ARTICLE

High variation in handling times confers 35-year stability to predator feeding rates despite community change

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Abstract

Historical resurveys of ecological communities are important for placing the structure of modern ecosystems in context. Rarely, however, are snapshot surveys alone sufficient for providing direct insight into the rates of the ecological processes underlying community functioning, either now or in the past. In this study, I used a statistically reasoned observational approach to estimate the feeding rates of a New Zealand intertidal predator, *Haustrum haustorium*, using diet surveys performed at several sites by Robert Paine in 1968–1969 and by me in 2004. Comparisons between time periods reveal a remarkable consistency in the predator's prey-specific feeding rates, which contrasts with the changes I observed in prey abundances, the predator's body-size distribution, and the prey's proportional contributions to the predator's apparent diet. Although these and additional changes in the predator's per-capita attack rates seem to show adaptive changes in its prey preferences, they do not. Rather, feeding-rate stability is an inherently statistical consequence of the predator's high among-prey variation in handling times which determine the length of time that feeding events will remain detectable to observers performing diet surveys. Though understudied, similarly high among-prey variation in handling (or digestion) times is evident in many predator species throughout the animal kingdom. The resultant disconnect between a predator's apparent diet and its actual feeding rates suggests that much of the temporal, biogeographic, and seemingly context-dependent variation that is often perceived in community structure, predator diets, and food-web topology may be of less functional consequence than assumed. Qualitative changes in ecological pattern need not represent qualitative changes in ecological process.

KEYWORDS
adaptive dynamics, attack rate variation, context independence, correlation of ratios, diet survey, digestion time, functional response, historical resurvey, process rates, spurious correlation

INTRODUCTION

Historical resurveys of ecological communities provide an important means to document change and contextualize the state of modern ecosystems (Chen et al., 2009; Moritz et al., 2008; Sorte et al., 2017; Tingley et al., 2009). Although such resurveys typically involve the comparison of only pairs of points in time, their advantages include the

ability to quantify change relative to time periods before the onset of time-series monitoring, which rarely extends prior to the 1970s (Hughes et al., 2017; Kuebbing et al., 2018). Overall, many historical resurveys have documented substantial changes in community structure (i.e., species composition and abundances), changes that are often, but not always, attributable to climate change, land use, and other human impacts (Perry et al., 2005; Riddell et al., 2021; Rowe & Terry, 2014).

Rarely, however, is it possible to use snapshot surveys to go beyond the characterization of community structure to quantify the rates of the biological processes that underlie how communities function, such as growth, predation, and competition (McCoy & Pfister, 2014; Paine, 1966, 1980, 2010; Urban et al., 2016). Studies in which this has been possible have revealed sometimes unexpected insights. For example, Rowe et al. (2011) combined historical and modern surveys of small mammal species and their body-size distributions with metabolic scaling laws to relate changes in community structure to marked declines in rates of total energy use within Great Basin communities since the late 1920s. These patterns contrasted markedly with the findings of Terry and Rowe (2015), who used the same approach to reveal that, despite substantial changes in small mammal body-size distributions and community structure, total energy use remained stable over the period of rapid climate warming that occurred at the terminal Pleistocene. Studies that quantify process rates can therefore provide levels of insight into underlying drivers of change (or stasis) that surveys of community structure alone may miss.

Unfortunately, most survey studies that quantify process rates have had to rely on macroscopic, species-agnostic theory or empirical relationships (such as metabolic and allometric scaling laws; e.g., Rowe and Terry, 2014; Terry and Rowe, 2015) or have depended on the existence of parameter-rich physiology-based models. For example, Atcheson et al. (2012) used a bioenergetic model to combine estimates of apparent diet and prey availability with estimates of individual growth rates from scale circuli to simulate and compare rates of prey biomass consumption by steelhead fishes over 18 years in the North Pacific. Although the mechanistic basis and structural assumptions of such models are often well grounded and empirically validated, their appropriateness to historical time periods can be difficult to affirm or rely upon given compounding estimation uncertainties.

In this study, I used an alternative, statistically reasoned approach to estimate and assess changes in the species-specific feeding rates of a predatory intertidal whelk, *Haustrum haustorium*, whose diet was surveyed at several northern New Zealand sites by Robert (Bob) T. Paine (Dayton et al., 2016; Estes et al., 2016; Palumbi et al., 2017; Power et al., 2018) in 1968–1969 and which I resurveyed in 2004. The approach I used to estimate feeding rates contrasts with the aforementioned theory and model-based approaches in minimally requiring data on only two aspects of predator foraging: estimates of a predator's apparent diet proportions from feeding surveys and estimates of the length of time that feeding events remain detectable to observers performing the feeding surveys (henceforth referred to as "detection times," which are typically prey-specific and functions of the predator's handling and/or digestion times; see *Data analysis* below).

Based on the 35-year time span and prior observations of nonequilibrial, dynamically changing species abundances and interactions in the region (e.g., Benincà et al., 2015) and intertidal systems in general (e.g., Katz, 1985; Menge et al., 2022; Sorte et al., 2017), I naively expected to see a weak correspondence between the feeding rates of the two time periods. Instead, my comparisons revealed a remarkable stability in *H. haustorium*'s prey-specific feeding rates that contrasted with the changes I observed in prey abundances, *H. haustorium*'s body-size distribution, and the proportional contributions of *H. haustorium*'s prey species to its apparent diet. Additional analyses implicated similarly large changes in *H. haustorium*'s prey-specific prey preferences.

I recognized the inevitability of *H. haustorium*'s feeding-rate stability only in hindsight. The underlying statistical mechanism—effectual because of the wide range of *H. haustorium*'s handling times across its many prey species—has nonetheless been recognized for 125 years as a consequence of correlated denominators on the correlation of ratios (Pearson, 1897).

