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When Sea Urchins Dine: The Roles of Friends, Food and Fear and Implications to Kelp Forest Conservation

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Abstract. Kelp forests are vital "blue carbon" sinks and biodiversity hotspots, yet increasingly threatened by sea urchin overgrazing, which can convert them into barren seascapes. Understanding the behavioral drivers of urchin feeding—such as group dynamics, food availability, and predation risk—is therefore critical for effective conservation and ecosystem-based management.This study investigates the behavioral drivers behind overgrazing by the sea urchin Strongylocentrotus intermedius through controlled laboratory experiments, focusing on the roles of group size, diet composition, and predator cues. Results indicate that solitary urchins exhibit lower overall consumption and a preference for drift kelp, whereas grouped urchins show significantly higher feeding rates and shift toward live kelp, intensifying grazing pressure on kelp forests. Diet composition further modulates foraging behavior, with drift kelp abundance sustaining urchin populations even when live kelp is limited. Predator cues suppress total feeding but do not alter the preference for live kelp. The interplay between food availability and predation risk highlights that grazing dynamics are shaped by both bottom-up and top-down factors. The findings underscore the need for integrated conservation strategies that manage urchin densities, prevent aggregation, maintain kelp bed integrity, and consider predator roles to mitigate kelp forest degradation.

Keywords: Sea urchin grazing, Kelp forest conservation, Feeding behavior, Predator-prey interactions, Ecosystem management

1. Introduction

Kelp forest is a natural resource in the fight against climate change due to their high carbon sequestration capacity. For example, certain kelp species like the giant kelp (Macrocystis pyrifera) grow up to two feet in a day, rapidly storing carbon in their biomass. They are vital ecosystems that combat climate change by absorbing around 4.9 megatons of carbon dioxide annually, reducing greenhouse gases [1]. Through carbon dioxide absorption and fixation by photosynthesis, kelp beds function as high-capacity "blue carbon" sinks that can mitigate global warming while, simultaneously, increasing biodiversity because the complex physical structure of the forest creates niches for countless species, ranging from juvenile fish to sea stars and sea urchins. Also, kelp forests play a key role in maintaining coastal and marine ecosystem health and resilience by buffering wave energy and preventing coastal erosion, thus protecting shorelines. Ecologically, kelp forests provide diverse habitat, cover, and food for a wide range of marine organisms from small invertebrates to important commercial fish species. These ecosystems enhance biodiversity with the maintenance of complex food webs and offering protective refuges from predators. Functionally, kelp forests act as natural nutrient regulators and water purifiers, removing pollutants while providing high-quality water to sustain marine and human coastal populations through filtration and oxygenation, which supports fisheries and aquaculture.

Their importance extends beyond ecology to socioeconomic and cultural realms, sustaining fisheries [2], ecotourism-supported coastal economies [3], and culturally significant resources for local and Indigenous communities who rely on them for subsistence and culture [4]. Despite these benefits, kelp forests are now under siege by a number of stressors, one of the most imperative being overgrazing by sea urchins. This process, typically triggered by the loss of natural predators like sea otters, has the potential to rapidly convert dense kelp bed habitat to barren habitat. Protecting kelp forests should be a central focus of ecosystem-based management, and understanding the behavioral mechanisms driving urchin overgrazing is key to designing effective restoration and conservation strategies [2,5,6].

Sea urchins act as keystone grazers, serve as regulating agents of algal communities and stabilize ecological equilibrium [7]. Yet they can also act as a cause of leading to devastating grazing that converts productive kelp forests into barren seascapes known as "urchin barrens." These transitions are not only calamitous for marine diversity but also undermine fisheries, destabilize food webs, and exact severe economic costs on coastal communities based on kelp-associated resources. The decline of kelp assemblages into barrens emphasizes the need to understand the ecological mechanisms controlling the behavior of sea urchins and the tipping points at which their grazing becomes deleterious.

While previous investigations have documented urchin effects on kelp, less had been known about the behavioral drivers of these regime shifts. It is well established that sea urchin feeding behavior exhibits remarkable plasticity, which may in fact be the underlying cause of overgrazing events [8,9]. Studies have shown that when sea urchin populations are large and densities high, individuals tend to feed preferentially on live kelp, whereas at low population densities, urchins consume proportionally more drift kelp [10-12]. This shift is interpreted as an adaptive foraging strategy in response to environmental context and population density. Previous research has also demonstrated that predator presence and associated risk cues can profoundly modify urchin behavior, even in the absence of direct predation, leading to reduced feeding activity or altered dietary preference from live to drift kelp [13,14]. When drift kelp becomes scarce, however, sea urchins increase grazing pressure on live kelp, accelerating the transition toward barren states [12]. Based on these observations, we hypothesize that sea urchins adjust their feeding behavior according to perceived predation risk in the environment, with drift kelp serving as a safer and more conservative food option. Understanding these behavioral mechanisms is critical for predicting the thresholds of overgrazing and informing future conservation and restoration strategies for kelp forest ecosystems.

