Short Note

Spawning ascent durations of pelagic spawning reef fishes

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Abstract
Predation risks have been hypothesized to influence spawning behaviors of coral reef fishes that broadcast gametes pelagically. The duration of spawning ascents of 13 species were measured from video footage at a single spawning site for multiple coral reef fishes to investigate if this behavior was influenced by varying risks of predation. Fishes that spawned in pairs had ascents of longer duration than group-spawning species. Duration of spawning ascents did not vary between fishes spawning at daytime and dusk, nor between group-spawning species with specific anti-predatory morphological adaptations. These results indicate that risk of predation may not significantly influence the duration of spawning ascents of pair spawning reef fishes at our study site, while group-spawning behaviors are influenced by predation. Avoidance of egg predation by benthic organisms and female mate choice are more likely to influence the pelagic spawning behaviors of all fishes observed [Current Zoology 58 (1): 95–102, 2012].

Keywords
Reef fishes, Behavior, Spawning, Predation, Mate selection

Benthic or demersal fishes with pelagic or broadcast spawning behaviors generally exhibit a spawning ascent that involves adult fishes swimming through the water-column away from the substrate to release gametes (Randall, 1961; Thresher, 1984; Myrberg et al., 1989). This spawning ascent or spawning rush behavior has been hypothesized to diminish egg predation rates by benthic planktivores (Johannes, 1978; Hobson, 1973; Barlow, 1981), reduce male sperm competition by males with alternative mating strategies (Myrberg et al., 1989; Sancho, 1998) and facilitate mate selection by females (Hutchings et al., 1999). Pelagic spawning ascents are often accompanied by increased predation risks to spawning adults (Clifton and Robertson, 1993; Sancho 2000; Sancho et al., 2000a), since broadcast spawning implies swimming away from the shelter provided by the substratum (Jones, 1968; Hixon, 1993). This risk of adult predation has been hypothesized to be a factor determining spawning location of small fishes (Hugie and Dill, 1994; Sancho et al., 2000a), courtship behavior (Warner and Dill, 2000) and spawning rush height (Thresher, 1984; Nemtsov, 1994), but has not been shown to influence the height of spawning ascents in toxic trunkfish species (Sancho, 1998).

This study attempts to further consider which factors influence the duration of spawning ascents by comparing differences in spawning behaviors of pelagic broadcast spawning coral reef fishes at a single spawning aggregation site. This approach allowed us, based on specific characteristics of different mating systems and potential adult predation risks, to make predictions on the duration of swimming ascents, a variable that can be precisely measured from video recordings and is directly related to the swimming distance (height) and speed of spawning fishes, variables much harder to measure accurately in the field.

Pelagic spawning events can be categorized into pair and group-spawns (Thresher, 1984). Pair-spawning events involve courtship behaviors by a male with a female, eventually both ascending together to release their gametes above the substrate. On occasion, other males (streakers) will join a pair-spawning ascent by suddenly darting upwards and release sperm close to the main spawning pair, an event that commonly elicits aggressive behaviors by the dominant male after spawning (Thresher, 1984). Group-spawns involve groups of more than one male courting and ascending together with a single female, competing among them to fertilize her eggs. For the purpose of this study, group-spawning events were defined as those when no dominant courting male could be identified, and three or more fishes performed a spawning rush to release gametes

In pair-spawning coral reef species, male courtship behavior is hypothesized to act as a safety indicator for
interested females, assuring that mortality risks from visual predators are low (Warner, 1987). This hypothesis suggests that male courting behavior and bright colorations are of greater influence/importance to females as safety indicators than as assurance of male quality, and therefore females may be then choosing decreased mortality risk over desirable male qualities and/or attributes.

Adult predation risks during spawning events (per spawning rush) are greater for group-spawning species than for those spawning in pairs at the site where this study took place (Sancho et al., 2000a). In group-spawning events, risk of predation can be influenced by the number of individuals participating in spawning activities, and individual mortality risk can be reduced simply due to increased spawning population density (Krause and Godin, 1995). Though the individual risk of predation per individual male in a spawning rush is reduced with increasing group size, male fish participate in multiple spawning events per day, increasing their overall predation risk with respect to females that may only spawn once every few days (Clifton and Robertson, 1993; Sancho et al., 2000a). Diel timing of spawning also affects adult predation risks, since predation rates can vary along the day based on visibility and predator abundance and activity (Hobson, 1973). At the spawning location of this study, predation risks on group-spawning fishes are lower at dusk than during the daytime period (Sancho et al., 2000a). Also, the existence of anti-predatory morphological adaptations (spines, deep bodies, large sizes) should reduce the predation risks during spawning for those species that possess them (Smith, 1997; Godin, 1997).

