



Planktivorous fishes as selective agents for reproductive synchrony

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Received 25 October 1995; revised 21 May 1996; accepted 5 July 1996

Abstract

Most shallow-water crabs release larvae during nocturnal maximum amplitude high tides, when larvae are rapidly transported by strong ebb tides to deeper waters at night. Larvae released at this time may avoid being eaten by planktivorous fishes, which abound in shallow water and feed during the day. *Eurypanopeus planus* (Smith, 1869), *Uca beebei* (Crane, 1941) and *Pachygrapsus transversus* (Gibbes, 1850) live on the Pacific coast of Panama and often release larvae during the day. *Eurypanopeus planus* also releases larvae without regard to tidal amplitude. Unlike most crabs, larvae of these three species will encounter, not avoid, planktivorous fishes. The predator avoidance hypothesis predicts that these larvae should be relatively well protected from predation compared to larvae of species that are released when predators are avoided. We tested this prediction experimentally by exposing larvae of these species and the sympatric crab, *Cataleptodius taboganus* (Rathbun, 1912), which exhibits the common hatching pattern, to silversides, *Membras gilberti* an abundant diurnal planktivore that feeds where all species release larvae. The rank order of silversides' prey preferences matched that predicted from the timing of larval release. Larval vulnerabilities to predation were related to the apparent conspicuousness of larvae, which is determined by the color of yolk and chromatophores. A survey of 30 other species of crabs further indicates that conspicuously colored larvae are released when they best avoid predators and that inconspicuously colored larvae may be released at other times. Copyright © 1997 Elsevier Science B.V. All rights reserved.

Keywords: Biological timing; Larval release; Hatching; Predation; Visibility; Chromatophores; Crabs

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1. Introduction

Synchronous bursts of reproduction dramatically punctuate the lives of many plants (Janzen, 1976; Aide, 1988) and animals, especially marine animals (Thompson, 1919; Korringa, 1947; Babcock et al., 1986). Predation on small, poorly defended seeds, gametes and larvae often has been invoked as the cause of reproductive synchrony. Synchronous reproduction may reduce predation on propagules because they are produced (1) when predators are rare or not feeding—the avoidance hypothesis, or (2) in such abundance that predators are sated thereby increasing the survival probability of each propagule—the swamping hypothesis (Rathcke and Lacey, 1985; Aide, 1988; Ims, 1990).

The timing of reproduction is known for 46 species of crabs from nine families worldwide (Morgan, 1995; Morgan and Christy, 1995). Despite diverse adult ecologies, 35 (76%) species release larvae synchronously on a monthly or biweekly schedule, and 27 of these (77%) hatch at the same time, within about an hour of large amplitude nocturnal high tides. The timing of larval release relative to the light-dark cycle is known for 38 species, and 32 (84%) of them release larvae only at night.

Three features of the natural history of crabs indicate that synchronous reproduction promotes larval avoidance, not swamping, of planktivorous fishes, which probably are the most important predators of crab larvae (Morgan, 1989, 1990, 1992). First, larvae enter the water column when planktivorous fishes are least likely to be foraging. Few planktivorous fishes feed at night and especially at dusk (Hobson and Chess, 1978; Zaret, 1980; Lazarro, 1987; Morgan, 1990). Second, contrary to the most basic prediction of the swamping hypothesis, crab larvae are rare or absent in the diets of fishes even though, shortly after hatching, they may be the most abundant zooplankton in intertidal and shallow subtidal habitats (DeCoursey, 1979; Christy and Stancyk, 1982; Salmon et al., 1986; Morgan, 1990). Third, in estuaries and other coastal environments, the density of planktivorous fishes, especially larvae and juveniles, decreases with increasing distance from shore (see Morgan, 1986, for review). Crab larvae that hatch on the largest amplitude lunar or semilunar tides are transported by ebb currents at maximum velocities from shallow to deeper waters, where the risk of predation is reduced (Christy, 1982; Christy and Stancyk, 1982; Morgan, 1987a, 1990). Therefore, larvae may avoid predation in space as well as time. Hence, substantial circumstantial evidence supports the avoidance, but not the swamping hypothesis. Here we report the results of the first experimental test of the avoidance hypothesis.

