Trophic cascades and the transient keystone concept

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Abstract

Apex predator reintroductions are commonly motivated by the imperative to restore populations and wider ecosystem function by precipitating trophic cascades that release basal species. Yet evidence for the existence of such cascades is often equivocal, particularly where consumptive interactions between apex and intermediate predators are weak or absent. Here, using a tri-trophic skate-crab-bivalve study-system, we find that non-consumptive interactions between apex skate and intermediate crabs cascade down to consumptive interactions between crabs and basal bivalves, significantly reducing bivalve mortality. However, skate only functioned as keystones where crabs foraged for bivalves in the absence of mature bivalve reef: where reef was present, bivalve mortality was not significantly different. By facilitating the establishment of basal species which, in turn, diminish apex-intermediate interactions, the skate's keystone function is subject to negative regulation. Thus, we propose that keystone functionality can be transient with respect to environmental context. Our findings have two central implications for apex predator reintroductions and basic ecology: (i) species hitherto not considered as keystone may have the capacity to act as such transiently, and; (ii) keystones are known to regulate ecosystems, but transience implies that ecosystems can regulate keystone function.

1. Introduction

The keystone species concept is one of the most influential in all of contemporary ecology (Davic, 2003; Mills et al., 1993; Power et al., 1996). As planet Earth undergoes a so-called trophic downgrading (Estes et al., 2011) there are urgent societal, fundamental and applied motivations to better understand keystone-ecosystem interactions. Widespread declines in keystone apex predator populations have been implicated in the release of mesopredators, associated declines in basal species populations, and reductions in biodiversity (Stier et al., 2016). Yet, despite decades of research, keystone species can be difficult to define—as can the trophic cascades that result from their presence or absence (Polis et al., 2000; Ripple et al., 2016). Moreover, apparently incontrovertible examples of apex predator-mediated cascades are often disputed because it is difficult to establish the strength or existence of consumptive interactions between apex and intermediate predators (Grubbs et al., 2016).

Apex-mediated cascades that were once thought to be primarily driven by consumptive effects often turn out to have strong non-consumptive or behavioural elements (Peckarsky et al., 2008). Moreover, fear of apex predators alone is sufficient to initiate and maintain cascades (Suraci et al., 2016). The recognition that non-consumptive effects are central mediators of cascades (Peckarsky et al., 2008; Werner and Peacor, 2003) is particularly relevant to understanding the functional role of elasmobranchs, because evidence for consumptive mediation or apex function is often equivocal or disputed (Grubbs et al., 2016; Roff et al., 2016). Further, because behavioural effects can be instantaneous and decoupled from demographic factors, they are liable to change abruptly between contexts, for example, where intermediate predators forage for basal species in risky or refuge habitats (Trussell et al., 2006). In addition, many basal species—kelp, seagrass, biogenic reefs—are directly responsible for driving changes in context through the provision of spatial structure (Barrios-O'Neill et al., 2016, 2015). Yet little consideration is given to the notion that apex-basal feedbacks might regulate cascades and/or the position of apex predators as keystones, despite the recognition that wider food web complexity can buffer cascades (Brose et al., 2005).

Here, we are motivated to investigate the potential for keystone apex-basal feedbacks because of relatively recent extirpations of large elasmobranchs (including the critically-endangered Flapper Skate, *Dipturus intermedia*) and population collapse of a priority reef-forming species (the Horse Mussel, *Modiolus modiolus*) in Strangford Lough, Ireland (refer to Supporting Information for details). Given the local extirpation of the species in question, we resort to experimental manipulations involving a proxy higher predator (the Painted Skate, *Raja microocellata*) with a comparable feeding ecology (Supporting Information), a representative intermediate crab (*Carcinus maenas*) and a reef forming basal bivalve (*Mytilus edulis*). Structural complexity is known to mediate interactions across foraging contexts (Barrios-O'Neill et al., 2016); thus, we hypothesised that any capacity of the apex predator to provide keystone function would be modulated by the presence of bivalves established in a size refuge, i.e. providing structural complexity whilst being invulnerable to predation. Our goals here are twofold: (i) to experimentally elucidate if and how potential cascading effects might be regulated via feedbacks in the tri-trophic system, and; (ii) to use this data to inform new hypotheses about the potential demographic effects of such feedbacks.