In a predation risk avoidance scenario (Warner, 1987; Hixon, 1993), spawning ascent durations should be shorter for fishes with higher risks, wherein attempting to minimize the distance and time spent away from their benthic refuges. Based on known behavior and abundance patterns of predatory fishes at the study spawning site (Sancho et al., 2000a), we can therefore predict various scenarios. Hypothesis 1: fishes spawning in groups are predicted to have shorter spawning ascent durations than those spawning in pairs, since group-spawning events are more commonly attacked by predators (Sancho et al., 2000a). This hypothesis supposes that the increase in predation risk per individual female due to spawning with a group of males targeted by predators is greater than the reduction in female individual predatory risk due to multiple (2–15) males participating in a single spawning rush. This supposition is more likely in species with smaller spawning group sizes. Hypothesis 2: daytime group-spawners should display shorter ascents than dusk group-spawning fishes, since predation risks are higher during daytime hours (Sancho et al., 2000a). Hypothesis 3: no differences should exist between daytime and dusk pair-spawners, since pair-spawning occurs when the dominant male perceives predation risks to be low (Warner, 1987; Warner and Dill, 2000). Hypothesis 4: group-spawning fishes with anti-predatory adaptations (surgeonfish) should have longer spawning ascent times than species without these adaptations (parrotfish).

Alternatively, female mate choice and sperm competition can also influence the duration of spawning ascents. If courtship displays in pair-spawning species are indicators of male quality or safety (Warner and Dill, 2000), then courtship associated displays by males during the spawning rush (see Thresher, 1984 for examples) are expected to increase the duration of spawning ascents. In pair-spawning mating systems, egg fertilization rates are increased when there is sperm competition from satellite streaker males (Petersen, 1991; Marconato et al., 1997). In aggregations of group-spawning species, sperm competition among males is expected to be high, though assortative mating does seem to occur, implying that mate selection is taking place (Hutchings et al., 1999; Bekkevold et al., 2002). If females control the speed and distance of the spawning ascents, and more importantly, the point of gamete release, then group-spawning females could choose mates by performing fast swimming ascents (and therefore shorter ascent durations) and select for the most attentive and fastest swimming males (a possible measure of fitness). Under these assumptions, females spawning with a single male partner (pair-spawn) are predicted to have longer ascent durations than females spawning with more than one male in group-spawns (hypothesis 1).

This study measured the duration of spawning ascents for 13 pelagic spawning coral reef fishes. While spawning behaviors of reef fishes can be plastic and vary in response to local environmental conditions characteristic of different spawning sites (Warner, 1991, 1997), we compared spawning behaviors of different species under the well described local conditions of a single spawning site (Sancho et al., 2000a,b). To investigate the influence of predation risks and mate choice on spawning ascent durations of reef fishes we compared the following groups of observations: (1) group-spawners vs. pair-spawners, (2) day pair-spawners vs. dusk pair-spawners, (3) day group-spawners vs. dusk group-spawners, (4) group-spawners without anti-predatory
morphological adaptations vs. those with anti-predatory adaptations.

1 Materials and Methods

Behaviors of pelagic spawning reef fishes were studied during April and May of 1994 at the Mustin’s Gap resident spawning aggregation site at Johnston Atoll, Central Pacific (Sancho et al., 2000a, b). Multiple reef fish species were observed spawning in both pairs and groups at this shallow (average depth of 4.5 m.) reef channel, characterized by a strong bi-directional tidal and waved-induced current regime (Sancho et al., 2000b). Video recordings of spawning ascents or rushes were made by scuba divers employing an 8-mm video camera inside an underwater housing.

Video recordings were transferred into a digital video system, and using digital video analysis software (Final Cut Pro 3.0), the duration of spawning ascents was measured by counting the total number of frames (29 frames s⁻¹). Spawning ascent times were measured for 189 spawning events from 13 pelagic-spawning species: two-barred goatfish *Parupeneus insularis*, multibarred goatfish *Parupeneus multifasciatus*, teardrop butterflyfish *Chaetodon unimaculatus*, yellowtail coris *Coris gaimard*, slingjaw wrasse *Epibulus insidiator*, ringtail wrasse *Oxycheilinus unicristatus*, stareye parrotfish *Calotomus carolinus*, bullethead parrotfish *Chlororus sordidus*, bluelined surgeonfish *Acanthurus nigrolineatus*, goldring surgeonfish *Ctenochaetus strigosus*, yellow tang *Zebrasoma flavescens*, peacock flounder *Bothus mancus* and spotted trunkfish *Ostracion meleagris* (Table 1).