METHODS

Data collection

Study system

H. haustorium is a muricid whelk that is endemic to the North and South Islands of New Zealand (Tan, 2003). Its fossil record shows *H. haustorium* to have grown to 80 mm shell length (Tan, 2003), but in modern times its size rarely exceeds 55 mm (Novak, 2008). (Paine's notebook records his having measured the shells of 15 large individuals, 65.0, 65.5, 65.7, 66.2, 67.5, 68.0, 68.3, 68.5, 68.6, 69.4, 69.6, 71.9, 73.1, 74.0, and 76.8 mm in length, in a Maori midden of unknown age found somewhere

between North Cape [Otou] and Parengarenga Harbor.) Its diet varies through ontogeny (Novak, 2008) but primarily consists of herbivorous limpets, chitons and snails, filter-feeding barnacles and mussels, and its congener *H. scobina* (formerly *Lepsiella scobina*) with whom it shares many prey species (Luckens, 1975; McKoy, 1969; Morton & Miller, 1968; Novak, 2010, 2013; Ottaway, 1977; Patrick, 2001; Walsby, 1977). *H. haustorium* drills through the shells of its prey and/or flips them over to digest and ingest the "soup" through its extended proboscis (Figure 1). A feeding event can last hours to more than a day (and can thus be detected by an observer through one or more low-tide periods) depending on the temperature,

FIGURE 1 *Haustrum haustorium* feeding on the limpet *Cellana ornata* surrounded by additional prey species: *Xenostrobus pulex* mussels, *Epopella plicata*, and *Chamaesipho columna* barnacles, *Austrolittorina antipodum* snails, and its congeneric intraguild prey *H. scobina* (center right).

the prey's identity, and the sizes of the whelk and prey individual (Novak, 2010, 2013).

Feeding surveys

Feeding surveys during low-tide periods are a standard means to determine the apparent diet of whelks and many other intertidal predators (e.g., Hughes & Burrows, 1991; Menge, 1974; Paine, 1963; Yamamoto, 2004). They consist of a systematic search of an area of rocky shore, carefully inspecting each found individual to determine whether or not it is feeding, measuring its shell length (± 1 mm) and, if it is feeding, identifying and measuring the size of its prey. Paine conducted such surveys at 10 sites along the northern coast of the North Island between November 1968 and May 1969 (Appendix S1: Table S1). In June 2004, using Paine's site names, descriptions, and hand-drawn maps, I was able to relocate and access five of the same sites to resurvey *H. haustorium*'s diet using the same protocols.

Prey abundance surveys

Paine also conducted abundance surveys of *H. haustorium*'s prey species at several sites, including three of the sites where he performed feeding surveys and which I was able to resurvey (Appendix S1: Table S1). Abundance surveys entailed the use of a 0.3×0.3-m quadrat that Paine placed randomly at 15 positions along a transect line (of unknown length) located haphazardly in the same area in which feeding surveys were subsequently conducted. All mobile prey species within the quadrats were counted. I repeated these surveys using 15 quadrats positioned randomly along a 20-m transect. Paine often distinguished among tidal zones (e.g., the "oyster zone" and "1 ft. above *Xiphophora* zone"), surveying a transect (or two) in each of them. I matched my survey areas to these zones as best I could, though sometimes zonation patterns were not as clear as they had apparently been for Paine.

Data analysis

Estimating feeding rates

The approach I used for estimating *H. haustorium*'s prey-specific feeding rates from diet surveys appears to have been first used by Charles Birkeland (Birkeland, 1974), who earned his Ph.D. with Paine as primary advisor. It was rederived by Novak et al. (2017) and ostensibly several

others (Bajkov, 1935; Englund & Leonardsson, 2008; Speirs et al., 2000; Woodward et al., 2005). The approach relies on the following information:

1. The count of the number of predator individuals that, in the course of a snapshot diet survey, are observed to be feeding on each focal prey species (n_i);
2. The count of the total number of predator individuals that are surveyed (n); and
3. An estimate of the (average) length of time (d_i) over which a feeding event on each focal prey species remains detectable to an observer performing the feeding survey.

A formal derivation is summarized as follows. Consider a generalist predator population whose diet consists of $i = 1, ..., S$ different prey species on which predator individuals feed only one prey item at a time. If f_i is the predator population's average feeding rate on the ith prey species (which we wish to estimate), then, over some time period T, an average individual will consume $f_i T$ individuals of prey i. If each of these feeding events remains detectable to the surveying observer for length of time d_i (because of the predator's handling or digestion of the prey individual, for example), then the total time that the predator individual could have been seen feeding in time period T is $f_i d_i T$ and the proportion of time it could have been seen feeding on prey i is $f_i d_i$. It follows that if we perform a snapshot feeding survey of n independent and equivalent predator individuals, the expected proportion of individuals we should observe feeding on each prey species, p_i, will also be $f_i d_i$. Since the maximum likelihood estimator of p_i is n_i/n, we can therefore estimate prey-specific feeding rates as

$$f_i = \frac{n_i}{n} \frac{1}{d_i}. \tag{1}$$

In using this approach, we make no assumptions regarding the mathematical form of the predator's functional response (besides the nonnegligible length of handling or digestion) and need not know prey or predator abundances (but see *Discussion* for their potential importance).

Clearly, the primary challenge of applying the approach to diet surveys is to have information on detection times, these likely being primarily determined by handling or digestion times and potentially altered by attributes of the predator, the prey, the abundance of other species, environmental conditions, and the observer (Novak et al., 2017; Preston et al., 2017; Stouffer & Novak, 2021). Indeed, a prey species that is frequently observed in a predator's apparent diet may in fact be only infrequently consumed by the predator if its detection time is long relative to that of other prey species (Fairweather & Underwood, 1983; Novak, 2010, 2013).

