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Planktonic predation risk: effects of diel state, season and prey life history stage

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Predation is considered an important source of mortality for plankton, but documenting variation in planktonic predation, particularly across interacting environmental cycles, remains logistically difficult, thus our understanding remains limited. To test for the combined effects of prey life history stage, diel or light level phase (including crepuscular periods) and seasonal upwelling on the risk of predation, we deployed tethered adult and larval brine shrimp *Artemia franciscana* using dock-based plankton tethering units (PTUs). Risk was higher overall during upwelling, but life history stage also interacted with season. There was no seasonal difference in risk for adults. Larvae were at significantly lower risk of predation during non-upwelling than during upwelling. Larvae were also at lower risk during non-upwelling than were adults during either season. During upwelling, there was no significant difference in risk between the two prey categories. With respect to the diel cycle, dusk was safer than daytime. For larvae, the diel pattern in risk remained consistent across seasons while risk for adults at night was slightly lower during upwelling than during non-upwelling. Variation in planktonic predation risk across diel and seasonal cycles differs for different life history stages and thus, generalizations fail to capture the complexity of interactions between factors.

KEYWORDS: size-dependent predation; plankton tethering unit; predator–prey interaction; mortality; diel cycle

INTRODUCTION

The risk of predation is a strong selective force that has been implicated in driving activity patterns, habitat use,

the timing of life history events and many other details of an animal's ecology. Predictable variation in predation risk across the daily cycle of light levels appears to drive

behaviours such as daily migrations between habitats (Bollens and Frost, 1989a; Yahel *et al.*, 2005b; Sato *et al.*, 2013). For many marine organisms, the timing of spawning or hatching of embryos linked with the diel, tidal and tidal amplitude cycles is believed to decrease predation on embryos, newly hatched young or reproducing adults (Christy, 2011). Differences in behaviour across ontogeny or size classes such as differences in the strength or timing of diel vertical migration among different sized plankton have been attributed to predictable changes in predation risk among size classes (Zaret and Suffern, 1976; De Robertis *et al.*, 2000). When community structure is stable, patterns in risk associated with size and diel phase are more likely to be predictable. However, when community structure is variable, the relationships between predators and prey may also vary, resulting in complex patterns of predation risk.

In many seasonal marine environments, upwelling-induced variation in productivity causes seasonal variation in zooplankton community structure (Mann, 1993; Fernández-Álamo and Färber-Lorda, 2006; García-Reyes *et al.*, 2014). The community composition and abundance of predators of zooplankton also fluctuates strongly with seasonal changes in productivity (Ohman, 1988). In some cases, correlated seasonal variation in zooplankton abundances or behaviour and planktivore abundances have been attributed to predation (for example, Bollens and Frost, 1989a; Cury *et al.*, 2000; Sato *et al.*, 2013). Thus, it seems likely that predation risk varies seasonally with changes in upwelling strength or productivity. However, *in situ* studies of variation in planktonic predation risk are still uncommon (but see Bollens and Frost, 1989a). Using assays with tethered prey, Bullard and Whitlatch (Bullard and Whitlatch, 2008) reported increased predation risk during the more productive summer months, when larger numbers of fishes were present. While higher densities of predators or prey should increase encounter rates across the population, higher densities of prey may decrease encounter rates with predators on a *per capita* basis. Since changes in productivity can influence numbers of both predators and prey, the direction of change in planktonic predation risk across seasonal variation in productivity is not obvious.

Even less obvious is how environmental cycles and life history stage interact to produce patterns of planktonic predation risk. Due to the difficulties of studying predation on plankton, especially *in situ* (Vaughn and Allen, 2010), most studies have focused separately on variation in predation risk across an environmental cycle (Robertson and Howard, 1978; Bullard and Whitlatch, 2008) or changes in risk as organisms grow (Sogard, 1997; Allen, 2008) (but see studies of size-specific diel vertical migrations such as: De Robertis *et al.*, 2000; Yahel

et al., 2005a, b; Sato *et al.*, 2013). However, these factors likely function simultaneously to result in complex temporal variation in risk, as has been shown for comparisons of diel or lunar phase and habitat or location in the water column (Acosta and Butler IV, 1999; Allen and McAlister, 2007). Using dock-based assays of tethered adult and larval brine shrimp (*Artemia franciscana*), we previously demonstrated that diel patterns in risk of predation differ between life history stages. On the Caribbean coast of Panama, in Florida, and during the non-upwelling season in the Bay of Panama, early life history stage brine shrimp experience significantly lower predation risk at night than during the day, but by the time they are small adults, their risk of predation at night is higher than, but not significantly different from the risk that they experience during the day (Kerr *et al.*, 2014). Here, we build on this previous study by reporting on risk of planktonic predation in the Bay of Panama during all four diel periods (dawn, day, dusk and night) during both non-upwelling and upwelling seasons to test the hypotheses that (i) predation risk is lowest at night, (ii) predation risk varies with season and (iii) patterns in risk vary with prey size or life history stage.

METHOD

Plankton tethering units

Brine shrimp, *A. franciscana*, attached to PTUs (Fig. 1, based on Bullard and Whitlatch, 2008) were deployed from a floating dock to assess the relative risk of predation attempts on standardized prey items across diel and seasonal cycles. We used nauplii and sexually immature individuals that have the adult morphology (hereafter referred to as adults) to test for effects of prey life history stage on predation risk. Since tethered prey cannot escape, tethering studies provide estimates of relative risk

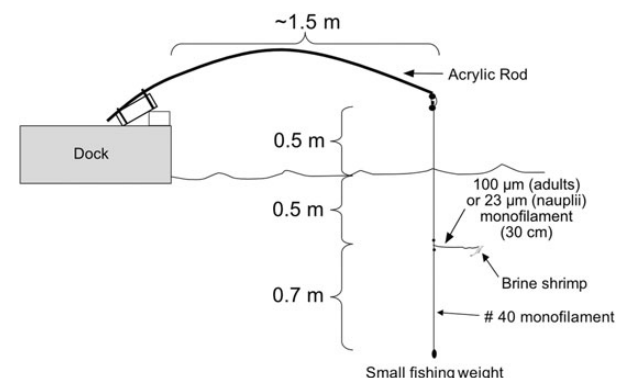


Fig. 1. Dock-based PTU used for predation risk assays (reproduced from Kerr *et al.*, 2014; based on Bullard and Whitlatch, 2008).

rather than quantitative measurements of mortality from predation. In addition, brine shrimp may be more vulnerable to predation than other zooplankton due to their non-cryptic coloration, particularly if they have recently eaten, and their lack of protective spines, which many marine crustaceans such as crab larvae possess. PTUs are an effective method for the measurement of relative rates of predation risk as they are free of biases of losses that are not due to predation, attraction or deterrence of predators, and PTUs do not alter the range of planktivorous fishes that consume the prey when not tethered (Bullard and Hay, 2002). We have also shown that losses that are not the result of predation are rare, and are not significantly different between adult and nauplii prey categories (Kerr *et al.*, 2014). Throughout the paper, we refer to losses of our prey items as “risk” or “predation risk” rather than “mortality”.