We describe laboratory experiments on the sea urchin Strongylocentrotus intermedius to quantify how group size, diet composition, and predator cues interactively regulate feeding behavior. In establishing baseline physiological and behavioral responses, we illuminate the processes that regulate overgrazing thresholds and outline potential conservation and management approaches for kelp forests.

2. Materials and methods

2.1. Sea urchins

Two hundred sea urchins Strongylocentrotus intermedius (37.45 ± 1.43 mm test diameter, 19.40 ± 1.39 g body weight) were transported from a local aquafarm to the Key Laboratory of Mariculture & Stock Enhancement in the North China's Sea, Ministry of Agriculture and Rural Affairs. Upon arrival, all individuals were acclimated and fed Laminaria japonica ad libitum for one week in six tanks (50 × 35 × 30 cm) with seawater at 13.8 ± 0.53 °C, under a 12D:12L light regime, and pH 7.83 ± 0.06. To standardize feeding motivation, sea urchins were starved for 48 h prior to each experiment.

Fresh kelp was collected from the field and used as food. Each kelp blade was cut into pieces of approximately 12 × 15 cm and was used in the experiment. Two types of kelp were prepared: live kelp, which was fixed upright in the tanks using stones and floats, and drifting kelp, which was placed horizontally on the tank bottom with the same size and weight as live kelp.

The sea urchins were reused across experiments. Considering that predator cues may induce stress responses, all individuals were allowed to recover for seven days after each trial. To ensure consistency, the same recovery period was also applied to experiments without predator treatments, even though feeding alone was unlikely to affect sea urchin condition.

2.2. Experiment 1. effect of group size on feeding rate and food preference

To examine the effects of population size on feeding rate and preference, three density groups were established: 1-urchin, 5-urchin, and 10-urchin groups, containing one, five, and ten individuals per group, respectively. Sea urchins were placed in tanks (50 × 35 × 30 cm) with 50 g of fresh kelp and 50 g of drifting kelp for 24 h. After the trial, the amount of kelp consumed was measured. Each treatment was replicated six times. The mean consumption per urchin was calculated as the total food consumed in each tank divided by the number of sea urchins in that tank.

2.3. Experiment 2. effect of diet composition on feeding behavior

To assess the effects of food supply on sea urchin feeding behavior, two diet treatments were established, each containing 10 sea urchins per group. The treatments consisted of a live kelp dominated diet (70 g fresh kelp + 30 g drifting kelp) and a drift kelp dominated diet (30 g fresh kelp + 70 g drifting kelp). Each treatment was replicated six times. The weights of kelp were recorded before and after the 24 h trial to determine total consumption, live kelp consumption, and drift kelp consumption.

2.4. Experiment 3. effect of predator on feeding behavior

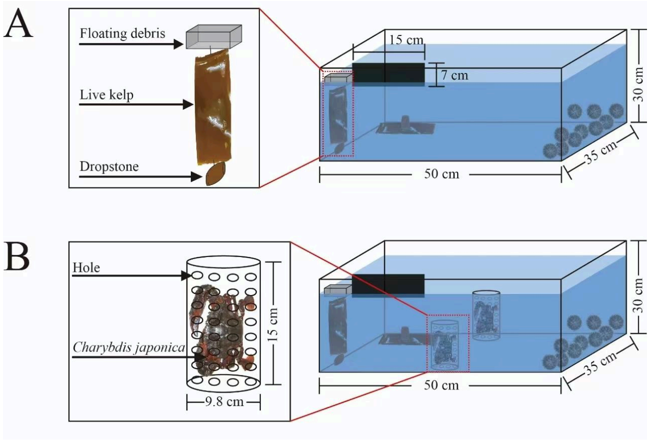

Figure 1. Experimental setup for feeding behavior assays of the sea urchin Strongylocentrotus intermedius. (A) The treatment showing placement of live and drift kelp in the tank (50 × 35 × 30 cm). (B) Predator-cue treatment with a swimming crab (Charybdis japonica) confined in a perforated PVC cylinder allowing cue diffusion without direct contact

