for understanding sexual selection because the females display strong preferences for a male with no obvious benefits in return. There are potential costs and benefits associated with lek and lek-like systems within mating or spawning aggregations. These mating systems are advantageous because they allow females to choose their mate, and different mates are in close proximity to each other for the female to compare, however this is not always the case. The most notable counterexample is the elephant seal, *Mirounga angustirostris*, in which leks are arenas for extremely intense competition among males, thus reducing the mate-choice availability (Andersson 1994). An advantage for mating in dense leks is that breeding in dense aggregations may increase mating rates. Wikelski et al. (1996) found that the reproductive success of the small marine iguana, *Amblyrhynchus cristatus* (Iguaidae), is directly related with lek size. Alternatively, one disadvantage for mating or spawning in close proximity to others is that sperm competition can be intense. This has been shown in colonial birds and fishes. In this scenario, individual males may fertilize significantly fewer eggs due to the presence of their neighbors (Brown and Bomberger Brown 1989, Jennings and Philipp 1992).

It is not uncommon that a single or few males will perform the majority of mating or spawning in these leks across all taxa (Arita and Kaneshiro, 1985, Durães et al. 2009, Emlen and Oring 1977, Kirkpatrick and Ryan 1991, McDonald and Potts 1994, Moyer and Yogo 1982; Gill et al. 2021). In fact, some studies show that one to two males will perform 70-90% of the spawning (Fiske et al. 1998, Cestari et al. 2016), indicating that there is an extremely skewed success among species that spawn in leks. Though this highly skewed success is common, it is

not well understood. In the orangefin wrasse, *Halichoeres melanochir* (Labridae), mating system, males set up continuous territories daily during breeding season, and centrally located lek territories tend to have more spawning success than peripheral territories (Moyer and Yogo 1982). Similarly, *G. varius* was found to have highly skewed success in the center outermost territory that was located prominently on the edge of the reef in an area exposed to currents that likely disperse eggs produced there (Gill et al. 2021). Furthermore, lek-like systems in birds, mammals, and fishes are often correlated with extreme sexual dichromatism (Warner 1975, Wiley 1973), which again holds true for *G. varius*, a sexually dichromatic and protogynous species. The lek-like mating systems of coral reef fishes are species-specific and have not been studied thoroughly.

If a spawning site is used by multiple species, there may be higher levels of interspecific aggression. Fiske et al. (1998) found that territory attendance, display frequency, and aggression rates were positively correlated with male mating success, with territory attendance being the most correlated. Intrasexual competition for leks of larger sizes results in higher display efforts for both dominant and non-dominant males (Cestari et al. 2016).

### ***Oceanographic conditions of spawning aggregations***

Oceanographic conditions are important factors in determining the timing and location of spawning aggregation formation. Fish spawn in tidal and current conditions that optimize the dispersal of their eggs and discourage egg predation (Robertson and Hoffman 1977). For many Indo-West Pacific resident aggregating species, spawning occurs after high tide during the outgoing flow (Bell and Colin 1986). Alternatively, should the spawning area be suitable and safe for larvae development, fish may spawn at times that optimize larvae retention (Johannes

1978). The timing of most spawning aggregation formation is generally predictable, as they occur at times and sites with tidal flows, non-tidal current speed, and/or direction that predictably differs from random sites (Colin 2012b). However, some species do not time their aggregations to coincide with tidal nor current regimes at all (Colin 1992).

Although it is largely assumed that spawning occurs at times that maximize larval distribution, such as during a heavy outgoing tide, spawning in aggregations that form in locations or times of weak current flow may result in large-scale mixing of the gamete cloud, and perhaps increase fertilization rates (Kiflawi et al. 1998). In locations where tidal currents are weak, time of day or light intensity may facilitate spawning behavior in labrids (Thresher 1984). The timing of spawning may depend on local conditions (Robertson and Hoffman 1977). Temporal segregation of spawning time within the same species may have evolved to reduce hybridization probability (Monteiro et al. 2016). Temporal spawning patterns can substantially differ within and between species at different locations, even at the same latitude (Colin 2012b, SCRFA 2020). Generally, reef fish spawning seasons are linked to temperature, winds, currents, and rainfall (Johannes 1978, Robertson 1991). There is, however, a dearth in the literature which assesses the role of temperature regimes in relation to spawning over broader geographic ranges (Colin 2012b). Recently, labrid assemblages traditionally consisting of temperate species were shown to shift to tropical and sub-tropical dominated species as sea surface temperatures increased (Parker 2019). For resident spawners found at lower latitudes and longer mating seasons, annual variability is often negligible (Choat 2012), however most tropical labrids rely more on tidal activity than their transient spawning counterparts (Thresher 1984). Within species, spawning patterns associated with tidal, diel, or lunar periodicity can also depend on location (Appeldoorn et. al 1994, Colin and Bell 1991, Domeier and Colin 1997).

Reef topography and complexity are hypothesized to be important factors in determining spawning location, as more complex reefs serve as protection from predation (Gladstone 2007, Sancho et al. 2000). Aggregations often form around a promontory, or reef projection, that fish might use as “signposts” that direct them where to spawn (Moyer 1989, Warner 1995, Kobara 2010). The continued use of a spawning aggregation site over time may be due to its traditional use over generations rather than its physical parameters (Warner 1988), which suggests that not all parts of the reef thought to promote spawning success are used at one time. The near shore oceanographic physics may interact with reef topography to reduce offshore larvae dispersion (Hamner & Largier 2012). Furthermore, non-aggregating (strictly harem and pair spawning) species generally have a greater range of spawning sites on a given reef than aggregating species, and resident aggregation sites tend to be more numerous than transient aggregations in a given area (Colin 2012b). Because harem, pair-spawning, and lek-like mating systems exist in resident and transient aggregations, it is important to identify these spawning sites and examine the oceanographic differences between species’ use.

Migration distance may be a constraint for many researchers studying species of reef fishes due to reef isolation or the aggregation occurring at an inhospitable depth (Kramer and Chapman 1999). The latter constraint is an issue for both transient and resident spawning species, especially as new species of mesophotic fishes are being discovered and simply cannot be studied in their environment as comprehensively as their shallow-water counterparts. To compensate for the lack of field-based behavioral studies of fishes in these poorly accessed areas, thorough behavioral analyses of more accessible species, coupled with phylogenetic methods for predicting relationships, are critical for understanding and predicting how species reproduce in aggregations that form in these environments.

### *Patterns of larvae dispersal*

Among reef fish species with external fertilization of eggs, most spawn either on the bottom (demersal) or in open water (pelagic). Most species with spawning aggregations are pelagic spawners, although some (rabbitfishes - Siganidae, many triggerfishes - Balistidae), spawn demersally (Juario et al. 1985, Gladstone 1994, Kawase 1998). Pelagic eggs are positively buoyant and may be kept out of range from potential benthic predators while drifting in the current (Colin 2012b). Bluehead wrasse (*Thalassoma bifasciatum*, Labridae) tend to group spawn at sites that optimize off-reef transport of pelagic eggs (Hensley et al. 1994), which may imply that this labrid species relies on oceanographic conditions that disperse larvae.

The pelagic larval stage of many fishes is assumed to be a dispersal mechanism (Barlow 1981). The distance traveled by pelagic larvae drifting in the current invariably exceeds that of adults, and often this is the only life history stage in reef fishes that can cross water barriers. Therefore, it is crucial that the successful dispersion of larvae is achieved because it is primarily responsible for the structure of many reef fish populations (Hamner and Largier 2012). There are three hypotheses that share the assumption that spawning sites are selected because of the significant water movement passing over a site: to reduce near-reef egg predation (Johannes 1978), to maximize dispersal (Barlow 1981), or to increase the probability that larvae will settle in food patches (Doherty et al. 1985).

Self-recruitment was previously assumed to be rare because of the opportunity for ocean currents to distribute larvae, however, fish larvae have the ability to return to their natal reef should the conditions be optimal for growth (Jones et al., 1999), or if genetic barriers exist between subpopulations (Jackson et al. 2014). For island reef fish populations, dispersal patterns that maximize larvae retention may be typical of many resident spawning aggregation species in

order to sustain their local population, especially if the species is endemic and/or the island is geographically isolated. Eddies that form at an island's down-current end induce circulation that may help in retaining eggs and larvae nearby (Hamner and Hauri 1981). Heppell et al. (2009) released current-tracking drifters at a Nassau grouper spawning aggregation site in the Cayman Islands and found those released on the night of spawning showed eddy formation tending to retain eggs and larvae near the aggregation site. Hamner et al. (2007) found that in the first few days, tidal currents and eddies are important in both initial transport away from the reef and allow for retention of larvae relatively close to their natal location, even bringing a small number of early larvae to return back to their initial spawning sites. Eggs from some species of parrotfish and surgeonfish on a forereef in Palau were exported alongshore after initial transport by tidal currents off the reef.

### ***Aspects of the spawning of the study species *Gomphosus varius****

*Gomphosus varius* (Labridae) is a common tropical wrasse (Labridae) on Indo-West Pacific reefs, with a widespread geographic range from Cocos-Keeling to the Hawaiian, Marquesan, and Tuamotu Islands, Japan to Rowley Shoals, Lord Howe, and Rapa Islands, as well as throughout Micronesia (Myers 1999). In the Indian Ocean, it is replaced by *Gomphosus caeruleus* (Myers 1999). Considering that isolated or geographically different populations may have different spawning aspects for fish of the same species (Claydon 2004), it is important to consider the local geographic and oceanographic differences when examining these mating systems.

There are seven published studies concerning the reproduction of *Gomphosus spp.* At Enewetak Atoll in the Marshall Islands, *G. varius* was reported to pair-spawn in a lek-like



mating system (Colin and Bell 1991) with spawning occurring on 20 days out of the 28-day lunar month. It was increasingly frequent before and during full moon, peaked at high tide, and occurred for the duration of the day. Boyle and Cox (2009) and Tricas and Boyle (2014) recorded acoustic signaling related to courtship and spawning behavior from male *G. varius* in Hawaii, which were emitted at a lower frequency and narrower sound band than the sympatric species, *Thalassoma duperrey* (Labridae), with whom it shares its mating site with. Kuwamura et al. (2016) reported for Okinawa (sub-tropical) that the spawning of *G. varius* occurred after high tide on days with morning high tides while on days with high tide later in the day, spawning occurred before high tide. In Guam, where the present study was done, Gill et al. (2021) found that spawning by *G. varius* occurred daily within the outermost central mating territory at a spawning aggregation site. Spawning was highly skewed in terms of reproductive success, and that planktivorous fish predation on released *G. varius* eggs increased linearly with spawning frequency.

Victor (1986) examined the planktonic larval stage of 105 species of Pacific and Atlantic labrids using otolith increment length analyses on mostly juvenile fishes and found the mean larval duration for *G. varius* collected from Palau was 51.6 days (SD=6.4) based on daily otolith increment measurements and settlement markings from species while those from Hawaii was 65.3 days (n=3, SD=5.8). Victor (1986) also indicated that *G. varius* has a relatively long larval life and extensive range compared to other labrids, and that geographical variation influences larval duration period (i.e. generally, Hawaiian locality had significantly longer larval periods than conspecifics in the Western Pacific). For other species in the genus, Desvignes et al. (2017) found at Reunion Island (tropical western Indian Ocean) that *Gomphosus caeruleus* alternated

between harem and lek-like mating, and its spawning period was closely tied to the full moon phase of the lunar cycle.

## **OBJECTIVES**

In this study, I used *Gomphosus varius* as a model species for analyzing some of the ecological characteristics of reef fish spawning aggregations. *Gomphosus varius* can form resident spawning aggregations if local population densities are relatively high (Gill et al. 2021). The objectives of this study were to (1) understand the social and territorial dynamics of its lek-like mating system, (2) determine the oceanographic and environmental conditions at a given site associated with spawning at an aggregation site, and (3) determine the dispersal patterns of pelagic *G. varius* eggs from this site.

Fiske et al. (1998) found that territory attendance, display frequency, and aggression rates were positively correlated with male mating success in a meta-analysis of lekking species. In this study, I was interested if a male who invests more time into defending his territory will be rewarded with more mating opportunities. On the other hand, a male that is investing excessive time into territory defense may allow other males to have the opportunity to court and spawn instead. With this information, it was hypothesized that rates of spawning and mating territory defense would be positively linearly correlated.

