

Predator-prey relations at a spawning aggregation site of coral reef fishes

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ABSTRACT: Predation is a selective force hypothesized to influence the spawning behavior of coral reef fishes. This study describes and quantifies the predatory activities of 2 piscivorous (*Caranx melampygus* and *Aphareus furca*) and 2 planktivorous (*Melichthys niger* and *M. vidua*) fishes at a coral reef fish-spawning aggregation site in Johnston Atoll (Central Pacific). To characterize predator-prey relations, the spawning behavior of prey species was quantified simultaneously with measurements of predatory activity, current speed and substrate topography. The activity patterns of piscivores was typical of neritic, daylight-active fish. Measured both as abundance and attack rates, predatory activity was highest during the daytime, decreased during the late afternoon, and reached a minimum at dusk. The highest diversity of spawning prey species occurred at dusk, when piscivores were least abundant and overall abundance of prey fishes was lowest. The abundance and predatory activity of the jack *C. melampygus* were positively correlated with the abundance of spawning prey, and therefore this predator was considered to have a flexible prey-dependent activity pattern. By contrast, the abundance and activity of the snapper *A. furca* were generally not correlated with changes in abundance of spawning fishes. Spawning prey fishes were more common over substrates with complex topography, where refuges from piscivores were abundant. Piscivores differentially selected group-spawning species during spawning rushes over pair-spawning and non-spawning fishes. Overall attack rates by piscivores on adult spawning fishes were higher than by planktivores feeding on recently released eggs. The triggerfishes *M. niger* and *M. vidua* fed most actively at dusk and selected as prey those species of reef fishes that produced eggs of large size.

KEY WORDS: Predator-prey interactions · Predation · Piscivory · Planktivory · Spawning · Coral reef fishes

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INTRODUCTION

Predation is an important force in the evolution of fishes and in the regulation of fish populations in coral reef ecosystems (Hixon 1991). Predation affects fishes at different life stages, such as eggs and larvae (via planktivory) as well as juveniles and adults (via piscivory). For example, predation of juvenile fishes has been hypothesized to be a major post-settlement process that influences the numbers of adult fishes on coral reefs

(Hixon 1991, Jones 1991, Hixon & Carr 1997, Caselle 1999). Many hypotheses formulated to explain the reproductive behavior of reef fishes are based on risks from piscivorous or planktivorous predation, including explanations for the timing, location and behavior of reproduction in coral reef fishes (Johannes 1978, Lobel 1978, Thresher 1984, Shapiro et al. 1988, Robertson et al. 1990, Robertson 1991). However, both the high variance in predation reported and the lack of quantitative data on several aspects of predation and reproductive behavior make it difficult to adequately test these hypotheses (Robertson 1991). In this paper we examine the hypotheses concerning the influence of predation on the reproductive biology of coral reef fishes.

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Mating can often be a period of increased vulnerability to predators, and piscivory can be intense on adult reef fishes while they are spawning (Thresher 1984, Moyer 1987). The same traits that may enhance mating success in fishes, such as increased activity and visibility in males, can also increase their susceptibility to piscivory (Lima & Dill 1990). Predation of reef-fish eggs can also be very intense during spawning (Robertson 1983, Moyer 1987). The effects of planktivores on fish populations can be direct, through the consumption of propagules (Hobson 1991), or indirect, by influencing the reproductive behavior of reef fishes (Johannes 1978).

Several hypotheses can be used to make predictions concerning diel activity of predators, predator selectivity, and the relationship between prey spawning-behavior and vulnerability to predators. For this study, hypotheses regarding predator-prey relationships among piscivores, planktivores and spawning fishes (Hobson 1968, Johannes 1978, Thresher 1984, Shapiro et al. 1988, Robertson 1991) were used to generate alternative predictions that were tested using simultaneous observations of predator and prey species at a single study site. These hypotheses are:

(1) *Predator activity exhibits some fixed or random diel pattern at spawning sites.* This hypothesis suggests that physical or biological processes other than prey behavior may influence the timing of predator activity on coral reefs. The changes in absolute intensity of light during crepuscular periods may make fishes most vulnerable to piscivory during these times (Munz & McFarland 1973). Alternatively, predation might decrease at the end of the day after long successful periods of piscivory due to satiation of diurnally active predators. In these cases we would not expect predation patterns to follow patterns of prey availability at spawning sites. In fact, if predation influences the timing or location of spawning of prey fish, prey would be expected to spawn during moments and locations of low predatory activities.

(2) *Predators change their activities in response to prey reproductive behavior.* Because the timing and location of spawning in coral reef fishes is somewhat predictable, predators might be more common or active at spawning locations during times of heightened reproductive activity. This assumes that some reproductive behaviors lead to an increase in prey vulnerability, which appears to be true (Moyer 1987, reviewed by Lima & Dill 1990). Under this hypothesis, predator activity at the spawning site is expected to increase in some way with the reproductive activity of vulnerable or preferred prey species.

(3) *Risk of predation determines the choice of spawning location by prey.* Hypotheses regarding the effect of predation on the choice of spawning sites by reef

fishes predict that they will spawn at locations with abundant refuges from piscivores (Hugie & Dill 1994), or at locations with fast, outflowing current speeds that will reduce the exposure of eggs to benthic predators (Johannes 1978). Small coral reef fishes typically use holes and crevices in the substrate as refuges when attacked by piscivores (Hixon 1991, Hixon & Carr 1997). Many studies describe reef fishes spawning over specific substrate formations (see Lobel 1978, Shapiro et al. 1988, Warner 1988), but no quantitative measurements of the availability of refuges at spawning locations exist. By estimating the availability of refuges in both spawning and non-spawning sites, the importance of piscivory in determining location of spawning sites can be inferred. Reef fishes often migrate to spawning aggregation sites which have strong currents (Robertson 1983, Thresher & Brothers 1985, Moyer 1989, Colin & Bell 1991), but within these aggregation sites current speeds have rarely been compared between discrete spawning and non-spawning areas (Appeldoorn et al. 1994).

(4) *Interspecific variation in predation risk is influenced by prey morphology and behavior.* Predation risks can vary not only with the behavior of the prey, but also with the body morphology of prey. Piscivores should select species lacking morphological adaptations that make ingestion difficult, such as deep bodies, defensive spines or toxic substances (Godin 1997). Planktivores feeding on recently spawned eggs should select prey species in an analogous manner, selecting species with large visible eggs over those with small inconspicuous ones. This hypothesis predicts that predators with flexible diel activity patterns should act independently of the activity patterns of species with significant anti-predatory adaptations, but be influenced by the activity patterns of those species without adaptations.

The interspecific variation in vulnerability to predators may also affect how reef fishes respond to piscivores. Fishes that are less vulnerable to predators, for whatever reasons, should be less likely to spawn at the safest times and places on the reef if other places provide increased fitness benefits to offspring (Gladstone & Westoby 1988).