To evaluate the effect of predator on sea urchin feeding behavior, two treatments were established: with predator and without predator. In the with-predator treatment, a live crab (Charybdis japonica, a natural predator of sea urchins) was placed inside a transparent plastic container (diameter 9.8 cm, height 15 cm) with multiple perforations. The container allowed water exchange, enabling the crab to breathe and release chemical signals, while preventing direct physical interaction with the sea urchins. In the control treatment, no crab was introduced. Sea urchins (10 individuals per tank) were exposed to the two treatments for 24 h, with six replicates for control, the treatment without predator, and 12 for the with-predator group. Food consumption was measured by weighing kelp before and after the trial.

2.5. Experiment 4. combined effects of predator cues and diet composition on feeding behavior

To examine the combined effects of predator cues and food composition on sea urchin feeding behavior, two treatments were conducted under predator cue conditions: live-dominated diet (70 g fresh kelp + 30 g drifting kelp) and drift-dominated diet (30 g fresh kelp + 70 g drifting kelp). Each treatment contained 10 sea urchins per tank, lasted for 24 hours and was replicated six times. The design of experiment 4 corresponded to the two diet treatments in Experiment 2 and 10-urchins group in experiment 1 which served as the without predator cue controls with different food supply. And also corresponded to the with-predator group in experiment 3, which served as the equal food supply control. Thereby these six groups forming a two-factor experiment (predator cue × diet composition).

2.6. Feeding consumption calculations

Total food consumption, live kelp consumption, and drifting kelp consumption were calculated as the difference between the initial and final food weights for all four experiments:

$$\mathrm{C}_{\text{total}} = \mathrm{W}_{\text{initial, total}} - \mathrm{W}_{\text{final,total}} \tag{1}$$

$$C_{\mathrm{live}} = W_{\mathrm{initial,live}} - W_{\mathrm{final,live}} \tag{2}$$

$$C_{\mathrm{drift}} = W_{\mathrm{initial,drift}} - W_{\mathrm{final,drift}} \tag{3}$$

where C represents consumption (g), and $W_{\mathrm{initial}}$and W_{final}represent the weights (g) of food before and after the 24 h feeding trial, respectively.

2.7. Data analysis

Normality and homogeneity of variances were tested using the Shapiro–Wilk test and Levene's test, respectively. One-way ANOVA with Tukey's HSD test, Welch's ANOVA with Games–Howell test, and independent t-tests were used for normally distributed data with equal or unequal variances. When assumptions of normality or homogeneity were not met, non-parametric tests (Wilcoxon signed-rank test or Mann–Whitney U test) were applied. Two-way ANOVA with Tukey's HSD test was used to analyze the effects of predator presence and different diet compositions. Since the assumption of homogeneity of variance for total feeding amount and live kelp consumption in Experiment 4 was violated ($p < 0.05$), we used the robust Pillai's Trace statistic for multivariate testing, and conducted simple effect analyses using independent-samples t-tests and one-way ANOVA.

All statistical analyses were performed in R (version 4.3.1; R Core Team, Vienna, Austria). Two-way ANOVA and subsequent post hoc tests (Tukey HSD) were conducted using the package car and emmeans. Normality was assessed with the Shapiro–Wilk test and homogeneity of variances with Levene's test (car package). A significance level of $p < 0.05$ was adopted for all analyses.

3. Results

3.1. Group size affects sea urchin feeding behavior

The food consumption per urchin differed significantly among the three groups ($F = 20.97$, $P < 0.001$). The mean values were 0.87 ± 0.28 g in the 1-urchin group, 1.70 ± 0.31 g in the 5-urchin group, and 1.64 ± 0.09 g in the 10-urchin group. There is a significantly lower consumption in the 1-urchin group compared with both the 5-urchin ($P < 0.001$) and 10-urchin groups ($P < 0.001$), whereas no difference was detected between the 5- and 10-urchin groups ($P = 0.896$).

Live kelp consumption also differed significantly among the three groups ($F = 142.67$, $P < 0.001$). The mean values were 0.17 ± 0.08 g, 0.85 ± 0.27 g, and 1.02 ± 0.08 g for the 1-, 5-, and 10-urchin groups, respectively. The 1-urchin group consumed significantly less live kelp than both the 5-urchin ($P = 0.001$) and 10-urchin groups ($P < 0.001$), while no difference was observed between the 5- and 10-urchin groups ($P = 0.210$).

