Nonlinear foraging response of a large marine predator to benthic prey: eagle ray pits and bivalves in a New Zealand sandflat

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Abstract

The density-dependent foraging response of eagle rays (*Myliobatis tenuicaudatus*) to infaunal bivalves (*Macomona lilliana*) was measured in a New Zealand sandflat. Disturbance pits provided unequivocal indicators of ray feeding activity, and pits were counted on a plot (250 m × 500 m) which had prey density mapped in a 200 cell (25 m × 25 m) grid. Although foraging response increased significantly with prey density treated as a nominal (class, ANOVA-type) variable, treating bivalve density as a ratio scale (continuous, regression-type) variable provided more information about characteristics of the response. Eagle rays exhibited a nonlinear segmented response to prey density, in which ray foraging activity was low and independent of prey density at low *Macomona* densities, while foraging increased sharply above a threshold density of prey but did not reach satiation at the highest prey densities in our site. By counting ray pits repeatedly over a 31 day period, we showed that the levels and slope of the foraging response (no. of ray pits per 707 m^2 per 4 days) varied temporally during the season, but the nonlinear characteristic and the threshold of prey density were consistent. Correlation analysis showed that the distribution of bivalve prey and ray foraging was spatially constant during the season. Comparison of 3 estimators of prey density showed that a fitted polynomial density was the best predictor of ray foraging, and indicated that rays were responding to prey patches on a scale of 75–100 m. The temporal features of the response to prey density were incorporated into a nonlinear segmented model and integrated with respect to time for each cell of the study grid. The impact of ray foraging estimated from the integral indicated that only about 1.6% of the *Macomona* population was consumed and 5.0% of the total plot was disturbed by rays during one month of study. However, the nonlinearity of response indicated that foraging impacts were concentrated

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disproportionately on high density patches of prey, which suffered up to 4% mortality and 13% disturbance. *Macomona* gained a refuge from predation and disturbance at low density, which would stabilize prey populations and even out prey distribution.   © 1997 Elsevier Science B.V.

1. Introduction

Foraging behaviors help animals optimize the intake of energy in response to variation in prey density (Stephens and Krebs, 1986). The total foraging response describes density-dependent prey mortality and reflects a combination of two components of predator behavior as a function of prey density: the functional response, which describes the number of prey consumed per predator; and the aggregative response, which describes the number of predators at a site (Holling, 1959). When foraging on prey resources with patchy distributions, predators are expected to select the most energetically rewarding (e.g., highest density) prey patches (Charnov, 1976). These predators are expected to exhibit an aggregative response characterized by the ''Ideal Free Distribution'', in which predators aggregate on prey patches in proportion to prey density (Fretwell and Lucas, 1970; Fretwell, 1972; Tregenza, 1995).

For any predator, the density-dependent characteristics of the foraging response are crucial components of predator–prey dynamics (Holling, 1959). Even though experimental and field studies in marine ecosystems are limited, nonlinear variation in density-dependent effects of predator functional responses are probably common; and the shape of the functional response may determine local extinction or persistence at low prey densities, reflecting refuge characteristics of microhabitats (Abrams, 1982; Lipcius and Hines, 1986; Eggleston, 1990; Eggleston et al., 1992; Dittel et al., 1995; Piersma et al., 1995). However, there has been little experimental consideration of variation in the characteristics of the aggregative response, especially in marine ecosytems (Tregenza, 1995; but see Goss-Custard, 1970, 1977; Goss-Custard et al., 1991). Holling (1959) considered the aggregative response to exhibit 3 simple forms of density dependence (density-independent and increasing or decreasing density-dependence), but there has been limited effort to model this component (but see Holmgren, 1995). Nonlinearity in predatory response to prey would implicate threshold densities in predator–prey interactions.

An important aspect of determining the foraging response of a predator is measuring prey resource density and distribution at spatial scales which match the predator's assessment of variation in prey resources (Gotceitas and Colgan, 1991). While studies of shorebird foraging consider the importance of scale-dependent analysis (Piersma et al., 1993; Schneider, 1994), the scale of predator behavioral responses is often difficult to know in animals with diverse sensory capabilities and movement patterns. In marine systems, the limitation of acquiring data on aggregative responses is partly due to the fact that most predators feed underwater, where greatly reduced visibility makes counting predators difficult and often prevents direct observation of feeding activities.

Rays (Elasmobranchii) are common marine predators which feed on infaunal prey (especially bivalves) in soft-bottom habitats, and which provide a way of measuring the foraging response in a low visibility marine ecosystem. Ray foraging activities often create extensive disturbance of the sediment that may significantly affect benthic community structure (Orth, 1975; Reidenauer and Thistle, 1981; Woodin, 1981; Van Blaricom, 1982; Grant, 1983; Sherman et al., 1983; Levin, 1984; Thrush et al., 1991); however, little is known concerning their response to variation in prey density. Eagle rays (*Myliobatis tenuicaudatus* Hector) forage with variable intensity on the intertidal sandflats of New Zealand, causing major sedimentary disturbance (Thrush et al., 1991). New Zealand eagle rays feed by pumping water from their mouth to liquify sediment, creating elliptical cone-shaped pits (Gregory et al., 1979), from which they primarily consume infauna, especially tellinid bivalves *Macomona lilliana* (Iredale) (Thrush et al., 1991). The feeding pits, therefore, provide an unequivocal indicator of foraging activity which can be compared to bivalve prey density and distribution.