Fish spawning patterns of the family Labridae are largely related to ebb (falling) tide and time of the day (Claydon 2004; Choat 2012; Claydon et al. 2014), however interspecific variation is dependent upon population locality. In the sub-tropical climate of Okinawa, *G. varius* was found to time spawning either before or after high tide, depending on lunar phase (Kuwamura et al. 2016). At Reunion Island *G. caeruleus* spawning is closely tied to the waxing gibbous phase

of the lunar cycle (Desvignes et al. 2017). Based upon these findings, I predicted that peak spawning would coincide with the high tide, full moon, early morning hours, and show no patterns of seasonality.

While there is the opportunity for the eggs to be transported passively by ocean currents, their movement in the water column is first determined by the currents present at their natal reef. I predicted that *G. varius* eggs would be distributed away from Finger Reef but retained inside Apra Harbor for the first 24 hours after spawning takes place. Apra harbor is a largely enclosed, protected embayment and probably has high retention rates for water masses. Initial eddy formation and tidal currents after spawning are important oceanographic conditions that can facilitate larvae retention at the aggregation site (Hamner et al. 2007; Hamner & Hauri 1981).

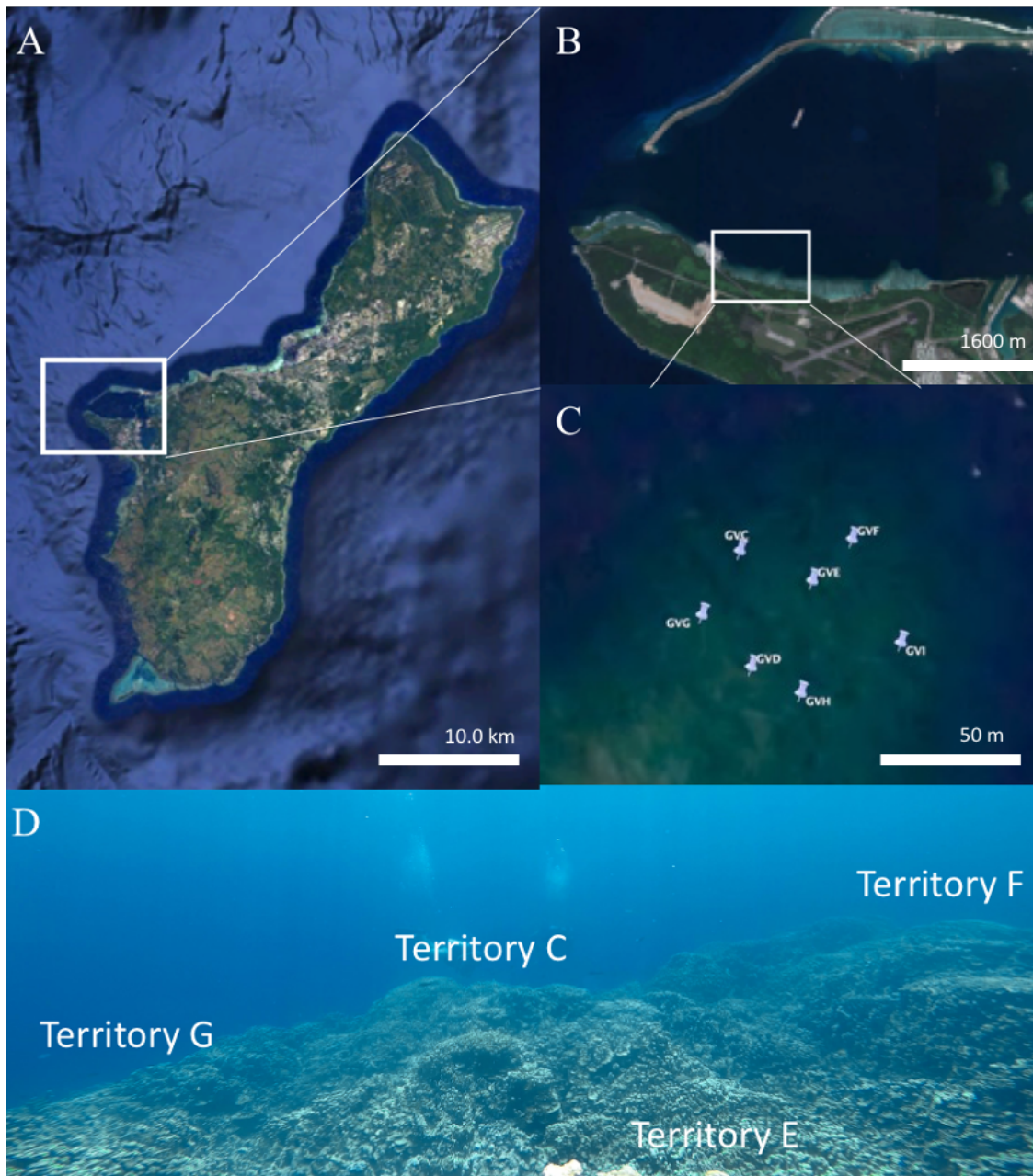
Alternatively, the mean larval duration period for *G. varius* is relatively long and may have extensive range, however geographical variation can influence larval duration period for members of the same species. Victory (1986) found that the mean larval duration for *G. varius* otoliths collected in Hawaii was 13.5 days longer than *G. varius* from Palau in the Western Pacific, which is consistent with their finding that fish populations from Hawaii had significantly longer larval durations than their conspecifics in the Western Pacific. Similarly, levels of larvae retention in corals and reef fish were found to be largely independent of pelagic larval duration, but rather were influenced by geographic setting, such as the geographic isolation and spacing of reefs (Jones et al. 2009). Larvae duration and retention are largely influenced by the local geographic factors that influence an ecosystem, and thus, conspecifics in different regions may have dissimilar larval behavior. Because of this intraspecific variation, it is important to study a species' larval dispersal with regards to local oceanographic characteristics.

## METHODS

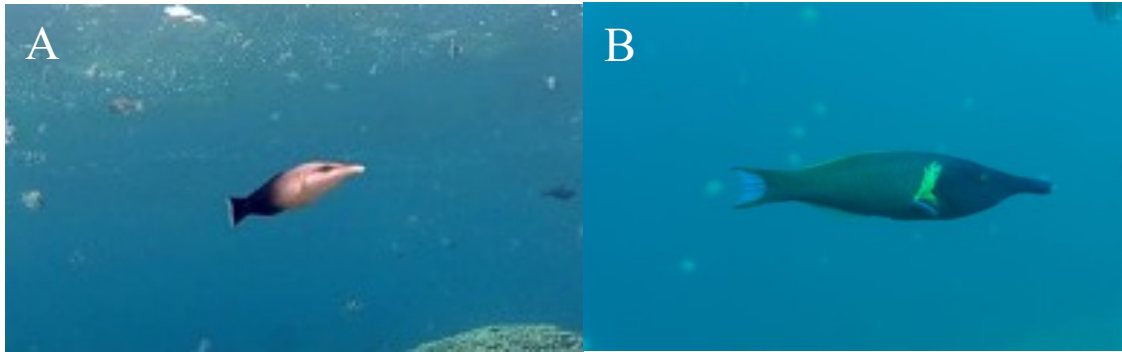
### *Study Site & Species*

Apra Harbor is located on the western coast of Guam, the largest island of the Mariana Archipelago. Finger Reef (13° 26' 41.136" N, 144° 38' 11.2626" E) is a popular scuba diving and snorkeling destination located on the southern end of Apra Harbor (Fig. 1), which is also part of a strategic U.S. naval base. Tourist divers and snorkelers regularly feed fishes on the reefs there, making them relatively more approachable to humans than on other reefs around Guam. The benthic composition of Finger Reef consists predominantly of *Porites rus* coral colonies. Additionally, Orote Point (Fig. 1) is located at the mouth of Apra Harbor and approximately 1.54 km ENE of Finger Reef and a site there was used to analyze surface currents with respect to larval drift. Guam experiences mixed semi-diurnal tides and fringing coral reefs may be exposed during times of low tide (Péguignet et al. 2011).

*Gomphosus varius* can be identified by its elongated snout in the adult form. Females are generally smaller with black and white coloration, while males are slightly larger and display bright green and blue coloration (Fig. 2). *Gomphosus varius* courts and spawns at Finger Reef using a lek-like mating system within this spawning aggregation, although not all males forming mating territories there actually mate (Gill et al. 2021). This species also exhibits protogynous hermaphroditism, meaning that individuals are born as initial phase (IP) females and may transition into terminal phase (TP) males if sex ratios or social conditions facilitate a sex change (Myers 1999, Avise and Mank 2009).



**Figure 1.** Map of study site. Guam, Mariana Islands (a). Apra Harbor (b), Finger Reef ( $13^{\circ} 26' 41.136''$  N,  $144^{\circ} 38' 11.2626''$  E) is along the southern shore of Apra Harbor and marked by the white box (b). Orote Point is located at the mouth of Apra Harbor and is marked by a white circle (b). Seven tagged temporary mating territories at Finger Reef using GPS (c). Territories G, C, E, and F (d). GoogleEarth Image © DigitalGlobe.



**Figure 2.** Study species: initial phase female (a) and terminal phase male (b) *Gomphosus varius* at Finger Reef, Apra Harbor, Guam.

### ***Behavioral Observations***

The locations of six temporary male mating territories within the study site were determined previously based upon initial observations of fish behavior (i.e., a male *G. varius* displaying courtship behavior around a coral head). These locations were tagged by affixing color-coded zip ties to the bottom (Fig. 1c). For each observation, a weighted stationary video camera was set up on the bottom (depth ranging 1-3 m) facing the mating territory to record behavior and validate in-field observations. A total of three stationary cameras were used to record multiple territories at once. One camera surveyed up to four mating territories at random *in situ* per day while the remaining two cameras recorded behaviors occurring at other randomly selected territories at the same time. Up to 12 replicates of 30-minute surveys were recorded per observation day. Visual observations were made subsequently if there was at least one male occupying the territory. For each observation period, the following data were recorded: the number of courtship attempts, the number of successful spawning events, the time of day and

tidal heights recorded for each courtship attempt and spawning event, the sex of the individual aborting each courtship attempt, and the number of attacks on other fish by the defending male.

### ***Oceanographic Data***

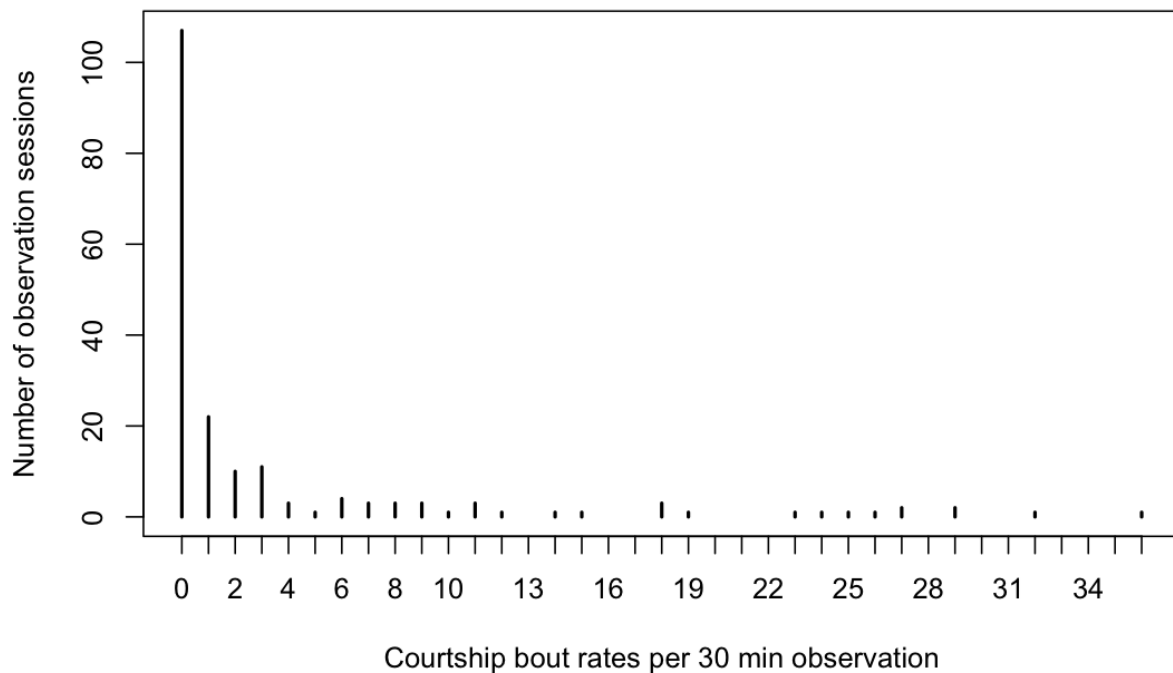
Tidal heights, lunar stage, and lunar age (days after new moon) were obtained from the NOAA 1630000 Apra Harbor Station, Guam (data publicly accessed from NOAA Tides and Currents). Seasonality (i.e. dry season in the winter/spring months, rainy season in the autumn/summer months) was also recorded. Spawning activity was compared with each of these parameters to determine which has the greatest influence on peak spawning time. To model the patterns of egg dispersal, four Pacific Gyre Microstar Lagrangian Drifters were released for a total of 32 replications at similar times and tidal heights relative to spawning frequency. The drifter's drogue is 1m deep, and is propelled by the surface current, rather than wind. Two drifters were released at high, low, ebb, and flood tides of four lunar phase categories: lunar age 0-7 (new/crescent waxing), 8-14 (first quarter/waxing gibbous), 15-21 (full/waning gibbous), and 22-28 (last quarter/waning crescent). GPS coordinates were transmitted every thirty minutes for approximately 24 hours for each drifter release replication, then retrieved the next day. The GPS points from each drifter release replication were plotted on a map of western Guam. ArcGIS was used to plot the range and area of short term egg dispersal from different spawning times.