The present study analyzes the behavior of 2 piscivorous (*Caranx melampygus* and *Aphareus furca*) and 2 planktivorous (*Melichthys niger* and *M. vidua*) predators at a spawning aggregation site of reef fishes. By quantifying predator and prey abundance, current speed and bottom topography, the timing and location of spawning events, and the rate of attempted and successful piscivorous attacks, we hoped to shed light on the relative importance of predatory processes in shaping the spawning behavior and predator-prey relationships of coral reef fishes.

MATERIALS AND METHODS

Data for this study were collected during April/May of 1994 and 1995 at Johnston Atoll (Central Pacific), in a reef channel which was used as a resident spawning aggregation site (*sensu* Domeier & Colin 1997) by various species of pelagic-spawning reef fishes. This channel is called Mustin's Gap, is 70 m long and 28 m wide, with an average depth of 4.5 m, and crosses the NW reef crest of the Atoll (Fig. 1A). Substrate composition consists of a mix of live tabular coral formations dispersed among dead coral boulders and fine rubble. Currents at the reef channel are bi-directional, influenced by both tides and waves (Sancho et al. 1997, 2000).

Behavior of predators and prey. Observations of the behavior of piscivores and prey were done by a single observer (G.S.) while SCUBA-diving. Data sampling was limited to a rectangular area of 170 m² (Fig. 1B). Observations were made from a fixed position located at a distance of 5 m from the sampling area, annotating each minute the presence of any piscivores above the sampling area (score = 1), or their absence (score = 0). This 1–0 scoring (Altmann 1974) was done continuously for 2 consecutive 15 min periods. Abundance of piscivores was expressed as the percentage of 1 min sampling intervals when predators were present above the sampling area, during a 15 min period. The 2 piscivorous species that were routinely observed attacking reef fishes at Johnston Atoll were the 2 species monitored: *Caranx melampygus* (Carangidae, commonly known as jacks) and *Aphareus furca* (Lutjanidae, or snappers). *C. melampygus* typically shows active roaming predatory behaviors over shallow reefs during daytime hours (Potts 1980, Holland et al. 1996), feeding mostly on shallow-water reef fishes (Potts 1981, Sudekum et al. 1991). *A. furca* is found in the same shallow-reef habitats across the tropical Indo-Pacific region as *C. melampygus* (Myers 1991). Little information is available on the diet and predatory behaviors of this snapper, but casual observations indicate that reef fish are an important component of its diet and it is less mobile than *C. melampygus* (Randall 1955, Hobson 1974, Potts 1981, G.S. pers. obs.). Other large transient piscivorous species that were sighted during this study, but not observed attacking reef fishes, included the sharks *Triaenodon obesus* (Hemigaleidae) and *Carcharhinus amblyrhynchos* (Carcharhinidae), as well as *Caranx ignobilis*, *C. lugubris*, *C. sexfasciatus*, *Scomberoides lysan* (Carangidae) and *Sphyraena barracuda* (Sphyraenidae).

Inside the sampling area, attacks by piscivores on reef fishes were recorded, as well as the hunting strategy employed by the attacker (Sancho 2000) and the specific motor pattern displayed by the intended prey

fish at the moment of the attack. Two spawning-related motor patterns, 'bobbing' and 'rushing' were identified in these observations. 'Bobbing' consisted of courtship-related behaviors by pre-spawning fishes and involved fish interacting while swimming above the substrate (0.1 to 2 m approximately). This motor pattern combines what was described for *Thalassoma cupido* as 'bobbing' and 'milling' behaviors (Meyer 1977, Moyer 1987). 'Rushing' consisted of spawning ascents up into the water column.

Spawning in fishes that release pelagic eggs typically occurs after the individuals rapidly swim upwards through the water column (0.5 to 4.5 m above the bottom). A pair-spawn consists of a female and male rushing upward, with both releasing gametes at the apex of the spawning rush. Occasionally 1 or more additional males (streakers) join the pair just as they are spawning. Group-spawning consists of a female courting and

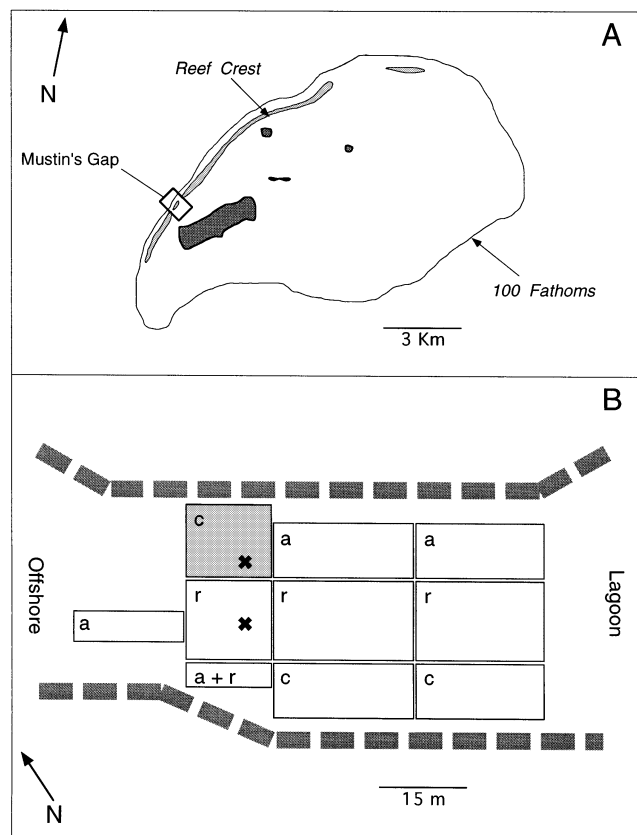


Fig. 1. (A) Map of Johnston Atoll showing location of spawning aggregation site, Mustin's Gap. (B) Schematic representation of reef channel of Mustin's Gap showing position and size of 10 sampling areas used in topographical and fish-census measurements; dominant substrate elements in each area are *Acropora* spp. (a), broken coral heads (c) and fine coral rubble (r). (✕) Positions of current meters. The shaded area (c) shows where behavioral observations of piscivores and spawning fish were made

mating with a group of >1, typically 4 to 20, males in a spawning rush. Successful attacks or kills were recorded when prey capture by a piscivore was observed.

In the spring of 1994, a total of 31 h of behavioral observations of predators took place between dawn and dusk (07:00 to 20:00 h), while in the spring of 1995 a total of 46.5 h observations were concentrated in the early afternoon (13:00 to 16:30 h) and dusk (19:00 to 20:00 h) periods. Spawning and abundance of prey species were simultaneously recorded during these observations periods (Sancho et al. 2000). Spawning sequences of various species were video-recorded in May of 1994, and the duration of spawning rushes was measured from the video-recordings by counting the total number of frames per rushing event (24 frames s^{-1}). The time spent rushing by each species at the spawning grounds was estimated by multiplying the average spawning rush duration by the total number of spawns observed for each species in a given time. Only data from times when fish were actively spawning were used for this calculation (Sancho et al. 2000).

During observations of piscivorous fishes, all observed cases of predation by mobile planktivores (*Melichthys niger* and *M. vidua*) on recently released propagules were also recorded. Both of these triggerfish (Balistidae) species were observed following spawning fishes during their ascent and feeding on clouds of gametes. Data on egg sizes of prey species observed spawning at Johnston Atoll were obtained from published values of the individual species if possible, or otherwise from a member of the same genus.