The purpose of this study was to measure the foraging response of eagle rays to variations in bivalve prey density in a large New Zealand sandflat. We used the characteristic pits as a marker of ray feeding activity and abundance. We also assessed three related estimators of bivalve density (see Section 2 below) as predictors of the predators' aggregative response. The estimators allowed us to assess the predators' response to prey density at different spatial scales. From the nonlinear feeding response determined in this study and from the distribution of prey determined in a companion study (Legendre et al., 1997), we were also able to extrapolate the predatory impact of this large mobile predator upon infaunal prey populations as a function of spatial variation in prey density.

2. Methods

2.1. Study site

This study was conducted at the intertidal sandflats on the shore of Wiroa Island, Manukau Harbor, New Zealand (37 °02′ S, 174 °41′ E) (Fig. 1). The study site (250 m × 500 m) was situated in the mid-tide zone of a relatively large sandflat (6.25 km^2) and appeared relatively homogenous in terms of sedimentary and biological characteristics. A general description of the area is presented in Thrush et al. (1997a), with detailed analysis of the spatial variation in biological and physical components given in Legendre et al. (1997). The bivalves *Macomona liliana* and *Austrovenus stutchburyi* (Gray) are the dominant macro-infauna of the sandflat.

2.2. Estimation of spatial patterns of prey abundance: mapped Macomona densities

To narrow our consideration to prey species and sizes relevant to eagle rays, we examined data on infaunal abundances available for the study site during the same period (Thrush et al., 1997b; Legendre et al., 1997). Although approximately a dozen infaunal invertebrates were common in the study site, only two common species of
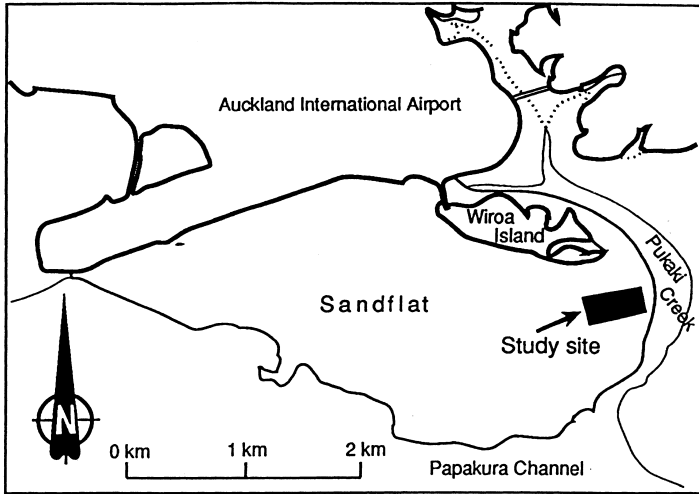
Fig. 1. Map of Wiroa Island showing location of study plot.

bivalves comprised $> 97\%$ of the macrofaunal biomass: *Macomona lilliana* and *Austrovenus stutchburyi*. On 22–23 January *Macomona* > 15 mm comprised aproximately 84% of the bivalve individuals and $> 95\%$ of the biomass in samples of the infauna in the study site: mean density ($\pm$SE) per 0.25 m^2 of *Macomona* > 4–15 mm $= 5.68 \pm 0.67$; *Macomona* > 15 mm $= 38.2 \pm 2.02$; *Austovenus* > 4–10 mm $= 0.55 \pm 0.19$; *Austrovenus* > 10 mm $= 0.94 \pm 0.23$. Therefore, we assert that *Macomona* > 15 mm was the only infaunal invertebrate in the study site which was a prey category relevant to foraging eagle rays.

We determined three estimators of bivalve prey density (enumerated below), corresponding to different spatial scales. To map the spatial variation in density of *Macomona* in the study plot, the rectangle was partitioned at 25 m intervals into a grid of 200 cells (Fig. 2). On 22–23 January 1994, each cell was sampled by positioning a 0.25 m^2 quadrat at a random location within the cell (Legendre et al., 1997). The sediment in the quadrat was excavated to a depth of 15 cm and sieved on a 4 mm mesh screen. Bivalves were sorted into 4 species-size categories: *Macomona* 4–15 mm; *Macomona* > 15 mm; *Austrovenus* 4–10 mm; and *Austrovenus* > 10 mm shell lengths. From these data, the following variables of bivalve abundance were calculated: (1) observed density (i.e. raw counts); (2) the neighborhood density (the mean of each cell $+ 8$ cells surrounding it, which precluded values for cells on the periphery of the plot) and (3) fitted polynomial density (as calculated by Legendre et al., 1997). These three variables provided estimators of prey abundance integrated over somewhat different scales: the observed density sampled at the 25 m interval of the cells in the grid; the neighborhood density averaged *Macomona* densities across the 75 m distance of 3 adjoining cells; and the fitted polynomial density smoothed the observed distribution at a scale > 75 m but within the 250×500 m boundaries of the study plot.