2. Methods

Experimental stock (*Raja microocellata*, *Carcinus maenas* and *Mytilus edulis*) was obtained in the locality of Strangford Lough (54.48102° N, 5.58841° W). Each species was maintained separately in flow-through mesocosms at Queen's Marine Laboratory prior to experimental trials (Supporting Information). Because of the primacy of size over personality in determining interaction strengths (Schröder et al., 2016) we subsampled narrow size-classes of mussels and crabs for trials: *M. edulis* (valve length $\bar{x}/SD$ = 19.8 mm/2.1) and *C. maenas* (carapace width $\bar{x}/SD$ = 43.4 mm/2.1). Given the locally endangered status of *R. microocellata* we selected two closely size-matched individuals for trials (lengths: 490 mm and 510 mm)—on account of this unavoidable pesudoreplication we refrained from analysing data on skate movement.

Arenas (2200 L and 1800-by-1300 mm footprint) contained one marginally-positioned Perspex refuge (40 mm tall, 130-by-200 mm footprint) and one centrally-positioned Perspex reef patch (350-by-350 mm footprint) furnished with 40 previously settled mussel prey (hereafter 'juveniles', i.e. a size class vulnerable to predation). Reef patches were either 'complex' (4 large silicone-filled *Modiolus* bivalves, 57-110 mm valve length) or 'simple' (lacking *Modiolus*). 16 h trials were initiated on the introduction of predator mixtures (presence/absence of 1 skate and presence/absence of 3 crabs) into arenas between 16:00-18:00: surviving mussels were counted on termination. Trials were block-randomised with *n* = 10 (reflecting the maximum experimental turnover practical in 2 months) at each predator/complexity treatment combination, including predator-free controls. During the second hour of a random subset of trials (*n* = 6-8) we recorded behaviour using camcorders and quantified the following for skate and a randomly selected crab respectively: (i) time spent moving (i.e. moving across the arena floor); (ii) time spent on the reef patch, off the patch, or in the refuge.

All analyses were performed in R (R Core Team 2016). Mussel survival was 100% in predator-free controls and skate-only mixtures, therefore we used a simple two-by-two analysis of variance (ANOVA, categorical predictors: skate presence/absence and simple/complex reef) and Tukey's *post hoc* tests with respect to the focal crab-mussel interaction. Crab location constitutes a non-discrete compositional response—therefore, to satisfy model assumptions we applied an isometric planar transformation (van den Boogaart and Tolosana-Delgado, 2008) and assessed location with respect to the same categorical predictors using multivariate analysis of variance (MANOVA). Crab movement is also a compositional response, but with two options here we opt to treat proportion of time spent moving as the response in a standard two-way ANOVA. Assumptions of heteroscedasticity were met for all fitted models (all Bartlett's tests p >0.05).

3. Results

The presence of skate reduced consumption of mussel juveniles by crabs only in the absence of mature reef (Fig. 1a: open half). Conversely, in the presence of reef, skate slightly enhanced consumption of mussel juveniles by crabs (Fig. 1a: shaded half), resulting in a significant main effect of skate ($F_{1,36} = 4.45$, $p = 0.042$, $\eta_p^2 = 0.11$) and a significant skate-reef interaction ($F_{1,36} = 9.36$, $p = 0.004$, $\eta_p^2 = 0.21$). Reef presence did not significantly enhance consumption of mussels, but still had a comparable effect size to skate presence ($F_{1,36} = 3.22$, $p = 0.081$, $\eta_p^2 = 0.08$). Consumption of mussel juveniles by crabs was highest in the absence of skate and mature reef (Fig. 1a: open half) and was significantly higher here than in all other treatments (*post hocs*: skate/reef absent $p = 0.004$; skate/reef present $p = 0.043$; skate absent/reef present $p = 0.008$). Crabs did not change location in response to the presence of mature reef or skate (Fig. 1b. Skate presence/absence $F_{1,23} = 0.82$, NS; reef presence/absence $F_{1,23} = 1.39$, NS; skate-reef interaction $F_{1,23} = 0.02$, NS) but instead significantly reduced their movement where skate were present (Fig. 1c: shaded boxes. Main effect: $F_{1,23} = 18.71$, $p < 0.001$, $\eta_p^2 = 0.45$; *post hocs* between all skate present treatments and all skate absent treatments significant at $p < 0.05$). In contrast, skate tended to move less in the presence of mature reef, and did not appear to respond to the presence of crabs (Fig. 1d open *versus* shaded half).