This hypothesis predicts that larvae released when they best avoid predation should be more vulnerable to planktivorous fishes than those released at riskier times. Therefore, species sharing the common pattern of releasing larvae on nocturnal maximum amplitude high tides should be especially vulnerable to planktivorous fishes, whereas atypical species that release larvae during the day, on low amplitude tides or on low tides should be better defended. None of the 46 species studied worldwide releases larvae at the riskiest time: daytime, minimum amplitude, low tides (Morgan, 1995). However, we recently discovered three species (*Eurypanopeus planus*, *Uca beebei*, *Pachygrapsus transversus*) of sympatric intertidal crabs from the Pacific coast of Panama that release larvae during the daytime while planktivorous fishes are foraging

Table 1
Timing of larval release relative to tidal amplitude, tidal and diel cycles by four species of crabs from the Pacific coast of Panama (Morgan and Christy, 1994, 1995)

Species	Family	Hatching		Morphology			Color		Vulnerability		
		Tidal Amplitude	Tidal	Diel	Body size	Spine length	Spine number	Color	Hatching	Morphology	Color
<i>Eurypanopeus planus</i>	Xanthidae	Asynchronous	HT	D-N	Large	Long	4	Pale green	Low	Low	Low
<i>Uca beebei</i>	Ocypodidae	MAT	HT	D-N	Small	Short	2	Pale ochre	Medium	High	Medium
<i>Pachygrapsus transversus</i>	Grapsidae	MAT	HT	D-N	Small	Short	3	Green-brown/green	Medium	High	Medium
<i>Cataplepodius taboganus</i>	Xanthidae	MAT	HT	N	Large	Long	4	Red	High	Low	High

Vulnerabilities of larvae to planktivorous fishes are predicted from the timing of hatching, larval morphology and larval color. The maximum complement of larval spines is four: one dorsal, one rostral, one pair of antennal and one pair of lateral spines. Symbols: MAT = maximum amplitude tide, HT = near high slack tide, N = night, D = day.

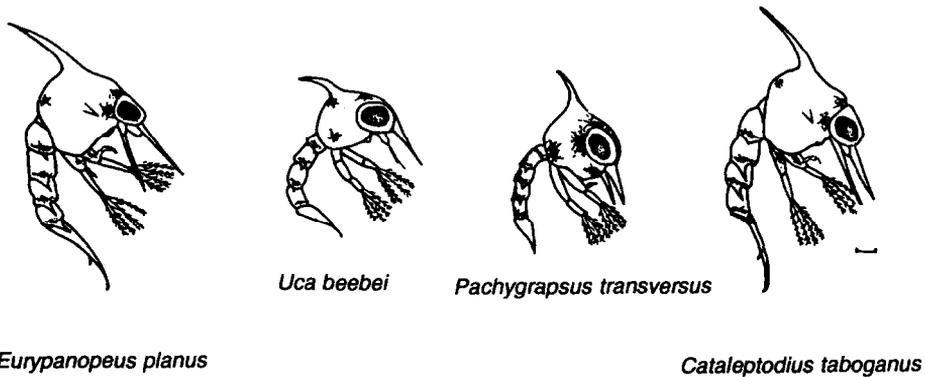


Fig. 1. Larvae of four crabs from Panama. Chromatophores are representations and do not reflect their precise location and number. Scale bar = 0.1 mm.

(Table 1). One of these species (*E. planus*) also releases larvae on small amplitude tides, when they would be transported slowly from shorelines, further increasing the risk of predation. A fourth species (*Cataleptodius taboganus*), released larvae during the safe period and should be most vulnerable to planktivorous fishes. The timing of larval release and predicted larval vulnerabilities of the four species are summarized in Table 1. We tested the avoidance hypothesis by determining whether the feeding preferences of fish matched the risk of predation predicted from hatching patterns.