Because we counted ray pits repeatedly over a seasonal period when ray foraging

Fig. 2. Study plot (250 m × 500 m) with grid of 200 cells in which bivalve densities were sampled on 22–23 January. Dark shading indicates location of 38 cells in which eagle ray pits were counted on 6 dates.

activity was changing markedly (see below), we wanted to ascertain if change in abundance and/or distribution of bivalve prey could account for change in predator behavior. To test for potential short-term change in prey abundance during the study period, we took advantage of the intensive sampling of bivalve prey in parallel studies on the study plot (Legendre et al., 1997), in which a subset of 22 of the pre-selected cells were re-sampled on 16 February 1994. Bivalves were re-sampled with four 0.25 m^2 quadrats located at 1.5 to 2 m away from the first sample and about 3 m apart from each other, providing a mean nested density for the cell. As before, each plot was excavated to 15 cm depth, and bivalves retained on a sieve of 4 mm mesh were counted. Densities of *Macomona* > 15 mm on 22 February were significantly correlated with the densities of 22–23 January, with a major axis regression (Mesplé et al., 1996) of $Y = 0.879X + 5.66$ (where Y is 22 Feb density and X is 22–23 Jan density). The slope (95% C.I. = [0.631, 1.394]) and intercept (95% C.I. = [−3.55, 11.35]) of this regression do not differ significantly from 1 and 0, respectively. This indicates that the density and spatial distribution of *Macomona* > 15 mm did not change significantly during the time period of the study.

2.3. Estimation of predator feeding activity: eagle ray pits

As a measure of the foraging activity of predators on bivalves, we counted pits created by eagle rays in the sand flat substrate. Preliminary sampling by trawling and traps in the study area showed that other potential predators of large bivalves were either uncommon (e.g., portunid crabs) or did not forage directly on whole bivalves (e.g., siphon nipping flat fish) (see also Thrush et al., 1997a; Whitlatch et al., 1997). Newly formed pits on the sandflat at Wiroa Island were distinctive and often surrounded by clear impressions of the eagle ray's outline showing the blunt nose, wings, and sometimes even the tail (Fig.
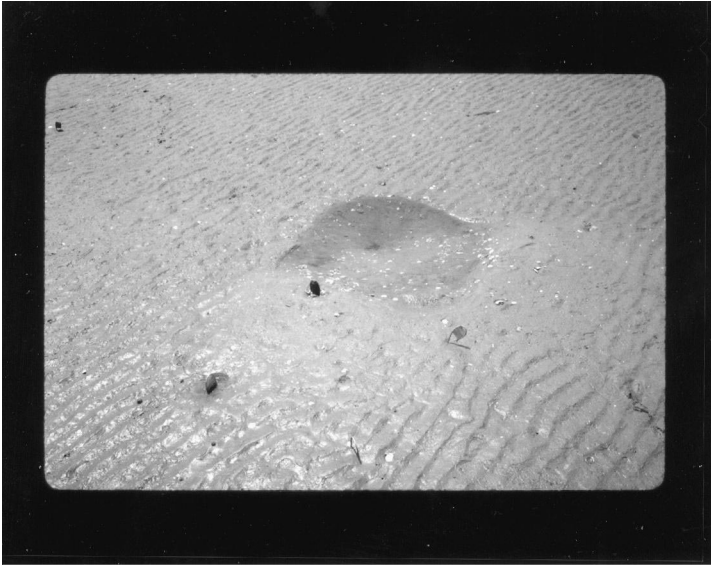
Fig. 3. Photo of newly formed large ray pit showing area disturbed and core of feeding area made by an eagle ray (*Myliobatis tenuicaudatus*) on the study plot of the sandflat at Wiroa Island, New Zealand.

3). The area of disturbance by a ray pit averaged about 0.5 m^2 including the disturbance of the wings, while the area of predatory impact averaged about 0.015 m^2 (average disturbance diameter = 0.8 m, average feeding diameter = 0.14 m; see also Thrush et al., 1991). The depth of the sediment disturbed by the wings of the rays was 2–5 cm; and the depth of the feeding hole was consistently about 15 cm (range 10–20 cm), and much of the sediment jetted out of the feeding pit often formed a mound of dark anaerobic color on the pit's down-current side. This depth of the pits exceeded the maximum burial depth (ca. 5 cm) of *Austrovenus* and the average burial depth (10 cm) of large *Macomona*, and extended to *Macomona*'s maximum burial depth (ca. 15 cm), where a layer of shell hash frequently occurred in the study site. Eagle rays appeared to be effective at removing bivalves from the sediment, because new pits formed on the previous tide contained few large *Macomona* compared to the surrounding sediment, although the pits were rapidly recolonized (Thrush et al., 1991).