We chose to use *A. franciscana* as bait for this study, despite the fact that they do not occur naturally in the study area. *Artemia* can be easily raised in the lab year-round, providing a consistent prey item for use across the year. In addition, since *Artemia* are not well defended from predators (morphologically, behaviourally or chemically), they should be vulnerable to many different types of predators. If we had chosen a prey species that is, for example, morphologically defended via cryptic coloration, visual predators may not have detected them. The use of *Artemia* as a prey item allowed us to test for the effect of size/life history stage on the risk of predation by being available to all (most) predators that are found in the area and are able to consume prey of these sizes.

Larval brine shrimp (nauplii aged 2–4 days old, average size = 0.60 mm \pm 0.110 SD, n = 511 measured) were used as our small prey category and are similar in size to many crustacean larvae such as crab zoea. Immature adults, individuals that have the adult form, but are not yet sexually mature (males without claspers and females that were not carrying eggs), averaging 3.4 mm in length (\pm 0.70 SD, n = 2406) were used as our large prey life history stage. Brine shrimp were raised from eggs in aerated, locally sourced seawater, maintained at 20–24°C in the lab. Nauplii were fed only the single-celled alga *Isochrysis galbana* daily for \sim 2–5 days, after which their diet was supplemented with a commercial powdered brine shrimp food mixture (Zac’s Brine Shrimp Food, distributed by Xoscientific) every 1–2 days. Brine shrimp were glued to the ends of 30 cm tethers that were tied to the PTU. Tethers were attached to the brine shrimp by touching the end of the thread to a small drop of cyanocrylate glue and then gently laying the thread on the dorsal side of the brine shrimp. Tethers for the nauplii were 23 μ m diameter PET (polyester) monofilament (Biogeneral Advanced Fiber Technology).

Tethers used for the adults were \sim 100 μ m diameter invisible thread available from sewing supply stores.

During each assay, 6–10 PTUs baited with each prey category were deployed, for a maximum total number of 20 PTUs deployed (10 nauplii and 10 adults). Each PTU was deployed for 30 min and the two categories of prey were distributed on the dock in an alternating fashion, placed \sim 2 m apart. Further details of the method of attachment of prey to the tethers, transport to the dock (\sim 300 m away from the lab) and deployment are described in Kerr *et al.* (Kerr *et al.*, 2014).

Controls testing for a difference in losses between the two prey categories that are not due to predation (prey falling off the tethers) were conducted in a water table in the laboratory. Ten 30-min deployments of eight adults and eight nauplii resulted in no significant difference in losses of prey items between the two categories (see Kerr *et al.*, 2014 for more detail). Controls testing for a bias in losses resulting from the different diameters of the tethers were conducted during daytime high tides at the Naos dock during non-upwelling conditions. Assays were done separately for the two prey types and consisted of 6–10 PTUs with prey (adults or nauplii) attached to 23 μ m monofilament and 6–10 PTUs with prey attached to 100 μ m thread. Eight 30-min assays for each prey category were conducted in the same manner as the experimental deployments. Losses of nauplii when attached to the thin or thick threads were statistically indistinguishable. Adults were lost at a higher rate when attached to the thin thread (see Kerr *et al.*, 2014 for more detail). The use of thicker thread for adults and thinner thread for nauplii maintained a similar prey-to-thread size ratio between the prey categories and resulted in more conservative estimates of risk for adults than if we had used the thin thread for both prey categories.

Study area: Isla Naos, Bay of Panama, Panama

Our study was conducted at the Smithsonian Tropical Research Institute’s (STRI) Naos Marine Laboratory dock on the Pacific coast of Panama (8°55.041’ N, 79°31.978’ W). The floating dock where sampling was conducted measures 7 by 21 m. Tidal amplitude is large, averaging 4.01 m (range during our study = 2.03–6.37 m), and tides are semidiurnal. Water depth at the dock ranges from 5.5 to 9.5 m at high tide. Water clarity is variable. During our study, Secchi disk depths ranged from $<$ 0.5 to $>$ 5 m, but the bottom was never visible (Fig. 2). The habitat under the dock is muddy-sand with rocky boulders located slightly inshore. Planktivorous fishes were present near the dock; sergeant majors (*Abudefduf troschelii*, diurnal feeders) were consistent residents and schools of silversides

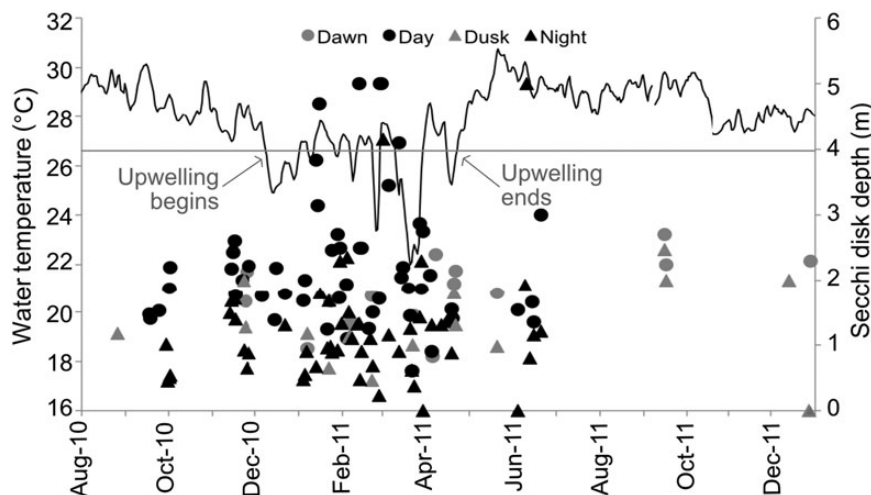


Fig. 2. Water temperature and Secchi disk measurements at Naos from August 2010 to January 2012. Seasons (upwelling versus non-upwelling) were defined based on water temperature as described in the text. Data are combined daily measurements in the Naos laboratories aquariums and *iButton* datalogger measurements from 1 m depth at Naos dock. Secchi disk measurements taken after the recovery of the PTUs are shown as circles (dawn = gray, black = day) and triangles (dusk = gray, night = black).