Feeding preference analysis revealed that in the 1-urchin group, consumption of drifting kelp was significantly higher than live kelp ($F = 3.000$, $t = 5.394$, $P < 0.001$). In the 5-urchin group, no difference was detected between the two food types ($F = 0.295$, $t = 0.046$, $P = 0.964$). In the 10-urchin group, live kelp consumption was significantly higher than drifting kelp (Mann-Whitney = 0.000, Wilcoxon $W = 21.000$, $P = 0.002$).

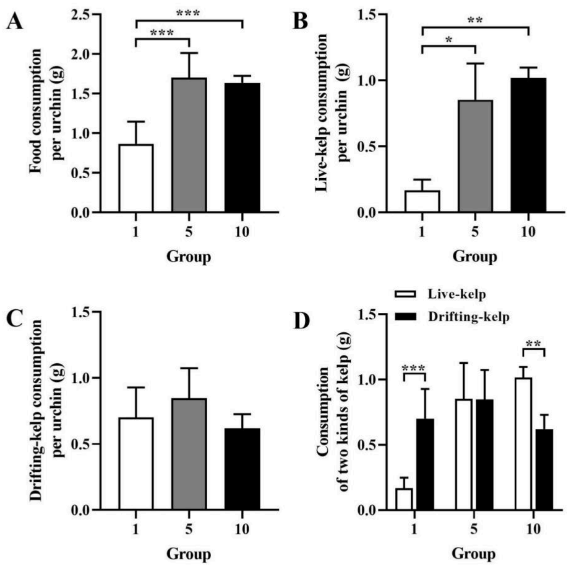

Figure 2. The result of experiment 1, *, **, *** refer to P< 0.05; P <0.01, and P < 0.001. 3.2 Diet composition affect sea urchins feeding behavior

3.2. Diet consumption affects sea urchin feeding behavior

Across the three diet treatments (70 g live + 30 g drift, 30 g live + 70 g drift, and equal supply), total kelp consumption differed significantly (F = 5.359, P = 0.018). Pairwise comparisons revealed that the drift-dominated group consumed more kelp than the live-dominated group (P = 0.017), while no significant difference was found between the equal supply group and either of the dominant groups (live-dominated vs. equal: P = 0.080; drift-dominated vs. equal: P = 0.707).

Live kelp consumption also varied significantly among treatments (Kruskal–Wallis = 12.684, P = 0.002). Urchins in the live-dominated group consumed more live kelp than those in the drift-dominated group (P = 0.001), while no significant difference was detected between the equal supply group and the other two groups (P > 0.05).

By contrast, drift kelp consumption showed a strong dietary effect (F = 45.348, P < 0.001). Urchins in the drift-dominated group consumed the highest amount of drift kelp, followed by those in the equal supply group, and the lowest intake occurred in the live-dominated group. All pairwise comparisons indicated significant differences (P < 0.05), except for the drift-dominated vs. equal supply comparison, where drift consumption was still higher in the drift-dominated group (P = 0.018).

Preference analyses further indicated that urchins exhibited consistent selection patterns within each diet treatment. In the live-dominated group, live kelp was significantly preferred over drift kelp (t = 8.900, P < 0.001). Similarly, in the equal supply group, urchins also preferred live kelp (Wilcoxon W = 21.000, P = 0.002). In the drift-dominated group, however, drift kelp was consumed in significantly greater quantities (t = 4.972, P = 0.001).

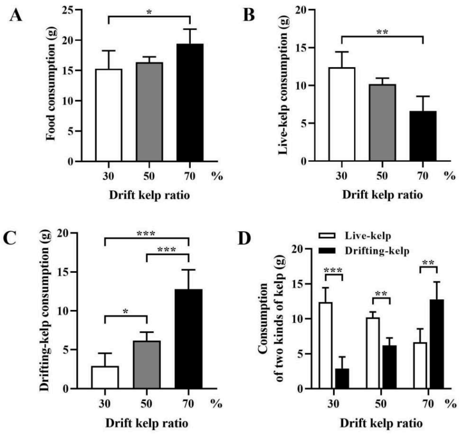

Figure 3. The result of experiment 2, *, **, *** refer to $P < 0.05$; $P < 0.01$, and $P < 0.001$

3.3. Predator presence affects sea urchin feeding behavior

Total kelp consumption was significantly lower in the with predator group (6.43 ± 0.98 g, n = 12) than in the without predator group (17.87 ± 2.12 g, $P = 1.39 \times 10^{-5}$). Live kelp consumption was lower in the with predator group (4.83 ± 0.82 g) than in the without predator group (11.88 ± 1.83 g; $P = 1.0 \times 10^{-4}$). Drift kelp consumption was also reduced in the with predator group (1.60 ± 0.72 g) compared with the without predator group (5.98 ± 1.83 g; $P = 1.49 \times 10^{-3}$).