To estimate the feeding response of eagle rays to spatial variation in prey densities, we counted ray pits in a subset of 38 cells of the mapped grid of bivalve densities (Fig. 2). The subset of cells was selected using the neighborhood density of prey to represent cells with low (> 26–36 individuals per 0.25 m^2), medium (> 36–46 individuals per 0.25 m^2), or high (> 46–56 individuals per 0.25 m^2) density of large (> 15 mm) *Macomona*. Twenty–two of the cells were chosen as representatives of the full range of bivalve densities with the lowest standard deviation of neighborhood density as a part of other experiments (see also Thrush et al., 1997b). The 16 other cells were selected to increase the sample size and spatial coverage across the grid. We counted ray pits within circular plots (707 m^2) centered at the randomly positioned location of the bivalve

sampling quadrats for each cell. We used a 15 m measuring tape pivoted as a radius around the plot when counting the pits.

Seasonal variation in eagle ray foraging on the Wiroa sandflat was estimated qualitatively and quantitatively. Qualitative observations were made during monthly visits to the site from 1988–1994 (see also Thrush et al., 1991, 1994). In quantitative studies, ray pits were counted repeatedly in the 38 cells of the study site during low tides on 6 dates in 1994 (5, 7, 10, 22 Feb and 1, 8 March). The feeding pits aged rapidly with oxidization of sulfide sediments and slumping/filling of the pit, although the rate of aging depended upon weather. During windy conditions and rough seas, pits did not persist for more than 2 days. During typically moderate weather conditions, pits persisted up to 4.5 days before becoming indistinguishable from surrounding sediment, which is consistent with Thrush et al. (1991). Therefore, to meet the assumption of independence among samples, counting dates should be separated by at least 5 days for statistical analysis of data. This condition of independence was met by all of our counting dates except 7 February, and we excluded those data from tests of significant differences among counting dates.

2.4. Statistical analyses

We compared treatment of the independent variable of bivalve density as a ratio scale (regression-type) variable with treatment of the independent variable as nominal (ANOVA-type) variable. We used general linear models (GLM) to test for interaction between prey density categories (high, medium and low) and ray pit counting dates. After initially testing linear regression models for goodness of fit, we used nonlinear segmented regression models to describe the response of large ray pits to variation in density of bivalve prey (Gallant, 1975; SAS Institute, 1992). The parameters of the nonlinear segmented model were estimated by the GLM procedure, which also estimates their confidence intervals. We used R^2 values to compare the goodness of fit of the three estimators of prey density in predicting predator response (number of eagle ray pits) in the nonlinear segmented models. To incorporate a seasonal component of predator foraging activity into the model, we allowed the parameters of the nonlinear segmented model to vary with time by adding a polynomial function of sampling date into each parameter of the nonlinear segmented model. The temporal component was added to the parameters successively, and we tested for significance in the improvement of R^2 value due to the added parameters, as for multiple regressions (Sokal and Rohlf, 1981).

3. Results

3.1. Temporal variation in predator foraging activity

Eagle rays exhibited a seasonal cycle in feeding on the Wiroa Island sandflat. Our qualitative observations found that pits began to appear on the sandflat in November 1993 and were abundant, although clumped in spatial distribution, during surveys of the study site during January 1994. Thus, when our quantitative spatial sampling of ray pits

began on 5 February 1994, the season of eagle ray foraging activity was well underway. After dropping the 7 February data for violating the assumption of independence among samples, the total number of ray pits differed significantly among counting dates (ANOVA, $F_{1,117} = 0.20$, $P < 0.001$), reflecting the pattern of seasonal activity which peaked in February and declined to minimal levels by mid-March (Fig. 4). The number of ray pits on each of the subsequent counting dates were significantly correlated with the first counting date (Fig. 5) (range of $R^2 = 0.73–0.88$). The significant regressions of ray pits versus *Macomona* density across sample dates indicates that the foraging activity of the eagle rays exhibited a consistent spatial pattern. Note, however, that the slope of these regressions declined progressively as ray foraging activity declined during the season (Fig. 5). Considering both qualitative observations and quantitative sampling, our counting dates spanned approximately the second half to last third of the season of foraging by eagle rays on the sandflat.