I estimated *H. haustorium*'s prey-specific detection times (in days) on the basis of extensive laboratory experiments that I had previously performed for *H. haustorium* populations of New Zealand's South Island (Novak, 2013, 2014). These experiments involved placing *Haustrum* individuals of various sizes into isolated aquaria, providing them focal prey of various sizes and identities, and subsequently classifying each whelk as either feeding or not feeding on a nearly hourly basis or continuously with video surveillance. Whelk and prey size combinations maximized or exceeded the range of relative sizes observed in the field. The temperature was varied between 10°C and 18°C by placing the aquaria in temperature-controlled rooms. For each prey species I regressed the difference between the feeding start and end times on whelk size, prey size, and experimental temperature (all variables $\log_e$-transformed) to obtain regression coefficients describing the size-dependent sensitivity of the detection times to each of the variables (see Novak [2013] for details). These regression coefficients exhibit substantial variation across prey species (Appendix S1: Figure S1). For the present study, I then used the regression coefficients to back-calculate the expected detection time of each feeding event that Paine and I had observed in the field, thereby allowing for potential changes between time periods in temperature and the sizes and size ratios of predators and prey at the individual level. In doing so, I used the mean water temperature measured in the given year and month at the Leigh Marine Laboratory for all surveyed sites (Costello, 2015; Evans & Atkins, 2013), it being centrally located to all sites and providing the only in situ temperature record that extends to the 1960s. Prey for which I had not estimated detection-time regression coefficients in the experiments were matched to the most similar species for which they had been estimated (Appendix S1: Table S2). Feeding observations in which the size of either the prey or whelk was unknown (typically because the prey was "swallowed" when the whelk closed its operculum too quickly) were assigned the species' mean detection time across all observations.

Comparisons of 1968–1969 and 2004

I used several measures of correlation and deviation to quantify the similarity of feeding rates between 1968–1969 and 2004. I ignored prey species not observed in *H. haustorium*'s diet at a given site in both time periods and used all remaining time-period pairs of site-specific prey species from across all five sites to calculate similarities. As is typically the case (e.g., Preston et al., 2019),

feeding rates varied over several orders of magnitude and exhibited a right-skewed frequency distribution. I therefore calculated the correlation between time periods in three ways: using Pearson's linear correlation coefficient on the natural scale (r), using Pearson's correlation coefficient after $\log_{10}$-transformation (r_{10}), and using Spearman's rank correlation coefficient (r_s). I also calculated the mean logarithmic difference (MLD) and the mean absolute logarithmic difference (MALD) between feeding-rate pairs, these both being measures of relative similarity, since $\log_{10}(x) - \log_{10}(y) = \log_{10}(x/y)$. I repeated these same calculations for the prey-specific diet proportions ($p_i = n_i/n$) and the field-calculated detection times (d_i), restricting these comparisons to the same site–prey pairs that were included in the comparison of the feeding rates.

To determine whether (dis)similarities between time periods in any of the just-mentioned three variables were associated with changes in *H. haustorium*'s or its prey's sizes, I plotted histograms of whelk and prey sizes and formally assessed differences between time periods using Kolmogorov–Smirnov (KS) tests. I also used multiple linear regression to regress whelk size ($\log_e$-transformed) on prey size ($\log_e$-transformed), time period, and their first-order interaction to determine whether there was a change in *H. haustorium*'s prey-size selectivity.

Finally, to determine whether (dis)similarities between time periods in *H. haustorium*'s feeding rates were associated with changes in its prey preferences, I used the estimator derived by Novak and Wootton (2008) and clarified by Wolf et al. (2017) to calculate *H. haustorium*'s per-capita attack rates. This estimator uses the same information as is used to estimate feeding rates (i.e., the n_i prey observations and d_i detection times) but also makes use of the number of surveyed individuals that are observed to be not feeding (n_0), requires knowledge of each prey's abundance (N_i), and necessitates the specification of a functional-response model (Novak et al., 2017). I assumed the multispecies extension of the Holling Type II functional response (e.g., Murdoch, 1973) and that *H. haustorium*'s handling times equaled its detection times (i.e., $h_i = d_i$). Under these assumptions, which are well justified for *H. haustorium* (see Novak, 2010, 2013; Novak et al., 2017), the estimator for *H. haustorium*'s per-capita attack rate on prey i is

$$a_i = \frac{n_i}{n_0} \frac{1}{h_i N_i}. \tag{2}$$

In absolute terms, these per-capita attack rates (also known as space clearance rates) reflect the prey eaten per predator per day per available prey, with abundances reflecting densities (here per square meter; see Arditi et al., 2021). They reflect predator and prey velocities, the distance over which predator's perceive prey, the probability that they attack perceived prey individuals, and the probability that attacks will be successful, and so forth, so they may be influenced by myriad biotic and abiotic factors (DeLong, 2021; Jeschke et al., 2002; Wootton et al., 2021). In relative terms, they reflect the predator's prey preferences accounting for differences in prey handling times and prey abundances (Chesson, 1983; Fairweather & Underwood, 1983; Novak & Wootton, 2008). Systematic variation in the attack rates or their analogs is thus often treated as a form of so-called adaptive dynamics, assuming other aspects of foraging remain unchanged (Kondoh, 2003; Valdovinos et al., 2010).

Because the attack rate estimator (Equation 2) requires estimates of prey abundances, I calculated *Haustrum*'s per-capita attack rates only for the subset of three sites where both Paine and I had estimated these using quadrat surveys. I then calculated the between time-period correlations and deviations of the attack rates, feeding rates, diet proportions, detection times, and prey abundances for these sites as described earlier. Finally, I used multiple linear regression to regress feeding rates ($\log_e$-transformed) on prey abundances ($\log_e$-transformed), time period, and their first-order interaction to determine whether there was an effect of time period on the density dependence of *H. haustorium*'s feeding rates (i.e., on its across-species "functional response").

RESULTS

Feeding survey sites

Across the five sites at which both Paine and I performed feeding surveys, Paine observed 232 of 1101 total individuals feeding on 10 different species (Table 1). In my resurveys, I observed 160 of 1567 total individuals feeding on 16 different species. Across sites, the proportions of feeding individuals ranged from 11.8% to 65.9% for Paine and from 5.2% to 27.3% for me. Paine observed *H. haustorium* feeding on two species that I did not observe (one observation each, totaling 0.9% of all Paine's feeding observations), whereas I observed it feeding on eight species that Paine did not (totaling 20 observations, 12.5% of all my observations). Together we observed *H. haustorium* feeding on 18 different species.

There were seven species on which both Paine and I observed *H. haustorium* feeding at the same site. For these seven species, there were 17 site-species feeding-rate pairs for me to compare between 1968–1969 and 2004 (Figure 2a). These varied over two orders of magnitude (from 1.71×10^{-3} to 0.51×10^{-1} prey per predator per day), were positively correlated between time periods for

TABLE 1   Summary of Paine's 1968–1969 and my 2004 feeding observations.