(multiple species, nocturnal and diurnally feeding species are present in the area) near the dock were also often observed. Artificial lighting over the dock was turned off during sampling. Although some artificial light from streetlights located 50 m away, and light pollution from nearby Panama City, was present, light levels were low on the dock at night and potential attraction of visual predators to the dock by light was considered minimal.

Upwelling of cold water occurs in the Bay of Panama between December and April, resulting in strong seasonal changes in water temperature and productivity (D’Croz and O’Dea, 2007). For our comparison of seasons, we defined the upwelling season as beginning on the day when temperature dropped below 26.6°C (based on the Panama Canal Authority’s indices of upwelling) and ending when it rose above this temperature and did not drop again (Fig. 2). Water temperature was measured hourly at the dock by an *iButton* datalogger (Maxim Integrated, thermochron DS1922L) located 1 m below the water surface. *iButton* data were not available for the entire time series; therefore, we used linear regression to determine the relationship between temperature measurements taken twice a day in the aquariums at Naos Laboratories (water intake located ~5 m from the location of PTU and *iButton* deployments) and *ibutton* data at the dock (linear regression equation: $y = 1.0935x - 1.9$, $R^2 = 0.913$). We then adjusted the aquarium temperature time series based on this relationship to fill missing data in the *iButton* temperature time series. This compiled daily temperature time series was then smoothed using a 3-day moving average.

Temperature during the non-upwelling (wet) season averaged 28.7°C (± 0.82 SD) between 4 August and 6 December 2010 and 20 May and 28 December 2011

when we conducted data collection. During upwelling, water temperature can drop by as much as 10°C for short periods. We sampled from 15 December 2010 to 21 April 2011, during which time variable but generally weak upwelling resulted in an average water temperature of $26.3^\circ\text{C} \pm 1.40$ SD (Fig. 2). Dates of sampling are shown in Fig. 2 as Secchi disk measurements (32 days during non-upwelling, 58 days during upwelling). Deployments were conducted during both high tides (day and night or dawn and dusk) on 3 days during large amplitude tides and 3 days during small amplitude tides. Assays conducted during dawn, or dusk, were defined as those for which the high tide occurred <1 h before the time of sunrise, or sunset, respectively, and thus occurred during the time periods when light levels were rapidly changing. Data collected during day and night of the non-upwelling season (35 of the 139 deployments reported here) have been previously published (Kerr *et al.*, 2014). Data from dawn and dusk during non-upwelling and from all four diel states during upwelling are published for the first time here.

Data analysis

Statistical analyses were conducted in R (version 3.1.0, www.R-project.org). Counts of the number of prey items lost or retained on the tethers were analysed using generalized linear models with a binomial error distribution and logit link function. Predictor variables included diel state (day, night, dawn or dusk), prey size category (adults versus nauplii), season (upwelling versus non-upwelling), prey size category (adults versus nauplii), season, tidal amplitude and their interactions. Data points that were flagged as potential outliers on diagnostic plots of

residuals and detected as outliers using the package “outliers” in R were categorized as outliers (1 adults/night/upwelling, 1 nauplii/dusk/upwelling and 2 adults/day/non-upwelling) (Komsta, 2011). Data from both prey categories for these four deployments were excluded from the analyses. Analyses run with and without outliers give the same general results, but with an increased, but still statistically significant, P -value for diel state. Overdispersion was detected so standard errors were corrected using a quasi-GLM (Crawley, 2007; Zuur et al., 2009). Model selection was conducted by comparing nested models using F -tests (Crawley, 2007). When two nested models did not differ significantly, the simpler (reduced model) was selected. Results obtained for the reduced model are presented. Multiple comparison Tukey’s all-pair comparison tests were conducted using the “multcomp” package in R (Hothorn et al., 2008). Proportion of prey items lost, rather than

counts, is presented in figures since the number of prey items deployed differed among assays (ranging from 6 to 10 prey items per prey category).

RESULTS

Risk differed significantly across the diel cycle ($P_{\text{diel}} = 0.009$, Table I). Dusk is the safest time period with significantly lower risk than daytime (Fig. 3A, *post hoc* Tukey’s tests, $P < 0.05$). Other paired contrasts among diel phases were not significant (*post hoc* Tukey’s tests, $P > 0.05$). Risk was greater overall during upwelling than during non-upwelling ($P_{\text{season}} = 0.006$, Table I) and season and prey category interacted to affect risk ($P_{\text{prey:season}} = 0.002$, Fig. 3B). The seasonal effect is mainly driven by a significant increase in risk from non-upwelling to upwelling for nauplii (*post hoc* Tukey’s test, $P < 0.05$, Fig. 3B: triangles) as there was no significant difference in risk for adults between the seasons (*post hoc* Tukey’s tests, $P > 0.05$, Fig. 3B). Risk for nauplii during non-upwelling was significantly lower than risk for adults during either season (*post hoc* Tukey’s tests, $P < 0.05$, Fig. 3B: stars and circles). During upwelling, there was no significant difference in risk for nauplii and adults (*post hoc* Tukey’s tests, $P > 0.05$, Fig. 3B). The diel pattern was generally consistent across the seasons (Fig. 4). When tidal amplitude was included in the model, a marginally significant interaction effect between prey category, season and tidal amplitude was detected ($P = 0.048$). However, tidal amplitude and diel state are confounded: the largest amplitude tides tend to occur during dawn and dusk. When

Table I: Generalized linear model of proportion of prey items lost

Model term	df	Deviance	Residual df	Residual deviance	F	P -value
Null			277	630.72		
Diel	3	21.79	274	608.93	3.92	0.009
Prey	1	1.08	273	607.85	0.58	0.447
Season	1	14.31	272	593.55	7.73	0.006
Prey:season	1	17.37	271	576.18	9.38	0.002

Analysis of deviance table for a generalized linear model of prey items lost (prey items deployed–recovered) using a binomial error distribution adjusted for overdispersion (quasibinomial). Diel state includes day, night, dawn, dusk. Season was categorized as upwelling versus non-upwelling. Prey refers to adults versus nauplii categories. P -values of variables with significant effects on the loss of prey items are shown in bold.