3.2. Predator response to prey density

Numbers of ray pits differed significantly among categories of neighborhood prey density (high, medium and low densities of *Macomona* > 15 mm per 0.25 m^2) and among counting dates; but there was not a significant date–density interaction (two-way ANOVA; Fig. 6). For each of the counting dates, one-way ANOVA indicated that the number of large ray pits differed significantly among the three levels of prey for the three estimators of *Macomona* density (Observed, Neighborhood, Fitted Polynomial) (Table 1). Numbers of eagle ray pits were greatest at high prey density for each of the estimators of bivalve density (SNK tests, $P < 0.01$), while ray feeding did not differ significantly between low and medium prey densities (SNK tests, $P > 0.05$) (e.g., Fig. 6).

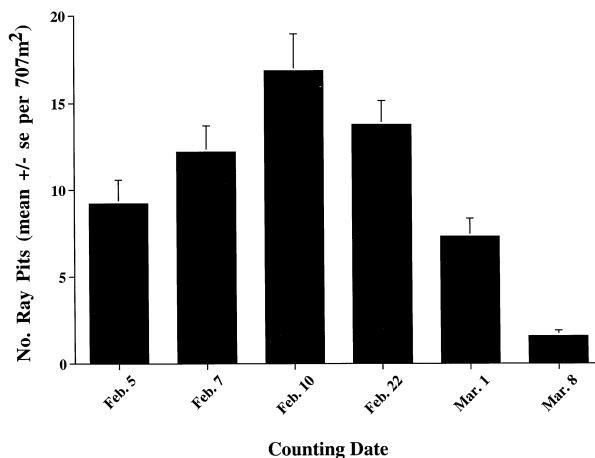The response of eagle ray foraging (number of ray pits per 707 m^2) to variation in

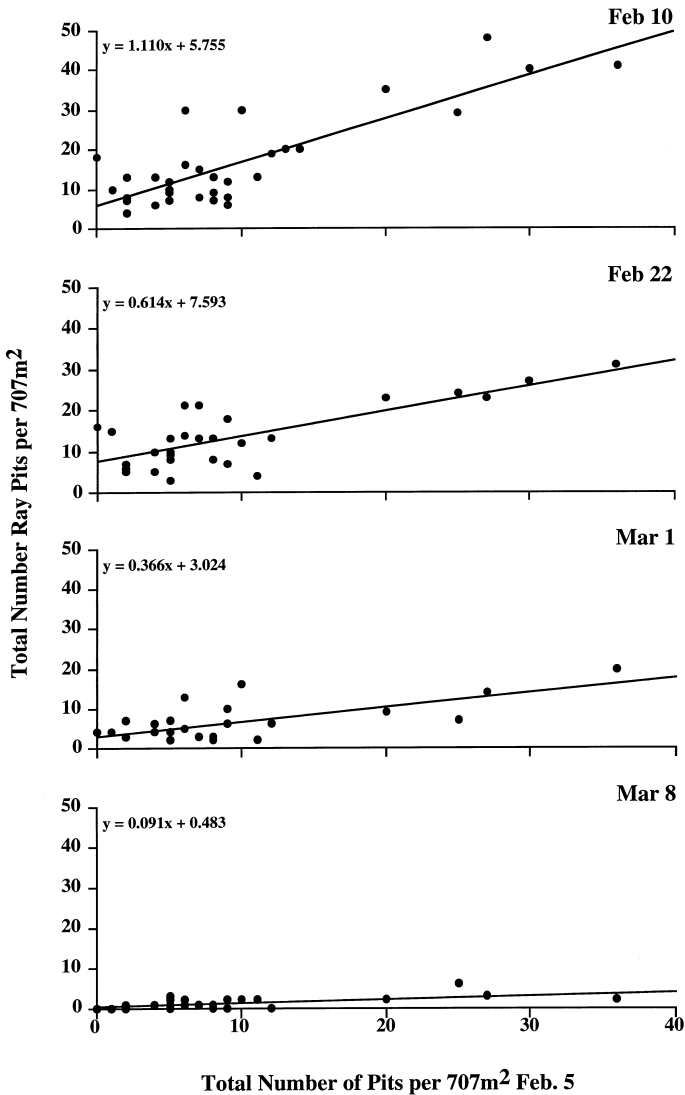Fig. 4. Number (mean±SE) of eagle ray pits on the six counting dates. Note seasonal cycle of ray foraging activity.

Fig. 5. Number (mean±SE) of eagle ray pits counted on 5 dates indicated as a function of 3 levels of Neighborhood Prey Density (*Macomona* >15 mm per 0.25 m^2). Results of two-way ANOVA for main effects and interaction are indicated.