The start of an individual spawning ascent was determined to be the moment the female began her ascent into the water column from her initial benthic location. The conclusion of the ascent was defined as the moment after the female had released her eggs at the apex of her swimming trajectory and begun her descent. Sperm release by males immediately followed, which could be observed more readily. When females could not be morphologically recognized from males, it was interpreted that the individual leading the spawning rush was the female. We did not consider quantifying spawning descents for these analyses because of the difficulty in defining the termination moment of the behavior from our recordings.

The durations of spawning ascents for the 13 species were analyzed according to spawning behavior (pair or group), the time of day of spawning (day or dusk) and phylogeny (grouped by species and order). Pair-spawning

<table>
<thead>
<tr>
<th>Order / Family</th>
<th>Species</th>
<th>Spawning Behaviors Recorded</th>
<th>No. Spawn Events Recorded</th>
<th>Time of Spawning</th>
<th>Mean Ascent Duration</th>
</tr>
</thead>
<tbody>
<tr>
<td>Acanthuriformes</td>
<td><em>Acanthurus nigrolineatus</em></td>
<td>Group</td>
<td>44</td>
<td>Day/Dusk</td>
<td>0.58</td>
</tr>
<tr>
<td><em>Ctenochaetus strigosus</em></td>
<td>Group (pair)</td>
<td>21 (4)</td>
<td>Day/Dusk</td>
<td>0.24 (0.29)</td>
<td></td>
</tr>
<tr>
<td><em>Zebrasoma flavescens</em></td>
<td>Group</td>
<td>29</td>
<td>Day/Dusk</td>
<td>0.60</td>
<td></td>
</tr>
<tr>
<td>Labridae</td>
<td><em>Calotomus carolinus</em></td>
<td>Pair</td>
<td>4</td>
<td>Daytime</td>
<td>5.44</td>
</tr>
<tr>
<td><em>Chlorurus sordidus</em></td>
<td>Group (Pair)</td>
<td>52 (3)</td>
<td>Daytime</td>
<td>0.68 (1.08)</td>
<td></td>
</tr>
<tr>
<td><em>Epibulus insidiator</em></td>
<td>Pair</td>
<td>15</td>
<td>Daytime</td>
<td>4.39</td>
<td></td>
</tr>
<tr>
<td><em>Oxycheilinus unicristatus</em></td>
<td>Pair</td>
<td>3</td>
<td>Daytime</td>
<td>6.41</td>
<td></td>
</tr>
<tr>
<td>Mullidae</td>
<td><em>Parupeneus insularis</em></td>
<td>Pair</td>
<td>3</td>
<td>Dusk</td>
<td>5.90</td>
</tr>
<tr>
<td><em>Parupeneus multifasciatus</em></td>
<td>Pair</td>
<td>2</td>
<td>Dusk</td>
<td>5.34</td>
<td></td>
</tr>
<tr>
<td><em>Chaetodon unimaculatus</em></td>
<td>Pair (Sneaker)</td>
<td>1 (1)</td>
<td>Dusk</td>
<td>8.14 (5.75)</td>
<td></td>
</tr>
<tr>
<td>Pleuronectiformes</td>
<td><em>Bothus mancus</em></td>
<td>Pair</td>
<td>1</td>
<td>Daytime</td>
<td>6.07</td>
</tr>
<tr>
<td>Tetraodontiformes</td>
<td><em>Ostracion meleagris</em></td>
<td>Pair</td>
<td>2</td>
<td>Dusk</td>
<td>20.18</td>
</tr>
</tbody>
</table>

Orders represent monophyletic groupings, and represent the phylogeny of percomorph fishes (Wiley and Johnson, 2010)
events were defined as those involving only one dominant courting male and one female. Dominant male fishes were observed making courtship displays directed at specific females positioned near the substrate. Occasionally, secondary non-courting streaker males were observed rushing upwards attempting to simultaneously release sperm in competition with the principal dominant male (see Thresher, 1984). These events were categorized as pair-spawning with streakers, only observed once in our recordings. Group-spawning events consisted of an individual female ascending in the water column closely followed by two or more males. In this case many fishes were involved in group courtships (milling), with no dominant males displaying in the water column. Nine species were categorized as pair-spawners and four species were classified as group-spawners (Table 1). However, seven pair-spawning events were recorded among species categorized as group-spawners, usually at moments of low fish density, before group-spawning occurred.