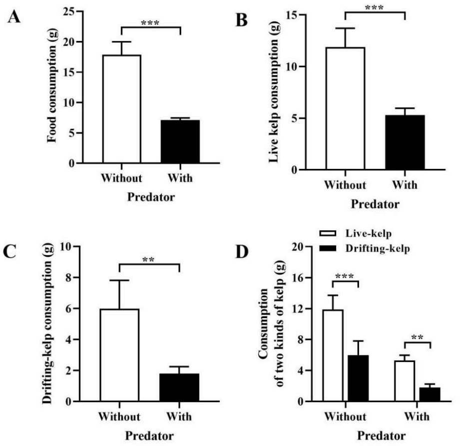

Figure 4. The results of experiment 3, **, *** refer to $P < 0.05$; $P < 0.01$, and $P < 0.001$

3.4. Combined effects of predator presence and diet composition

A two-way ANOVA revealed that both predator presence and food ratio significantly influenced sea urchin feeding behavior. For live kelp consumption, the main effect of predator was not significant ($P = 0.933$), whereas the effect of food ratio was highly significant ($F= 41.50$, $P < 0.001$). Importantly, a strong Predator × Ratio interaction was detected ($F= 18.77$, $P < 0.001$), indicating that predator presence altered the effect of food ratio on live kelp intake.

For drift kelp consumption, both predator presence ($F = 97.41$, $P < 0.001$) and food ratio ($F= 36.60$, $P < 0.001$) showed highly significant effects. Moreover, their interaction was also significant

(F= 27.50, P < 0.001), suggesting that predators strongly suppressed drift kelp consumption and that the influence of food ratio differed depending on predator presence.

Total kelp consumption was also significantly affected by predator presence (F = 55.32, P < 0.001), food ratio (F= 15.61, P < 0.001), and their interaction (F= 20.80, P < 0.001). In general, predator presence markedly reduced total intake, particularly by lowering drift kelp consumption.

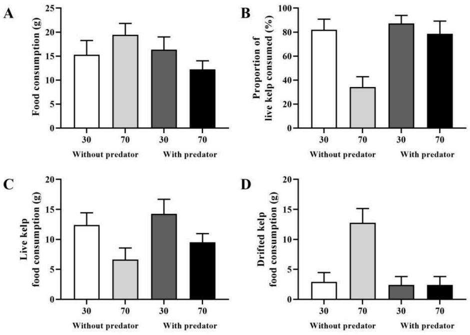

Figure 5. The results of experiment 4, 30 and 70 refer to the ratio (%) of drifting kelp

4. Discussion

4.1. Group size as a driver of feeding behavior change

In this study, food consumption per urchin was significantly lower in the 1-urchin group compared with both the 5-urchin and 10-urchin groups, supporting our initial hypothesis that solitary urchins feed more cautiously, resulting in reduced intake [13,15]. In contrast, no significant difference was detected between the 5-urchin and 10-urchin groups, indicating that once sea urchins form a group, per-urchin food consumption stabilizes and is not further influenced by larger group size [16,17]. This pattern may reflect a shift in feeding mode, with solitary individuals exhibiting cautious behavior, whereas group-living individuals feed more boldly, such that increasing group size does not further alter consumption [18].

Feeding preference also varied with group size. When alone, sea urchins showed a clear preference for drifting kelp, while no significant difference between the two food types was observed in the 5-urchin group. In contrast, in the 10-urchin group, consumption of live kelp was significantly higher than that of drifting kelp. This indicates that group formation not only enhances feeding rate but also promotes a stronger preference for live kelp [19,20]. Notably, the amount of drifting kelp consumed did not differ significantly among the three groups, whereas live kelp consumption was significantly higher in the 5- and 10-urchin groups than in solitary urchins. These results further support the hypothesis of two distinct feeding modes, and demonstrate that the bolder feeding behavior observed in groups is primarily expressed through increased consumption of live kelp [21].

From an ecological perspective, this behavior represents a potential threat to kelp forest conservation, as group foraging by sea urchins can disproportionately increase damage to live kelp [16,22]. Therefore, in addition to controlling overall sea urchin abundance, management strategies should also aim to reduce local densities and prevent aggregation, thereby mitigating their impact on kelp forests [9,23].