The vulnerabilities of crab larvae largely may be determined by their body size, spination, and color (Christy, 1986; Morgan, 1987b, 1989, 1990), because planktivorous fishes typically select the largest manageable and most visible prey (Zaret, 1980; Lazarro, 1987). Crab larvae do not evade fishes by swimming but their sharp multiple spines make them difficult for fishes to ingest (Morgan, 1987b, 1989, 1990). Crab larvae with few short spines, small bodies and conspicuous red or brown-black pigments may be most vulnerable and may hatch during nocturnal maximum amplitude high tides. Conversely, larvae with many long spines, large bodies and inconspicuous yellow–green pigments may be best defended against planktivorous fishes and may be released when the risk of predation is high. The vulnerabilities of larvae that are well defended morphologically but conspicuously colored or that are inconspicuously colored but poorly defended morphologically may be moderate, and they may depend on whether fish select prey based primarily on larval morphology (Morgan, 1987b, 1989, 1990) or color (Christy, 1986). Relative larval vulnerabilities of the four species were predicted from larval morphologies and colors (Fig. 1, Table 1). We also surveyed 30 other species of crabs to further examine the relationship between the timing of larval release, larval morphology and larval coloration.

2. Materials and methods

We tested these predictions by conducting feeding trials in the Bay of Panama using

silversides, *Membras gilberti* as a predator. This atherinid fish commonly foraged in large schools over intertidal habitats where the four species of crabs released larvae. Indeed, silversides are one of the most abundant planktivorous fishes in nearshore habitats at most latitudes and may strongly influence the timing of larval release by crabs (see Morgan, 1986 for review). Silversides 30 to 40 mm long (SL) were used in predation experiments because they commonly eat crab larvae (Morgan, 1990). Smaller silversides have difficulty eating crab larvae, and larger fish prefer juvenile fishes and benthic invertebrates.

Silversides and ovigerous crabs of all four species were collected from intertidal habitats near Naos Marine Laboratory on the Pacific coast of Panama from October to November 1987. The xanthid crabs, *Eurypanopeus planus* (Smith, 1869) and *Cataleptodius taboganus* (Rathbun, 1912), live in the lower intertidal zone on cobble beaches on the exposed coasts. The ocypodid fiddler crab, *Uca beebei* (Crane, 1941), lives on open muddy sand flats in the middle intertidal zone in estuaries. The grapsid, *Pachygrapsus transversus* (Gibbes, 1850), lives in the middle intertidal zone on both rocky shores and in mangroves, often within meters of the other species. Ovigerous crabs of a fifth species, the xanthid, *Xanthodius sternberghii*, also lives on cobble beaches. During preliminary feeding trials, larvae of this species sometimes were used instead of *C. taboganus* larvae. The larval morphology and color of these two xanthids are nearly identical.

Silversides were collected at night using a light and dipnet. The three xanthids were collected by overturning stones, *U. beebei* was dug from burrows and *P. transversus* was collected near the tide line at night by using a flashlight. All crabs were collected during low tides.

Silversides were held in flow-through seawater tables at ambient seawater temperature and salinity (approximately 30°C, 35 ppt) and were fed *Artemia* nauplii. Fish were not fed 24 h before feeding trials to standardize hunger level. Silversides were placed individually in 19-l (48 cm high × 27 cm dia) clear glass carboys with filtered seawater the night before experiments to accustom them to their surroundings.

Crabs were held individually in the compartments of plastic trays that floated in seawater tables in an outdoor pavilion. Seawater circulated around females through screened holes in the bottom of the trays. For 2 to 3 days twice each month (1 to 3 days after the full and new moons), some females of all species released larvae. Hence, newly hatched (< 12 h old) larvae of all species were obtained and fed to planktivorous fishes on the same day.