prey density (*Macomona* >15 mm per 0.25 m^2), however, was best described by a nonlinear segmented model, in which there was a constant feeding level at low bivalve densities and a rapidly increasing linear response at bivalve densities above a threshold level of prey density (Fig. 7). At the maximum prey densities sampled in the study site, ray foraging did not reach a satiation level, and the number of ray pits as a function of *Macomona* density increased without forming an asymptote. Thus, the model is:
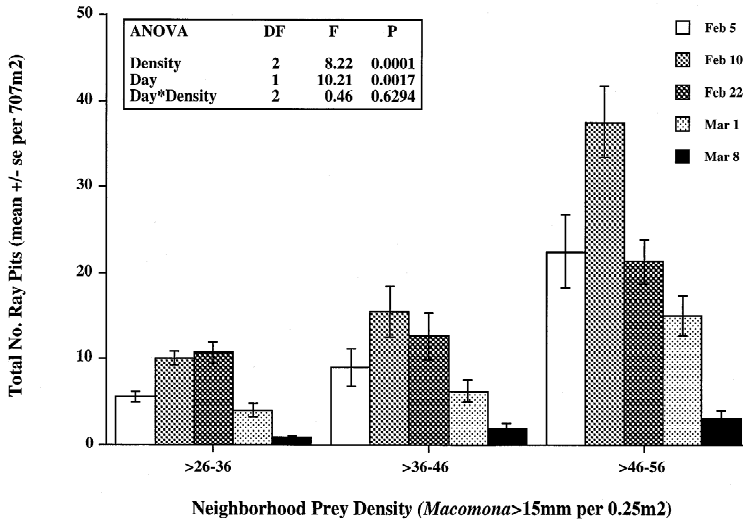
Fig. 6. Regressions of number of large eagle ray pits per 707 m^2 for 4 dates indicated versus number of eagle ray pits per 707 m^2 on 5 February in the 38 counting cells. Regression equations indicated are all significant (ANOVA, $P < 0.02$).

If prey density $< C$, then ray pits $= A$;

or else ray pits $= B$(prey density $- C) + A$,

where C is the threshold prey density; A is a constant number of ray pits at low prey levels; and B is the slope of the linear foraging response at prey levels above the threshold in prey density. Although tests of regression models for linear and log-transformed functions also showed significant least-squares fit, the amount of variation explained by these models (range of R^2: 0.38 to 0.58) was always appreciably lower than the corresponding nonlinear segmented model (range of R^2: 0.51 to 0.85). Therefore, the following analysis considers only nonlinear segmented models. All three

Table 1
Effects of 3 estimators of bivalve prey density on ray foraging revealed in one-way ANOVA of log number of ray pits as a function of *Macomona* >15 mm density (low, medium and high levels)

Density Estimator		5 Feb	10 Feb	22 Feb	1 Mar	8 Mar
Observed	P	0.054	0.008	0.054	0.014	0.015
	R^2	0.158	0.254	0.201	0.273	0.269
Neighborhood	P	<0.001	<0.001	<0.016	<0.001	0.041
	R^2	0.360	0.547	0.274	0.561	0.211
Fitted Polynomial	P	<0.001	<0.001	<0.001	<0.001	0.015
	R^2	0.394	0.600	0.421	0.485	0.268

P and R^2 values and are given for five counting dates. R^2 values allow comparison of goodness of fit among the estimators.
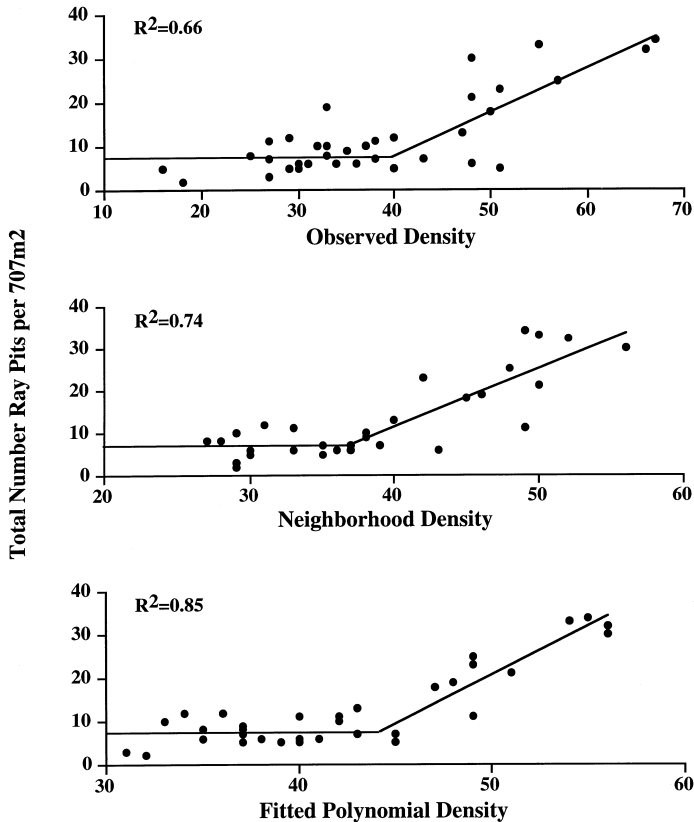
Fig. 7. Density-dependent response of eagle rays to bivalve prey. The plots compare the goodness of fit for nonlinear segmented regression models of ray pits versus 3 estimators of prey density (*Macomona* >15 mm per 0.25 m^2). See text for explanation of the 3 estimators. R^2 values for each model are indicated.

estimators of prey density were significant predictors of the nonlinear response of ray foraging (Fig. 7); however, the Neighborhood Density improved the fit compared to the Observed Density and the Fitted Polynomial Density provided the best fit (highest R^2) (Fig. 7). Subsequent analysis that derived the parameters (*A*, *B*, *C*) of the model considered only this best-fitting estimator for use in estimating the impact of ray foraging.