Topographical and current-speed measurements. In order to study the potential effects of predation in the choice of prey spawning grounds, we measured the topographical complexity of the substrate, water velocity above the substrate, and abundance of spawning reef fishes at the reef channel. A large section (1820 m^2) of the reef channel was delineated and divided into 10 defined sampling areas (Fig. 1). The bottom topography was quantified using a modification of the ratio of linear versus contoured distance technique (Risk 1972). This method was chosen because it is highly sensitive in detecting bottom structures with deep crevices and holes (McCormick 1994), which are used as refuges by prey fish (Hixon & Beets 1989, Hixon 1993). Five quadrates (1 m^2 each) were randomly positioned in each of the 10 sampling areas. The contoured distance was measured with a fine-link chain applied over the substrate along the 2 middle axes (1 m in length) of all 50 quadrates. A topographic index (TI), referred elsewhere as substrate rugosity index, was calculated as the ratio of linear distances (1 m) to contoured distances (McCormick 1994). Flat

surfaces have TI values of 1, while more complex surfaces have values closer to 0.

Two current meters (S4 InterOcean, San Diego) were mounted on PVC tripods at 2 contiguous sampling areas (Fig. 1B) with different topographic complexity values. The first current meter was mounted 1.5 m above a complex substrate composed of broken coral heads, while the second one was located 1.7 m above a smooth substrate composed of coral rubble. They recorded current velocity simultaneously every second. Simultaneous data used for comparative analyses were recorded on 21 May (10:05 to 11:05 h) and 25 May (13:45 to 14:59 h) of 1994, for which consecutive 1 s recordings of current speed were combined into 1 min averages.

Fish censuses at the reef channel were performed on 14 occasions during May 1995 by swimming down the reef channel and estimating the number of fishes above each of the 10 sampling areas. Sampling was done in the afternoon (13:00 to 16:00 h) and only fishes showing courting and spawning behaviors were counted.

Data analyses. Observed diel distributions of predatory activities were compared with expected distributions, based solely on the relative sampling effort, by using *G*-tests for goodness of fit modified with a William's correction. To detect differences between daytime and dusk predatory activity rates, Mann-Whitney *U*-tests were used. The statistical independence of pairs of variables was analyzed using 2-way *G*-tests for independence at a 95% significance level. The distribution of successful piscivorous attacks at different time periods and among different prey species was analyzed by a Fisher's exact-probability test. Simultaneous current speed recordings were compared through a paired *t*-test analysis for equal variances. Significance of correlations among variables was established through Spearman rank-correlation tests. All statistical procedures were done according to Sokal & Rohlf (1995).

RESULTS

Diel spawning patterns

A total of 9642 spawns by 34 fish species were observed during monitoring of predatory activities at the Mustin's Gap spawning grounds (Table 1). The diel distributions of spawning fish abundance and spawning activity in 1994 (Fig. 2) were significantly different (*G*-test; $p < 0.001$) from those expected when considering sampling effort alone. Highest abundance and spawning rate values occurred during the afternoon hours (13:00 to 19:00 h), with the lowest values

recorded at dusk (19:00 to 20:00 h). The diel distribution pattern of the 2 most abundant species spawning at the sampling site, *Chlorurus sordidus* (Scaridae) and *Acanthurus nigroris* (Acanthuridae), had shorter periods of peak abundance and activities (13:00 to 17:00 h) and a more drastic decrease in activities in the late

afternoon period (17:00 to 19:00 h) than the total prey abundance distribution (Fig. 2). Neither of these 2 abundant species was observed spawning at dusk (19:00 to 20:00 h).

The number of different fish species observed spawning over discrete time intervals in 1994 increased as

Table 1. Spawning activities of reef fishes and attacks by piscivores at spawning aggregation site. Reproductive data are from all species observed spawning during 1994 and 1995 spring sampling seasons. n: no. of spawns; Mode: predominant spawning mode showing pair (P) and group (G) spawning rushes. Total attacks: total no. of piscivorous attacks; % rushing: % of attacks on rushing fish; Attack success: total attack-success rate. Proportion of spawns attacked and attack-success rates by piscivores were calculated using data on attacks and kills by *Caranx melampygus* and *Aphareus furca* from 1994 and 1995 sampling seasons combined

Family Species	n	Mode	Total attacks	% rushing	No. of kills	Attack success (%)
Aulostomidae						
<i>Aulostomus chinensis</i>	1	P				
Mullidae						
<i>Parupeneus bifasciatus</i>	59	P				
<i>Parupeneus cyclostomus</i>	1	P				
<i>Parupeneus multifasciatus</i>	90	P				
<i>Parupeneus pleurostigma</i>	1	P				
Chaetodontidae						
<i>Chaetodon citronella</i>	3	P				
<i>Chaetodon ornatissimus</i>	2	P				
<i>Chaetodon trifasciatus</i>	3	P				
<i>Chaetodon unimaculatus</i>	17	P				
<i>Megaprotodon trifascialis</i>	1	P				
Labridae						
<i>Cheilinus unifasciatus</i>	93	P				
<i>Coris gaimard</i>	105	P				
<i>Epibulus insidiator</i>	62	P				
<i>Labroides phthiophagus</i>	1	P				
<i>Gomphosus varius</i>	2	P				
<i>Novaculichthys taeniourus</i>	1	P				
<i>Thalassoma duperrey/lutescens</i>	2	P, G				
<i>Thalassoma purpuraceum</i>	3	P				
Scaridae						
<i>Calotomus carolinus</i>	14	P				
<i>Scarus perspicillatus</i>	1	P				
<i>Scarus psittacus</i>	76	G	4	100	0	0
<i>Scarus rubroviolaceus</i>	1	P				
<i>Chlorurus sordidus</i>	3749	G	135	84.4	7	5.2
Acanthuridae						
<i>Acanthurus achilles</i>	9	G				
<i>Acanthurus oliveaceus</i>	4	P				
<i>Acanthurus nigroris</i>	3461	G	98	85.7	2	2.0
<i>Ctenochaetus strigosus</i>	770	G	6	93.3	1	16.7
<i>Zebрасoma flavescens</i>	939	G	5	60.0	0	0.0
<i>Naso lituratus</i>	10	P				
Zanclidae						
<i>Zanclus cornutus</i>	5	P, G				
Bothidae						
<i>Bothus mancus</i>	8	P				
Ostraciidae						
<i>Ostracion meleagris</i>	142	P				
<i>Ostracion whitleyi</i>	5	P				
Total	9642		248	84.7	10	4.0

the day progressed (Fig. 2C). Only 3 species spawned in the morning hours, while a maximum of 16 species were observed spawning at dusk.