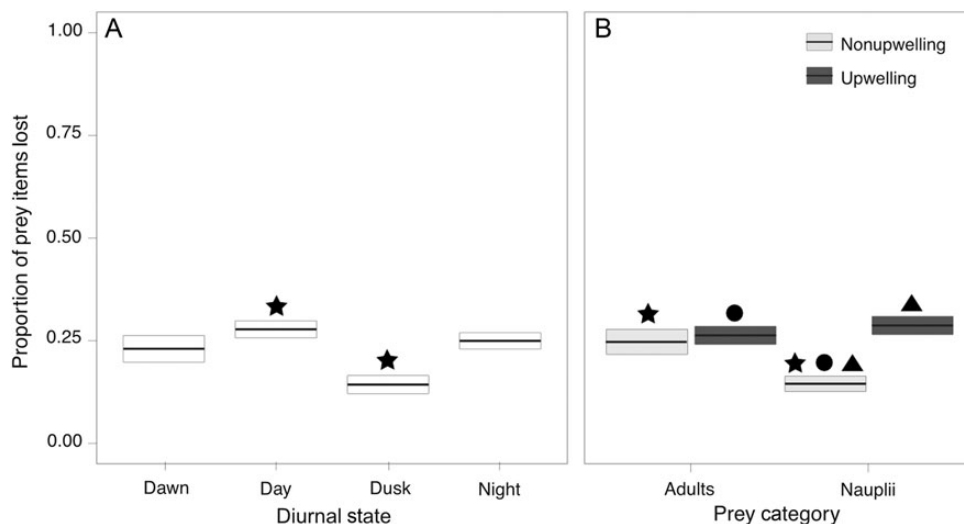


Fig. 3. Proportion of prey items (*A. franciscana*) lost at Naos dock (A) across the diel cycle (prey and seasonal categories pooled) and (B) between seasons for each prey category (diel phase categories pooled). Rectangles represent the mean (centre line) and standard error (upper and lower limits of rectangles). In B, upwelling season data are indicated by dark grey rectangles and non-upwelling is indicated by light grey rectangles. Paired symbols (stars, circles and triangles) represent paired comparisons with significant differences.

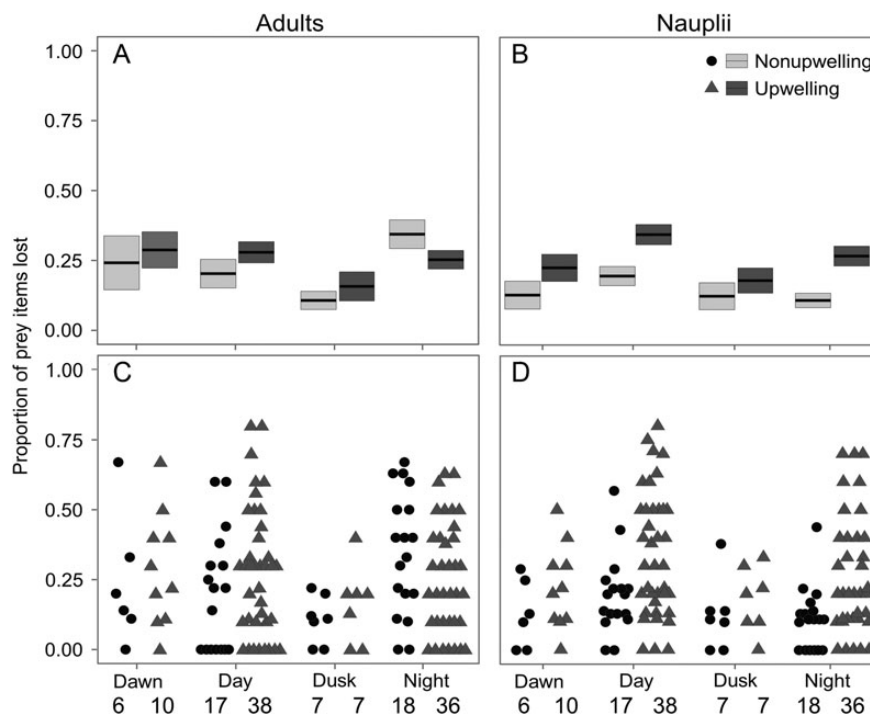


Fig. 4. Seasonal differences in proportion of prey items lost at Naos dock across the diel cycle for the two brine shrimp life history stages (nauplii versus adults) used as prey categories. The upper panels (A and B) show the mean (centre line of rectangles) and standard error (upper and lower limits of rectangles) for each group (dark grey = upwelling, light grey = non-upwelling). Bottom panels (C and D) show the raw data points (triangles = upwelling and circles = non-upwelling) from each assay. Sample sizes are listed below the x-axis.

dawn and dusk are excluded, the interaction effect is no longer significant. Despite the marginally significant effect of prey, season and amplitude, the inclusion of tidal amplitude and its interactions with other variables did not significantly improve the model and thus was excluded from the final analysis.

To examine the relative risk for adults and nauplii during individual assays, paired data for each assay were plotted as a proportion of adults lost versus proportion of larvae lost and compared with the line of equality (Fig. 5). Consistent deviations from the line of equality indicate that one prey category was consistently lost at a higher rate relative to the other. During non-upwelling, adults were more likely to be lost relative to nauplii during each nocturnal assay, but that trend disappeared during upwelling (Fig. 5). For day, dawn and dusk, we found no directional loss of prey items per assay with respect to their size category (Fig. 5).