One hundred larvae of each of the four species were added to each carboy (400 larvae total). As a control, we also added 400 larvae to carboys without fish. Carboys were corked and suspended 0.5 or 2.5 m below the surface and within 100 m of shore. Therefore, silversides selected prey in nearly natural lighting. Five trials at each depth were run concurrently. Fish were allowed to feed for 3 to 6 h between 0930 and 1630. Trial durations were adjusted to maximize the number of fish that consumed between 20 and 80% of the larvae. However, some fish ate more than 80% or fewer than 20% of the larvae, and these trials were excluded from the analysis. Fish in these trials may have been stressed or larvae of only one species may have remained, which obscured prey preferences. Consequently, the number and duration of trials at each depth varied.

Thirteen trials were conducted at 0.5 m and 20 trials were conducted at 2.5 m. Larvae remaining at the end of feeding trials were collected on a 230 μ m-mesh sieve. All larvae were recovered from 6 fishless control carboys.

This experiment determines the preferences of fish when an interspecific patch of crab larvae is encountered. Regardless of whether fish encounter the patch in bottles or in the plankton, the ratio of prey will change as foraging proceeds. Peterson and Renaud (1989) argue that the assumption of independence is violated in prey choice experiments, because the consumption of each species depends on the changing ratios of prey available. If so, routine statistical analysis is inappropriate because suitable parametric and nonparametric tests both assume statistical independence. However, prey choices of silversides are similar regardless of whether different prey types are fed to fish separately or together, suggesting that the assumption of independence is not violated in prey preference experiments (Morgan, 1989). Therefore, we have analyzed log transformed data by the analysis of variance to detect interspecific differences in larval survival at the two depths. A planned comparison of mean larval survival among species was conducted. Allowing fish to feed until as much as 80% of the prey were consumed provided a conservative test for prey preferences, because fish switch to alternative prey as preferred prey decline (Werner and Hall, 1974; O'Brien, 1979; Zaret, 1980; Lazarro, 1987). Preferred prey will be consumed first but the number remaining may not change substantially thereafter while fish consume alternative prey.

Body size, spine length, spine number and color of larvae were documented for the species of crabs that were used in experiments and other species of crabs for which the timing of larval release is known. Body size was classified as large or small and spine length (relative to body size) was classified as long or short. Four was the maximum number of larval spines or pairs of spines: one dorsal, one rostral, one pair of antennal and one pair of lateral carapace spines. Very small spines were not counted. Chromatophores and yolk remaining at hatching determine larval color. We recorded larval colors by observing larvae in daylight and using a dissecting microscope in transmitted and reflected light.

3. Results

The relative predation rates by silversides on the four species of crab larvae (Fig. 2) matched those predicted by the avoidance hypothesis (Table 1). Silversides ate significantly more *C. taboganus* larvae than *U. beebei* or *P. transversus* larvae ($F_{1, 128} = 10.14$; $p < 0.002$) or *E. planus* larvae ($F_{1, 128} = 26.31$; $p < 0.001$). Furthermore, *U. beebei* and *P. transversus* larvae were preferred to *E. planus* larvae ($F_{1, 128} = 7.45$; $p = 0.007$). When *X. sternberghii* larvae were used in preliminary feeding trials, silversides ate more of them than larvae of *E. planus*, *U. beebei* and *P. transversus*.

Fish were allowed to feed longer at 0.5 m (5.4 ± 0.7) than at 2.5 m (3.4 ± 0.5 h), and they ate significantly more at the shallower depth (Fig. 2, Table 2). Preferences of silversides for the four species of crab larvae did not differ significantly between depths.