Site	Observations		Percentage feeding	
	1968–1969	2004	1968–1969	2004
Leigh—echinoderm reef	228	72	13.6 (9.7–18.7)	13.9 (7.7–23.7)
Leigh—tabletop rocks and boulders	44	268	65.9 (51.1–78.1)	5.2 (3.1–8.6)
Leigh—waterfall rocks	275	1060	17.5 (13.4–22.4)	10.1 (8.4–12.1)
Rangitoto Island—Whites Beach	93	130	11.8 (6.7–19.9)	20.8 (14.7–28.5)
Red Beach—Whangaparaoa	461	37	24.5 (20.8–28.6)	5.4 (1.5–17.7)
Sum/average	1101	1567	26.7	11.1

Note: Observations refer to total no. whelks inspected. Percentage feeding refers to proportion of observed whelks that were feeding. Parentheticals are the binomial confidence interval (95% coverage probability) calculated using the Wilson method.
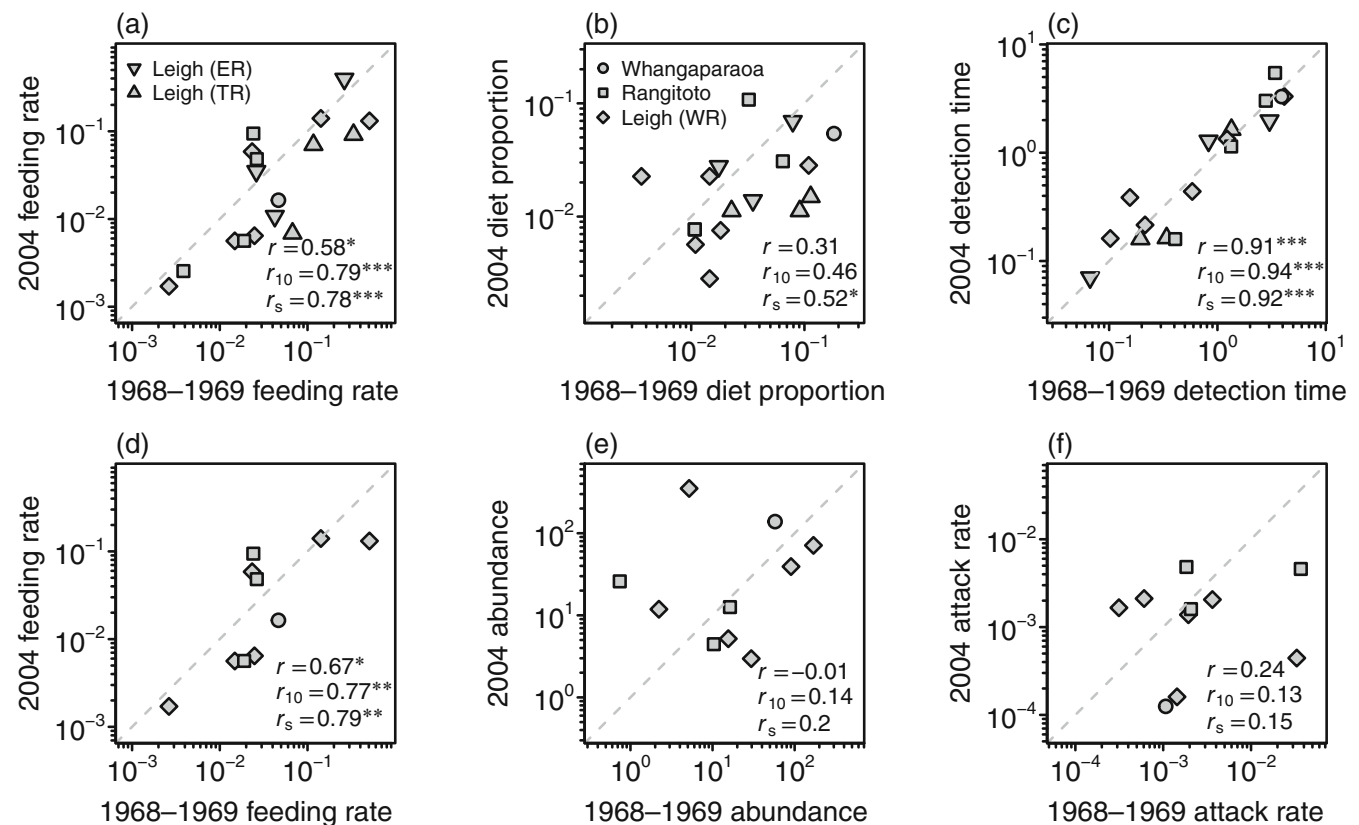
FIGURE 2   The between time-period correlation of prey-specific (a) feeding rates (prey predator^{-1} day^{-1}), (b) apparent diet proportions (unitless), and (c) detection times (days) among all sites where Paine and I surveyed *Haustrum haustorium*'s diet and of prey-specific (d) feeding rates, (e) abundances (prey m^{-2}), and (f) per-capita attack rates (prey prey^{-1} predator^{-1} day^{-1}) for the subset of sites where Paine and I also surveyed prey abundances. I calculated three correlations for each comparison to assess the linearity and monotonicity of the time-period (dis)similarities: Pearson's correlation (r), Pearson's correlation after log$_{10}$-transformation (r_{10}, as plotted), and Spearman's rank correlation (r_s). The probability of observing a correlation at least as extreme as the observed correlation under the null hypothesis of no correlation (two-tailed test) is indicated by asterisks: ***$p < 0.001$; **$p < 0.01$; *$p < 0.05$; otherwise, $p > 0.1$. Dashed diagonal lines reflect the 1:1 relationship.

all three correlation measures ($r = 0.58$, $p = 0.01$; $r_{10} = 0.79$, $p < 0.001$; $r_s = 0.78$, $p < 0.001$) and tended to be greater in 1968–1969 than in 2004 (mean deviation and 95% bootstrapped confidence interval: MLD = 0.220 [0.020, 0.418], MALD = 0.404 [0.294, 0.520]).