Daytime spawns were defined as spawning events occurring before 19:00 h (10:14–18:53) and dusk spawns as those occurring after 19:00 h local time (19:03–19:52), in low light levels but bright enough to record fish behaviors. Based on this classification our species were categorized as both daytime and dusk spawners (Table 1). However, in our recordings, group-spawning surgoenfishes (A. nigroris, C. strigosus, and Z. flavescens) were considered to possess anti-predatory morphological adaptations (defensive spines and laterally compact bodies), which are absent in the parrotfish C. sordidus (Thresher, 1984; Godin, 1997).

Non-parametric statistical tests (Mann-Whitney U and Kruskal-Wallis H) were employed to compare spawning ascent data grouped by species (Kruskal-Wallis $H=120.02$; $P<0.001$; $n=13$ categories), families (Kruskal-Wallis, $H=92.14$; $P<0.001$; $n=7$ categories) and orders (Kruskal-Wallis $H=67.85$; $P<0.001$; $n=5$ categories) indicate differences in spawning ascent times between these phylogenetic groupings. But further analyses show that these differences are driven by the short group-spawning ascents performed by 3 surgeonfish and 1 parrotfish species), which were significantly shorter (median $=0.48$ s; range $=0.14–2.03$ s) than pair-spawning events (median $=5.00$ s; range $=1.88–21.79$ s) (Mann-Whitney U test; $U=512$; $n_1=138$; $n_2=45$; $P<0.001$; Fig. 1). Only one family of fishes (Scaridae) had daytime spawning species that spawned in pairs (Calotomus carolinus) and predominantly in groups (Chlorurus sordidus), displaying very different ascent durations (5.44 and 0.68 s respectively).

Each pair-spawning species was observed spawning at either day or dusk, but never during both periods. No significant differences were found when grouping pair-spawns into daytime and dusk periods (Mann-Whitney U test; $U=73$; $n_1=28$; $n_2=9$; $P=0.06$). There were no differences in duration of pair-spawning ascents between species (Kruskall-Wallis $H=9.59$; $P=0.295$; $n=9$ categories; Fig. 1) nor when pair-spawning species were grouped by taxonomic orders (Kruskall-Wallis $H=6.20$; $P=0.102$; $n=4$ categories). The species with the longest spawning ascent was Ostracion meleagris, a dusk spawning toxic trunkfish with poor swimming capabilities (Walker, 2000), and the pair-spawning species with the shortest was Epibulus insidiator, a daytime spawning wrasse. The butterflyfish Chaetodon unimaculatus was recorded twice, a single pair-spawning ascent of 8.14 seconds and another ascent with a third streaking male of 5.75 seconds.

Fig. 1 Average spawning ascent durations (+ standard error) for species spawning in pairs at daytime (white background) and at dusk (dark gray), and in groups (light gray; daytime and dusk combined)
All four group-spawning species were recorded spawning at both daytime and dusk periods (Fig. 2). The duration of spawning ascents did not vary significantly between day and dusk spawning events within each species (Mann-Whitney U tests; P > 0.05; see Fig. 2 for details). After combining daytime and dusk group-spawns for each species, the surgeonfish *C. strigosus* showed significantly shorter ascent durations than the other three group-spawning surgeonfish species (Kruskal-Wallis $H=41.67; P < 0.001; n=4$ categories; Fig. 2).

![Fig. 2](image)

Figure 2: Average spawning ascent durations (± standard error) for group-spawning species at daytime (□) and dusk (■), showing no intra-specific diel differences

$A. nigroris$ $U=66; n1=39; n2=5; P=0.25$; $C. strigosus$ $U=26; n1=12; n2=5; P=0.87$; $Z. flavescens$ $U=68; n1=20; n2=8; P=0.56$. Asterisks indicate inter-specific significant differences in ascent duration by a Kruskal-Wallis H-Test for overall spawning durations (day and dusk data combined) ($H=41.67; P < 0.001; n=4$ categories).