DISCUSSION

Differences in activity patterns and habitat use of predators and prey from day to night or among prey size classes have been fairly well documented, especially with respect to diel vertical migration, but data on how planktonic predation risk varies with multiple, potentially

interacting physical and biological factors are still relatively sparse (Bollens and Frost, 1989b; Bollens and Stearns, 1992; Vaughn and Allen, 2010; Sato *et al.*, 2013). Our results demonstrate that interactions between such factors can cause patterns of risk to change or reverse across environmental cycles or during ontogeny. Despite a weak upwelling year in 2011, risk varied significantly with season, and prey life history stage interacted with this seasonal effect. During non-upwelling, nauplii were safer at night than during the day and were at lower risk than adults (Kerr *et al.*, 2014). Their risk increased overall during upwelling. In contrast, risk for adults tended to be higher at night than during other times of the day during non-upwelling, but risk at night decreased slightly during upwelling resulting in similar risk during all diel periods. Relative risk between the prey categories also varied with the seasons: at night during non-upwelling, adults were more likely to be eaten than nauplii during each deployment, but there was no difference in relative risk per assay between the prey categories during upwelling.

Seasonal variation in size-biased predation

The direction of size selectivity of prey is dependent on predator identity (Rumrill, 1990; Allen, 2008). Thus, the

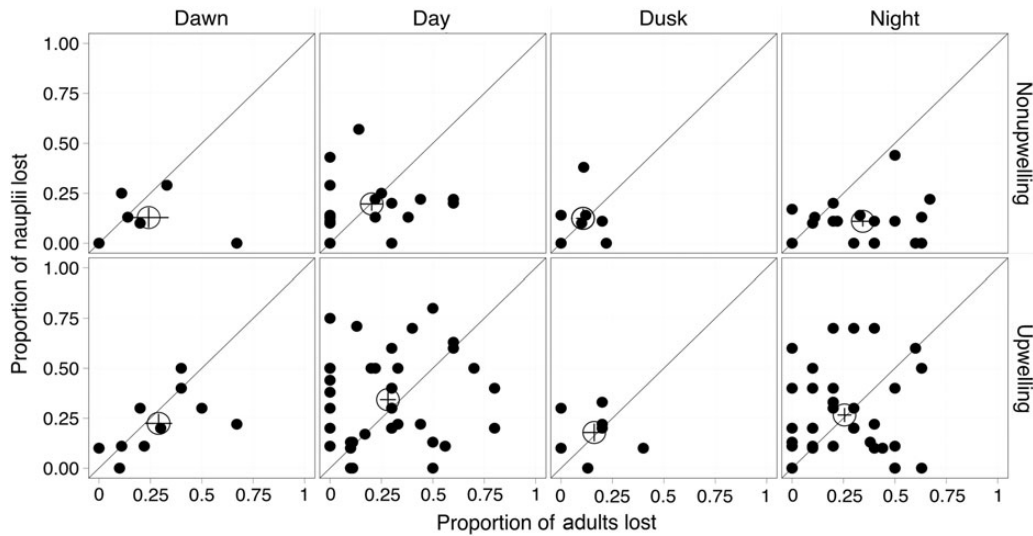


Fig. 5. Proportion of *Artemia* nauplii lost with respect to proportion of *Artemia* adults lost per assay during each diel state for both seasons (filled circles). The diagonal line represents the one-to-one relationship between these proportions. Points above the line indicate a higher loss of nauplii relative to adults. Average relative risk is shown as larger open circles. Error bars represent standard error.

dominant predators, their abundance, size, gape limitations (if any) and their activity patterns will drive diel patterns of risk resulting from size-dependent predation. Research on size-selective predation shows that many predators select smaller prey, supporting the “bigger is better” hypothesis for predator avoidance (Sogard, 1997; Allen, 2008). However, other studies have contradicted this hypothesis (Cowan and Houde, 1992; Litvak and Leggett, 1992; Scharf *et al.*, 2000). Planktivorous fish, for example, are visual predators that tend to select for larger prey regardless of the time of day (Hobson, 1991). Further, planktivorous fish that feed at night cannot detect small plankton ($< \sim 1$ mm in size) because their visual resolution is poor (Holzman and Genin, 2003, 2005). Thus, larger zooplankton will be at higher risk throughout the diel cycle if the dominant planktivores are fish. In contrast, some non-visual predators are not affected by light patterns or are not limited by gape and thus may not show diel or size-dependent patterns in predation. Our results during non-upwelling point towards planktivorous fishes as the dominant predators: size selectivity towards the relatively larger adult brine shrimp was evident at night (Fig. 5), and they experienced generally higher risk compared with the smaller nauplii throughout the diel cycle (Fig. 4). During upwelling, however, risk for nauplii increased to become similar to that for adults, and the size selectivity bias towards adults observed during non-upwelling was no longer present (Figs 4 and 5). These changes may reflect a seasonal shift in predator community.

In the Bay of Panama, large seasonal changes in oceanographic conditions associated with upwelling

bring seasonal changes in phytoplankton and marine fauna (D’Croz and Robertson, 1997; D’Croz and O’Dea, 2007, 2009; O’Dea *et al.*, 2012). Zooplankton, fish such as anchovetas and diving birds can all increase strongly in abundance during upwelling; however, it is unknown how these changes in community structure affect species interactions such as predation risk (Forsbergh, 1969; Glynn and Maté, 1997; Miglietta *et al.*, 2008). Seasonal variation in abundance of planktivorous fishes has been associated with seasonal variability in the strength of diel vertical migration in copepods off the coast of Washington (Bollens and Frost, 1989a). Bullard and Whitlatch (Bullard and Whitlatch, 2008) found a seasonal peak in daytime predation risk for tethered adult brine shrimp in New England during the summer, when productivity was highest. This peak in risk coincided with the highest abundance of planktivorous fish near the dock. Our results show that planktonic predation risk also increases during higher productivity in the Bay of Panama, potentially pointing to an overall increase in abundance of predators. However, the large seasonal increase in relative risk for nauplii at night, rather than an increase in risk for both prey categories, may indicate an increase in the abundance of non-visual or nocturnally feeding predators that prefer smaller prey.

Although the identities of the predators of our tethered prey are unknown, non-visual planktivores are present in the waters of our site. Chaetognaths are gape-limited predators that feed on prey within a size range that encompasses our small prey category only (Canino and Grant, 1985; Baier and Purcell, 1997; Lie *et al.*, 2012), and can feed regardless of light conditions (Nagasawa and

Marumo, 1972; Feigenbaum and Reeve, 1977; Feigenbaum, 1991; Terazaki, 1996; Baier and Purcell, 1997). They can be extremely abundant, exhibit large seasonal fluctuations and can be very important predators of smaller plankton (Baier and Purcell, 1997; Terazaki, 1998; Tse *et al.*, 2007). They are regularly found in plankton samples at Naos, but appear to vary in abundance (K.A.K. and R.C., pers. obs.).