Piscivores

A total of 254 attacks by piscivores were observed on 5 different prey species: *Chlorurus sordidus*, *Scarus*

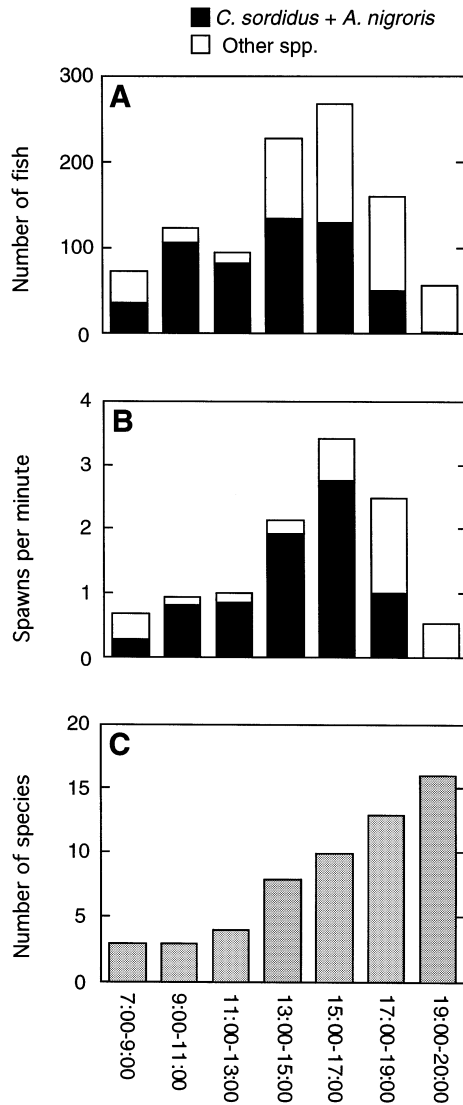


Fig. 2. Diel distribution of abundance of spawning fishes (A), spawning rate (B) and number of species (C) at Mustin's Gap during 1994. Data from 15 min observation periods ($n = 123$). Fish abundances are averages and include all species observed spawning ($n = 24$); spawning rate is expressed as average number of spawns (number of spawns observed = 3754) per minute observation. Black bars = abundance and spawning rate of *Chlorurus sordidus* and *Acanthurus nigroris* only, white bars = those for the other species. Abscissa: time of day (h)

psittacus (Scaridae), *Acanthurus nigroris*, *Zebrasoma flavescens* and *Ctenochaetus strigosus* (Acanthuridae). All 5 species are predominantly group spawners in the reef channels of Johnston Atoll, and all observed attacks occurred during bobbing or rushing of the prey, with no attacks observed on feeding or migrating fishes. The attack rates of the 2 piscivores, *Caranx melampygus* and *Aphareus furca*, were similar during 1994 and 1995 (Table 2). The proportion of attacks by *C. melampygus* and *A. furca* (50 vs 32 attacks in 1994; 123 vs 49 in 1995) did not vary significantly between the 2 sampling years (G -test of independence; $p > 0.05$).

Ten of these attacks resulted in the successful capture and ingestion of prey (Table 2). The combined total success rate of attacks, defined as the proportion of attacks leading to prey capture, was 3.9%. The attack success rates for *Caranx melampygus* (4.0%) and *Aphareus furca* (3.7%) were not significantly different (G -test of independence; $p > 0.05$).

Diel abundance of piscivores and attack distributions were significantly different from expected distributions based solely on the sampling effort at each time category for both *Caranx melampygus* and *Aphareus furca*, and for both years of sampling (G -test; $p < 0.001$). The abundance of *C. melampygus* at the spawning grounds during 1994 increased during the day, reaching a maximum during the early afternoon (13:00 to 15:00 h), then decreased in the late afternoon, reaching a minimum at dusk (Fig. 3). Abundance of *A. furca* was constant during all daytime periods, abruptly decreasing at dusk (Fig. 3). In 1995, the abundance values of *C. melampygus* and *A. furca* were significantly higher during the afternoon hours than at dusk (Mann-Whitney U -test; $p < 0.001$ for both species).

To further investigate the relation between predator and prey abundance, the abundance of the 2 prey species selected by piscivores (*Chlorurus sordidus* and *Acanthurus nigroris*) were compared with the specific values of predator abundance through a linear regression analyses over a short-time scale (15 min), using 123 paired measurements collected in 1994. For *Caranx melampygus*, the joint abundance of the 2 prey species explained an important portion ($R^2 = 0.52$, linear regression) of the variance in abundance of this piscivore at the spawning grounds (Fig. 4). Prey abundance was not significantly correlated with the pattern of abundance of *Aphareus furca* ($R^2 = 0.004$, linear regression; Fig. 4).

The timing of attacks on reef fishes was similar to the abundance distributions of the attacking piscivores. In 1994, *Caranx melampygus* attacked spawning fishes during the morning and the early part of the afternoon, with most attacks occurring at the time period when

Table 2. Attacks by *Caranx melampygus* and *Aphareus furca* on different prey species. Numbers in parentheses: successful attacks (kills). Motor pattern of prey fish was categorized as 'bobbing' or 'rushing' when attack was observed. Indiscriminate category represents attacks that occurred when (1) specific spawning behavior of prey was not observed, or (2) attack was directed to a mixed species aggregation

Year	Prey species	Motor pattern	Attacks		
			<i>C. melampygus</i>	<i>A. furca</i>	Total
1994					
	<i>Chlorurus sordidus</i>	Rushing	26 (1)	16 (2)	45
		Bobbing	8	1	9
	<i>Acanthurus nigroris</i>	Rushing	7 (2)	4	13
		Bobbing	2	2	4
	<i>Zebrasoma flavescens</i>	Rushing	2	0	2
		Bobbing	1	0	1
	<i>Scarus psittacus</i>	Rushing	0	4	4
		Bobbing	0	0	0
	Indiscriminate		1	3	4
1995					
	<i>Chlorurus sordidus</i>	Rushing	56 (3)	10	69
		Bobbing	10	2	12
	<i>Acanthurus nigroris</i>	Rushing	37	34	71
		Bobbing	8	2	10
	<i>Zebrasoma flavescens</i>	Rushing	1	0	1
		Bobbing	1	0	1
	<i>Ctenochaetus strigosus</i>	Rushing	4 (1)	0	5
		Bobbing	1	0	1
	Indiscriminate		1	0 (1)	2
Total					
		Rushing	140	70	210
		Bobbing	31	7	38
		All	173	81	254

jacks were most abundant (13:00 to 15:00 h). The attack rates for *Aphareus furca* were highest in the early morning (07:00 to 09:00 h) and in the afternoon (15:00 to 17:00 h). During 1994, no attacks were observed for either species after 17:00 h (Fig. 3). In 1995, *A. furca* was only observed attacking during the afternoon, with no attacks at dusk, while *C. melampygus* was observed attacking spawning fishes during the afternoon and dusk. Both species had significantly lower attack rates at dusk than during the daytime period (Mann-Whitney *U*-test; $p < 0.004$ for *C. melampygus* and $p < 0.02$ for *A. furca*).

All successful attacks (10 kills) occurred between 11:07 and 15:29 h, except for 1 attack by *Caranx melampygus* directed at 3 rushing *Ctenochaetus strigosus* which occurred at 19:34 h and resulted in the capture of 1 spawning individual. However, the difference in the number of successful attacks by piscivores at daytime versus dusk was not statistically significant (Fisher's exact-probability test; $p > 0.05$) when compared with the sample size of observations recorded during each diel period.

