Tiny Tables Turned: early juveniles of the keystone sea star *Asterias forbesi* selectively prey upon juveniles, *Asterias rubens,* an interfertile intraguild predator

Both cannibalism and intraguild predation (IGP; defined as predation occurring among individuals of competing species) are widespread in nature (Polis 1981, Polis et al. 1989, Elgar and Crespi 1992, Arim and Marquet 2004). Cannibalism and IGP are similar in that each entails the removal of a potential competitor. The analogy between these two processes is particularly obvious when competing species are taxonomic relations. For instance, tadpoles exhibiting cannibalism-promoting polyphenisms voraciously consume both conspecific and heterospecific tadpoles (Salt, 1961; Pomeroy, 1981; Polis, 1989). Unlike IGP, however, cannibalism can reduce the inclusive fitness of predator individuals if prey conspecifics are kin (Pfennig, 1997). Predators could avoid such fitness downsides by 1) detecting and avoiding consumption of kin when cannibalizing and 2) preferentially consuming guild-mates over conspecifics. Kin-avoidant cannibalism has been demonstrated in many taxa (Klahn and Gamboa, 1983; Nummelin, 1989; Pfennig et al., 1993; Fisher et al., 2021). Selective engagement in IGP over cannibalism has received less attention, but recent theoretical studies suggest that predator persistence may sometimes depend on (Toscano et al., 2017).

The interplay between cannibalism and IGP may be especially complex when intraguild prey and predator are interfertile, as is the case in our study system examining the sea stars *Asterias forbesi* and *Asterias rubens*. On the east coast of North America, *A. forbesi* and *A. rubens* overlap in range, hybridize, and act as keystone species, controlling populations of the competitively dominant blue mussel, *Mytilus edulis* (Harper and Hart, 2007; Giakoumis et al., 2023; Menge, 1982). Both species cannibalize infrequently as adults, and *A. rubens* is also known to prey upon *A. forbesi* on occasion (Menge 1979). Furthermore, juveniles of *A. forbesi* cannibalize voraciously beginning only four days after the completion of larval settlement, with rates of mortality exceeding 90% at high densities (Brocco French and Allen, 2021). A remarkable instance of such density-dependent mortality has been observed in the field: Witman et al. (2003) describe a wave of massive *Asterias* recruitment that was effectively terminated by widespread predation among juveniles. Because individuals were not identified to species, however, it is unclear how much of this predation was *bona fide* cannibalism versus IGP.

*A. forbesi* and *A. rubens,* like many other echinoderms, tend to settle and recruit in occasional but intense episodes (Balch and Scheibling 2000; Uthicke et al., 2009). Predation among juveniles during these episodes may contribute to juvenile mortality (cite Jennings and Hunt), which is known to be extreme across marine invertebrate taxa (Gosselin and Qian, 1997; Hunt and Scheibling, 1997). However, cannibalism is a strong driver of growth and could allow cannibalistic juveniles to escape the hazardous early juvenile period through rapid attainment of size refuges. The growth benefits of cannibalism, thought to derive from the stoichiometric compatibility of consumer and resource (MacArthur and Pianka, 1966; Mitra and Flynn, 2005), have been demonstrated in juveniles of the sea star *Pycnopodia helianthoides*, which grow faster when consuming one another than on any other food source (Hodin et al. 2021). IGP could provide the nutritional advantages of cannibalism while also removing competitors and avoiding reductions in inclusive fitness, but such behavior among juvenile sea stars has only been anecdotally reported in one instance (Sewell and Watson 1993). IGP may be less drawback-free in the case of interfertile competitors like *A. forbesi* and *A. rubens*, as ‘heterospecifics’ may be potential future mates and hybrids may be kin.

We conducted a series of experiments to assess evidence for selective cannibalism and cannibalism-avoidant IGP in *A. forbesi*. First, we examined rates of cannibalism in the presence of various levels of an alternative food source, juveniles of the mussel *Mytilus edulis*. We predicted that rates of cannibalism would increase with decreasing *M. edulis* abundance. Second, we offered early juvenile *A. forbesi* equal numbers of related and unrelated conspecifics and observed their predation preferences, predicting that they would preferentially consume non-relatives. Third, we offered early juvenile *A. forbesi* equal numbers of unrelated conspecifics and juveniles of *A. rubens* and observed their preferences, predicting that they would selectively consume juveniles of *A. rubens* over conspecifics.

USE DENSITY FIGURE FROM WITMAN PAPER!!

Stats

Try Fisher’s exact test

Try a paired t test or something like that

**Discussion outline**

We found statement (maybe with short summary of background before we found statement)

Statement on kinship thing and dispersal?

Maybe our finding’s unsurprising (see if there’s any lit on negative results)

Then again, high relatedness among dispersing larvae

Cannibalism in many MIs, little study of kin effect, more studies to determine whether avoidance correlates with l-h (and maybe make this negative results point explicitly)

Cannibalism para—

Widespreadness of canni in cstars

Apparently widespread in juvs, despite few studies

Taxonomic var—asterias and pycnos yes, acanthaster and pisaster probs not (pers obs, the paper that cites Pearce)

Why??