### ***Statistical Analyses***

Courtship rate data had an excess of zeros, was right-skewed, and did not pass the Shapiro-Wilks test for normality (Fig. 3). A two part zero-inflated negative binomial hurdle model was used to analyze courtship rate data. This is the same model used in a similar study by

Gill et al. (2021). Five other regression models were compared using the Akaike information criterion (AIC) and the Bayesian information criterion (BIC) to ensure the best fitting model for this type of count data: General linear model (GLM) Poisson, GLM negative binomial, zero-inflated Poisson, zero-inflated negative binomial, and zero-inflated hurdle (Table 2.) The zero-inflated hurdle negative binomial had the lowest AIC and BIC values, as well as a hanging rootogram with the least deviations of statistical values below the reference line (Fig. 4).

Data was further analyzed using non-parametric Spearman rank coefficient tests to determine the relationships between courtship, aggression, and population density. A Kruskal-Wallis non-parametric test was also performed on courtship rates between lunar age groups.

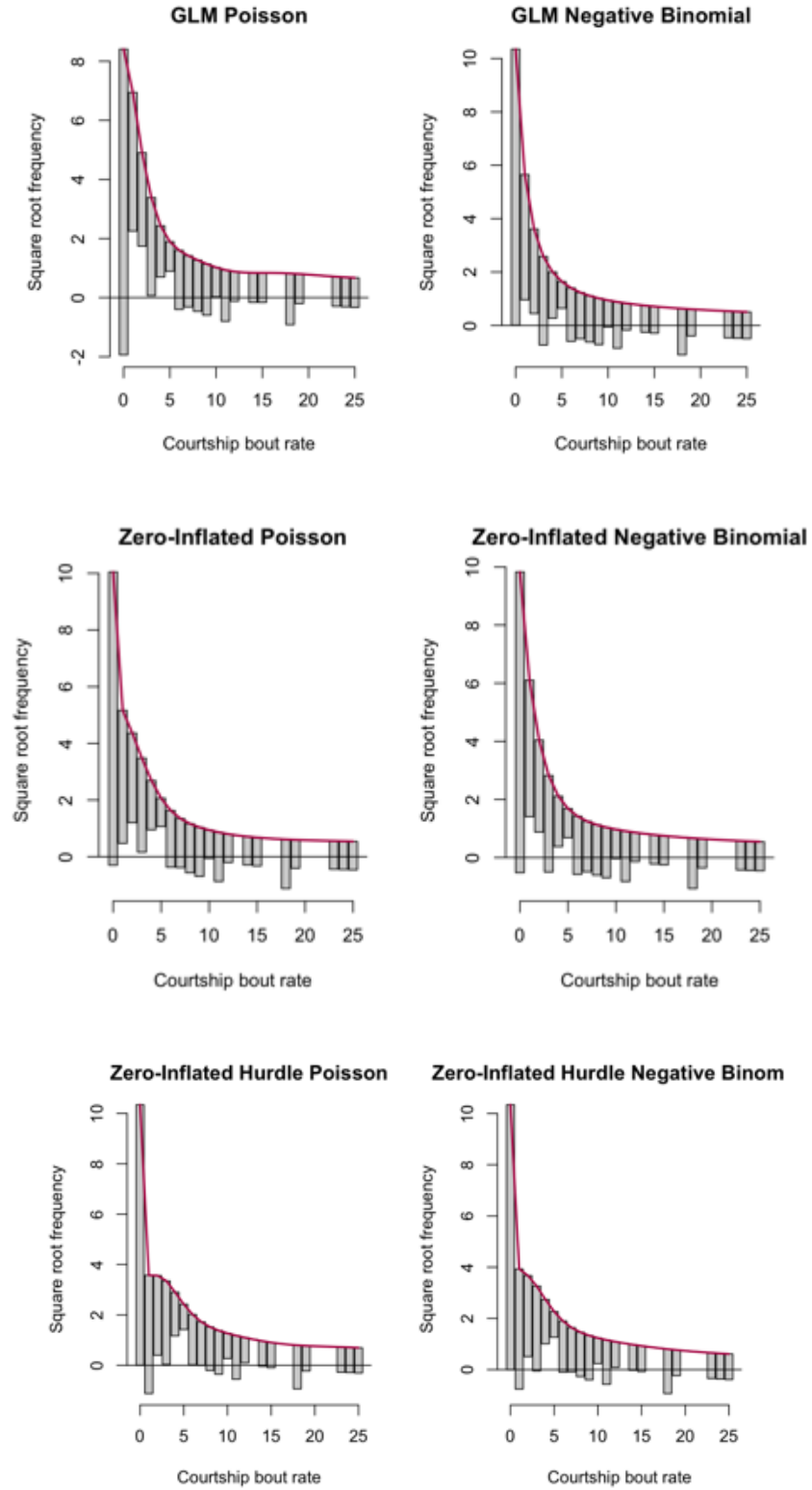


**Figure 3.** Courtship rate frequency given as the total rate of courtship bouts per 30-minute observation period. Courtship rate data is right-skewed due to an excess zero-count observations; therefore, a count-data model was used.



<b>Model</b>	<b>AIC</b>	<b>BIC</b>
<b>GLM Poisson</b>	631.4725	683.2556
<b>GLM Negative Binomial</b>	567.4219	619.205
<b>Zero-Inflated Poisson</b>	603.7044	681.379
<b>Zero-Inflated Negative Binomial</b>	574.251	655.162
<b>Zero-Inflated Hurdle</b>	477.5275	581.0936
<b>Zero-Inflated Hurdle Negative Binomial</b>	<b>471.8063</b>	<b>578.6089</b>

**Table 1.** Common count-data models tested using AIC and BIC fitted to number of courtship bouts per 30-minute observation. The zero-inflated hurdle negative binomial model has the lowest AIC and BIC and is therefore the best fitted model for analysis.



**Figure 4.** Hanging rootograms of total courtship bouts per 30-minute observation. Six models were considered as they were commonly used for count data with excess zeros.

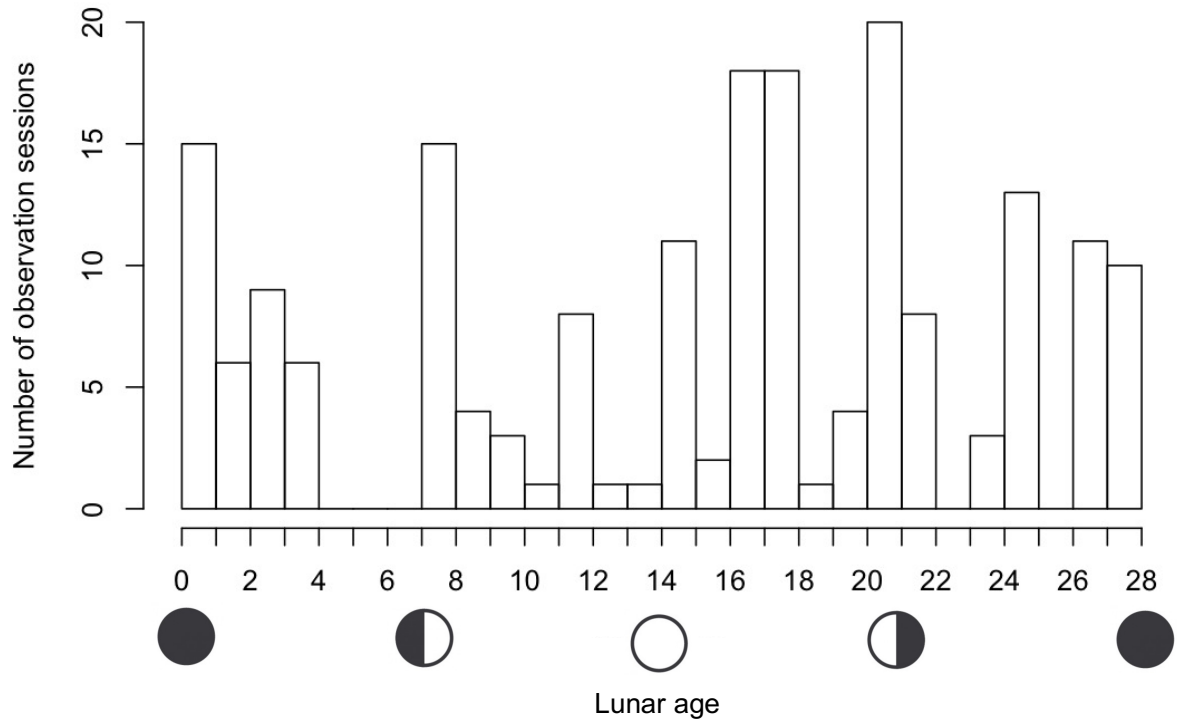
## RESULTS

Over the course of this study, 194 observation surveys were conducted at the field site (Table 2). At least one observation was made on lunar days 0-3 and 8-28 (Table 2). Figure 5 indicates the frequency of surveys for each lunar age including surveys that have no spawning behavior recorded. Tidal level was assigned for each spawning ascent (Fig. 6). Spawning behavior was most frequently observed at higher tidal levels, and lowest at low and medium tidal levels (Fig. 6). My results indicate that spawning and courtship are concentrated around times of first high tide, which shift in time of day with lunar age (Fig. 7), similar to the pattern of a monthly tidal chart. Unsuccessful courtship attempts (female and male interrupted events) tended to appear before and after peak clusters of successful spawns daily (Fig. 7). Territory C is the outermost central mating territory and, historically, males defending and courting in it have had the most reproductive success (Gill et al. 2021). My results indicated that the male occupying Territory C contributed 90.5% of the total courtship bouts, 96.8% of successful spawns, and 83.9% of aggression attempts for the duration of the study. This confirms that this mating territory is the most active and attractive spawning site within the study area. Territory C also accounted for 59.4% of observed females, and 30.4% of observed males throughout the study, indicating that other mating territories were occupied and that females at least considered these other territories in the area.