Although the dominant prey species remained dominant, in contrast to the feeding rates, *H. haustorium*'s apparent diet proportions showed relatively little similarity between time periods (Figure 2b). That is, although the diet proportions exhibited similar variation within each time

period (varying from 2.83×10^{-3} to 1.8×10^{-1}), their between time-period correlations were lower and less clearly different from zero ($r = 0.31$, $p = 0.22$; $r_{10} = 0.46$, $p = 0.06$; $r_s = 0.52$, $p = 0.03$). They also tended to be greater in 1968–1969 than in 2004 (MLD = 0.233 [0.018, 0.439], MALD = 0.433 [0.313, 0.599]). On the other hand, mean detection times were very similar between time periods (Figure 2c). These varied over two orders of magnitude (from 1.6 to 130.8 h), were highly correlated between time periods for all three measures ($r = 0.92$, $p < 0.001$; $r_{10} = 0.94$, $p < 0.001$; $r_s = 0.92$, $p < 0.001$), and were not distinguishable between time periods (MLD = 0.011 [−0.079, 0.100], MALD = 0.149 [0.094, 0.210]).
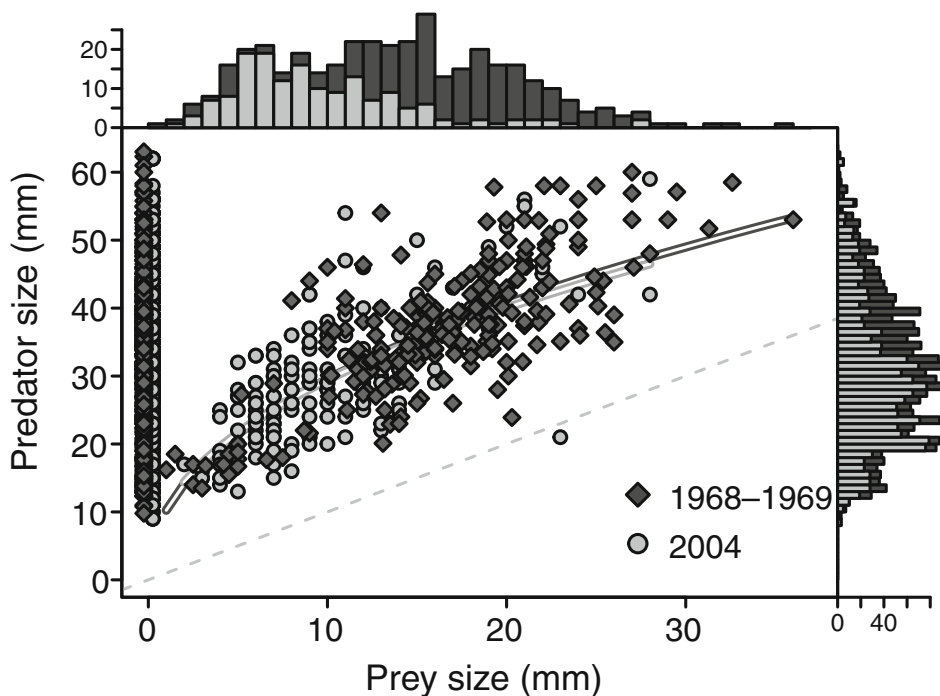
Although *H. haustorium*'s size range was unchanged between time periods, its size distribution showed a clear shift toward smaller individuals in 2004 relative to 1968–1969 (Figure 3; 1968–1969: 9.8–63.0 mm, $\bar{x} = 34.7$ mm; 2004: 9.0–62.0 mm, $\bar{x} = 30.0$ mm; KS test: $D = 0.30$, $p < 0.001$, all five sites combined). The size distribution of prey individuals was also shifted toward smaller individuals in 2004 (Figure 3; 1968–1969: 1.0–36.0 mm, $\bar{x} = 16.5$ mm; 2004: 2.0–28.0 mm, $\bar{x} = 10.2$ mm; KS test: $D = 0.55$, $p < 0.001$). *H. haustorium*'s relative prey-size selectivity, however, appeared unchanged between time periods, with multiple regressions providing no support for main or interactive effects of time period (Figure 3,

Appendix S1: Tables S3–S5, $\log_e[\text{predator size}] = 2.34 + 0.46 \times \log_e[\text{prey size}]$, $F_{1,381} = 629.9$, $p < 0.001$, $R^2_{adj} = 0.62$ for both periods combined).

Feeding and abundance survey sites

Feeding rates were even more clearly similar between time periods for the 10 pairs of site-species estimates (six prey species) from the three sites where Paine and I performed both feeding and abundance surveys (Figure 2d; $r = 0.67$, $p = 0.03$; $r_{10} = 0.77$, $p < 0.01$; $r_s = 0.79$, $p < 0.01$; MLD = 0.15 [−0.116, 0.394], MALD = 0.40 [0.283, 0.508]). As seen when considering all five sites, the between time-period similarity of the apparent diet proportions was lower (not shown; $r = 0.35$, $p = 0.32$; $r_{10} = 0.51$, $p = 0.13$; $r_s = 0.62$, $p = 0.053$; MLD = 0.147 [−0.165, 0.416], MALD = 0.447 [0.322, 0.574]), but the similarity of mean detection times was high (not shown; MLD = −0.006 [−0.138, 0.123], MALD = 0.161 [0.085, 0.250]).

Prey abundances varied over two orders of magnitude within both time periods (varying from 0.74 to 351 individuals m^{-2}) but showed no relationship between the two time periods (Figure 2e; $r = -0.009$, $p = 0.98$; $r_{10} = 0.14$, $p = 0.71$; $r_s = 0.2$, $p = 0.58$; MLD = −0.178 [−0.746, 0.338], MALD = 0.718 [0.420, 1.073]). This was


FIGURE 3 Predator and prey size distributions and their individual-level relationships by time period. Although *Haustrum haustorium* and their prey were smaller in 2004 than in 1968–1969, *H. haustorium*'s size selectivity was unchanged between time periods. See Appendix S1: Tables S3–S5 for regression summaries. The values near a prey size of 0 mm indicate the sizes of nonfeeding whelks and are omitted from the prey-size frequency histogram. Note that this figure includes the *H. haustorium* and prey individuals of all observations made at the five focal study sites (rather than just the subset of temporally paired estimates considered in Figure 2).

similarly true for the estimates of *H. haustorium*'s per-capita attack rates, which also varied over three orders of magnitude within time periods (varying from 5.2×10^{-6} to 1.5×10^{-3} prey per predator per day per prey available) but showed no relationship between time periods (Figure 2f; $r = 0.24$, $p = 0.50$; $r_{10} = 0.13$, $p = 0.72$; $r_s = 0.15$, $p = 0.68$; MLD $= 0.348$ [-0.116, 0.835], MALD $= 0.685$ [0.402, 1.017]).