4.2. Diet composition as a driver of feeding behavior

Our results demonstrate that food composition strongly affected the feeding behavior of S. intermedius. When diets were dominated by live kelp, consumption of live blades increased, whereas in drift-dominated diets, consumption shifted toward drifting kelp. Across treatments, sea urchins adjusted their feeding patterns according to the availability of each food type. This flexible foraging strategy is consistent with observations that sea urchins modify feeding intensity depending on resource distribution [18,24].

Ecologically, these findings highlight the role of drifting kelp in reinforcing a feedback cycle. Grazing on live kelp can lead to frond detachment, generating drifting material. Once present, this drifting kelp is readily consumed, thereby sustaining sea urchin populations even when live kelp biomass is reduced. This drift–grazer cycle has been noted as a critical factor maintaining urchin barrens and inhibiting kelp recovery [21,23].

For conservation and management, these results suggest that strategies should not only aim to control sea urchin densities but also to maintain the structural integrity of kelp beds. Preventing excessive detachment of kelp fronds can reduce the supply of drifting material that otherwise sustains overgrazing populations [9,25].

4.3. Predator presence and its effect on feeding

Our results clearly demonstrate that the presence of predator cues strongly suppressed the feeding activity of S. intermedius. Total kelp consumption was significantly lower in the with-predator group than in the without-predator group, and this reduction was consistently reflected in both live and drifting kelp. Such non-consumptive predator effects on sea urchins have been widely reported, where chemical cues of predators suppress foraging intensity and movement [26,27].

Although overall intake was reduced, the relative preference pattern remained unchanged. In both predator and non-predator treatments, live kelp consumption was significantly higher than drifting kelp. This indicates that predator cues suppressed total feeding but did not alter the direction of food preference. Similar findings have been observed in other echinoid species, where predator risk reduced grazing but did not completely eliminate resource selectivity [24,28].

Taken together, these results suggest that predator presence primarily has a quantitative effect, reducing how much is consumed rather than changing which resource is preferred. From an ecological perspective, this implies that even under predation risk, sea urchins may continue to exert disproportionate pressure on live kelp, thereby maintaining a potential threat to kelp forests [16,22].

4.4. Combined effects of food composition and predator presence

The gradient of increasing drift kelp proportion (70:30 → 50:50 → 30:70) revealed a clear substitution effect in feeding behavior. In the absence of predators, live kelp consumption decreased whereas drift kelp consumption increased, resulting in the highest total intake in the 30:70 group. This indicates that sea urchins flexibly adjust their foraging strategies in response to food composition, shifting towards drift kelp when it becomes more abundant. Drift kelp may be energetically more accessible, as it requires lower handling costs compared to attached kelp, thereby allowing consumers to maximize net energy intake [29,30]. In contrast, predator presence suppressed both total consumption and food-type differences, supporting the safety-first principle of foraging theory and suggesting that risk avoidance overrides nutritional optimization [31,27].

From an ecological perspective, these results imply that fluctuations in drift kelp availability, which are common in kelp forest ecosystems due to seasonal detachment and storm events, may enhance herbivore consumption and accelerate energy transfer to higher trophic levels when predator pressure is low [23,32]. However, this bottom-up effect of drift subsidies is constrained in predator-rich environments, where top-down forces dominate feeding behavior [24,33]. Such context-dependent interactions highlight the importance of jointly considering both bottom-up and top-down processes in understanding energy flow and trophic dynamics in coastal ecosystems [5,34].

At the applied level, these findings provide practical insights for aquaculture and resource management. In controlled culture systems where predator cues are absent, increasing the proportion of drift macroalgae could be an effective strategy to stimulate overall feeding and growth performance [18,35]. Conversely, under conditions of strong predation risk or simulated predator cues, adjusting feed composition may have limited benefits since feeding activity is largely suppressed. Therefore, optimizing feed strategies should be coupled with predator management to fully realize the growth-promoting potential of drift algal supplementation.

Together, the present study demonstrates that feeding strategies are shaped by the interplay between food availability and predator risk. At the individual level, sea urchins trade off between energy maximization and risk avoidance; at the ecosystem level, drift kelp inputs can enhance trophic transfer but only under low-risk conditions; and at the applied level, aquaculture systems can harness drift kelp subsidies to improve efficiency when predation stress is minimized. This multi-scale perspective underscores the necessity of linking behavioral ecology with ecosystem processes and aquaculture practices to achieve both ecological understanding and practical outcomes.

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