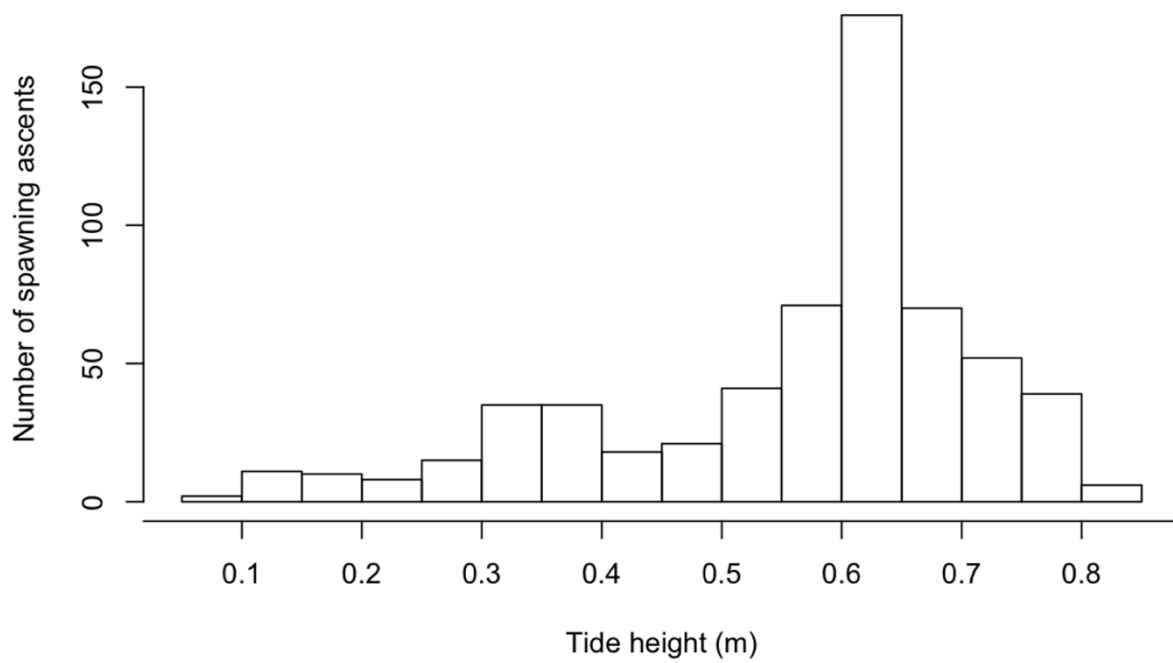
<b>Study Period</b>	<b>Lunar age (days)</b>	<b>No. of surveys</b>	<b>Start time of observation sessions (h)</b>	<b>Sunrise time (h)</b>	<b>Sunset time (h)</b>	<b>Seasonality</b>
Oct. 15 - Nov. 19, 2018	20, 25, 27	9	0956-1355	0611-0621	1750-1802	Rainy
Jan. 31 - May 2, 2019	8, 10, 15, 21 – 28	35	1016-1406	0559-0648	1820-1844	Dry
June 06 - Aug. 28, 2019	0 – 4, 8, 12, 15 – 28	89	1008-1444	0552-0609	1833-1852	Rainy
Oct. 02 - Nov. 20, 2019	4, 22	10	1238-1553	0610-0622	1750-1810	Rainy
Feb. 26 - Apr. 14, 2020	0 – 2, 17, 21	30	0854-1329	0608-0641	1828-1833	Dry
July 02 - Aug. 4, 2020	9, 11, 15	16	1052-1224	0557-0606	1847-1852	Rainy

**Table 2.** Study periods, lunar age, number of observation sessions, start time of observation

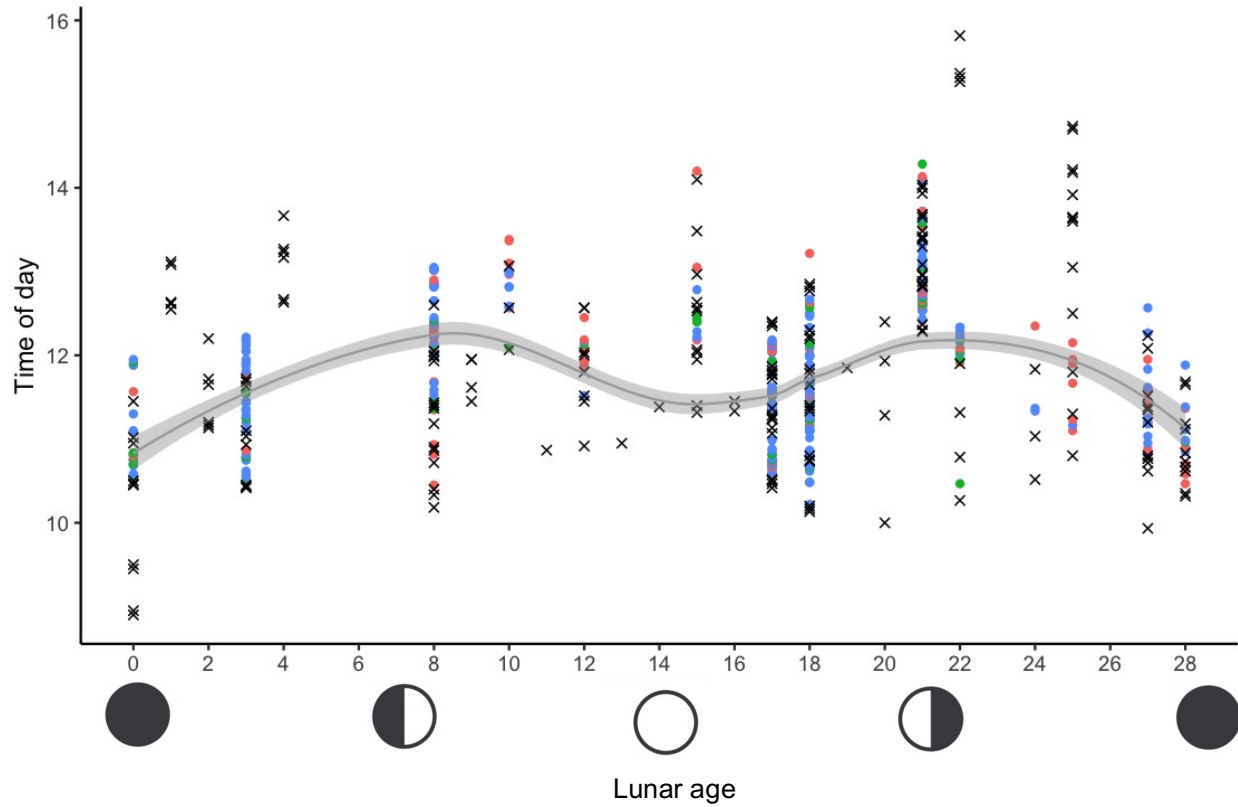
sessions, sunrise and sunset times, sea surface temperature, and tidal velocity range. Study period is noted approximately by local seasons (dry winter/spring months, rainy summer/fall months), and observation sessions were made somewhat continuously over a two-year period (weather and boat availability permitting). The duration of observation sessions was 30 minutes each.



**Figure 5.** The number of 30-minute observations sessions by lunar age. n=194.



**Figure 6.** Frequency of spawning ascents (n=610) in relation to tidal height water levels (NOAA Water Levels – Station ID 1630000 Apra Harbor).



**Figure 7.** *Gomphosus varius* courtship bouts observed by time of day, courtship type, and lunar age. Female interrupted (red), male interrupted (green), spawning success (blue), observation session (x), mean time spawning (black line), standard error (grey). Each observation session is 30 minutes.

### *Zero-inflated model for courtship rate*

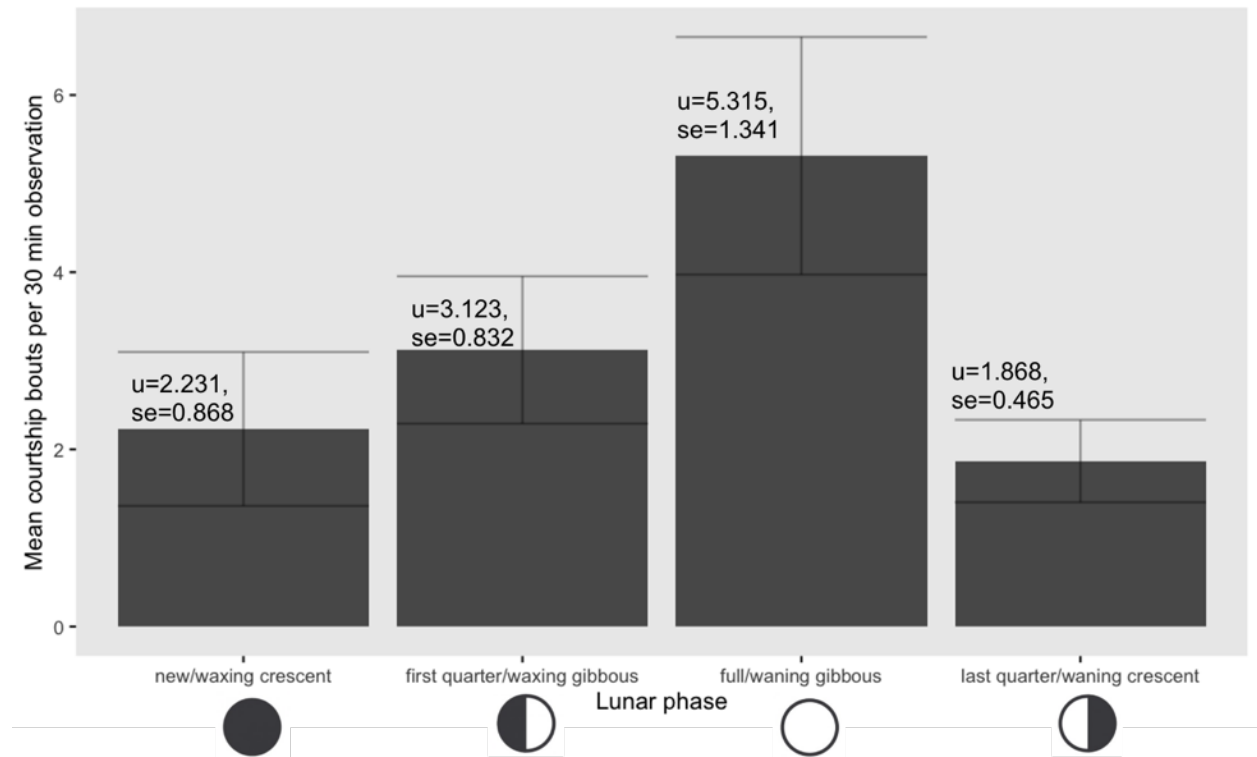
Aggression rate is a significant predictor for courtship rate for both non-zero (z-statistic=4.248,  $p<0.05$ ) and zero-count (z-statistic=3.210,  $p<0.05$ ) model outputs. The number of males present was not statistically significant for both model outputs (z-statistic=1.702,  $p=0.089$  for non-zero counts, z-statistic=1.865,  $p=0.062$  for zero-counts). The number of females was not a significant predictor for non-zero or zero-counts, and there may be a certain threshold of females that must be present for any spawning to occur at all. Lunar phase, tide direction, and seasonality were not statistically relevant to either model outputs.

### *Non-parametric tests*

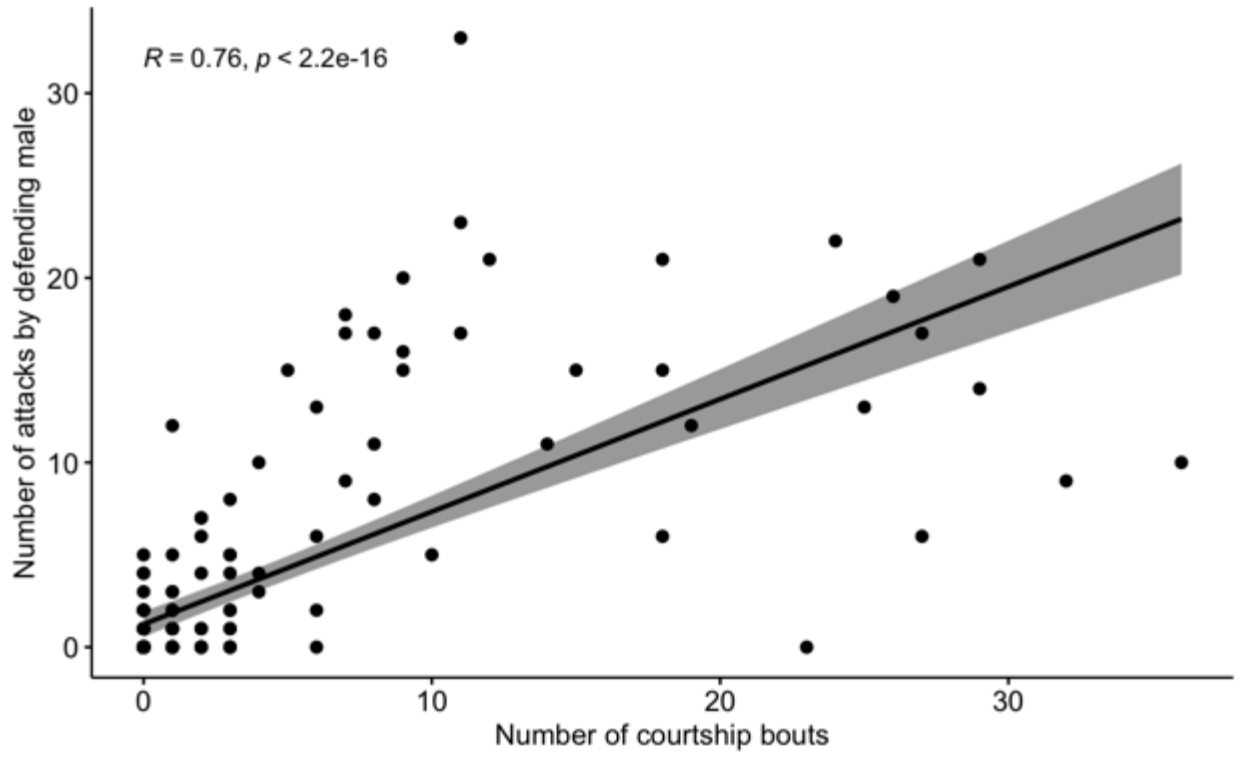
Mean courtship rate per 30-minute observation for all territories was highest during the full/waning gibbous lunar phase (mean=5.315, se=1.341), followed by first quarter/waxing gibbous (mean=3.123, se=0.832) and new/waxing crescent (mean=2.231, se=0.868), and lowest during last quarter/waning crescent (mean=1.868, se=0.465) (Fig. 8). Mean courtship rates among lunar age categories were not significantly different, using a Kruskal-Wallis test. Data was further analyzed using non-parametric Spearman rank coefficient tests. Courtship rate was positively correlated with aggression rate ( $R=0.76$ ,  $p<0.05$ ) indicating that male fish have higher reproductive success when more effort is put into defense of a mating territory (Fig. 9). Similarly, courtship rate was positively correlated with the number of females present at a mating territory ( $R=0.65$ ,  $p<0.05$ ) indicating that more spawning occurs when there are more females present with which to mate (Fig. 10). However, the zero-inflated hurdle model did not suggest that there was a significant relationship between courtship rate and the number of females (z-statistic=0.701,  $p>0.05$ ). Aggression rate was also positively related to the number of