Regressing feeding rates on prey abundances did not show main or interactive effects of time period on the density dependence of *H. haustorium*'s across-species "functional response" (Appendix S1: Tables S6 and S7), with the simpler model combining time periods revealing that feeding rates increased with a decelerating rate as prey abundances increased (Figure 4, Table S8, $\log_{10} f_i = -2.26 + 0.52 \cdot \log_{10} N_i$, $F_{1,23} = 8.41$, $p = 0.008$, $R^2_{\text{adj}} = 0.24$).

DISCUSSION

That feeding rates are dynamic and respond to many aspects of a predator's environment is a central, well-supported thesis. The importance of predator and prey abundances, their body sizes, and environmental temperature has elicited particularly strong research attention within the vast literatures relating to predator foraging ecology, food webs, and the impacts of climate change
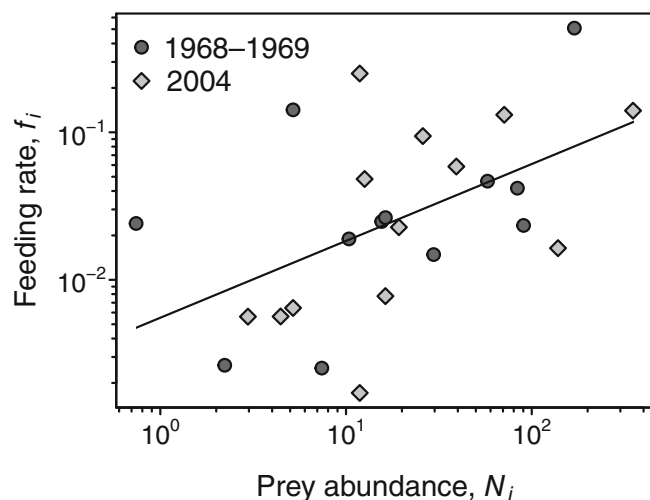
FIGURE 4 The relationship between *Haustrum haustorium*'s prey-specific feeding rates (prey eaten per predator per day) and prey abundances (m^{-2}) by time period. Feeding rates increased as a decelerating function (logarithmic slope < 1) of prey abundance and were not distinguishable by time period (Appendix S1: Tables S6–S8). Note that this regression includes five temporally unpaired estimates that reflect feeding rate and abundance estimates for prey species which only Paine or I observed (rather than just the subset of temporally paired prey-specific estimates considered in Figure 2).

thereupon. Although water temperatures in northern New Zealand have not exhibited a systematic trend to date (Shears & Bowen, 2017), my resurveys of Bob Paine's study sites revealed significant differences in *H. haustorium*'s apparent diet between 1968–1969 and 2004. My resurveys further showed an overall reduction in *H. haustorium*'s body size which, though not associated with changes in the relative size of chosen prey individuals, was accompanied by substantial changes in community structure. These changes in apparent diet proportions and prey abundances inferred by my main analyses were corroborated by additional comparisons using alternative analyses that included (rather than excluded) species observed by only Paine or only me (see Appendix S1: Section S1.5).

Given these observations and their consistency with the dynamic nature of rocky intertidal systems (e.g., Benincà et al., 2015; Katz, 1985; Menge et al., 2022; Sorte et al., 2017), I expected *H. haustorium*'s prey-specific feeding rates to have been similarly altered in the 35 years that separated Paine's and my surveys. Instead, as estimated by a statistically reasoned approach that did not rely on species-agnostic scaling laws, parameter-rich energetic models, or even the specification of a particular functional-response model, *H. haustorium*'s feeding rates showed a remarkable stability between the two time periods (Figure 2a,d). That is, although feeding rates were overall higher in 1968–1969 than in 2004 (possibly due to the change in *H. haustorium*'s body size, but see *Generality and assumptions* below), prey-specific feeding rates evidenced a high degree of temporal consistency in their relative within time-period magnitudes regardless of the metric of similarity I employed.

On the face of it, this contrast between *H. haustorium*'s feeding-rate stability versus the changes in its prey's abundances and apparent diet contributions implies a substantial compensatory response in *H. haustorium*'s prey preferences. This inference was underscored by my comparison of *H. haustorium*'s per-capita attack rates at the subset of sites where these could be estimated assuming a multispecies Type II functional response. That is, regardless of how their similarity was quantified, attack-rate estimates in 1968–1969 showed no similarity to the estimates of 2004 (Figure 2f). Indeed, the temporal consistency of the relationship (albeit loose) between *H. haustorium*'s feeding rates and its prey's abundances (i.e., its across-species "functional response", Figure 4) that was associated with these changes in attack rates could be inferred to indicate an adaptive response in prey preferences to altered prey abundances (sensu Abrams, 1999; Kondoh, 2003; Valdovinos et al., 2010).

I believe this final inference to be incorrect, however. Instead, I attribute the stability of *H. haustorium*'s feeding rates to the high variation in handling times that

H. haustorium exhibits among its diverse prey species. The underlying mechanism is statistical in nature and was recognized in 1897 soon after the formal definition of Pearson's measure of correlation itself.