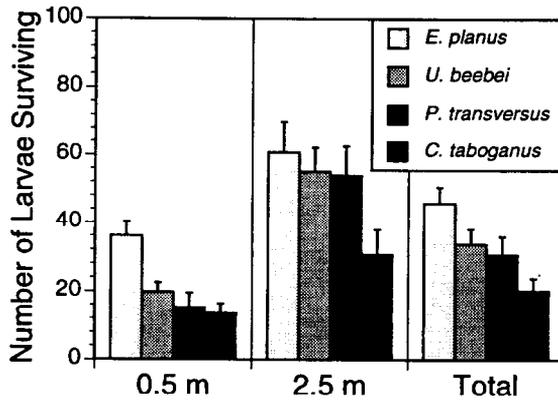


Fig. 2. Mean survival (± 1 SE) of crab larvae that were fed to silversides, *Hubbesia gilberti*, 30 to 40 mm long for 3 to 6 h at depths of 0.5 and 2.5 m in the Bay of Panama.

4. Discussion

Differences in sizes, spines, and especially colors of these crab larvae may explain differences in vulnerability to predation (Fig. 1, Table 3). From morphology, silversides should have eaten more poorly defended *U. beebei* and *P. transversus* larvae than well-defended *C. taboganus*, *X. sternberghii* and *E. planus* larvae. However, large spiny larvae were the most (*C. taboganus*, *X. sternberghii*) and least (*E. planus*) preferred prey. A striking difference in larval color may explain this apparent paradox (Christy, 1986). Red yolk and chromatophores of newly hatched *C. taboganus* and *X. sternberghii* larvae contrast strongly with the background spectral radiance of yellow–green coastal waters and may render these larvae highly visible to fishes (Lythgoe, 1979). In contrast, *E. planus* larvae are pale green and probably are cryptic to fishes even in illuminated shallow waters. The pale ochre larvae of *U. beebei* may be relatively difficult for fishes to see, which should limit otherwise high predation rates on these small short-spined larvae (Morgan, 1987b, 1989, 1990). Larvae of *P. transversus* also may be only moderately visible, because they have highly reflective blue–green pigment that may mask large chromatophores.

Table 2

Analysis of variance of the survival of four species of crab larvae that were fed to silversides, *Membras gilberti* 30 to 40 mm SL for 3 to 6 h at depths of 0.5 and 2.5 m in the Bay of Panama

Source	df	MS	F	P
Depth	1	5.22	39.31	< 0.001
Species	3	3.72	9.35	< 0.001
Depth \times species	3	0.98	2.47	0.065
Error	124	16.46		

Table 3
Larval vulnerabilities to planktivorous fishes of 34 species of crabs from North and Central America as predicted from hatching relative to lunar, tidal amplitude, tidal and light–dark cycles, larval morphologies and larval colors