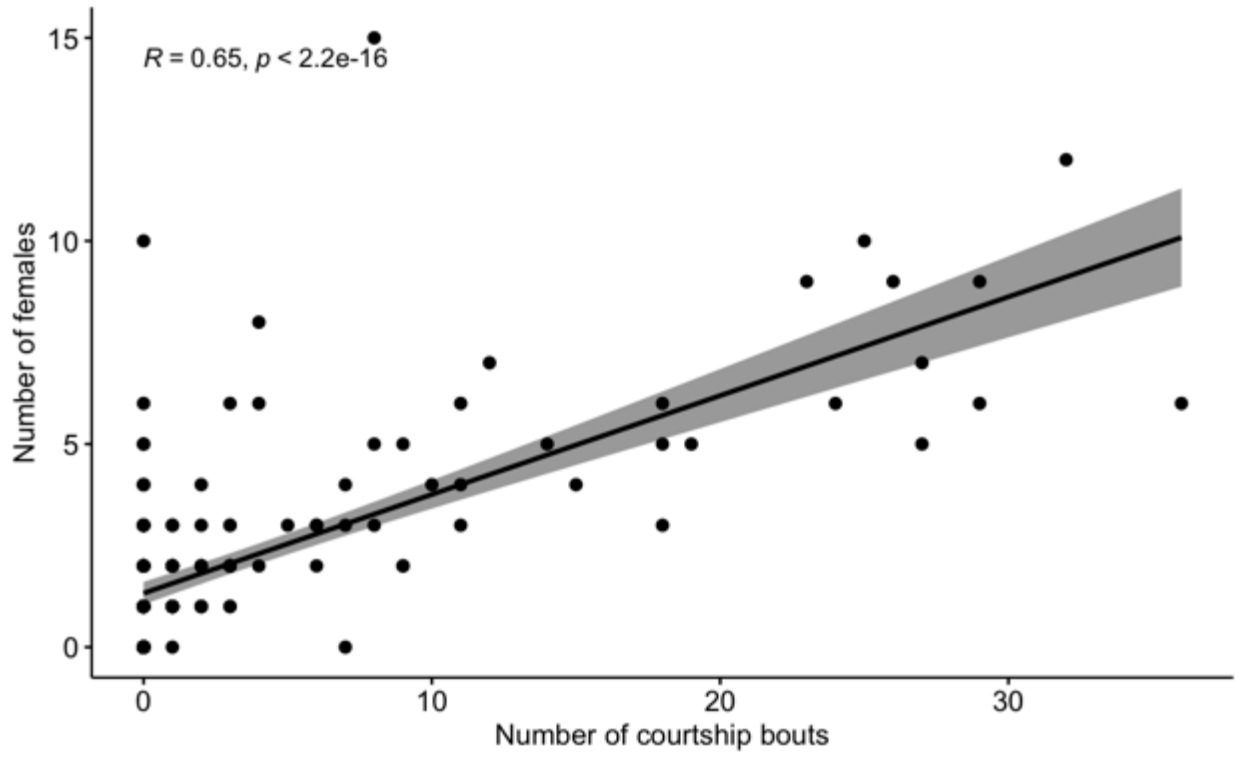
females ( $R=0.52$ ,  $p<0.05$ ) implying that males must defend more when there are more females in their mating territory (Fig. 11).



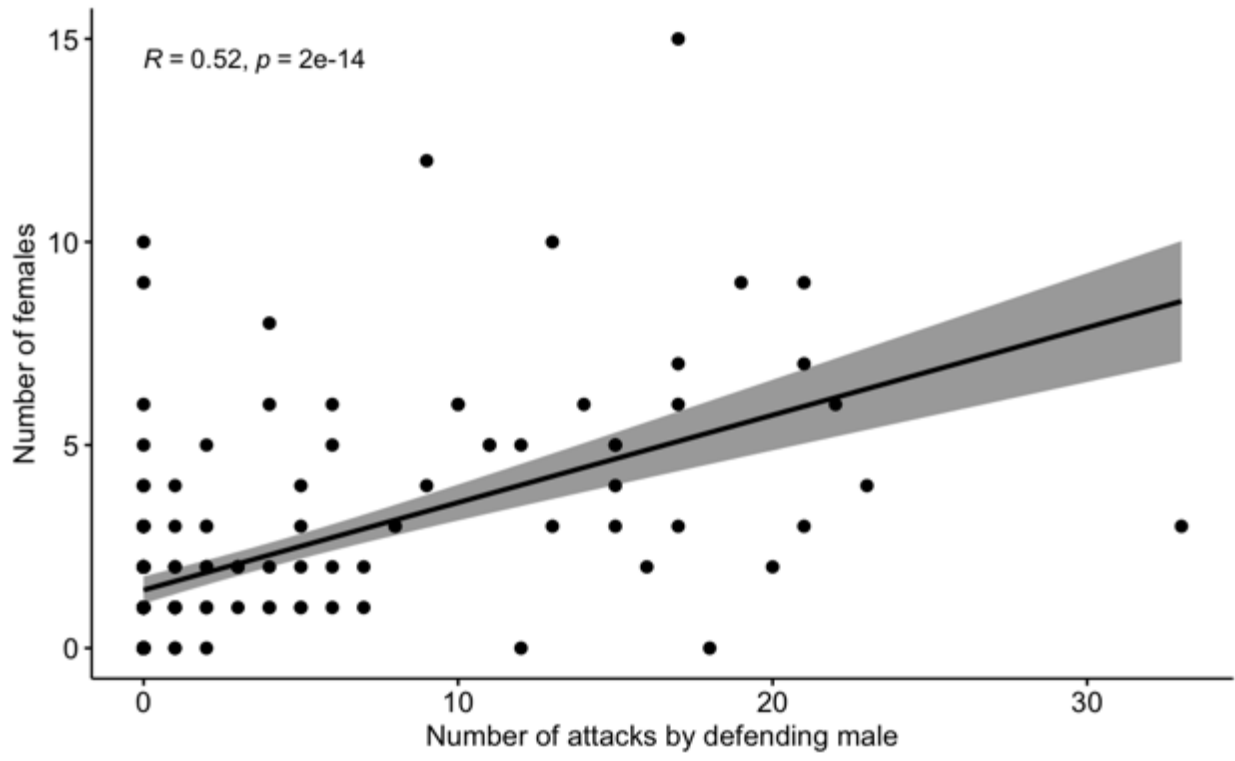
**Figure 8.** Mean rate of courtship bouts by lunar phase category with standard error. Full and waning gibbous have the highest courtship rate by lunar phase. First and last quarter, new, and full moon phases are reported on their specific day (NOAA Water Levels – Station ID 1630000 Apra Harbor).



**Figure 9.** The number of courtship bouts vs the number of attacks by defending male per 30-minute observation. (Spearman rank correlation,  $\rho = 0.7571975$ .)



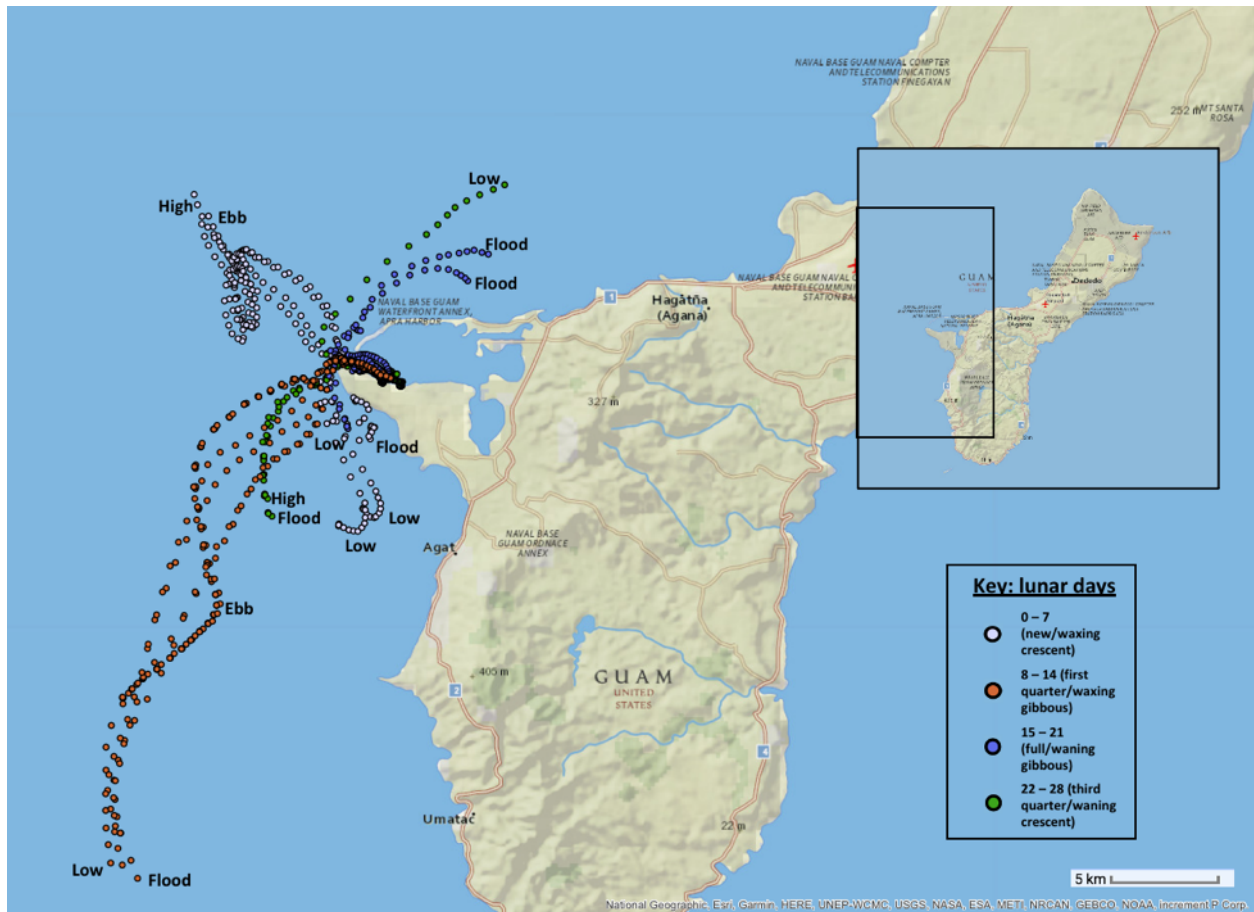
**Figure 10.** The number of courtship bouts vs the number of females present per 30-minute observation. (Spearman rank correlation,  $\rho = 0.6503636$ .)



**Figure 11.** The number of attacks by defending males vs the number of females present per 30-minute observation. (Spearman rank correlation,  $\rho = 0.5201386$ .)