To evaluate which prey were most vulnerable to attacks, we measured the duration of the spawning rush for different species; this varied between 0.9 and 2 s in duration (Table 3). By combining these data with the number of spawns observed in the observation area, the proportion of time spent rushing by each species while aggregated at the spawning site was calculated (Table 3); it ranged between 7.9 and 0.8%.

Of all the attack sequences observed in their entirety (Table 2), 210 attacks (84.7%) were on prey ascending into the water column in a spawning rush, while only 38 attacks (15.3%) were on fish involved in pre-spawning bobbing and milling behaviors. Comparison of the proportion of attacks by piscivores during spawning rushes with the actual time spent by each species rushing (Table 3) indicated that predators preferentially attacked their prey while they rushed above the substrate, avoiding fishes located near the substrate (*G*-test; $p < 0.001$). This selection for attacks on rushing fishes is significant, even if we consider that spawning fishes could spend up to 50% of their time rushing to release eggs (*G*-test; $p < 0.001$).

Most attacks (93.9%) were directed towards 2 prey species: *Chlorurus sordidus* and *Acanthurus nigroris*, the 2 most frequent spawning fishes at the sampling site (Table 1), that together account for 80.2% of the total number of spawns by group-spawning species at the reef channel. Comparison of the number of attacks observed with the number of spawns by each prey species revealed that both *Caranx melampygus* and *Aphareus furca* preferred *C. sordidus*, *A. nigroris* and *Scarus psittacus* as prey items over the other group-spawning species (*G*-test of independence; $p < 0.001$). Considering the total number of spawns observed, we calculated, for each individual prey species, the proportion of spawning rushes that were attacked by piscivores (Table 1). *C. sordidus* (3.0%), *A. nigroris* (2.4%) and *S. psittacus* (5.3%) suffered significantly more attacks per spawning rush (*G*-test of independence, $p < 0.001$) than did *Ctenochaetus strigosus* (0.6%) and *Zebrasoma flavescens* (0.3%).

Most attacks occurred on groups of ≥ 4 spawning fishes; only 1 attack was observed on a pair-spawning event and 1 attack on a group of 3 spawning individuals (principal male, female and streaker male). Com-

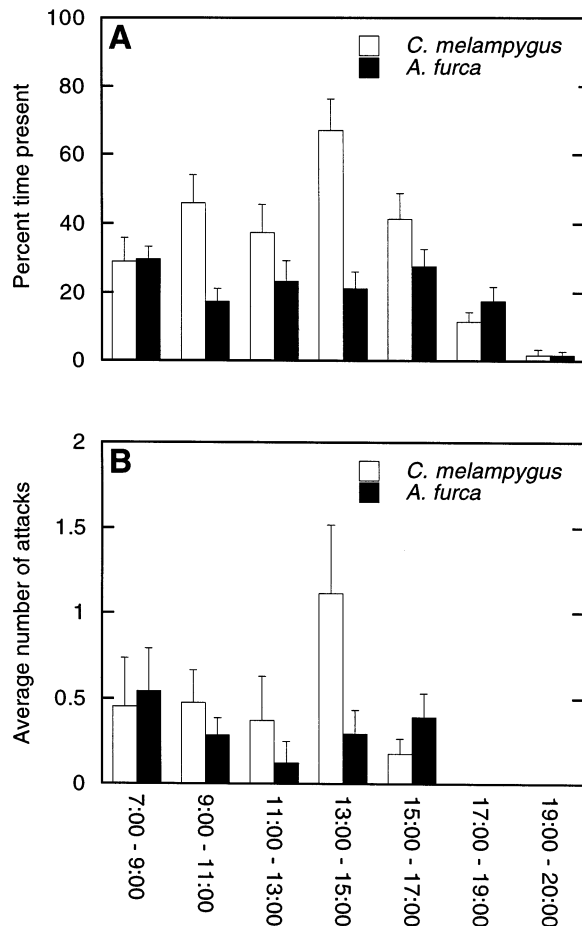


Fig. 3. *Caranx melampygius* and *Aphaeus furca*. Abundance (A) and attacks (B) during 1994. Data are averages from 15 min observations (+SE). Abscissa: time of day (h)

paring this distribution of attacks with the number of spawns involving 2 and 3 spawners (494 spawning events) versus group spawns with >4 individuals (8501 spawning events), piscivores preferred to attack prey spawning in groups, rather than in pairs or trios (*G*-test of independence; $p < 0.001$).

Considering only piscivorous attacks for which the identity of the intended prey was clearly identified by the observer (248 attacks), the total attack-success by piscivores on group-spawning fish species was 4.0% (Table 1). Attack-success rates on different group-spawning species were not statistically different (Fisher's exact-probability test; $p > 0.05$), even though they varied between 17% (*Ctenochaetus strigosus*) and 0% (*Scarus psittacus* and *Zebbrasoma flavescens*), because of the low power of the statistical test at very low specific-attack rates. The proportion of group-spawning rushes which suffered a successful predatory attack was estimated to be 0.1%.

Planktivores

Melichthys niger formed aggregations of from 2 to 15 individuals, and spent most of their time close to the surface, among breaking waves as described by Lubbock (1980), while *M. vidua* were usually observed in pairs or as single fish close to the substrate.

Attacks were observed at all times of the day (09:22 to 19:41 h), but a higher proportion of attacks occurred during the dusk period (0.303 attacks per 15 min \pm 0.144 SE) than during daytime hours (0.125 attacks per 15 min \pm 0.029 SE; *G*-test of independence; $p < 0.005$). The attack behaviors of the 2 planktivorous species on planktonic gametes were almost identical: planktivores would quickly approach groups and pairs of spawning fishes during their spawning ascent and proceed to bite in the center of the released cloud of ga-

