Toxic prey can alter foraging strategies of key marine predators

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Harmful algal bloom (HAB) toxins have been shown to mediate the strength of consumer-prey interactions, and thus ecosystem patterns and processes, by altering the foraging behavior of principal predators in coastal marine systems. In a series of companion studies examining the role HABs play in structuring marine vertebrate/invertebrate predator-prey relationships, we compared the foraging behavior and diet of key marine mammal and avian predators with prey abundance and seasonal/spatial variation of paralytic shellfish poisoning toxins (PSPT) in selected invertebrate prey species. Results of these foraging studies suggest that some high-level marine predators are able to detect and avoid consumption of lethal concentrations of HAB toxins by altering their foraging strategies, as demonstrated by site avoidance, prey switching, and selective tissue rejection behaviors. Consequently, the ability of prey species to retain toxins may deter or exclude these ecologically important predators from areas affected by HABs, potentially altering ecosystem structure and function. The ecological implication of this shifting of predation pressure away from preferred prey has yet to be determined.

Research Approach

Sea Otters and chronically toxic prey in southeast Alaska

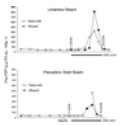
Prior to 1991, Sea otters in southeast Alaska were found only along the outer coast, where they preyed primarily upon populations of *Saxidomus giganteus* (butter clams) with no history of paralytic shellfish poisoning (PSPT) toxicity. The Inside Passage, however, is well known for large populations of butter clams containing chronically high levels of PSPT. We tested the general hypothesis that PSPT distribution regulated sea otter foraging by determining: 1) whether or not the expanding southeast Alaskan sea otter population occupied Inside Passage sites where butter clams are abundant but contain biologically significant levels of PSPT, and 2) if so, whether the sea otters either shifted their diet away from their primary butter clams prey to alternate non-toxic species, or are continuing to eat butter clams, while discarding the most toxic body parts.

Study areas for comparison were selected based on documented patterns of butter clams toxicity and recent sea otter range expansion. Prior to selecting specific observation sites, each area was subdivided and thoroughly surveyed by small boat. Specific sampling stations within sites were selected where sea otters were observed to be actively feeding. Because previous work with captive sea otters suggests that 149 µg PSPT 100g^{-1} in butter clams is a threshold level for sea otters, sites or prey were not considered toxic unless average levels were above this value.

Within each study area we sought to assess and quantify sea otter diet and foraging behavior, as well as prey availability, composition, abundance, and PSPT toxicity. **Methods** included direct observation of sea otter diet composition, feeding behavior (including dive times, surface intervals, feeding rate and foraging success), SCUBA diver sampling of prey shells and discarded tissues (particularly the large siphon of butter clams), as well as live prey abundance. With these data we determined the threshold concentrations of PSPT avoided by free-ranging sea otters, and how this avoidance translated to differences in the prey population status.

Shorebirds and seasonally toxic prey in California

Our general approach was to document and correlate changes in the foraging behavior of free-ranging avian predators with seasonal changes (spatial and temporal) in harmful algal bloom (HAB) related toxicity of their invertebrate prey in two different habitat and community types. Habitats included: 1) Rocky shores where Black Oystercatchers (*Haematopus bachmani*) forage primarily on sea mussels (*Mytilus californianus*), and, 2) Exposed sandy beaches where a diversity of shorebirds forage on extremely abundant sand crabs (*Emerita analoga*). Each of these prey species are known to accumulate PSPT during HAB events (F1). These two systems provided ideal study sites for determining the ecological role of phytotoxins in benthic communities. Pairing each sandy site with a rocky site separated by only a few hundred meters not only minimized field effort, but enabled comparisons of prey toxicity and predator behavior in different habitat types exposed to very similar bloom conditions.



F1. Synchronous rise and fall of PSPT concentrations (µg STX eq ·100g^{-1}) in sand crabs and sea mussels at the study sites. Data points represent single values resultant of standard mouse bioassay analyses.

Observations of foraging birds were made every two weeks during the lowest tides of the month at pre-selected rocky and sandy beach sites from April through October. Foraging data was collected using a "continuous focal sample" method. Type and duration of the bird's activities were recorded to the nearest second, as well as habitat used, and weather and surf conditions. Major activity categories included: searching, prey handling, inactive periods of foraging due to wave interruption, resting, interacting with other birds (especially kleptoparasitism), and out-of-view. All prey captured during a focal sample was identified and recorded. Rejection and partial consumption of prey was also noted. PSPT levels in tissue samples (sea mussels and sand crabs) were analyzed using the standard mouse bioassay.