### *Surface drifters*

Drifters released at high and ebb tides during the 0-7 (new/waxing crescent) lunar phase traveled northwest directly out of the mouth of the harbor, then south during the morning tidal change, and returned on a northwest track before being retrieved. Drifters released during low and flood phases traveled southeast along the coastline (Fig. 12). All drifters released in the 8-14 (first quarter/waxing gibbous) lunar phase drifted immediately into the current line due south on the western side of Guam (Fig. 12). These drifters traveled the furthest distance from the natal reef and were released during typical dry season conditions in late February, which is when there are increased trade winds and wind-driven forces. Drifters meant to be released during high tide were released at ebb tide instead because of difficulties in locating the drifters released previously that day. During the 15-21 (full/waning gibbous) lunar phase, drifters released at flood tide exited Apra Harbor and traveled along the northern coast of the harbor, and one low tide drifter traveled south but remained close to the harbor entrance (Fig. 12). The remaining drifters traveled too close to shore and became lodged on the beach or reef. The wind and waves were very calm during these days, likely slowing the water movement so much that these drifters became trapped in the waves breaking along shore. Drifters released at high and flood tides during the 22-28 (last quarter/waning crescent) lunar phase traveled south, although not as far as category 8-14 (Fig. 12). Drifters released at low tide traveled northward and further than those drifters released during the full/waning gibbous phase (Fig. 12). Overall, drifters released during typical dry season conditions (0-7 and 8-14) further or integrated into the main ocean current; drifters released during typical rainy season (15-21, 22-28) remained close to the coast and may be indicative of larvae retention.



**Figure 12.** Released drifter tracks. Each path is labeled with the tide at Finger Reef from which the drifter was released. White tracks (0-7) indicate drifters released during new and waxing crescent days, which went northwest and south of Finger Reef. Orange tracks (8-14) indicate drifters released during first quarter and waxing gibbous days, were released on a windy days, and drifted the furthest south. Blue tracks (15-21) indicate drifters released during full and waning gibbous days, particularly on calm days, and drifted primarily northeast of Finger Reef. Green tracks (22-28) indicate last quarter and waning crescent days, drifted both north and south, and were also released on particularly calm days.

## DISCUSSION

### *Timing of spawning*

Spawning occurred almost every day but did not occur on days when the tidal conditions were suboptimal. Unlike the results of Kuwamura et al. (2016), who found that the timing of *Gomphosus varius* spawning occurred during all daylight hours, spawning generally did not commence at Finger Reef until after 1000H and only occurred up until the early afternoon. This is likely due to this site being used by multiple resident spawning aggregation species, as well as the prolonged presence of dive boats visiting and fish feeding by divers and snorkelers.

A male interrupted courtship attempts often occur when the defending male observes another conspecific male or egg predator (i.e. *Thalassoma hardwicke*, *Abudefduf sexfasciatus*, *Abudefduf vaigiensis*, and *Chromis atripectoralis*) in his mating territory (Gill et al. 2021), and a female interrupted courtship attempts may occur when there are many males lekking in the available area. A female was more likely to cease courtship if multiple males were attempting to court her. These interrupted courtship attempts occurred before and after peak spawning time daily, or on days where there was very little spawning at all.

### *Tidal and lunar patterns*

The results of this study show that tidal direction and lunar phase were not significant predictors for courtship behavior, and therefore, do not support my second hypothesis. The vast majority of recorded courtship bouts observed at tidal levels between 0.60-0.65m, which suggests that *G. varius* time their spawning closely with high tide. Reports of *G. varius* spawning tied to high tide in the Marshall Islands (Colin and Bell 1996) and Okinawa (Kuwamura et al.

2016) have been noted previously, as well as various other tropical labrids studied elsewhere (i.e., Claydon 2004).

In this study, *G. varius* was predicted to time spawning during lunar days around full moon, and while there was no significant difference between different lunar phases, it is worth noting that the most reproductively active periods occurred around times of full moon. Lunar phase alone was not a significant predictor of spawning rate, however, the full/waning gibbous lunar phase was the most reproductively active period in this study, followed by first quarter/waxing gibbous phases. Similarly, *Gomphosus caeruleus* at Reunion Island displayed peak spawning behavior closely tied to the waxing gibbous lunar phase. (Desvignes et al. 2017). This suggests that lunar pattern alone is an important secondary factor for these species' reproductive strategies in the sense that lunar rhythm controls tidal shifts. This is the case for many small residential tropical labrid species, which rely on tidal activity more than larger transient species (Thresher 1984, Choat 2012).

### ***Territoriality***

Spawning rates were very similar to data collected from a previous study by Gill et al. (2021), especially with the use of Territory C as the primary temporary mating territory. Spawning rates and mating territory defense were predicted to be positively linearly correlated, which is supported both by my results and by studies of other lekking species (Nooker and Sandercock 2008). In a meta-analysis of mating success in lekking males, Fiske et al. (1998) found that aggression rate, display frequency, and territory attendance were positively correlated with male mating success across different taxa, however territory attendance was the most correlated. Over 90% of spawning occurred at Territory C in this study and Gill et al. (2021). This suggests that there could be female preference for a specific mating territory, or a



hierarchical order for males to hold the most successful mating territory. While I was not able to quantitatively assess territory attendance in this study, I did observe that the same male would stay at his mating territory for the entire duration of females present at Finger Reef. I noticed that there were three reasons a male may leave his territory unattended. A male would leave his territory temporarily, usually to chase away other planktivorous fishes that would prey on spawned larvae (Gill et al. 2021) or other male *Gomphosus varius* that attempt to mate with females in this territory. This usually occurred around peak spawning times, when *G. varius* behavior, as well as overall reef activity, was at its highest. The second reason is when there was inconsistent or infrequent spawning activity. During these slow days, males would often travel around the Finger Reef vicinity, almost as if he was visiting competing males' territories or seeing if there were other females present elsewhere. Males would usually return to their post within a few minutes. The third reason for leaving a territory is if a male is abandoning his mating territory altogether because no females are visiting (usually the case for the less visited territories), or if spawning is done for the day.

Territory abundance and lek size are indicators of male reproductive success across other taxa (Fiske et al. 1998, Cestari et al. 2016). While my results indicate that neither number of males nor number of females were significant predictors for courtship alone, the number of females was positively related to the number of attacks. Because number of attacks is a significant predictor, it would be useful to develop a population model which utilizes male and female population densities in relation to reproductive success in these smaller aggregate spawning species. On Reunion Island, Devignes et al. (2017) reported that the number of observed spawning ascents were positively and linearly correlated to the number of females

present. This context suggests that differences in specific habitat and population dynamics between different locations plays a more important role than population densities alone.

### ***Implications for commercially important fisheries***

*Gomphosus varius* practices an array of reproductive strategies, some of which may be applied to other species that are understudied, less accessible, commercially important and data-limited, or a combination of these, and share some of these behavioral or physical characteristics. For codfishes (Gadidae) in the northern Atlantic, it is suggested that some semi-pelagic species have a lek-like mating system, and is notoriously an over-exploited group of fishes. Skjæraasen et al. (2012) found that drumming muscles and sexually dimorphic pelvic fin lengths are possibly linked to this taxa's complex mating system, in this case sex-biased spawning shoals. The authors call for further morphological studies to shed light into the reproductive behavior of these heavily harvested species. *Gomphosus varius* also drum when spawning (Boyle and Cox 2009) and are sexually dimorphic, so similarly, morphological analyses could further contextualize our understanding of its mating system.

Many aggregate spawners rely on sound to spawn, so this isn't necessarily a huge tie, but I do think it's interesting that sound plays such an important role in spawning behavior and is intrinsically tied to reproductive success in many species. In Hawaii, *G. varius* and *Thalassoma duperrey* (Labridae) are sympatric species that spawn in the same time and location (Boyle and Cox 2009). Differences in spawning sound frequency were suggested to be a mechanism which prevents cross-species hybridization during spawning times. Because Finger Reef is a multi-specific spawning aggregation site and located along a heavily trafficked shipping and Navy channel, I did not attempt to quantify sound at this site. It would be interesting to see how reef

fishes in densely populated or noisy habitats compensate for the lack of auditory communication that is so important in other spawning species.

### ***Behavioral changes after the onset of the COVID-19 pandemic***

When the island COVID-19 pandemic lockdown initially began, all commercial dive and snorkel boats ceased operations. Prior to the pandemic, these boats would visit Finger Reef almost daily, some of which were anecdotally known to feed fishes here and likely created an unnatural reliance on human visitations. Further, limited boat operations out of the UOG Marine Laboratory made it challenging for me to visit Finger Reef. To observe any changes in behavior, I continued to access the site from shore at Guam Navy Base via snorkeling at Gab Gab Beach. I found that *G. varius*, as well as other species inhabiting the site, appeared nearly “asleep” before 1000H and were not as curious about approaching humans as they were before the lockdown began. Individuals observed appeared generally smaller in size and less energetic than before. Spawning of *G. varius* occurred less frequently overall, but I was unable to visit the site often enough to confirm this with statistical confidence.

### ***Implications for larval dispersal***

I predicted that *G. varius* eggs would be distributed by the current away from Finger Reef but would be retained inside Apra Harbor for the first 24 hours after spawning. This prediction was largely unsupported by my results. While Apra Harbor is a largely enclosed embayment, Finger Reef is located in relatively close proximity (17 km) to the harbor’s entrance along the southern edge. In a United States Geological Service (USGS) report, Storlazzi et al. (2014) stated that the strongest measured surface currents along Guam’s western coast occur at the entrance and along the northern perimeter of Apra Harbor. The different drifter trajectories from this

study are very interesting because that part of the study took place during the transitional period between local dry and rainy seasons. Seasonality has been known to be an important factor in larval dispersion dynamics (Saenz-Agudelo et al., 2012) and I attempted to capture the effect of this by conducting the drifter experiment during transition months.

Changes in the water column also occur during shifts in seasonality. Waters are cooler and more saline during the dry season, and shift to warmer and less saline conditions when the wind-driven forces decrease and rainfall increases (Storlazzi et al. 2014). Several drifters were trapped on the reef flat and did not make it out of the harbor's entrance. This was anticipated, especially for days when windspeed and tidal movements were slow, and also, because the drifter release point was just off the tip of the reef flat. Numerical modeling of local near surface currents suggests that surface currents in deep water areas are primarily controlled by the wind, and currents over shallow reef flats are controlled by wave motion (Storlazzi et al. 2014). So, even though some of the drifters deployed became stuck on the reef flat this may suggest that at least a portion of larvae might also be trapped nearshore by wave-driven water movements.

Drifters were released under different tidal and lunar conditions, so these results may be applicable towards understanding where larvae travel after being spawned in and around Apra Harbor. Finger Reef is a highly productive and multi-species resident spawning aggregation site but is certainly not the only one along the western coast of Guam.

### ***Evidence for self-recruitment***

Larvae retention may be typical of many resident spawning aggregate species, especially for island endemic or geographically isolated populations. In other island drifter release studies, tidal currents and eddy formations are important in initial transport and allow for a significant

portion of eggs and early larvae to return back to their initial spawning sites (Hamner et al., 2007, Heppel et al. 2009). Kendall et al. (2015) used drifters and modeling to determine that Guam relies on self-recruitment for more than 15% of its larval supply for pelagic larval durations (PLD) of 30-50 days, and 3% for PLDs of 60-100 days, which are the highest recruitment rates of the Mariana Archipelago. *Gomphosus varius* has a relatively long PLD of 51.6 days (Victor 1986), however the physical processes at a different locality would likely influence this larval duration, and should be examined.

Guam is located between the north equatorial current which flows west, is driven by the trade winds, and is slowest in the summer, and the north equatorial counter current which flows eastward and is slowest in the spring (Kendall & Poti, 2014; Kendall & Poti, 2015). This creates eddies, which are associated with larvae retention, and affects the long term distribution and distance that exported larvae will travel to. Also, slow moving currents often facilitate self-recruitment (Kendall et al. 2018). It's interesting to see these very subtle shifts in surface current patterns create this variety of initial dispersal over the course of just a few weeks. Short term drifter release experiments, such as these, can better inform us of the immediate physical and oceanographic processes that affect larval connectivity in large scale biophysical ocean modeling

### ***Conclusions***

In Guam, the reproductive behavior of *Gomphosus varius* is tied closely to male territorial behavior and daily tidal fluctuations, specifically the first diel high tide. Male reproductive success is correlated with aggressive territory defense behavior. Lunar phase and population density are secondary contributors to reproductive success because they are tied intrinsically to the tidal changes and male territoriality that drive this reproductive system,

respectively. Eggs and larvae from Finger Reef are initially dispersed away from the reef and generally drift into the main ocean current during windy season. A proportion of the larvae may self-recruit during rainy season, or become trapped in nearshore wave-driven water movements. *Gomphosus varius* spawns continuously despite shifts in seasonality, however, seasonal changes affect where larvae may ultimately disperse.