IG predation we’re first in lab studies, but previously reported pycno on pis

(HERE?) need to see what’s up with hybrids!!

The theme of unique trophic ecology of perimetamorphic stage

CoTS

Pycnos

Maybe also cite sprat eating cod example

Maybe this is the closing note

**Discussion**

Longstanding theoretical and empirical work suggests that predators should selectively avoid cannibalizing kin; more recent theory suggests that predator population stability maybe be higher if intraguild predation is preferred to cannibalism. We found that early juveniles of the sea star *Asterias forbesi* engage in cannibalism in the presence of alternative food sources. This confirms the findings of Brocco French and Allen (2021), and suggests that cannibalism is a feature of the post-settlement ecology of this species, rather than an artifact of laboratory conditions. While cannibalistic predators of diverse taxa have been shown to selectively avoid consuming kin, we found that relatively large early juveniles of *A. forbesi* consume related and unrelated conspecifics at similar rates. However, we found that *A. forbesi* given the choice between smaller unrelated conspecifics and individuals of the congener *Asterias rubens* consumed the latter at higher rate. The apparent preference in early juvenile *A. forbesi* for IGP over cannibalism is consonant with recent theory suggesting that predators with the opposite preference may “short circuit” their own populations.

Though Brocco French and Allen (2021) found that *A. forbesi* cannibalize regardless of the presence of alternative food sources, we predicted that presence of a known prey, juveniles of the mussel *Mytilus edulis*, would reduce rates of cannibalism and thus increase survival. However, because cannibalism is an extremely strong driver of growth, we predicted that mean growth would be highest when no alternative food was presented, and the emergence of a small number of cannibalistic “victors” was thus favored. We found that batches of *A. forbesi* offered 0, 5, or 50 mussels did not differ in either survival or mean growth; however, there were non-significant trends towards highest growth in the 0-mussel treatment and highest survival in the 50-mussel treatment, with 5-mussel batches intermediate. GULF OF MAINE

Kin-avoidant cannibalism has been shown to be widespread in nature, including in the early life-history stages of amphibians, insects, etc. (). We made, to our knowledge, the first attempt to examine potential for kin selection in an echinoderm, and find that juveniles of *A. forbesi* do not appear to selectively avoid consuming kin. The evident lack of a mechanism for kin detection is perhaps unsurprising in view of the substantial (30+ day) planktonic duration of larvae of this species, during which siblings seem likely to be separated, along with evidence that sea stars with dispersive larvae tend to have low population genetic structure (Harley et al. 2006). However, mounting evidence suggests that even highly dispersive marine species can exhibit kin structure, and further studies of potential kin-selective behavior in marine taxa are warranted. It would be particularly interesting to investigate whether the early juveniles of brooding sea stars like *Leptasterias* sp., which are released near siblings as well as individuals from other broods, might exhibit kin-avoidant cannibalism.

The ecological important of sea stars is proverbial, and the community-wide consequences of “booms” and “busts” in sea star populations have been demonstrated in marine systems across the world (cite, cite, cite, cite). However, little is known about the factors modulating sea star recruitment and abundance, due to a lack of information on early life-history stages (Menge and Sanford 2013). Mounting evidence suggests that cannibalism may be a widespread feature of sea star ontogeny. In studies or observations of early juvenile sea stars known to the authors, cannibalism has been reported in x/y cases (Table S1). That juveniles of 2/y species do not exhibit cannibalism may be interpreted as an exception proving the rule that such cannibalism is a feature of species-specific ecology, rather than a laboratory artifact. Moreover, in the two asteroid species in which cannibalism has been most intensively studied, this behavior is extremely prevalent among early juveniles and comparatively rare among adults, indicating that this behavior is ontogenetically determined. FURTHER RESEARCH? SOMETHING ABOUT DENSE RECRUITMENT?

More generally, our findings represent a fresh addition to a growing body of literature on the cryptic ecology of early benthic life-history stages of marine organisms. While the ecological significance of planktonic propagules has long been appreciated, the challenge of observing early benthic stages has bred tacit assumptions that these minute forms either operate as mini-adults or possess less well-defined ecological roles than their larger counterparts. In our study as in others, it appears the interactions of early juveniles can be highly defined and strikingly different from those of adults. Without laboratory experiments, it would have been impossible to guess that, for instance, that notoriously coral-killing *Acanthaster* are initially wary of their prey (Deaker et al. 2020), or that gametophytes of the kelp *Ecklonia* can survive, thrive, and potentially disperse through grazing. We propose that the next step in the opening of the so-called “black box” of recruitment is for marine ecologists to develop new molecular and aquacultural techniques to study the ecology of early benthic stages in the field.

SOMETHING ABOUT—if you don’t know what eats the keystone, you don’t know what controls the ecosystem

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