Despite the good fit of the non-linear segmented model for individual sampling dates, a general nonlinear segmented model estimated by pooling data from all 6 dates had a low $R^2 = 0.34$, because the pooled model did not account for the large seasonal variation in ray foraging. As the rate of eagle ray foraging changed seasonally, both the level (*A*) of the constant predator response at low prey densities and the slope (*B*) of the increasing predator response to prey density above the threshold of prey density also changed significantly; but the threshold density (*C*) did not (Fig. 8, Table 2). We attempted to improve the fit by initially incorporating a polynomial function of time as
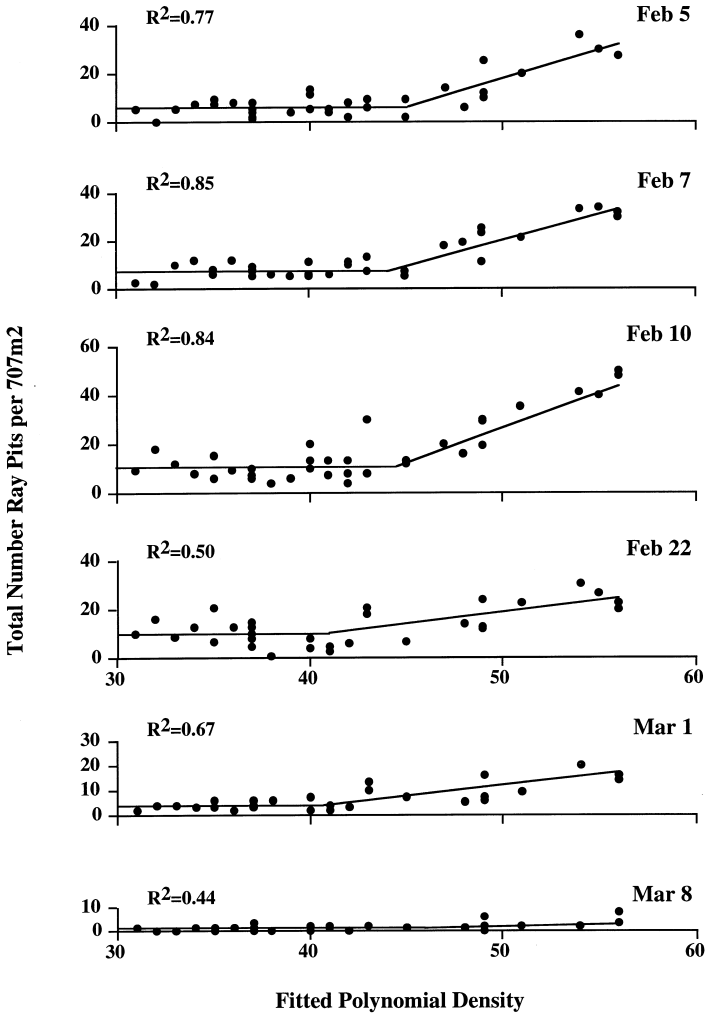
Fig. 8. Seasonal response surface of eagle ray pits versus prey density over the study period (julian day 35 to 67).

julian day (*T*) into all three parameters (*A*, *B*, *C*) of the model. However, a solution for this complex model was not found, in that the convergence criterion was not met in the iterative calculation process for estimating the parameters (SAS Institute, 1992).

Therefore, to incorporate time into the model we estimated the model separately for each counting date (Fig. 9, Table 2), and we used alternative approaches to test whether the parameters changed over time. The level of parameter *A* (number of ray pits at low prey densities) at each date varied directly with overall ray foraging activity and had 95% confidence limits which did not overlap among some of the counting dates (Table 2). Additionally, the number of large ray pits at prey densities <40 *Macomona* per m^2

Table 2
Parameters (and 95% confidence limits) for nonlinear segmented model of number of ray pits as a function of bivalve prey density

Date	A	(95% C.I.)	B	(95% C.I.)	C	(95% C.I.)	R^2
Feb 05	5.75	(5.75, 5.75)	2.47	(1.60, 3.34)	45.1	(42.9, 47.4)	0.77
Feb 07	7.54	(7.12, 7.96)	2.23	(2.13, 2.33)	44.1	(42.2, 45.9)	0.85
Feb 10	10.6	(9.09, 12.1)	3.22	(3.12, 3.32)	44.5	(43.1, 45.8)	0.84
Feb 22	10.0	(7.20, 12.8)	1.00	(0.35, 1.65)	41.0	(34.2, 47.8)	0.51
Mar 01	3.37	(2.05, 5.68)	0.88	(0.54, 1.22)	40.7	(36.6, 44.8)	0.67
Mar 08	0.90	(0.89, 0.91)	0.37	(0.34, 0.41)	46.0	(43.2, 48.8)	0.44