Carnivorous or omnivorous copepods are also potential predators that can detect prey in darkness via mechano- or chemoreception (Yen, 1985; Landry and Fagerness, 1988). Some lab experiments on feeding have used *Artemia* nauplii (Robertson and Frost, 1977; Gophen and Harris, 1981; Bailey and Yen, 1983) and the size range of natural prey indicates most species would be more likely to predate upon *Artemia* nauplii than adults (Yen, 1983, 1985; Turner *et al.*, 1984). Other crustaceans such as euphausiids, some decapods and demersal zooplankton such as amphipods and isopods, may also feed on zooplankton in the size range of our tethered prey. Some of these predators exhibit diel patterns in activity or vertical migrations and are more active at night (Yahel *et al.*, 2005a). However, there is no information available on seasonal variation in abundance of these groups in the Bay of Panama.

Other potential non-visual predators are ctenophores and cnidarian medusae. The abundance of both groups varies seasonally in many locations and intense blooms of hydromedusae (small jellyfish of the order Hydrozoa) occur during upwelling in the Bay of Panama (Larson, 1987; Miglietta *et al.*, 2008). Medusae and ctenophores prey upon zooplankton over a wide range of sizes, but some species, for example, the ctenophore *Mnemiopsis leidyi*, selectively prey upon zooplankton <1 mm in size when available (Larson, 1987; Cowan and Houde, 1992; Sullivan, 2014). Diel feeding rhythms for gelatinous predators are less well studied than other groups, and published studies demonstrate either no pattern in diel feeding or the pattern is not consistent among species (Sullivan, 2014). If the pattern of increased abundances of hydromedusae during upwelling in the Bay of Panama (Miglietta *et al.*, 2008) applies to other gelatinous predators, some of the high levels of predation risk we observed for both prey categories during day and night may be due to predation by these groups. Further studies on seasonal variation in zooplankton abundance and feeding ecology in the Bay of Panama are needed to better understand the causes of the observed variation in predation risk.

Diel variation in predation risk

Dusk was significantly safer than daytime in our study. In many locations, including Panama, the largest tides

during which many species of crabs release larvae occur near dawn or dusk (Christy, 2011; Kerr *et al.*, 2012; K. A. Kerr, submitted for publication). This may be a period of relatively low planktivore activity. Dawn and dusk are the change-over periods for diurnal and nocturnal planktivores on coral reefs and are periods of high activity of large piscivores, the predators of planktivorous fishes (Hobson, 1975). Nocturnal planktivores emerge a half an hour after sunset, their abundance peaks ~2 h after sunset and then declines to a level similar to sunrise and sunset ~2 h before sunrise (Holzman *et al.*, 2007). Large zooplankton that prey on smaller zooplankton also leave the water column an hour or two before sunrise (Yahel *et al.*, 2005b). Thus, risk from planktivorous fishes and predatory zooplankton is expected to be low at and just after sunset and before and during sunrise on reefs. Seagrass and mangrove areas also show patterns of movements between habitats by fishes during crepuscular periods with low abundances of active fishes at night in the mangroves (Sogard *et al.*, 1989; Rooker and Dennis, 1991). The relative safety of crepuscular time periods likely also depends on the relative size of prey and prey size preferences of predators. For organisms that vertically migrate such as euphausiids, the timing of movement into the upper water column often varies among size classes, with smaller individuals coming up at dusk, while larger individuals do not ascend until after dark (De Robertis *et al.*, 2000). On the other hand, the majority of crab larvae that were preyed upon by fishes in a temperate California estuary were eaten during twilight (Rasmuson and Morgan, 2013) and many zooplankton predators do not show strong diel patterns in feeding activity and thus would not exhibit a lull in predation pressure during crepuscular periods (Sullivan, 2014). In fact, chaetognaths have been documented actively feeding at dusk (Baier and Purcell, 1997). Thus, dawn and dusk may not be universally safe. While our results point to dusk being safer than daytime for nauplii, our small sample sizes for the crepuscular periods preclude us from making generalized statements about risk during these time periods. Further research on predation risk during crepuscular periods is warranted.

Studies on risk of predation across the diel cycle or with respect to prey size have provided valuable information on patterns in predation risk. Here, we add to that body of knowledge by demonstrating that interactions of multiple environmental and biological factors result in complex patterns in planktonic predation risk that cannot be easily generalized. Diel patterns in risk differed for the two prey categories. Nauplii experienced significantly higher risk overall during upwelling, while the diel pattern in risk for adults changed slightly between the seasons. The high levels of risk for nauplii during

upwelling may partially explain why some species with planktonic larvae do not reproduce during upwelling conditions. Further studies, in particular on understanding the drivers of variation in risk across seasonal cycles and during crepuscular periods, are necessary to increase our understanding of how predation risk influences zooplankton community dynamics and the timing of many biological events such as larval release and settlement of post-larvae.