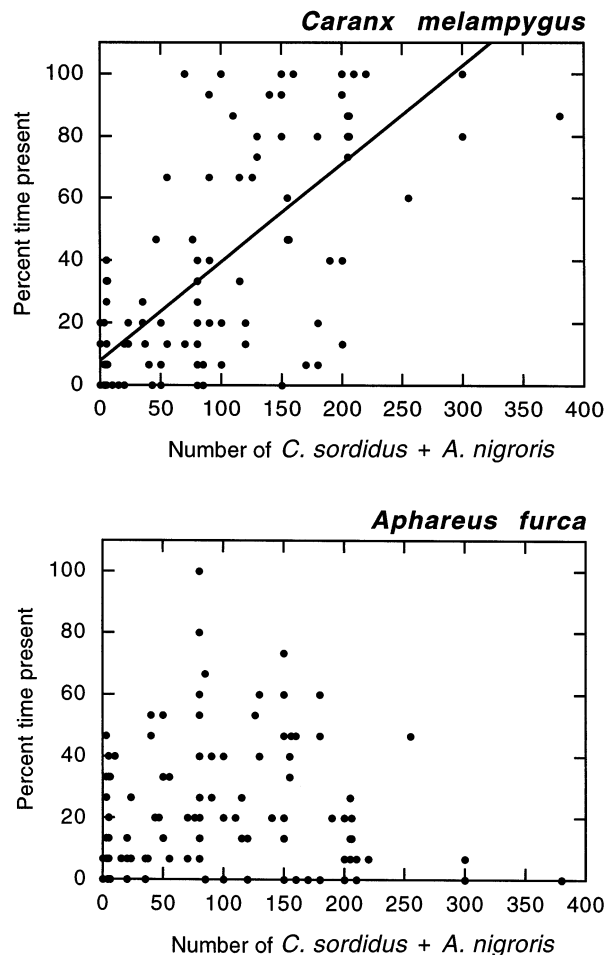


Fig. 4. Relationship between prey abundance (*Chlorurus sordidus* and *Acanthurus nigroris* combined) and abundance of piscivorous predators (*Caranx melampygius* and *Aphaeus furca*). Data points correspond to 15 min observation periods. Line indicates linear regression between *C. melampygius* presence and prey abundance ($R^2 = 0.52$)

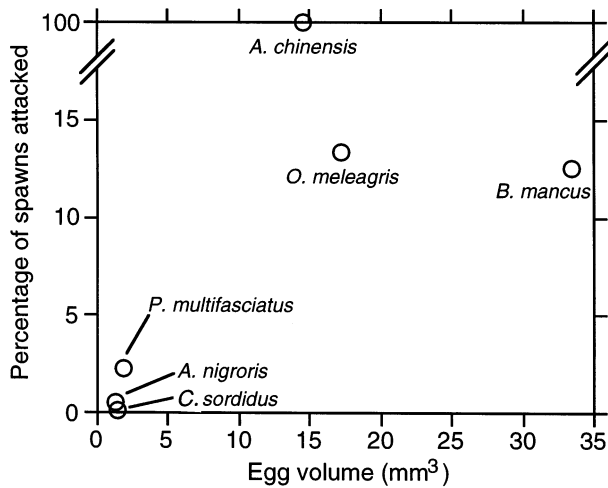


Fig. 5. *Melichthys niger* and *Melichthys vidua*. Relation between percentage of spawns attacked by mobile triggerfishes and egg volume of different spawning species. Egg volumes correspond to those of species *Aulostomus chinensis* (Watson & Leis 1974, as cited in Leis & Trnski 1989), *Chlorurus sordidus* (Colin & Bell 1991) and *Ostracion meleagris* (Leis & Moyer 1985); and of species from same genus of *Parupeneus multifasciatus* (*Parupeneus* sp.; Suzuki et al. 1980; as cited in Leis & Rennis 1983), *Acanthurus nigroris* (*A. triostegus*; Randall 1961) and *Bothus mancus* (*B. robinsi*; Jutare 1962; as cited in Martin & Drewry 1978)

metes as it drifted downcurrent. A total of 48 attacks on eggs by *Melichthys niger* (25 attacks) and *M. vidua* (23 attacks) were observed at the sampling site over the 2 yr of sampling, on both group-spawning (25 attacks) and pair-spawning events (23 attacks). The comparison of the proportion of attacks with the total number of group (7142) and pair (306) spawns recorded by the 6 species (*Aulostomus chinensis*, *Parupeneus bifasciatum*, *Chlorurus sordidus*, *Acanthurus nigroris*, *Bothus mancus* and *Ostracion meleagris*) attacked by triggerfishes revealed that these planktivores selected pair-spawning events over group-spawns (*G*-test of independence; $p < 0.001$).

One possible reason for the preference for pair-spawning species was that fishes with large eggs (Aulostomidae, Bothidae and Ostraciidae) tended to spawn in pairs at this site. Preliminary data from 151 spawns in 3 species with larger egg sizes indicate higher predation rates, suggesting that species with larger eggs are more vulnerable to predation by triggerfishes than species with small eggs (Fig. 5). Families with low proportions of spawning rushes subjected to planktivorous attacks all had small eggs, and contained pair-spawning (Mullidae) and

group-spawning (Scaridae and Acanthuridae) species. Two other families (Labridae and Chaetodontidae), with species often observed spawning in pairs at the reef channel, have small egg volumes (range of 1.20 to 1.32 mm³; Thresher 1984, Colin & Bell 1991), and were not attacked by planktivorous triggerfishes.

Spawning grounds

The abundance of group-spawning fishes was significantly correlated (Spearman's rank-correlation $r = -0.71$; $p < 0.05$) with the topographical index (TI) measurements at the reef channel (Fig. 6). Fish avoided spawning above areas of low topographical complexity, and were more abundant in areas with abundant crevices and holes (TI values < 0.5). This relation was also significant when considering individually the abundance of the 2 most abundant group-spawning species during May 1995: *Chlorurus sordidus* and *Zebrasoma flavescens* (Spearman's rank-correlation $r = -0.68$ and $r = -0.79$ respectively; $p < 0.05$).

Mean current velocities measured simultaneously at 2 adjacent sampling areas with different substrate morphologies (Site 1: TI = 0.48; Site 2: TI = 0.74), were significantly different on each of 2 independent sampling days (Student's *t*-tests; $p < 0.001$ for both days). The location with lower topographical complexity (Site 2) had slightly faster currents than the more complex area (Site 1) (47 vs 41 cm s⁻¹ average velocity), while the average density of spawning fishes was much lower at Site 2 than at Site 1 (0.06 and 0.77 fish m⁻², respectively). These results show an association between topographic complexity and current velocity at 1 pair of sites within our study location, but without data from a larger population of sites with varying TI our data are informative for our site, but may not reflect a general correlation between TI and relative water velocity.

Table 3. Duration of individual spawning rushes by 4 prey fishes (Duration), proportion of time spent rushing up into water column (Rushing time) and proportion of attacks by piscivores directed towards rushing fishes (Attacks). Selection by attacking piscivores of spawning rushes as the moment to attack their prey was established by comparing proportion of time spent rushing with proportion of attacks directed on rushing fishes

Prey species	Duration (s)	Proportion rushing time (%)	Attacks (%)	Selection ^a
<i>Chlorurus sordidus</i>	1.9	7.9	84.4	Yes
<i>Acanthurus nigroris</i>	1.1	4.9	85.7	Yes
<i>Ctenochaetus strigosus</i>	0.9	2.1	83.3	Yes
<i>Zebrasoma flavescens</i>	2.0	0.8	60.0	Yes