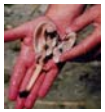
Results

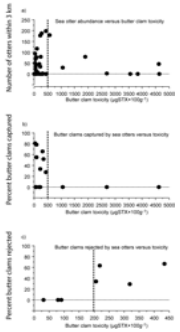
Site avoidance hypothesis not supported

No evidence was found in support of site avoidance by sea otters due to HAB related prey toxicity (F1a). Sea otters were found foraging in areas where butter clams and other high-value bivalve prey species contained the highest PSPT concentrations recorded during this study (1000 to >4500 µgSTX eq · 100g^{-1}).

Prey rejection at sites of intermediate prey toxic (200-500 µgSTX eq · 100g^{-1})

Sea otters were observed to reject and discard butter clam tissues only at sites where whole butter clam toxicity values were between 200-500 µgSTX eq · 100g^{-1} (F1c). It was also only at these sites that dense patches of discarded and highly toxic butter clam siphon tissues were found. Sea otters were never observed discarding tissues of any other captured prey species, nor from butter clams at any sites where the prey toxicity was below 200 µgSTX eq · 100g $^{-1}$. Statistically, there was a significantly higher frequency of sea otters discarding butter clams at sites where this species' toxicity was > 200 µgSTX eq · 100g^{-1} (t-test, df = 5, t = 6.49, p = 0.001), but sea otters were never observed even capturing butter clams in areas where their toxicity was > 500 µgSTX eq · 100g^{-1}.





F1. ***Enhydra lutris* and *Saxidomus giganteus*.** Scatter plots of data from individual sea otter feeding sites showing the relationship between butter clam toxicity and a) number of sea otters found within 3 km of prey sampling site, b) percentage of observed prey captured by feeding sea otters identified as butter clams, c) percentage of observed butter clam capture events in which sea otters discarded all or a portion of the captured individual. Vertical lines represent threshold concentrations of prey toxicity at which sea otter foraging behavior changed.

Sequestered PSPT as a refuge from sea otter predation

Butter Clam prey are more abundant and generally larger at toxic versus non-toxic foraging areas (T1).

	Abundance	Size	Biomass	N
Low toxicity	6.8 ± 7.7	60.4 ± 17.6	215 ± 330	21-22
High toxicity	16.5 ± 17.5	74.6 ± 10.2	541 ± 481	5
p	0.0261	0.0492	0.0403	

T1. ***Saxidomus giganteus*.** Abundance (ind. · 0.25m $^{-2}$), size (mm) and biomass (g · 0.25m $^{-2}$) were all significantly lower at sea otter occupied sites where butter clam paralytic shellfish poisoning (PSP) toxicity levels were low (<500 µg STX eq · 100 g^{-1} tissue weight) than at otter sites where butter clam PSP toxicity levels were high (>500 µg STX eq · 100 g $^{-1}$). Data are mean ± SD; N = number of sites

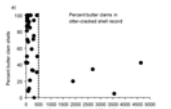
[Full results can be found in MEPS 271:233-243, 2004]

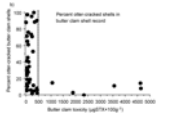
Butter clams were selected as the best overall indicator of the relationship between sea otter prey availability and status versus toxicity having the widest and most continuous range of PSPT toxicity values (non-detect to >4500 µg STX·100g^{-1}) found throughout the study areas.

Prey switching and testing at highly toxic sites (> 500 µgSTX · 100g^{-1})

There was strong evidence for prey switching at sites where the toxicity of the preferred butter clam prey exceeds a threshold concentration of 500 µgSTX eq · 100g^{-1}. At these highly toxic sites, foraging sea otters were never observed to capture butter clam prey (F1b), despite the high abundance of this species at these sites. Instead, otters were observed to forage on small and rare *Macoma* spp. clams, sea pens, and small green sea urchins, while avoiding (<1% captured) other highly toxic bivalve species that were much larger and more abundant. This prey avoidance behavior is very unusual for sea otters, a species with a well-documented preference for butter clams and other large energy-rich prey in disproportion to their relative abundance.

Butter clam mortality



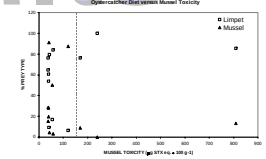


Butter clams constituted a significantly lower percentage of the sea otter diet at toxic sites. The majority of butter clam mortality by sea otters was greatest at sites of "intermediate toxicity" where sea otters were actively testing and discarding tissues. Although sea otters were never observed to capture butter clams at the highly toxic sites (>500 µgSTX eq · 100g $^{-1}$), the presence of a very few butter clam shells in the recent otter-cracked shell record (F2a) indicates that sea otters continue to capture, open and test a small number of butter clam prey above this threshold toxicity level.

F2. ***Enhydra lutris* and *Saxidomus giganteus*.** Scatter plots of shell record data from individual sea otter feeding sites showing the relationship between butter clam toxicity and a) the percentage of butter clam shells found among all collected bivalve shells that had been opened by sea otters, and b) the percentage of otter-cracked shells among all recently predated butter clam shells from all sources of mortality collected at each site.