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REFERENCES

- Acosta, C. A. and Butler, M. J. IV. (1999) Adaptive strategies that reduce predation on Caribbean spiny lobster postlarvae during onshore transport. *Limnol. Oceanogr.*, **44**, 494–501.
- Allen, J. D. (2008) Size-specific predation on marine invertebrate larvae. *Biol. Bull.*, **214**, 42–49.
- Allen, J. D. and McAlister, J. S. (2007) Testing rates of planktonic versus benthic predation in the field. *J. Exp. Mar. Biol. Ecol.*, **347**, 77–87.
- Baier, C. and Purcell, J. (1997) Trophic interactions of chaetognaths, larval fish, and zooplankton in the South Atlantic Bight. *Mar. Ecol. Prog. Ser.*, **146**, 43–53.
- Bailey, K. M. and Yen, J. (1983) Predation by a carnivorous marine copepod, *Euchaeta elongata* Esterly, on eggs and larvae of the Pacific hake, *Merluccius productus*. *J. Plankton Res.*, **5**, 71–82.
- Bollens, S. M. and Frost, B. W. (1989a) Zooplanktivorous fish and variable diel vertical migration in the marine planktonic copepod *Calanus pacificus*. *Limnol. Oceanogr.*, **34**, 1072–1083.
- Bollens, S. M. and Frost, B. W. (1989b) Predator-induced diel vertical migration in a planktonic copepod. *J. Plankton Res.*, **11**, 1047–1065.
- Bollens, S. M. and Stearns, D. E. (1992) Predator-induced changes in the diel feeding cycle of a planktonic copepod. *J. Exp. Mar. Biol. Ecol.*, **156**, 179–186.
- Bullard, S. G. and Hay, M. E. (2002) Plankton tethering to assess spatial patterns of predation risk over a coral reef and seagrass bed. *Mar. Ecol. Prog. Ser.*, **225**, 17–28.
- Bullard, S. G. and Whitdatch, R. B. (2008) Seasonal variation in planktivory risk in a Southern New England coastal habitat. *J. Exp. Mar. Biol. Ecol.*, **357**, 1–6.
- Canino, M. F. and Grant, G. C. (1985) The feeding and diet of *Sagitta tenuis* (Chaetognatha) in the lower Chesapeake Bay. *J. Plankton Res.*, **7**, 175–188.
- Christy, J. H. (2011) Timing of hatching and release of larvae by brachyuran crabs: patterns, adaptive significance and control. *Integr. Comp. Biol.*, **51**, 62–72.
- Cowan, J. H. and Houde, E. D. (1992) Size-dependent predation on marine fish larvae by ctenophores, scyphomedusae, and planktivorous fish. *Fish. Oceanogr.*, **1**, 113–126.
- Crawley, M. J. (2007) Generalized linear models. *The R Book*. John Wiley & Sons, Ltd, West Sussex, pp. 511–526.
- Cury, P., Bakun, A., Crawford, R. J. M. et al. (2000) Small pelagics in upwelling systems: patterns of interaction and structural changes in “wasp-waist” ecosystems. *ICES J. Mar. Sci. J. Cons.*, **57**, 603–618.
- D’Croz, L. and O’Dea, A. (2007) Variability in upwelling along the Pacific shelf of Panama and implications for the distribution of nutrients and chlorophyll. *Estuar. Coast. Shelf Sci.*, **73**, 325–340.
- D’Croz, L. and O’Dea, A. (2009) Nutrient and chlorophyll dynamics in Pacific Central America (Panama). *Smithson. Contrib. Mar. Sci.*, **38**, 335–344.
- D’Croz, L. and Robertson, D. (1997) Coastal oceanographic conditions affecting coral reefs on both sides of the Isthmus of Panama. *Proc. 8th Int. Coral Reef Symp.*, **2**, 2053–2058.
- De Robertis, A., Jaffe, J. S. and Ohman, M. D. (2000) Size-dependent visual predation risk and the timing of vertical migration in zooplankton. *Limnol. Oceanogr.*, **45**, 1838–1844.
- Feigenbaum, D. (1991) Food and feeding behaviour. In Bone, Q., Kapp, H. and Pierrot-Bults, A. C. (eds), *The Biology of Chaetognaths*. Oxford University Press, Oxford, pp. 45–54.
- Feigenbaum, D. and Reeve, M. R. (1977) Prey detection in the chaetognath: response to a vibrating probe and experimental determination of attack distance in large aquaria. *Limnol. Oceanogr.*, **22**, 1052–1058.
- Fernández-Álamo, M. A. and Färber-Lorda, J. (2006) Zooplankton and the oceanography of the eastern tropical Pacific: a review. *Prog. Oceanogr.*, **69**, 318–359.
- Forsbergh, E. (1969) On the climatology, oceanography and fisheries of the Panama Bight. *Inter-Am. Trop. Tuna Comm. Bull.*, **14**, 1–340.
- García-Reyes, M., Largier, J. L. and Sydeman, W. J. (2014) Synoptic-scale upwelling indices and predictions of phyto- and zooplankton populations. *Prog. Oceanogr.*, **120**, 177–188.
- Glynn, P. W. and Maté, J. L. (1997) Field guide to the Pacific coral reefs of Panamá. *Proc. 8th Int. Coral Reef Symp.*, **1**, 145–166.