## References Cited

- Andersson, M. (1994). *Sexual selection*. Princeton University Press, Princeton.
- Appeldoorn, R. S., Hensley, D. A., Shapiro, D. Y., Kioroglou, S., & Sanderson, B. G. (1994). Egg dispersal in a Caribbean coral reef fish, *Thalassoma bifasciatum*. II. Dispersal off the reef platform. *Bulletin of Marine Science* 54(1), 271–280.
- Arita, L. H., & Kaneshiro, K. Y. (1985). The dynamics of the lek system and mating success in males of the Mediterranean fruit fly *Ceratitis capitata* (Wiedemann). *Proceedings, Hawaiian Entomological Society* 25(2858), 39–48.
- Avise, J. C. and Mank, J. E. 2009. Evolutionary perspectives on hermaphroditism fishes. *Sexual Development* 3:152–163.
- Barlow, G. W. (1981). Patterns of parental investment, dispersal and size among coral-reef fishes. *Environmental Biology of Fishes* 6(1), 65–85.
- Beehler, B. M., & Foster, M. S. (1988). Hotshots, hotspots, and female preference in the organization of lek mating systems. *The American Naturalist* 131, 203–219.
- Bell, L. J., & Colin, P. L. (1986). Mass spawning of *Caesio teres* (Pisces: Caesionidae) at Enewetak Atoll, Marshall Islands. *Environmental Biology of Fishes* 15(1), 69–74.
- Boyle, K. S., & Cox, T. E. (2009). Courtship and spawning sounds in bird wrasse *Gomphosus varius* and saddle wrasse *Thalassoma duperrey*. *Journal of Fish Biology* 75(10), 2670–2681.
- Bradbury, J. W. (1981). The evolution of leks. In R. D. Alexander & D. W. Tinkle (Eds.), *Natural selection and social behavior* (pp. 138–169). Chiron Press, New York.
- Bradbury, J. W., & Gibson, R. M. (1983). Leks and mate choice. In R. D. Alexander & D. W. Tinkle (Eds.), *Mate Choice* (pp. 107–138). Cambridge University Press.
- Brown, C. R., & Bomberger Brown, M. (1989). Behavioural dynamics of intraspecific brood parasitism in colonial cliff swallows. *Animal Behaviour* 37(5), 777–796.
- Carr, M. H., Anderson, T. W., & Hixon, M. A. (2002). Biodiversity, population regulation, and the stability of coral-reef fish communities. *Proceedings of the National Academy of Sciences of the United States of America* 99(17), 11241–11245.
- Carvalho, N., Afonso, P., & Santos, R. S. (2003). The harem mating system and mate choice in the wide-eyed flounder, *Bothus podas*. *Environmental Biology of Fishes* 66, 249–258.
- Cestari, C., Loiselle, B. A., & Pizo, M. A. (2016). Trade-offs in male display activity with lek size. *PLoS ONE* 11(9), 1–12.
- Choat, J. H. (2012). Spawning aggregations in reef fishes; Ecological and evolutionary processes. In Y. Sadovy De Mitcheson & P. L. Colin (Eds.), *Reef fish spawning aggregations: Biology, research, and management* (pp. 85–116). Springer, New York.
- Chollett, I., Priest, M., Fulton, S., & Heyman, W. D. (2020). Should we protect extirpated fish spawning aggregation sites? *Biological Conservation* 241, 108395.
- Claydon, J. A. B. (2004). Spawning aggregations of coral reef fishes: characteristics, hypotheses, threats and management. *Oceanography and Marine Biology: An Annual Review* 42, 256–301.
- Claydon, J. A. B., McCormick, M. I., & Jones, G. P. (2014). Multispecies spawning sites for fishes on a low-latitude coral reef: spatial and temporal patterns. *Journal of Fish Biology* 84, 1136–1163.
- Colin, P. L. (1992). Reproduction of the Nassau grouper, *Epinephelus striatus* (Pisces: Serranidae) and its relationship to environmental conditions. *Environmental Biology of Fishes* 34(4), 357–377.

- Colin, P. L. (2012a). Aggregation spawning: Biological aspects of the early life history. In Y. Sadovy De Mitcheson & P. L. Colin (Eds.), *Reef fish spawning aggregations: Biology, research, and management* (pp. 191–224). Springer, New York.
- Colin, P. L. (2012b). Timing and location of aggregation and spawning in reef fishes. In Y. Sadovy De Mitcheson & P. L. Colin (Eds.), *Reef fish spawning aggregations: Biology, research, and management* (pp. 117–158). Springer, New York.
- Colin, P. L., & Bell, L. J. (1991). Aspects of the spawning of labrid and scarid fishes (Pisces: Labroidei) at Enewetak Atoll, Marshall Islands with notes on other families. *Environmental Biology of Fishes* 31, 229–260.
- Csanady, G. T. (1972). The coastal boundary layer in Lake Ontario: Part II. The summer-fall regime. *Journal of Physical Oceanography* 2, 168–176.
- Desvignes, T., Bourjon, P., & Chanet, B. (2017). Comportements reproducteurs du labre oiseau *Gomphosus caeruleus* dans un récif de l'île de la Reunion: mode de reproduction, facteurs environnementaux et alternance des stratégies reproductrices. *Comptes Rendus - Biologies* 341(1), 43–60.
- Doherty, P. J., Williams, D. M. B., & Sale, P. F. (1985). The adaptive significance of larval dispersal in coral reef fishes. *Environmental Biology of Fishes* 12(2), 81–90.
- Domeier, M. (2012). Revisiting spawning aggregations: definitions and challenges. In Y. Sadovy De Mitcheson & P. L. Colin (Eds.), *Reef fish spawning aggregations: Biology, research, and management* (pp. 1–26). Springer, New York.
- Domeier, M.L. and P. L. Colin. (1997). Tropical reef spawning aggregations: defined and reviewed. *Bulletin of Marine Science* 60(3), 698–726.
- Donaldson, T. J. (1990). Lek-like courtship by males, and multiple spawnings by females of *Synodus dermatogenys* (Synodontidae). *Japanese Journal of Ichthyology* 37(, 292–301.
- Donaldson, T. J. (1999). Assessing phylogeny, historical ecology, and the mating systems of hawkfishes (Cirrhitidae). *Proceedings, 5th Indo-Pacific Fish Conference, Noumea*, 789–796.
- Durães, R., Loiselle, B. A., Parker, P. G., & Blake, J. G. (2009). Female mate choice across spatial scales: Influence of lek and male attributes on mating success of blue-crowned manakins. *Proceedings of the Royal Society B: Biological Sciences* 276(1663), 1875–1881.
- Emlen, S. T., & Oring, L. W. (1977). Ecology, sexual selection, and the evolution of mating systems. *Science* 197(4300), 215–223.
- Erisman, B., Heyman, W., Kobara, S., Exer, T., Pittman, S., Aburto-Oropeza, O., & Nemeth, R. S. (2015). Fish spawning aggregation: where well-placed management actions can yield big benefits for fisheries and conservation. *Fish and Fisheries* 18, 128-144.
- Figenschou, L., Folstad, I., & Liljedal, S. (2004). Lek fidelity in male Arctic charr. *Canadian Journal of Zoology* 82, 1278–1284.
- Fiske, P., Rintamäki, P. T., & Karvonen, E. (1998). Mating success in lekking males: A meta-analysis. *Behavioral Ecology* 9(4), 328–338.
- Gill, A.M., Franklin, E.C., & Donaldson, T.J. (2021). Fore reef location influences spawning success and eggredation in lek-like mating territories of the bird wrasse, *Gomphosus varius*. *Environmental Biology of Fishes* 104, 451-461.
- Gladstone, W. (1994). Lek-like spawning, parental care and mating periodicity of the triggerfish *Pseudobalistes flavimarginatus* (Balistidae). *Environmental Biology of Fishes* 39, 249–257.
- Gladstone, W. (2007). Selection of a spawning aggregation site by *Chromis hypsilepis* (Pisces: Pomacentridae): habitat structure, transport potential, and food availability. *Marine Ecology*



- Progress Series 351, 235–247.
- Hamner, W. M., Colin, P. L., & Hamner, P. P. (2007). Export-import dynamics of zooplankton on a coral reef in Palau. *Marine Ecology Progress Series* 334, 83–92.
- Hamner, W. M., & Hauri, I. R. (1981). Effects of island mass: Water flow and plankton pattern around a reef in the Great Barrier Reef lagoon, Australia. *Limnology and Oceanography* 26(6), 1084–1102.
- Hamner, W. M., & Largier, J. L. (2012). Oceanography of the planktonic stages of aggregation spawning reef fish. In Y. Sadovy De Mitcheson & P. L. Colin (Eds.), *Reef fish spawning aggregations: Biology, research, and management* (pp. 159–190). Springer, New York.
- Hensley, D. A., Appeldoorn, R. S., Shapiro, D. Y., Ray, M., & Turingan, R. G. (1994). Egg dispersal in a Caribbean coral reef fish, *Thalassoma bifasciatum*. I. Dispersal off the reef platform. *Bulletin of Marine Science* 54(1), 271–280.
- Heppell, S. A., Semmens, B. X., Pattengill-Semmens, C. V., Bush, P. G., Johnson, B. C., McCoy, C. M., et al. (2009). Tracking potential larval dispersal patterns from Nassau grouper aggregation sites: evidence for local retention and the ‘importance of place’. *Proceedings of the 61st Gulf and Caribbean Fisheries Institute* 61, 325–327.
- Ishikawa, M., Mori, S., & Nagata, Y. (2006). Intraspecific differences in patterns of courtship behaviours between the Pacific Ocean and Japan Sea forms of the three-spined stickleback *Gasterosteus aculeatus*. *Journal of Fish Biology* 69, 938–944.
- Jackson, A. M., Semmens, B. X., Sadovy De Mitcheson, Y., Nemeth, R. S., Heppell, S. A., Bush, P. G., & Bernardi, G. (2014). Population structure and phylogeography in Nassau grouper (*Epinephelus striatus*), a mass-aggregating marine fish. *PLoS ONE* 9(5), e97508.
- Jennings, M. J., & Philipp, D. P. (1992). Female choice and male competition in longear sunfish. *Behavioral Ecology* 3(1), 84–94.
- Johannes, R. E. (1978). Reproductive strategies of coastal marine fishes in the tropics. *Environmental Biology of Fishes* 3(1), 65–84.
- Jones, G. P., Almany, G. R., Russ, G. R., Sale, P. F., Steneck, R. S., Van Oppen, M. J. H., & Willis, B. L. (2009). Larval retention and connectivity among populations of corals and reef fishes: history, advances and challenges. *Coral Reefs* 28(2), 307–325.
- Jones, G. P., Millcich, M. J., Emsile, M. J., & Lunow, C. (1999). Self-recruitment in a coral fish population. *Nature* 402(6763), 802–804.
- Kendall, M. S., & Poti, M. (2014). Potential larval sources, destinations, and self-seeding in the Mariana Archipelago documented using ocean drifters. *Journal of Oceanography*, 70, 549–557.
- Kendall, M. S., & Poti, M. (Eds.) (2015). *Transport pathways of marine larvae around the Mariana Archipelago*. (pp. 130). Silver Spring, MD: NOAA Technical Memorandum NOS NCCOS 193.
- Kendall, M. S., Poti, M., & Winship, A. (2018). Is Guam a regional source, destination, or stepping-stone for larvae of three fisheries species? *Fisheries Oceanography*, 1-12
- Kiflawi, M., Mazeroll, A. I., & Goulet, D. (1998). Does mass spawning enhance fertilization in coral reef fish? A case study of the brown surgeonfish. *Marine Ecology Progress Series* 172, 107–114.
- Kirkpatrick, M., & Ryan, M. J. (1991). The evolution of mating preferences and the paradox of the lek. *Nature* 350(6313), 33–38.
- Kobara, S., & Heyman, W. D. (2010). Sea bottom geomorphology of multi-species spawning aggregation sites in Belize. *Marine Ecology Progress Series* 405, 243–254.