Species	Family	Hatching		Morphology			Color		Vulnerability		References	
		Lunar/tidal amplitude	Tidal	Diel	Body size	Spine length	Spine number	Color	Hatching	Morphology		Color
<i>Sesarma rhizophorae</i>	Grapsidae	Monthly	HT	N	Small	Short	3	Brown	High	High	High	1
<i>Sesarma cinereum</i>	Grapsidae	Biweekly	HT	N	Small	Short	3	Yellow–brown	High	High	High	2
<i>Sesarma reticulatum</i>	Grapsidae	Biweekly	HT	N*	Large	Short	3	Dark/yellow–brown	High	Medium	High	3
<i>Araucana pisani</i>	Grapsidae	Biweekly	-	-	Small	Short	3	Dark brown	High	High	High	4,5
<i>Pachygrapsus transversus</i>	Grapsidae	Biweekly	HT	D–N	Small	Short	3	Green–brown/green	Medium	High	Medium	
<i>Uca oerstedii</i>	Ocypodidae	Monthly	HT	N	Small	Short	2	Yellow–brown	High	High	High	
<i>Uca galapagensis</i>	Ocypodidae	Monthly	HT	N	Small	Short	2	Brown	High	High	High	
<i>Uca beebei</i>	Ocypodidae	Biweekly	HT	D–N	Small	Short	2	Pale ochre	Medium	High	Medium	
<i>Uca rapax</i>	Ocypodidae	Biweekly	HT	N	Small	Short	2	Dark brown	High	High	High	6
<i>Uca minax</i>	Ocypodidae	Biweekly	HT	N	Small	Short	2	Yellow–brown	High	High	High	6
<i>Uca pugilator</i>	Ocypodidae	Biweekly	HT	N*	Small	Short	2	Yellow–brown	High	High	High	6
<i>Uca pugnax</i>	Ocypodidae	Biweekly	HT	N	Small	Short	2	Yellow–brown	High	High	High	6
<i>Cataprepodius floridanus</i>	Xanthidae	Biweekly	HT	N	Large	Long	4	Red	High	Low	High	5
<i>Cataprepodius taboganus</i>	Xanthidae	Biweekly	HT	N	Large	Long	4	Red	High	Low	High	7
<i>Xanthodius siemmergkii</i>	Xanthidae	Biweekly	HT	N	Large	Long	4	Red	High	Low	High	7
<i>Panopeus herbstii</i>	Xanthidae	Biweekly	HT	N	Large	Long	4	Brown–black	High	Low	High	8
<i>Panopeus simpsoni</i>	Xanthidae	Biweekly	-	N	Large	Long	4	Brown	High	Low	High	
<i>Panopeus obesus</i>	Xanthidae	Biweekly	-	N*	Large	Long	4	Brown	High	Low	High	
<i>Dyspanopeus tectana</i>	Xanthidae	Biweekly	-	N*	Large	Long	4	Yellow–brown	High	Low	High	9
<i>Dyspanopeus savi</i>	Xanthidae	Biweekly/ Asynchronous	HT	N	Large	Long	4	Yellow–brown	High	Low	High	10
<i>Eurypanopeus depressus</i>	Xanthidae	Asynchronous	-	N*	Large	Long	4	Yellow–brown	High	Low	High	11
<i>Eurypanopeus transversus</i>	Xanthidae	Biweekly	Flood	N	Large	Long	4	Yellow–black	High	Low	High	
<i>Eurypanopeus planus</i>	Xanthidae	Asynchronous	HT	D–N	Large	Long	4	Pale green	Low	Low	Low	7
<i>Rhithropanopeus harrisi</i>	Xanthidae	Asynchronous	HT	N	Large	Long	4	Brown	High	Low	High	12
<i>Pinnixa chaetoptera</i>	Pinnotheridae	Biweekly	HT	N	Small	Short	3	Yellow–brown	High	High	High	13
<i>Pinnotheres ostreum</i>	Pinnotheridae	Asynchronous	-	N	Small	None	0	Dark brown–black	High	High	High	13,14

The relationship between the timing of larval release, morphologies, colors and expected vulnerabilities to predation appears to be general (Table 3). The timing of larval release relative to the light–dark cycle was determined for 32 of the 34 species surveyed. Larvae of all 26 species (100%) that hatch at night have colors that should make them conspicuous to planktivorous fishes during the day. However, only 14 of these species (54%) would be vulnerable to fish based on their larval morphologies. All six species (100%) that release larvae during the day have inconspicuously colored larvae, but larvae of only one species (17%) are well defended morphologically. Colored yolk primarily may determine the conspicuousness and vulnerability of newly hatched larvae to fishes in clear tropical waters. Crab larvae typically metabolize yolk from 24 to 36 h after hatching, whereupon the conspicuousness of larvae may diminish and morphology may determine larval vulnerability.