- Gophen, M. and Harris, R. P. (1981) Visual predation by a marine cyclopoid copepod, *Corycaeus anglicus*. *J. Mar. Biol. Assoc. U.K.*, **61**, 391–399.
- Hobson, E. S. (1975) Feeding patterns among tropical reef fishes. *Am. Sci.*, **63**, 382–392.
- Hobson, E. S. (1991) Trophic relationships of fishes specialized to feed on zooplankton above coral reefs. In Sale, P. F. (ed). *The Ecology of Fishes on Coral Reefs*. Academic Press, San Diego, pp. 69–95.
- Holzman, R. and Genin, A. (2003) Zooplanktivory by a nocturnal coral-reef fish: effects of light, flow, and prey density. *Limnol. Oceanogr.*, **48**, 1367–1375.
- Holzman, R. and Genin, A. (2005) Mechanisms of selectivity in a nocturnal fish: a lack of active prey choice. *Oecologia*, **146**, 329–336.
- Holzman, R., Ohavia, M., Vaknin, R. *et al.* (2007) Abundance and distribution of nocturnal fishes over a coral reef during the night. *Mar. Ecol. Prog. Ser.*, **342**, 205–215.
- Hothorn, T., Bretz, F. and Westfall, P. (2008) Simultaneous inference in general parametric models. *Biom. J.*, **50**, 346–363.
- Kerr, K. A., Christy, J. H., Collin, R. *et al.* (2012) Reducing error in reproductive timing caused by temperature variation: interspecific differences in behavioural adjustment by fiddler crabs. *Mar. Ecol. Prog. Ser.*, **459**, 1–16.
- Kerr, K. A., Cornejo, A., Guichard, F. *et al.* (2014) Planktonic predation risk varies with prey life history stage and diurnal phase. *Mar. Ecol. Prog. Ser.*, **503**, 99–109.
- Komsta, L. (2011) *Outliers: Tests for Outliers*. R package version 0.14. <http://CRAN.R-project.org/package=outliers>.
- Landry, M. R. and Fagerness, V. L. (1988) Behavioral and morphological influences on predatory interactions among marine copepods. *Bull. Mar. Sci.*, **43**, 509–529.
- Larson, R. J. (1987) Daily ration and predation by medusae and ctenophores in Saanich Inlet, B.C., Canada. *Neth. J. Sea Res.*, **21**, 35–44.
- Lie, A. A. Y., Tse, P. and Wong, C. K. (2012) Diel vertical migration and feeding of three species of chaetognaths (*Flaccisagitta enflata*, *Aidanosagitta delicata* and *Aidanosagitta neglecta*) in two shallow, subtropical bays in Hong Kong. *J. Plankton Res.*, **34**, 670–684.
- Litvak, M. K. and Leggett, W. C. (1992) Age and size-selective predation on larval fishes: the bigger-is-better hypothesis revisited. *Mar. Ecol. Prog. Ser.*, **81**, 13–24.
- Mann, K. H. (1993) Physical oceanography, food chains, and fish stocks: a review. *ICES J. Mar. Sci. J. Cons.*, **50**, 105–119.
- Miglietta, M. P., Rossi, M. and Collin, R. (2008) Hydromedusa blooms and upwelling events in the Bay of Panama, Tropical East Pacific. *J. Plankton Res.*, **30**, 783–793.
- Nagasawa, S. and Marumo, R. (1972) Feeding of a pelagic chaetognath *Sagitta nageae* Alvarinho in Suruga Bay, Central Japan. *J. Oceanogr.*, **28**, 181–186.
- O’Dea, A., Hoyos, N., Rodríguez, F. *et al.* (2012) History of upwelling in the Tropical Eastern Pacific and the paleogeography of the Isthmus of Panama. *Palaeogeogr. Palaeoclimatol. Palaeoecol.*, **348–349**, 59–66.
- Ohman, M. D. (1988) Behavioral responses of zooplankton to predation. *Bull. Mar. Sci.*, **43**, 530–550.
- Rasmuson, L. K. and Morgan, S. G. (2013) Fish predation after weakly synchronized larval release in a coastal upwelling system. *Mar. Ecol. Prog. Ser.*, **490**, 185–198.
- Robertson, A. I. and Howard, R. K. (1978) Diel trophic interactions between vertically-migrating zooplankton and their fish predators in an eelgrass community. *Mar. Biol.*, **48**, 207–213.
- Robertson, S. B. and Frost, B. W. (1977) Feeding by an omnivorous planktonic copepod *Aetideus divergens* Bradford. *J. Exp. Mar. Biol. Ecol.*, **29**, 231–244.
- Rooker, J. R. and Dennis, G. D. (1991) Diel, lunar and seasonal changes in a mangrove fish assemblage off southwestern Puerto Rico. *Bull. Mar. Sci.*, **49**, 684–698.
- Rumrill, S. S. (1990) Natural mortality of marine invertebrate larvae. *Ophelia*, **32**, 163–198.
- Sato, M., Dower, J. E., Kunze, E. *et al.* (2013) Second-order seasonal variability in diel vertical migration timing of euphausiids in a coastal inlet. *Mar. Ecol. Prog. Ser.*, **480**, 39–56.
- Scharf, F. S., Juanes, F. and Rountree, R. A. (2000) Predator size–prey size relationships of marine fish predators: interspecific variation and effects of ontogeny and body size on trophic-niche breadth. *Mar. Ecol. Prog. Ser.*, **208**, 229–248.
- Sogard, S. M. (1997) Size-selective mortality in the juvenile stage of teleost fishes: a review. *Bull. Mar. Sci.*, **60**, 1129–1157.
- Sogard, S. M., Powell, G. V. N. and Holmquist, J. G. (1989) Utilization by fishes of shallow, seagrass-covered banks in Florida Bay: 2. Diel and tidal patterns. *Environ. Biol. Fishes*, **24**, 81–92.
- Sullivan, L. J. (2014) Apparent diel feeding by the ctenophore *Mnemiopsis leidyi* A. Agassiz 1865 (Ctenophora, Lobata). *J. Plankton Res.*, **36**, 1–16.
- Terazaki, M. (1996) Vertical distribution of pelagic chaetognaths and feeding of *Sagitta enflata* in the Central Equatorial Pacific. *J. Plankton Res.*, **18**, 673–682.
- Terazaki, M. (1998) Life history, distribution, seasonal variability and feeding of the pelagic chaetognath *Sagitta elegans* in the Subarctic Pacific: a review. *Plankton Biol. Ecol.*, **45**, 1–17.
- Tse, P., Hui, S. Y. and Wong, C. K. (2007) Species composition and seasonal abundance of Chaetognatha in the subtropical coastal waters of Hong Kong. *Estuar. Coast. Shelf Sci.*, **73**, 290–298.
- Turner, J. T., Tester, P. A. and Conley, W. J. (1984) Zooplankton feeding ecology: predation by the marine cyclopoid copepod *Corycaeus amazonicus*, F. Dahl upon natural prey. *J. Exp. Mar. Biol. Ecol.*, **84**, 191–202.
- Vaughn, D. and Allen, J. D. (2010) The peril of the plankton. *Integr. Comp. Biol.*, **50**, 552–570.
- Yahel, R., Yahel, G., Berman, T. *et al.* (2005b) Diel pattern with abrupt crepuscular changes of zooplankton over a coral reef. *Limnol. Oceanogr.*, **50**, 930–944.
- Yahel, R., Yahel, G. and Genin, A. (2005a) Near-bottom depletion of zooplankton over coral reefs: I: diurnal dynamics and size distribution. *Coral Reefs*, **24**, 75–85.
- Yen, J. (1983) Effects of prey concentration, prey size, predator life stage, predator starvation, and season on predation rates of the carnivorous copepod *Euchaeta elongata*. *Mar. Biol.*, **75**, 69–77.
- Yen, J. (1985) Selective predation by the carnivorous marine copepod *Euchaeta elongata*: laboratory measurements of predation rates verified by field observations of temporal and spatial feeding patterns. *Limnol. Oceanogr.*, **30**, 577–597.
- Zaret, T. M. and Suffern, J. S. (1976) Vertical migration in zooplankton as a predator avoidance mechanism. *Limnol. Oceanogr.*, **21**, 804–813.
- Zuur, A. F., Ieno, E. N., Walker, N. J. *et al.* (2009) *Mixed Effects Models and Extensions in Ecology with R*. Springer, New York.