3 Discussion

Adult predation risks are hypothesized to influence spawning behaviors of reef fishes, specifically the spawning ascents of pelagic spawning species (Johannes, 1978; Lima and Dill, 1990). At the study location of Mustin’s Gap in Johnston Atoll, the high complexity of the benthic substrate provides shelter and protection against piscivorous predators, and mortality rates of group-spawning reef fishes are considerably higher during spawning ascents than during courtship and non-spawning behaviors (Sancho, 2000; Sancho et al., 2000a). Predation attempts on pair-spawning fish were rarely observed at the spawning aggregation site, most attacks occurring on group-spawning events (Sancho et al., 2000a). As we initially hypothesized, group-spawning species had significantly shorter ascent durations than pair-spawning species. This finding suggests that pair-spawning ascent behaviors are not as influenced by elevated predation risks as group-spawning ascent behaviors, a result predicted by the safety assurance hypothesis which proposes that courtship displays by males in pair-spawning fishes indicate low predation risk at the mating site (Warner and Dill, 2000).

Our second hypothesis predicted that day spawning species would have shorter ascents than those spawning at dusk, based on diel changes in predation risk of adults, which were significantly higher at Mustin’s gap during daytime hours (Sancho et al., 2000a), since the main predator of reef fishes at the site, *Caranx melampygus*, is a diurnal piscivore (Potts, 1980; Sudekum et al., 1991; Holland et al., 1996). No changes in spawning ascent duration were detected between fishes spawning in pairs during the day and dusk, which suggests that successful spawning ascents in pair-spawning species are performed independently of the predatory fish diel activities at the spawning site. This again indicates the likely role of male courtship as a “safety assurance” to females before a pair-spawning ascent is initiated (Warner and Dill, 2000). Female fishes in this study were of small sizes, potentially susceptible to attacks by the piscivores observed at the spawning grounds. The exception was the relatively larger peacock flounder *Bothus mancus*, which displayed a spawning rush duration similar to the other smaller pair-spawning species, again indicating that predatory risks do not seem to influence pair-spawning rushes.

No clear influences of phylogeny on the spawning ascent durations measured were observed. Spawning differences among group-spawners did not match predicted phylogenetic patterns, and no significant differences were found among pair-spawning fishes. The study of possible influences of phylogeny on rushes of broadcast spawning reef fishes will benefit from broader and more extensive surveys, as well as further resolution of the phylogenetic relationships among perciform fish taxa (Wiley and Johnson, 2010).

The timing of the release of gametes during a pelagic spawning rush seems to be determined by the female, and it was estimated to occur when females (or the leading fish when sex could not be determined) stopped ascending, changed direction and initiated a descent (see Thresher 1984 for review). Direct observations of egg release were rare, though clouds of sperm released by males were observed. In pair-spawning species with differentiated sexes, females always initiated the
spawning descent before males, leading us to believe that they complete gamete release before their mates. Our observations suggest that in pair-spawns female mate choice occurs before initiating spawning ascents and females are likely responsible for determining the spawning ascent behavior. In pair-spawning species observed in this study, the spawning sequences loosely occurred as follows: (1) the female chooses a mate, on occasions among multiple males courting in the water column, and initiates a spawning ascent; (2) she leads the ascent through the water column with the male by her side or trailing slightly behind her, on occasions still performing courtship displays; (3) the female determines the end of the ascent by releasing eggs, quickly changing swimming direction and initiating a descent; (4) the trailing male releases sperm (visible in video recordings) at the location where eggs were released and eventually descends independently of the female. The long ascent durations of pair-spawners observed in the study could be explained as an adaptation by females to insure mate choice selection and avoid sperm competition from conspecific males (Myrberg et al., 1989). Our study can only provide anecdotal data from two recorded spawning ascents by the butterflyfish Chaetodon unimaculatus, displaying a longer ascent in a pair-spawn than in the presence of a streaker male, which conforms to the prediction of sperm competition avoidance by females. The trunkfish Ostracion meleagris has poor swimming capabilities (Walker, 2000) and displayed the longest spawning ascent duration of all species studied, an expected result since this toxic and armored species spawns in pairs at dusk, all characteristics that indicate a release from predatory risks. A previous study showed how height of spawning ascents in the trunkfish O. meleagris seems to be influenced by the presence of streaker males and not predation risks, thus resulting in spawning occurring further from the substrate when sperm competition is high (Sancho, 1998). An argument suggested against the avoidance of sperm competition as a possible mechanism influencing spawning behaviors are the higher fertilization rates achieved when spawning with multiple males (Marconato et al., 1997), though there is no direct evidence that females use differential fertilization success in their reproductive decisions (Petersen et al., 2001). Since predation risks during pair-spawns are low and females seem not to make reproductive decisions based on egg fertilization rates, the decision by females to stop the spawning ascent and release eggs is most likely influenced by the appreciated risk of eggs being preyed upon by benthic planktivorous predators (Johannes, 1978) and the avoidance of potential sperm competition from conspecific male fishes, which disrupts female mate choice. Further comparisons between pair-spawning rushes in the presence and absence of streaker males would help address the later hypothesis.