The general relationship between the timing of larval release by intertidal crabs and larval vulnerabilities to predation by shallow-water planktivorous fishes (silversides, anchovies, killifishes) may have arisen because these predators are abundant, widespread and prefer similar larval types. *Menidia menidia*, *Anchoa mitchelli* and *Fundulus heteroclitus* were the most abundant planktivorous fishes collected in bays and estuaries along the Atlantic coast of the USA (Morgan, 1990; Hovel, 1995), and congeners of these species (*Menidia peninsulae*, *Fundulus similis*) were the most abundant planktivorous fishes along shorelines of the Gulf coast (Morgan, unpubl. data). Larvae of all crabs studied on both of these temperate coasts were similarly colored brown–black but they differed in size and spination. Even though these fishes belong to different families and live on different coasts, they all preferred small short-spined crab larvae to large long-spined prey (Morgan, 1987b, 1989, 1990, unpubl. data; Hovel, 1995). In Panama, crab larvae also were morphologically diverse, but unlike the temperate species studied, they were variously colored red, green, yellow or black. Both silversides and killifish again were common, and silversides apparently selected the most visible rather than the most manageable crab larvae. Because prey color strongly affected the outcome of larval–fish interactions and various fishes prefer particular larval morphologies, it is likely that they share a preference for particular larval colors as well. Thus, the taxonomic composition of both crab and fish assemblages varies latitudinally, but the rules governing prey selection by fishes may not (O'Brien, 1979; Zaret, 1980; Lazarro, 1987). These common rules may explain why timing patterns and larval traits are associated across latitudes. In contrast, the wide variety of feeding modes, feeding habits and distributions of invertebrate planktivores are less likely to account for the relationship between larval traits and reproductive timing (Morgan, 1989, 1992, 1995).

Predation on adult crabs or embryos during larval release also may influence reproductive timing (Morgan and Christy, 1995). Females of intertidal species typically remain near refuges to release larvae, and therefore they must hatch during large amplitude tides when refuges are inundated. Three of the species (75%) studied here that release larvae biweekly (*U. beebei*, *C. taboganus*, *X. sternberghii*) live low on the shore, are inundated by all high tides and should not be constrained to release larvae on maximum amplitude tides. A total of 13 of 21 low intertidal and subtidal species (62%) surveyed also release larvae biweekly (Table 3). Therefore, predation on larvae rather than adults or embryos is more consistent with these hatching patterns. In addition, we

have tested alternative hypotheses that invoke high temperature, low salinity, ultraviolet radiation and colonization rates to explain the timing of larval release and have found little support for them (Christy, 1982, 1986; Morgan, 1987a; Morgan and Christy, 1995).

Our results support the hypothesis that intertidal crabs release conspicuous vulnerable larvae when they are least likely to be eaten by diurnally-foraging planktivorous fishes. The predator avoidance hypothesis is consistent with both intraspecific (Morgan and Christy, 1994) and interspecific (Morgan and Christy, 1995) differences in reproductive timing by this taxonomically and ecologically diverse group of marine invertebrates. In contrast, there presently is no support for the swamping hypothesis.

The explanatory scope of the avoidance hypothesis results from predictable spatial and temporal variation in predation. Synchronous reproduction by many closely related species may occur when offspring share traits that render them vulnerable to predators with similar foraging behaviors and ecologies. Other shallow-water marine animals also release eggs and larvae when many crabs do (Thompson, 1919; Korringa, 1947; Johannes, 1978) and the avoidance hypothesis advanced here may apply to them as well. Similarly, the majority of 32 species (21 families) of woody understory plants in a neotropical forest synchronously produce vulnerable leaves in the dry season when herbivorous insects are at an annual low (Aide, 1993).

We emphasize that the avoidance hypothesis does not explain the fitness benefits of producing offspring when predators are foraging. However, it does predict that such offspring should be better defended from predators than those that are produced when the risk of predation is minimal. Few intertidal crabs release larvae when the risk of predation by planktivorous fishes is high, and it is unlikely that many other organisms produce offspring at risky times. However, when rare reproductive timing patterns are discovered, the predator avoidance hypothesis can be tested experimentally.

Acknowledgments

We thank J. Bordua and S. McAfee for providing technical assistance and the Smithsonian Institution for providing financial support. Discussions with R. Cerrato regarding statistical approaches were helpful. We also thank J. Jackson and R. Palmer for commenting on early drafts of the manuscript.

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