4. Discussion

Across the biosphere, populations of apex predators are in widespread decline (Estes et al., 2011). The resultant trophic downgrading of ecosystems is particularly concerning because of the role that apex predators often fulfil as keystone species regulating biodiversity, disease and other critical ecosystem functions (Stier et al., 2016). Despite decades of research, ambiguity over operational definitions of keystone species (Davic, 2003), trophic cascades (Polis et al., 2000) and a focus on consumptive effects (Peckarsky et al., 2008) have all hindered more nuanced understanding of keystone-ecosystem interactions and feedbacks. Here, we demonstrate that the presence of and apex predator drives an intermediate-basal consumptive interaction only where that basal species isn’t established, and lacking individuals that are large enough to avoid predation. In doing so we provide preliminary evidence for an apex-basal feedback which prompts us to posit the existence of a hitherto unrecognised aspect of keystone species ecology: transience (Fig. 2). Although we must stress that short term feeding trials prevent an explicit link to demographic effects in the field, in the following section a re-examination data rich examples of trophic cascades would suggest that transience is a viable concept.

The behaviourally mediated wolf-elk cascade in Yellowstone (Fortin et al., 2005) can be viewed as a classic keystone cascade (our terminology: Fig. 2a) because it depends on a continuous apex-intermediate effect through time. In contrast, a consumptively mediated cascade initiated by orcas feeding on sea otters—cascading down to urchins and kelp—(Estes et al., 1998) is transient because the apex predator cannot be sustained in the locality and must move on once resources are locally depleted. We term this a positively regulated transient keystone cascade (Fig. 2c): if the intermediate predator (here, the otter) is locally extirpated then the alternate stable state (that of high urchin abundance) becomes independent of continued apex-intermediate effects through time. In the same system, where orcas are absent, otters regulate urchin abundance and release basal kelp but, given this release, kelp forms dense stands that, in turn, reduce urchin grazing (Konar and Estes, 2003). Thus, the function of the otter as keystone is reduced, but the cascade is maintained. We term this a negatively regulated transient keystone cascade (Fig. 2b). Our present study-system is a potential example of this form of transience. What we outline here is not prescriptive—there are likely numerous permutations beyond (Fig. 2b-c)—but the unifying diagnostic of transience is a system that is pushed into an apex-independent alternate stable state, regardless of the continued presence of that apex. Transience is distinct from the notion that wider complexity in food webs can regulate cascades (Brose et al., 2005) because it concerns the focal tri-trophic motif, rather than the effects of peripheral species on that motif. We suggest that food web models making broad assumptions about predator-prey interaction strengths may systematically underestimate the importance of apex predators if they fail to represent: (i) how changing foraging context can dramatically and systematically modulate interactions (Barrios-O'Neill et al., 2016; Pawar et al., 2012) and; (ii) how apex predators themselves might drive changes in context.

In Strangford Lough, elasmobranchs might function as transient keystones by facilitating the reestablishment of *Modiolus* reefs which, in turn, add structural complexity that can dampen interactions across the system (Barrios-O'Neill et al., 2016). Broadly, transience implies that species which don't obviously function as keystones in one context may come to do so in others, and may act as a buffer, facilitating the maintenance of stable states. Transience is therefore a form of functional redundancy that highlights the importance of biodiversity. Beyond the potential considerations and applications in conservation and restoration ecology, however, our findings highlight a key point: that although a keystone species may be characterised by disproportionate top-down effects on the wider ecosystem, these effects may themselves be subject to strong regulatory feedbacks.

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Supporting information

Sourcing stock, experimental setup and project details are available in the online supplement. Data is available at datadryad.org/xxxxx.