- Kramer, D. L., & Chapman, M. R. (1999). Implications of fish home range size and relocation for marine reserve function. *Environmental Biology of Fishes* 55, 65–79.
- Kuwamura, T., Suzuki, S., & Kadota, T. (2016). Interspecific variation in the spawning time of labrid fish on a fringing reef at Iriomote Island, Okinawa. *Ichthyological Research* 63(4), 460–469.
- Largier, J. L. (2003). Considerations in estimating larval distances from oceanographic data. *Ecological Applications* 13, 71–89.
- Loiselle, P., & Barlow, G. W. (1978). Do fishes lek like birds? In E. Reese & F. Lighter (Eds.), *Contrasts in behavior* (pp. 33–75). New York: Wiley Interscience.
- McDonald, D., & Potts, W. (1994). Cooperative display and relatedness among males in a lek-mating bird. *Science* 266(5187), 1030–1032.
- McKaye, K. R. (1983). Ecology and breeding behavior of a cichlid fish, *Crytocara eucinostomus*, on a large lek in Lake Malawi, Africa. *Environmental Biology of Fishes* 8(2), 81–96.
- Molloy, P. P., Côté, I. M., & Reynolds, J. D. (2012). Why spawn in aggregations? In Y. Sadovy De Mitcheson & P. L. Colin (Eds.), *Reef fish spawning aggregations: Biology, research, and management* (pp. 57–84). Springer, New York.
- Monteiro, C. A., Paulino, C., Jacinto, R., Serraõ, E. A., & Pearson, G. A. (2016). Temporal windows of reproductive opportunity reinforce species barriers in a marine broadcast spawning assemblage. *Scientific Reports* 6(July), 35–38.
- Monteiro, N. M., Carneiro, D., Antunes, A., Queiroz, N., Vieira, M. N., & Jones, A. G. (2017). The lek mating system of the worm pipefish (*Nerophis lumbriciformis*): a molecular maternity analysis and test of the phenotype-linked fertility hypothesis. *Molecular Ecology* 26, 1371–1385.
- Moyer, J. T. (1989). Reef channels as spawning sites for fishes on the Shiraho coral reef, Ishigaki Island, Japan. *Japanese Journal of Ichthyology*, 36(3), 371–375.
- Moyer, J. T., & Yogo, Y. (1982). The lek-like mating system of *Halichoeres melanochir* (Pisces: Labridae) at Miyake-jima, Japan). *Zeitschrift Für Tierpsychologie* 60(37), 209–226.
- NOAA water levels - NOAA tides & currents. Tides & Currents. (n.d.). Retrieved November 19, 2021, from <https://tidesandcurrents.noaa.gov/waterlevels.html?id=1630000>.
- Parker, J. R. C. (2019). Geographical and temporal changes of reef fish (Labridae) assemblages: A case study of South Western Australia. MP Thesis in Biology, Curtin University.
- Pequignet A. C., Becker J. M., Merrifield M. A., Boc S. J. (2011). The dissipation of wind wave energy across a fringing reef at Ipan, Guam. *Coral Reefs- Coral reef hydrodynamics special series*, 30:71-82.
- Petrie, M., Krupa, A. P., & Burke, T. (1999). Peacocks lek with relatives even in the absence of social and environmental cues. *Nature* 401(September), 155–157.
- Randall, J., & Randall, H. (1963). The spawning and early development of the Atlantic parrot fish, *Sparisoma rubripinne*, with notes on other scarid and labrid fishes. *Zoology* 48(2), 49–60.
- Robertson, D. R., & Hoffman, S. G. (1977). The roles of female mate choice and predation in the mating systems of some tropical labroid fishes. *Zeitschrift Für Tierpsychologie* 45(3), 298–320.
- Sadovy de Mitcheson, Y., Cornish, A., Domeier, M., Colin, P. L., Russell, M., & Lindeman, K. C. (2008). A global baseline for spawning aggregations of reef fishes. *Conservation Biology* 22(5), 1233–1244.

- Sadovy de Mitcheson, Y., & Erisman, B. (2012). Fishery and biological implications of fishing spawning aggregations, and the social and economic importance of aggregating fishes. In Y. Sadovy de Mitcheson & P. L. Colin (Eds.), *Reef fish spawning aggregations: Biology, research, and management* (pp. 225–284). Springer, New York.
- Saenz-Agudelo, P., Jones, G. P., Thorrold, S. R., & Planes, S. (2012). Patterns and persistence of larval retention and connectivity in a marine fish metapopulation. *Molecular Ecology*, 21(19), 4695–4705.
- Sancho, G., Petersen, C. W., & Lobel, P. S. (2000). Predator-prey relations at a spawning aggregation site of coral reef fishes. *Marine Ecology Progress Series* 203, 275–288.
- Saucier, M. H., & Baltz, D. M. (1993). Spawning site selection by spotted seatrout, *Cynoscion nebulosus*, and black drum, *Pogonias cromis*, in Louisiana. *Environmental Biology of Fishes* 36, 257–272.
- SCRFA Global Database. (2020). Hong Kong. Science and Conservation of Fish Aggregations (SCRFA) database. Updated November 2020. Available from [www.scrfa.org](http://www.scrfa.org).
- Sherman, P. W. (1999). Birds of a feather lek together. *Nature* 401(September), 119–120.
- Storlazzi, C.D., Cheriton, O.M., Lescinski, J.M.R., and Logan, J.B. (2014). Coastal circulation and water-column properties in the War in the Pacific National Historical Park, Guam – Measurements and modeling of waves, currents, temperature, salinity, and turbidity, April–August 2012: U.S. Geological Survey Open-File Report 2014-1130, 104p.
- Thresher, R. E. (1984). *Reproduction in reef fishes*. Neptune City, NJ: TFH Publications.
- Tricas, T. C., & Boyle, K. S. (2014). Acoustic behaviors in Hawaiian coral reef fish communities. *Marine Ecology Progress Series*, 511, 1–16.
- Victor, B. C. (1986). Duration of the planktonic larval stage of one hundred species of Pacific and Atlantic wrasses (family Labridae). *Marine Biology* 90(3), 317–326.
- Victor, B. C. (1987). The mating system of the Caribbean rosy razorfish, *Xyrichtys martinicensis*. *Bulletin of Marine Science* 40(1), 152–160(9).
- Warner, R. R. (1975). The adaptive significance of sequential hermaphroditism in animals. *The American Naturalist* 109(965), 61–82.
- Warner, R. R. (1988). Traditionality of mating-site preferences in a coral reef fish. *Nature* 335(6192), 719–721.
- Warner, R. R. (1995). Large mating aggregations and daily long-distance spawning migrations in the bluehead wrasse, *Thalassoma bifasciatum*. *Environmental Biology of Fishes* 44, 337–145.
- Warner, R. R., & Robertson, D. R. (1978). Sexual patterns in the labroid fishes of the western Caribbean: 1. The wrasses (Labridae). *Smithsonian Contributions to Zoology* 255, 1–26.
- Wikelski, M., Carbone, C., & Trillmich, F. (1996). Lekking in marine iguanas: Female grouping and male reproductive strategies. *Animal Behaviour* 52(3), 581–596.
- Wiley, R. H. (1973). Territoriality and non-random mating in sage grouse. *Animal Behavior Monographs* 6, 85–169.
- Windle, M. J. S., & Rose, G. A. (2007). Do cod form spawning leks? Evidence from a Newfoundland spawning ground. *Marine Biology* 150, 671–680.
- Yabuta, S., & Kawashima, M. (1997). Spawning behavior and harem mating system in the corallivorous butterflyfish, *Chaetodon trifascialis*, at Kuroshima Island, Okinawa. *Ichthyological Research* 44, 183–188.

## Appendix:

Table 1. Drifter release information. Drifter duration, distances, direction, velocity, lunar days, tide direction, wind dynamics for each drifter launched.

Release Date	Drifter Device Number	Deploy Time [ChST]	End Time [ChST]	Total Time [h:m]	Total Distance (m)	Net Distance (m)	Net Direction	Drifter Velocity (km/h)	Lunar Days	Tide Direction	Wind Direction	Wind Speed (m/s)	Gust Speed (m/s)
24-Feb-2021	OIST-I-0098	2/24/21 12:30	2/25/21 8:03	19:33	24165.83	21026.61	207.64	29.67	8-14	Low	76.44623656	3.264516129	5.66344086
24-Feb-2021	OIST-I-0099	2/24/21 12:30	2/25/21 8:01	19:31	23949.85	21205.66	208.85	29.45	8-14	Low	76.44623656	3.264516129	5.66344086
24-Feb-2021	OIST-I-0101	2/24/21 14:30	2/25/21 8:00	17:30	22247.05	19821.18	210.23	30.51	8-14	Flood	77.87349398	3.3	5.847590361
24-Feb-2021	OIST-I-0102	2/24/21 14:30	2/25/21 9:00	18:30	24105.29	21162.97	205.43	31.27	8-14	Flood	77.47159091	3.344318182	5.884659091
25-Feb-21	OIST-I-0098	2/25/21 10:30	2/26/21 7:31	21:01	19724.13	15662.36	219.14	22.52	8-14	Ebb	79.62857143	3.071904762	5.549047619
25-Feb-21	OIST-I-0099	2/25/21 10:30	2/26/21 8:30	22:00	19864.78	15669.87	219.08	21.67	8-14	Ebb	79.78181818	3.094545455	5.599090909
25-Feb-21	OIST-I-0101	2/25/21 10:30	2/26/21 7:30	21:00	20075.92	15655.02	219.49	22.94	8-14	Ebb	79.62857143	3.071904762	5.549047619
25-Feb-21	OIST-I-0102	2/25/21 10:30	2/26/21 7:30	21:00	19693.09	15461.71	219.08	22.51	8-14	Ebb	79.62857143	3.071904762	5.549047619
29-Mar-21	OIST-I-0098	3/29/21 14:30	3/30/21 8:03	17:33	8130.87	2508.83	219.05	11.12	15-21	Low	82.02840909	1.986363636	3.517045455
29-Mar-21	OIST-I-0101	3/29/21 16:30	3/30/21 10:00	17:30	8865.4	4652.97	38.55	12.16	15-21	Flood	80.89772727	2.06875	3.671022727
29-Mar-21	OIST-I-0102	3/29/21 16:30	3/30/21 10:00	17:30	9362.81	5954.84	38.4	12.84	15-21	Flood	80.89772727	2.06875	3.671022727
6-Apr-21	OIST-I-0098	4/6/21 12:30	4/7/21 8:30	20:00	9923.05	7090.2	220.55	11.91	22-28	Flood	155.4676617	1.219900498	1.975124378
6-Apr-21	OIST-I-0099	4/6/21 12:30	4/7/21 8:30	20:00	9572.99	7139.82	221.95	11.49	22-28	Flood	155.4676617	1.219900498	1.975124378
6-Apr-21	OIST-I-0101	4/6/21 14:30	4/7/21 8:30	18:00	9301.69	6984.81	221.44	12.40	22-28	High	154.3756906	1.220994475	1.997790055
6-Apr-21	OIST-I-0102	4/6/21 14:30	4/7/21 8:30	18:00	8603.13	6708.14	226.1	11.47	22-28	High	154.3756906	1.220994475	1.997790055
7-Apr-21	OIST-I-0102	4/7/21 11:30	4/8/21 12:00	24:30	13076.21	8277.79	29.4	12.81	22-28	Low	132.795082	3.40942623	4.523770492
12-Apr-21	OIST-I-0098	4/12/21 14:30	4/13/21 7:30	17:00	10597.78	5967.52	199.5	14.96	0-7	Low	80.09356725	2.470760234	4.595906433
12-Apr-21	OIST-I-0099	4/12/21 14:30	4/13/21 7:30	17:00	9966.06	5130.42	192.84	14.07	0-7	Low	80.09356725	2.470760234	4.595906433
12-Apr-21	OIST-I-0101	4/12/21 16:30	4/13/21 7:30	15:00	6929.42	1709.94	234.15	11.09	0-7	Flood	78.56291391	2.562251656	4.703311258
12-Apr-21	OIST-I-0102	4/12/21 16:30	4/13/21 7:30	15:00	7284.12	2585.53	199.18	11.65	0-7	Flood	78.56291391	2.562251656	4.703311258
13-Apr-21	OIST-I-0098	4/13/21 8:30	4/14/21 9:00	24:30	15499.19	9084.4	309.3	15.18	0-7	High	94	2.145121951	4.332520325
13-Apr-21	OIST-I-0099	4/13/21 8:30	4/14/21 9:30	25:00	16632.37	10097.03	313.23	15.97	0-7	High	94	2.145121951	4.332520325
13-Apr-21	OIST-I-0101	4/13/21 10:30	4/14/21 9:00	22:30	15445.91	9073.72	311.93	16.48	0-7	Ebb	95.34513274	2.103097345	4.285840708
13-Apr-21	OIST-I-0102	4/13/21 10:30	4/14/21 9:01	22:31	15106.77	8484.63	309.47	16.10	0-7	Ebb	95.34513274	2.103097345	4.285840708