The inevitability of feeding-rate stability

Pearson's correlation coefficient r is a measure of the linear association between two variables (Bravais, 1844; Pearson, 1895). Pearson (1897) was the first to note that two ratios (x/w and y/z) will be correlated when their denominator variables are correlated, even if the numerator variables are entirely uncorrelated. He derived the following expression with which to approximate this expected correlation of ratios using the correlations between each pair of variables and each variable's coefficient of variation (v, its standard deviation divided by its mean):

$$r_{\frac{x}{w}\frac{y}{z}} \approx \frac{r_{x,y}v_x v_y - r_{w,y}v_w v_y - r_{x,z}v_x v_z + r_{w,z}v_w v_z}{\sqrt{\left(v_y^2 + v_z^2 - 2r_{y,z}v_y v_z\right)}\sqrt{\left(v_w^2 + v_x^2 - 2r_{w,x}v_w v_x\right)}}. \quad (3)$$

Although it assumes that the coefficients of variation are small (Kim, 1999), and although an exact expectation may be obtained with a permutation-based approach (Appendix S1), Pearson's approximation provides useful insight into how a correlation between ratios will arise. In fact, in the context of understanding the stability of *H. haustorium*'s feeding rates (i.e., where $\frac{x}{w} = f_{1968-1969}$ and $\frac{y}{z} = f_{2004}$), the approximation may be further simplified by (*i*) letting the numerator variables (the x,y

apparent diet proportions; n_i/n in Equation 1) and the denominator variables (the w,z detection times; d_i in Equation 1) be uncorrelated with each other within and across time periods (i.e., $r_{y,z} = r_{w,x} = r_{w,y} = r_{x,z} = 0$) and (*ii*) letting the coefficients of variation of the two numerator variables and the two denominator variables each be the same across time periods (i.e., $v_n := v_y = v_x$ for the diet proportions and $v_d := v_z = v_w$ for the detection times). Under these simplifications, Pearson's approximation is reduced to

$$r_{\frac{x}{w}\frac{y}{z}} \approx \frac{r_{x,y}v_n^2 + r_{w,z}v_d^2}{v_n^2 + v_d^2}. \quad (4)$$

Since the denominator of Equation (4) simply scales the response between -1 and $+1$, it follows that feeding rates will tend to be positively correlated between time periods whenever the detection times are positively correlated and exhibit a sufficiently large coefficient of variation across prey species, even if the apparent diet proportions are uncorrelated or even negatively correlated (Figure 5). Feeding-rate stability can therefore occur despite substantial changes in the predator's prey preferences or its prey's abundances. The same logic applies using Spearman's rank correlation coefficient since it is just the Pearson correlation of rank-ordered values.

Pearson (1897) referred to the nonzero correlation of ratios involving uncorrelated numerator and correlated denominator variables as being spurious (but see Haig [2003] for a discussion of this term). When inference is being made regarding the relationship of the two numerator variables, the issue is indeed a major problem that has plagued—and continues to plague—diverse scientific
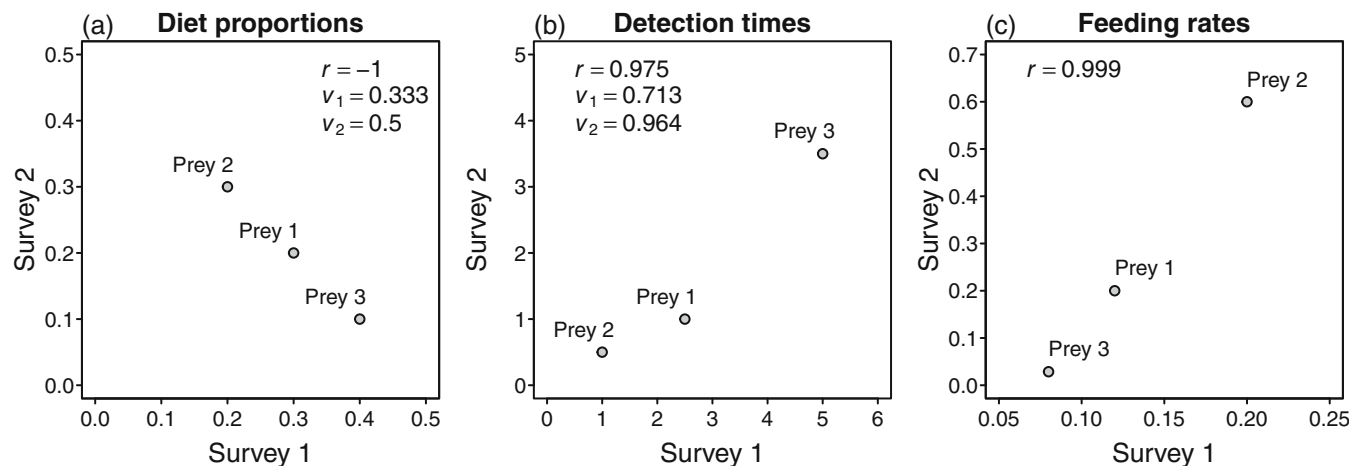
FIGURE 5 Hypothetical example of the statistical mechanism causing correlated ratios of which Pearson (1897) spoke. The panels show two surveys between which a predator's (a) apparent diet proportions on three prey species are perfectly negatively correlated ($r = -1.00$), but its (b) detection times are positively correlated ($r = 0.975$) and exhibit sufficiently high coefficients of variation (v) for its (c) feeding rates to be strongly positively correlated ($r = 0.999$) (given correlations are exact, not estimated using Equation 3 or 4).

disciplines (e.g., Atkinson et al., 2004; Håkanson & Stenström-Khalili, 2009; Jackson & Somers, 1991; Kenney, 1982; Williams et al., 2022), leading many to infer a relationship between measured variables when in fact none exists. Closely related issues can confound the interpretation of regression analyses (Freckleton, 2011; Spearman, 1904) as, for example, in the debate over density-dependent population regulation (Wolda et al., 1994). However, as first noted by Yule (1910), the relationship is not spurious when inference is being made regarding the ratios (Aldrich, 1995), as is the case in using Equation (1) to estimate feeding rates. That is, the correlation of ratios due to correlated denominator variables reflects (the linear aspect of) the true relationship between the ratios themselves. The stability of *H. haustorium*'s feeding rates between the two time periods is therefore not a spurious inference. Instead, it is the inevitable consequence of *H. haustorium*'s positively correlated and wide-ranging detection times that are themselves a direct consequence of the wide-ranging handling times that *H. haustorium* exhibits across its diverse diet.