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Figures

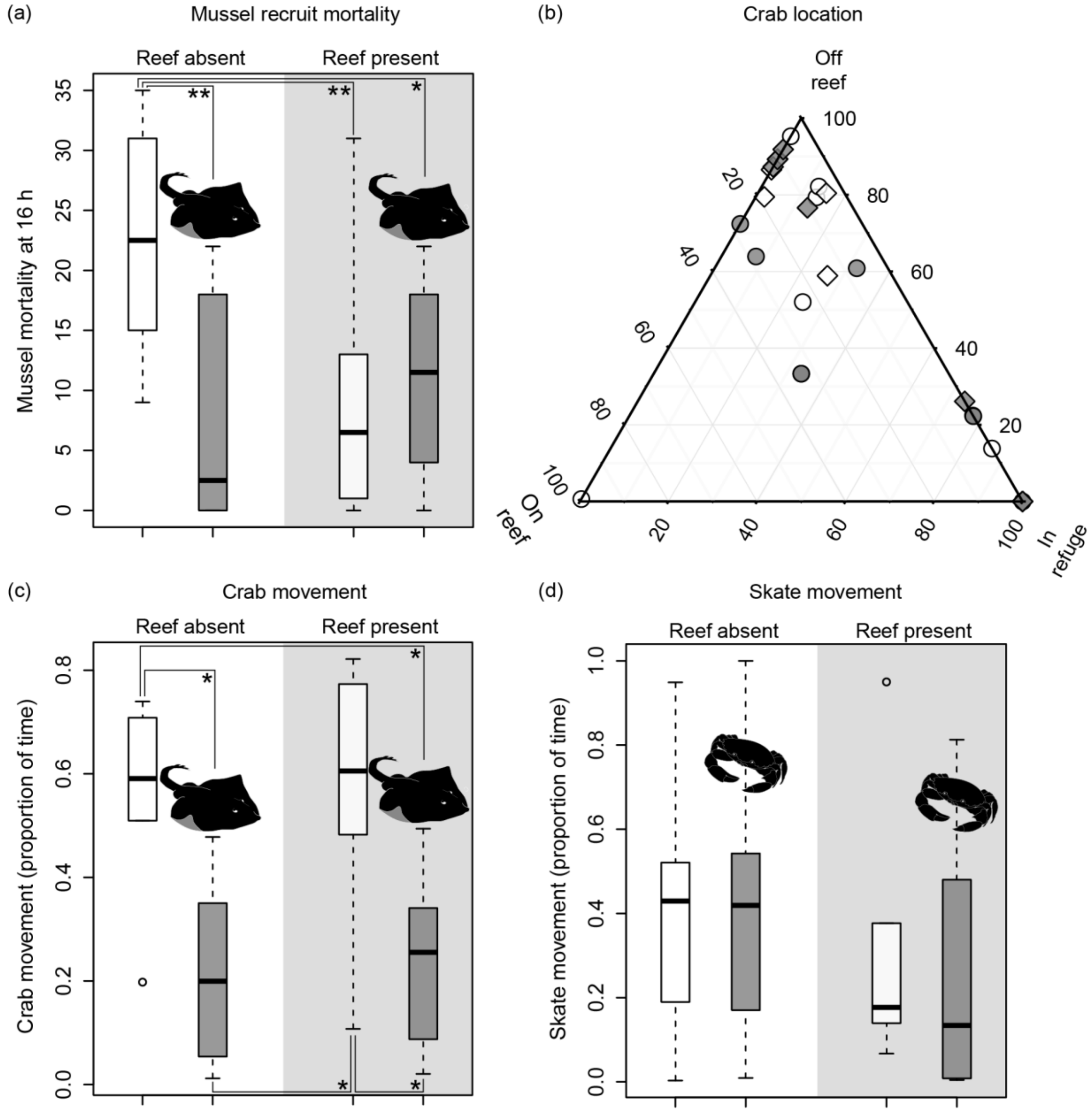

Figure 1 (a) Crab predation on mussel juveniles at 16 h; (b) crab location in the absence/presence (open/shaded) of skate and the absence/presence (diamond/circle) of mature reef; (c) crab movement in the absence/presence of mature reef and skate; (d) skate movement (pesudoreplicated) in the absence/presence of mature reef and crabs. Stars equate to significant differences following *post hocs*.