As mentioned above, overall group-spawning species had significantly shorter spawning ascent durations than pair-spawners. All group-spawning species observed were of relative small sizes, and were susceptible to predation by piscivores (Sancho et al., 2000a). We did not detect any changes in ascent duration within group-spawning species between daytime and dusk periods, though our data were very limited. The existence of anti-predatory morphological adaptations in certain group-spawners did not appear to have an influence in determining the ascent durations of the 3 surgeonfish species and the single group-spawning parrotfish Chlorurus sordidus, confirming earlier indications that caudal spines and deep bodies do not effectively protect spawning surgeonfishes from piscivorous jacks Caranx melampygus and snappers Aphareus furca at our study site (Sancho et al., 2000a). Of the four group-spawning species studied, the surgeonfish Ctenochaetus strigosus with the shortest spawning ascent duration defied two expectations based on the idea of predation risk avoidance influencing spawning ascent behavior: spawning when predation risk was lowest (dusk) and possessing potential anti-predatory adaptations characteristic of surgeonfish. But C. strigosus spawn in smaller group sizes (average of 3.7 individuals per rush) than the other three group-spawning species (all with averages >10 individuals per rush), and therefore has higher risks of predation per individual in a spawning rush. Therefore, predation risks of female C. strigosus are higher than for other group-spawning species since they spawn in smaller groups, which would explain the shorter spawning durations for this specific surgeonfish. These results indicate that changes in risks of predation due to spawning group size may influence the spawning ascent durations of group-spawners, but ascent duration is not influenced by diel activity cycles of predators or the existence of anti-predatory morphological adaptations in surgeonfishes. The short ascent durations of group-spawning species could partially be explained as an adaptation for mate selection by females, an idea supported by the longer ascent durations of group-spawning species with larger group sizes which benefit from decreased individual risks of predation of rush-leading females. However, our
observation of significantly shorter ascent durations of group-spawners than pair-spawning species also conforms to the alternative hypothesis of group-spawning females selecting mates by performing brief ascents, under the assumption that the most “fit” males will be the fastest individual able to reach the released eggs first. Behavioral studies on group-spawning Atlantic cod (Gadus morhua, L.) indicate that the initial courtship behavior of benthic circling of females by males prior to spawning ascent is a behavior controlled by females, giving them the opportunity to investigate the quality of the males and select specific individuals as mates (Hutchings et al., 1999). Overall, male paternal dominance in this temperate species seems to be positively influenced by male body size (Hutchings et al., 1999; Bekkevold et al., 2002). Genetic paternity analysis of an observed single spawning event showed how the male closest to the female urogenital opening at the time of egg release fertilized 83% of the eggs, with two other males fertilizing 11% and 4% of the remaining eggs (Hutchings et al., 1999). Body size is correlated with swimming speed in most fishes (Wardle, 1975), so females in spawning aggregations could easily select the largest mates by performing fast swimming ascents.

The conclusions in this study are based on the comparison of multiple species of reef fishes spawning at a single spawning location, responding to the specific set of local conditions found in the location (Sancho et al. 2000a, b). Further comparisons with spawning ascent measurements at other locations, if possible with the same species of fishes, are needed to confirm if the intra and interspecific patterns described in this study are observed across multiple spawning sites, and if spawning ascent behaviors change with locally varying predation risks and sperm competition regimes. Because of the plasticity of spawning behaviors of reef fishes in response to local conditions (see Warner 1991, 1997), we expect that spawning ascent durations will be different at other locations, but will follow the functional responses delineated in this paper. We conclude that longer spawning ascent durations in pair-spawning reef fish species are influenced by the threat of predation posed to spawned eggs and mate choice by females rather than the predatory risks faced by adults. Spawning ascent duration in group-spawning species are likely influenced by adult predation risks and female mate selection processes. In pair-spawning species, the duration of spawning ascents were not influenced by the risk of predation faced by spawning adults. For group-spawning species, spawning ascent duration was influenced by the size of the spawning group: shorter durations for small groups and longer for larger groups. Further investigations of spawning ascent heights and swimming speed determination of spawning ascents would help better understand selective forces influencing spawning rush behaviors and mate selection processes by females in marine pelagic spawning fishes, information that could be useful for management of fishes with small population sizes (Rowe and Hutchings, 2003; Adreani et al., 2004).

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