Generality and assumptions

At the species level, *H. haustorium*'s detection times were estimated to vary between 1.6 and 130.8 h. A wide range of detection times is typical for whelks (e.g., Yamamoto, 2004) and many other taxonomically diverse consumers—from fishes to birds, seastars, spiders, and flies (e.g., Campos & Lounibos, 2000; Hilton et al., 1998; Menge, 1972; Preston et al., 2017; Uiterwaal & DeLong, 2020)—and is the consequence of a wide variety of both general and specific prey attributes. These include differences in digestible tissue mass (e.g., acorn barnacles are smaller than mussels), chemical defenses (e.g., *H. scobina* exudes a dark purple substance when consumed by *H. haustorium* [personal observation] and takes much longer to consume than similarly sized gastropods [Novak, 2013]), and structural defenses (e.g., the pulmonate limpet *Siphonaria australis* with its mucous-rich foot is typically drilled while patellid limpets like *Cellana ornata* are simply flipped [Figure 1, personal observation]). For such fundamental aspects of biology to dramatically change in a way that reduces variation over ecological time scales seems unlikely.

The greatest weakness of the previously argued reason for *H. haustorium*'s feeding-rate consistency is therefore my inference that its detection times remained positively correlated between time periods (i.e., $r_{w,z} > 0$ in Equation 4). More specifically, although I did not assume a given species' detection time was the same between time periods, I did assume that whelks of a given size would exhibit the same detection time for a prey of a given identity and size at a given temperature. I thereby allowed for each of these variables to differ from observation to observation, site to site, and across time periods, assuming only that their relationship to detection times remained unchanged. This assumption seems defensible given the physiological and structural basis of whelk handling times (Carriker, 1981). However, detection times may be far more changeable in other predator–prey systems (e.g., when predation induces phenotypic plasticity in prey; Werner & Peacor, 2003), the potential for which could itself be dependent on the part of the feeding process on which feeding surveys rely (e.g., whether feeding events are observed during prey handling or by the examination of gut contents during digestion [Novak et al., 2017]). For some species, detection times could be just as dynamically labile as species abundances and prey preferences (Thompson, 1998) and could in fact respond to these as well (DeLong & Coblentz, 2021; Okuyama, 2010; Stouffer & Novak, 2021). (Anecdotally, populations of *H. haustorium* around Kaikoura on the east coast of the South Island, where mussels are rare, could not be brought to feed on them in the lab [although rare field observations thereof occurred], while populations from the west coast, where mussels are abundant, readily did so [Novak, 2008].) In such contexts where the consistency of detection times may be weak, among-prey detection-time variation will need to be large for the statistical mechanism of correlated ratios to contribute to feeding-rate stability.

Two additional considerations pertain more to methodological details. First, it is possible for a spurious correlation to occur when evaluating diet stability through diet surveys. This is because the apparent diet proportions (n_i/n of Equation 1) can themselves become correlated if the sample sizes (n) of both sets of surveys are correlated, just as Pearson (1897) warned. This was not the case in this study (Table 1; $r = 0.01$, $p = 0.98$; $r_{10} = -0.28$, $p = 0.65$; $r_s = -0.40$, $p = 0.52$) but may be quite likely to occur in other studies when sites exhibit a consistent gradient in predator abundances due to underlying environmental differences (e.g., Novak, 2013; Winemiller, 1990). Second, although it is likely that the lower overall feeding rate of *H. haustorium* in 2004 versus 1968–1969 was due to their decreased size, other reasons are also possible. Intertidal predators may adjust the length of time they spend foraging in response to conditions, spending longer periods of time foraging to compensate for lower prey availability, for example (Barahona & Navarrete, 2010). Although prey availability overall showed no relationship to time period in this study (Figure 2e), such deterministically caused variation in time T may affect additional responses in a predator's instantaneous feeding rates (as estimated by Equation 1), leading to biased inferences of change or lack thereof across surveys conducted at different prey

abundances. Further, it is also possible that Paine's and my feeding surveys differed with regard to our ability to find larger versus smaller or feeding versus nonfeeding individuals. On average, Paine was almost 2.5 times more likely to find feeding individuals than me (Table 1). However, given Paine's extensive experience with intertidal feeding surveys, the fact that he and his frequent field assistant, Terrence Beckett, compared and saw no difference between their independent surveys (as recorded in Paine's field notes), and the fact that smaller and nonfeeding individuals tend to be more difficult to locate (especially by relative novices like me in 2004), I consider biases due to differences in survey ability improbable. Such issues of potential bias for the observational approach and resurvey studies more generally require attention nonetheless, just as they do when manipulative experiments are repeated (Kimmel et al., 2021).

CONCLUSIONS

Overall, the results of my analyses speak to the importance of statistical thinking when interpreting survey data and to the importance of studying ecological process rates rather than variation in community and species interaction patterns alone. Specific to predator–prey interactions, they draw attention to the potential for the detection times of feeding events to alter the interpretation of predator diet data. Variation in detection times has been little studied relative to the substantial effort that has gone into the study of foraging strategies and prey preferences. Most relevant work has focused on the gut-evacuation rates of prey mass in fishes, but with little focus on generalist predators' diverse prey attributes (Preston et al., 2017). In the functional-response literature, handling and digestion times are primarily considered important only at high prey abundances, where feeding rates are limited by saturation or satiation (Coblentz et al., 2022; Jeschke et al., 2002). The potential for the effect of which Pearson (1897) warned to alter the interpretation of apparent diets for many more types of taxa indicates that more attention to detection times is warranted, and that factors to which handling and digestion times are sensitive may be more important for feeding rates than currently assumed even at prey abundances far below the point of saturation. Feeding rates may be far less variable than inferred from surveys of apparent diets and community structure alone, such that much of the apparent variation and seeming context dependency of species interactions may be functionally irrelevant. An improved understanding of detection times will thus be relevant not only for historical resurveys and other temporal analyses of community and interaction-network structure, but also for burgeoning efforts to understand their

spatial and biogeographic variation (Bartley et al., 2019; Bramon Mora et al., 2020; Paine, 1980; Preston et al., 2019; Tylianakis & Morris, 2017; Vázquez et al., 2022).

CONFLICT OF INTEREST

I declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

All code and data (Novak, 2022) are available in FigShare at https://doi.org/10.6084/m9.figshare.21518595.v1.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.