^a*G*-test for goodness of fit; $p < 0.001$

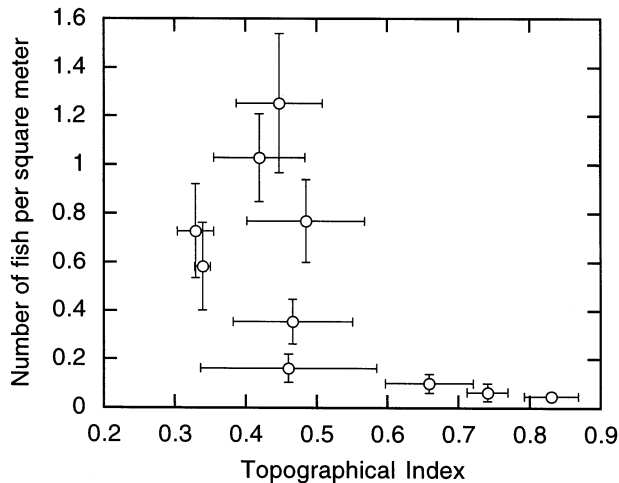


Fig. 6. Relation of density of spawning fishes (no. of fishes per m^2) with substrate topographical index (ratio of linear length to contoured length). Fish-density values (sum of *Chlorurus sordidus*, *Acanthurus nigroris* and *Zebrasoma flavescens*) are averages from 14 censuses (\pm SE); individual topographical indices values are averages from 2 diagonals from 5 quadrates (\pm SE)

DISCUSSION

Piscivores

An initial objective of this study was to describe the diel activity patterns displayed by predators at spawning aggregation sites of coral reef fishes. Predatory activities by *Caranx melampygus* and *Aphareus furca* were high during the day, decreased during the late afternoon, and were significantly lower at dusk. These results do not rule out the possibility of piscivores actively feeding at dusk somewhere else in the reef system, but predatory pressure clearly decreased at the spawning grounds in the later part of the day. These data are consistent with the diurnal activity patterns shown by other piscivores that feed on diurnal coral reef fishes (Sweatman 1984, Shpigel & Fishelson 1989, Clifton & Robertson 1993). Specifically, *C. melampygus* showed high daytime predatory activities at Aldabra Atoll (Potts 1980, 1981) and a diet mainly composed of diurnal reef fishes in the Hawaiian Islands (Sudekum et al. 1991). Sonic tracking studies in Hawaii show how *C. melampygus* actively patrol an extensive territory during daytime, while at nighttime they display 50% lower activity rates and are restricted to a distinctly smaller territory (Holland et al. 1996). Our results from Johnston Atoll are inconsistent with studies arguing for increased piscivore activities during crepuscular hours in coral reefs (Collette & Talbot 1972, Hobson 1973), an idea derived from observations of predators feeding in temperate waters (Hobson

1968) and supported by studies of piscivores feeding on schooling prey species over non-reef areas (Major 1977, Ogden & Ehrlich 1977).

The general patterns of abundance of piscivores and prey at the spawning aggregation site were similar (Figs. 2 & 3), supporting the hypothesis that predators change their activities in response to prey reproductive behavior. In addition, data from the 15 min observations showed a positive relationship between the abundance of *Caranx melampygus* and its most common prey (Fig. 4), indicating an interdependence between them (Hypothesis 2: see 'Introduction'). The reef channel where the spawning aggregation was sampled is interpreted to be part of a larger daytime hunting ground for various *C. melampygus* individuals, which patrol through it in search of food (Potts 1980). When large groups of suitable prey species aggregate to spawn, patrolling *C. melampygus* will likely locate them and stop patrolling to concentrate their hunting activities in the channel and exploit this food resource. This flexible activity pattern regulated through the abundance of prey could also explain the low abundance of *C. melampygus* at dusk, since this is the time of day when overall prey abundance is lowest. Prey-dependent changes in predator abundance have been observed in other transient carangids feeding on juvenile reef fishes (Hixon & Carr 1997).

Prey abundance was not significantly correlated with the pattern of abundance of *Aphareus furca* (Figs. 2, 3 & 4). Apart from a decrease of activity at dusk, the behavior of this species appeared independent of potential spawning prey. The limited information describing *A. furca* as a site-attached predator with low mobility (Randall 1955, Hobson 1974, Potts 1981, G. Sancho pers. obs.) supports the supposition that *A. furca* individuals were present at the spawning grounds at all times, but visual censuses only counted those individuals swimming above the substrate, during feeding and non-feeding periods, and ignored those hiding among coral formations. Thus, the abundance of *A. furca* was independent of changes in prey abundance at the spawning grounds, indicating that the presence of this predator was not affected by spawning activities of reef fishes (Hypothesis 1).

The decrease in piscivore activity at the study site at dusk (Fig. 3) could be caused by several factors, including a decrease in predator activity at low-light levels, low availability of preferred prey, or satiation. All appear possible. For example, with a measured capture rate of 3.9%, piscivores at the spawning site would need to perform approximately 25 to 50 attacks to reach an estimated daily ration of 1 to 2 prey fish per day (common for coral reef piscivores: Sweatman 1984, Kingsford 1992) and begin to approach satiation. This value seems plausible given attack rates reported for

ambushing lizardfishes averaging 27 attacks per day (Sweatman 1984), although how daily ration relates to satiation in these piscivores is not known.

Piscivores preferred to attack reef fishes when these rushed up into the water column to release gametes and temporarily became vulnerable by abandoning the reef substrate where refuges from predation exist (Hixon 1991, Hixon & Carr 1997). At the spawning aggregation site, successful attacks (kills) by piscivores only occurred on prey engaged in spawning rushes. In a similar study, Moyer (1987) described the same selection by piscivores of attacking during the rushing movements of their prey, but successful attacks were only observed on reef fishes that were bobbing close to the substrate. Both *Caranx melampygus* and *Aphareus furca* are large mobile predators, mostly performing high-speed midwater attacks (Sancho 2000). All piscivores from Moyer's study were small cryptic resident predators with ambushing attack behaviors, some with striking areas limited to a distance of only 6 to 7 cm from the substrate. The specific hunting behavior of different piscivores is likely to determine which behavioral motor pattern of spawning prey is most susceptible to predation.

Piscivores selected prey spawning in groups more than those spawning in pairs, indicating that mating behavior can affect predation patterns. Stomach-content analyses of *Caranx bartholomaei* revealed that male parrotfishes which typically spawn in groups were preyed on more often than more brightly colored males spawning in pairs (Clifton & Robertson 1993). Both results indicate that group-spawning is a riskier mating tactic than pair-spawning.

Piscivores showed a certain specificity when attacking group-spawning species: *Chlorurus sordidus*, *Scarus psittacus* and *Acanthurus nigroris* were selected as prey over *Ctenochaetus strigosus* and *Zebra-soma flavescens*. This selectivity pattern can be explained according to interspecific differences in timing of spawning and spawning behavior of the prey. The prey species that were subjected to high attack rates by piscivores spawned during the morning and early afternoon hours, while the 2 species that experienced low attack rates spawned late in the afternoon and at dusk (Sancho et al. 2000), when piscivores were less common at the study site. *Chlorurus sordidus* and *A. nigroris* also spent more time rushing into the water column than *C. strigosus* and *Z. flavescens*, therefore becoming more exposed to predation.

Certain anti-predatory morphological adaptations are expected to reduce the risk of predation for certain species (Godin 1997), but the observed patterns of prey selectivity by piscivores indicated that prey morphological characteristics are of low importance to piscivores at this study site. Deep bodies and defensive

caudal spines did not protect surgeonfishes (Acanthuridae) from piscivorous activity as expected. Selectivity of different group-spawning species by piscivores did not seem controlled by prey morphology, although prey behavior certainly influenced the attack rates of predators.