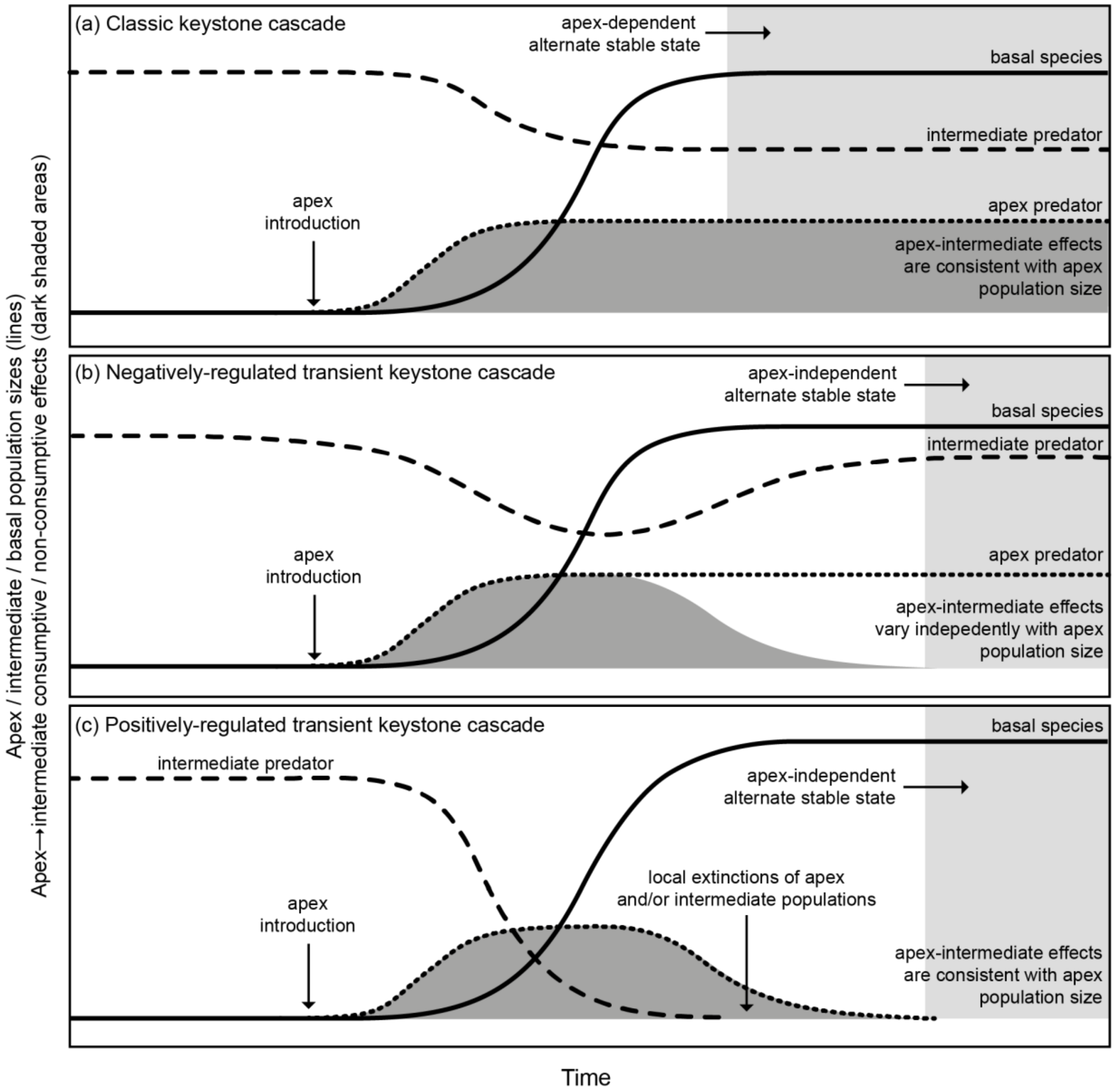

Figure 2 Classic trophic cascades depend on the continued effects of apex keystone predators on intermediate predators through time (a) but trophic cascades can also be precipitated when apex predators transiently act as keystones by releasing basal populations which, in turn, alter the context in which interactions occur. Negative regulation of this process may result in intermediate predator recovery (b), but where the cascade enhances intermediate risk extinctions may occur (c). In both cases the basal populations achieve an apex-independent alternate stable state.