Birds switch to alternate prey at high prey toxicity

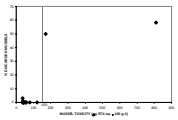
Oystercatchers shifted from a mussel-dominated diet to limpets during HAB periods when mussel PSPT concentrations were > 150 µg STX eq ·100g^{-1}. Although limpets were not tested for PSPT in this study, they forage by benthic grazing and are highly unlikely to accumulate measurable amounts of PSPT produced by planktonic dinoflagellates.

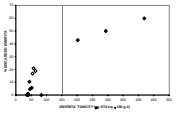


F2. ***Haematopus bachmani*, *Mytilus californianus* and *Lottia* spp.** Variation in the relative frequency of *Mytilus californianus* (sea mussels) and *Lottia* spp (limpets) in the observed diet of *Haematopus bachmani* (Black Oystercatcher) versus sea mussel PSPT concentration (µg STX eq ·100g^{-1}) at the rocky habitat study sites. Vertical dashed line marks PSPT concentration at which predator foraging behaviors changed

Birds discard a significantly greater percentage of captured prey at higher toxicity

Oystercatchers in rocky habitats, and shorebirds on sandy beaches all began rejecting a high percentage of their preferred prey (mussels and sand crabs respectively) at PSPT concentrations > 150 µg STX eq ·100g^{-1}. The shift in behavior occurred between 125 µg STX eq ·100g^{-1}, the highest prey PSPT concentration at which there was no observed predator response, and 150 to 200 µg STX eq ·100g^{-1}, the lowest values at which prey discarding and diet shift were observed.



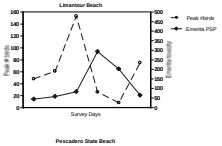


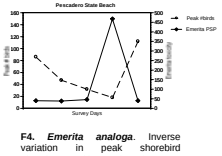
F3. ***Mytilus californianus* and *Emerita analoga*.** Percentage of observed *Mytilus californianus* and *Emerita analoga* captures that were discarded by shorebirds versus prey toxin concentration (µg STX eq · 100g^{-1}) at the study sites. Vertical line at 150 µg STX eq · 100g^{-1} marks the threshold prey PSPT concentration above at which predator foraging behaviors changed. ◇: samples where only egg masses were consumed.

[Full results can be found in MEPS 293:303-309, 2005]

Birds densities are locally reduced during periods of high prey toxicity

The significant decline in shorebird numbers observed at both the Limantour and Pescadero sandy beach sites during the HAB period when sand crab PSPT concentrations were >200 µgSTX·100g^{-1} supports a site abandonment hypothesis. Non-toxic control sites (not shown) showed no decline in bird abundance during the same time period.





F4. ***Emerita analoga*.** Inverse variation in peak shorebird abundance with sand crab PSPT concentrations (µg STX eq ·100g^{-1}) during the 13-week period bracketing the 1999 HAB period at the sandy habitat study sites.

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Conclusions

Although these results suggest that some high-level marine predators are able to detect and avoid ingestion of lethal concentrations of HAB toxins, this ability may only apply to cases in which the predator's feeding behavior, combined with the anatomical distribution of these toxins in the prey, enable the predator to "test" the prey prior to ingestion. Sea otters open or chew bivalve prey, shorebirds often dismember their prey before swallowing; both predatory behaviors expose the prey's soft organ tissues to contact with the inside of their mouth prior to swallowing. Thus, if these predators are able to "taste" or otherwise detect the presence of HAB toxins, they have the opportunity of rejecting these opened prey before swallowing them. The ability to test prey for HAB toxins is likely not the case for piscivorous species such as pinnepeds, whales and sea birds, the marine predators most commonly associated with HAB related mass mortalities. These species typically swallow their small fish prey whole, often during feeding frenzies, such that HAB toxins contained in the stomachs of their prey would not be released into the predators system until digestion takes place well after the feeding event. Under these circumstances, it is less likely that HAB toxins would alter feeding behavior or provide a deterrent to predation. The threshold values at which prey discards and diet shifting were observed reported in these companion studies (200 µg STX eq ·100g^{-1} & 500 µg STX eq ·100g^{-1} for sea otters, and 150-200 µg STX eq ·100g^{-1} for shorebirds) are similar to the concentrations in bivalve prey that promoted changes in feeding behavior during controlled experiments with free-ranging sea gulls (445 µg STX eq ·100g^{-1}) (Kvitek 1991b), captive sea otters (226 µg STX eq ·100g^{-1}) (Kvitek et al. 1991), and captive fish (135 µg STX eq ·100g^{-1}) (Kvitek 1991a).