Planktivores

Melichthys niger and *M. vidua* were active at all times of day and showed a higher proportion of attacks on recently spawned eggs at dusk. These mobile triggerfishes seem to feed only occasionally on pelagic eggs, since 70% of their diet consists of algae (Randall & Klausewitz 1973). The relative importance of fish eggs in the diet of triggerfishes at spawning aggregation areas is unknown, but satiation did not seem to occur in these predators. Planktivores have been hypothesized to feed less actively and to be less effective in locating eggs at dusk (Johannes 1978, Lobel 1978, Robertson 1983, Colin & Clavijo 1988), but this does not seem to be the case with planktivorous triggerfishes at Johnston Atoll.

Triggerfishes directed their feeding efforts towards those fish species with large egg sizes (Fig. 5), which may explain the increased feeding activity of these planktivores at dusk, since species with large eggs predominantly spawned at dusk in the reef channel. Triggerfishes displayed an activity pattern that matched the activity of prey species with a certain morphological characteristic (large eggs) that made them more vulnerable and attractive to these planktivores (Hypothesis 4). The selection of prey species was independent of prey abundance, which implies that triggerfishes can recognize the identity of rushing fishes.

Mobile planktivores attacking eggs from 2 surgeonfish species at reefs in Palau showed intraspecific preferences for gametes originated from group-spawning rushes over those produced in pair-spawning rushes (Robertson 1983). Group spawns might be preferred by planktivores for 2 reasons: (1) group spawns are typically more conspicuous than pair spawns, and (2) the larger amount of sperm released in group spawns (Shapiro et al. 1994) typically makes the gamete cloud visible in the water column for a longer period (Robertson 1983). Planktivorous triggerfishes selected pair-spawns at our sampling site. This difference is likely due to the preference of triggerfishes for species with large egg sizes, which predominantly spawned in pairs at Johnston Atoll.

The safety from immediate planktivory for species with small-sized eggs does not appear to be universal. Studies conducted at spawning sites where mobile planktivores are abundant have planktivorous species

which are more adapted to the ingestion of individual planktonic particles from the water column than are triggerfishes (Hobson 1991), and will readily prey upon gametes from species with small egg sizes (Colin 1978, Robertson 1983, Moyer 1987).

Choice of spawning location by reef fishes

The choice of spawning locations within a spawning aggregation site by group-spawning reef fishes is hypothesized to minimize reef-based predation of eggs (Johannes 1978) or to reduce predation risks on adult spawners (Hugie & Dill 1994). The spatial abundance pattern of group-spawning fishes along the channel was correlated with the topographical complexity of the underlying substrate at small scales (10 to 20 m), suggesting the importance of refuge availability in determining the spawning location of reef fishes (Hypothesis 3). Topographic complexity and availability of holes have been also shown to positively correlate with overall survivorship of juvenile and adult fishes (Luckhurst & Luckhurst 1978, Roberts & Ormond 1987, Hixon & Beets 1989, Connell & Jones 1991, Buchheim & Hixon 1992, Hixon 1993, Tupper & Boutilier 1997). Sites with fast current speeds are expected to minimize the exposure time of eggs to reef-based predators (Johannes 1978). Current-speed data from 2 adjacent locations with different topography showed that the site with low topographical complexity and fastest current speeds was not used by spawning fishes. Topography, and not current velocity, appears to have a more dominant role in determining spawning location for these 2 adjacent sites.

Predation effects on reef-fish populations

Predation pressures at spawning aggregation sites seem to vary greatly among different geographical locations (for review see Shapiro et al. 1988, Robertson 1991). In the present study, piscivores attacked 2.3% of all spawning rushes and mobile planktivores attacked the eggs from 0.6% of all spawning rushes. But these general predatory pressures should be viewed with caution, since they could be substantially higher for specific spawning species that are selected as prey by predators. Overall, spawning can be considered a dangerous activity compared with other non-reproductive behaviors (foraging, migration), since predatory attacks on adult fishes were always directed towards fishes displaying spawning-related behaviors.

The overall attack-success rate of piscivores feeding on spawning fishes measured in this study was 3.9%. The estimated mortality risk per individual spawning

rush for group-spawning fishes at the spawning aggregation was 0.1%. By estimating the number of spawning rushes that an individual fish makes in a spawning season, the yearly mortality rates of individual adult fishes due to piscivory at spawning aggregations sites can be calculated. Considering that about 15 individuals are typically involved in a group-spawning rush (G.S. pers. obs.), a 4 to 6 mo spawning season typical for many Hawaiian fishes (Lobel 1989), and a maximum spawning rate for female fish of 1 spawning rush per day (Hoffman & Grau 1989), the chances of an individual female being killed while performing a spawning rush during a whole spawning season appear low (1.2 to 0.8%). However, the estimated annual spawning mortality rates are very high (12 to 18%) for group-spawning males, which spawn multiple times per day. These calculations indicate that predation of group-spawning male fishes by large piscivores at spawning aggregation sites could be of crucial importance for the demography of group-spawning species. Prey selectivity by carangids feeding on parrotfishes in Panamá confirm the higher risks of male versus female fishes during spawning activities, specifically of males participating in group spawns (Clifton & Robertson 1993).

Predation effects on timing of spawning of reef fishes

An important question regarding the timing of spawning of reef fishes is whether they spawn at times when predation risks are reduced (Johannes 1978, Robertson 1991). In this study, dusk was the time when predator abundance and activity levels of piscivores were lowest. Dusk was also the period of the day with lowest overall abundance of spawning fishes and lowest spawning intensities. At the reef channel of Johnston Atoll, the largest diversity of spawning fishes occurred at dusk, a characteristic of other multispecific spawning sites (Johannes 1978, Lobel 1978, Thresher 1984).

These observations support the hypothesis that piscivores principally feed during the daytime on vulnerable group-spawning species and then, due to either changing light conditions or decreasing prey abundance, reduce their feeding activity during the late afternoon. Dusk could be used as the time for spawning by many species which exist in low abundance (but see Myrberg et al. 1989), since these would benefit from the reduced piscivorous activity levels at the spawning grounds during this period. This may constitute an example of how the abundance of certain species can affect the behavior and mortality rates of other species (Kingsford 1992).

Activity patterns of planktivorous fishes differed from those of piscivores. Spawning reef fishes with small eggs seem to benefit from reduced predatory rates on

their gametes during the daytime and dusk periods, since triggerfishes prefer species with large eggs.

Comparative studies at different locations are needed to further resolve the generality of the predator-prey relationships occurring at the spawning aggregation site described in this study. Changes in predatory pressures are expected to have behavioral and population effects on coral reef-fish communities. As a result of increasing fishing pressures in the coral reef environments, the populations of predators are declining, in particular those of large-sized piscivores (Roberts 1997). Predator-prey interactions in environments with abundant predatory populations, such as marine reserves and remote reefs, should be compared with those from locations impacted by fishing activities to better understand the effects of predation and human activities on the reproductive ecology of reef fishes.

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