See text for model. A=response level below threshold prey density; B=slope above threshold prey densty; and C=threshold prey density. Models were estimated for each of 6 dates that eagle ray pits were counted, as shown in Fig. 9. R^2 values of the regression models are indicated.

differed significantly among counting dates (one-way ANOVA, $F_{(1,115)}=22.38$, $P<0.001$). Accordingly, we derived a polynomial function for the parameter A fitted to the regression of the model-estimated values of A regressed against julian day (T), as:

$$A = -268.2 + 15.8T - 0.286T^2 + 0.00166T^3,$$

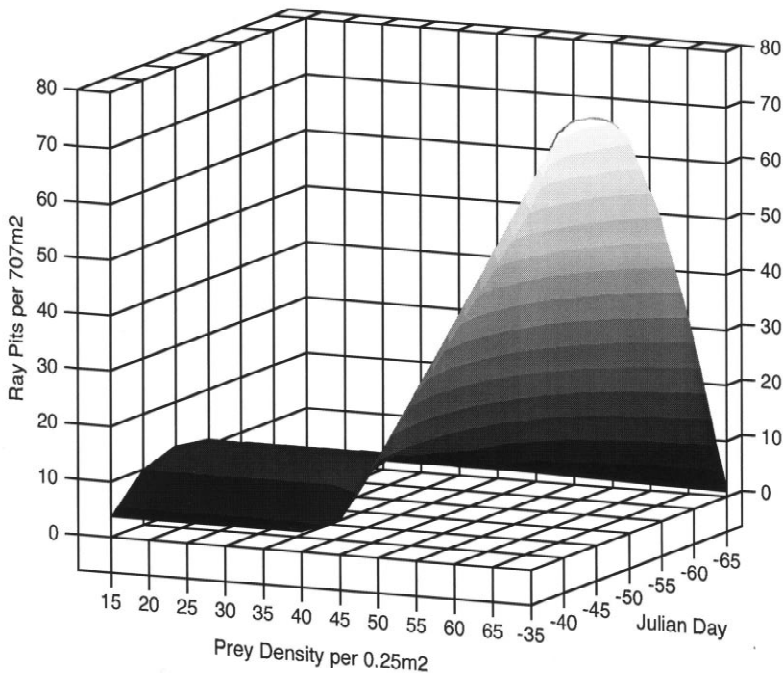which had an $R^2=0.98$. The slope (B) of the increasing foraging response above the

Fig. 9. Seasonal changes in density-dependent response of eagle rays to bivalve density. Nonlinear segmented regression models of ray pits versus fitted polynomial density of *Macomona* per 0.25 m^2. R^2 values for each model are indicated. Parameters of each model are given in Table 2.

threshold in prey density also varied directly with ray feeding activity and had 95% confidence limits which did not overlap among some of the counting dates (Table 2). In contrast, the threshold level (C) did not vary significantly among counting dates, and the 95% confidence limits were always overlaping among dates with a model estimated average of:

$$C = 43.9 \text{ } Macomona > 15 \text{ mm per } 0.25 \text{ m}^2.$$

The polynomial for A was substituted along with the constant for C into the non-linear segmented model to estimate a polynomial for the slope (B) as a function of julian day (T):

$$B = -6.426 + 0.428T - 0.00507T^2,$$

yielding a final model incorporating the three estimated parameters with a significantly improved $R^2 = 0.795$ ($P < 0.001$). Incorporating a temporal component into C did not significantly further improve the fit of the model ($P > 0.6$). The time-dependent parameters (A, B) are sharply constrained to the time period of our study; and application of these parameters outside this time interval yields values which are not interpretable (i.e., yields negative values of ray pit formation). The model estimates the seasonally changing rate of ray pit formation per 707 m^2 per 4 days as a function of *Macomona* density per 0.25 m^2 (Fig. 8).

3.3. Spatial variation in the impact of predator foraging

Considering the area disturbed by each ray pit as 0.5 m^2 and the core feeding area as 0.015 m^2, we estimated the impacts of eagle ray foraging for each grid cell of the study site by integrating the nonlinear segmented model of ray pits as a function of prey density with respect to the time period of our sampling (julian day 35 to 67). We assumed that rays consumed all of the *Macomona* within the feeding area of a pit; although we believe their feeding efficiency was quite high, it was probably less than 100 percent and our estimate thus represents a maximum. We adjusted the integral to units per cell (625 m^2) and time (31 days). Summed for the study period, the total impact of eagle rays across the entire 125 000 m^2 study site resulted in 6303 m^2 (5.04% of the total area) of disturbance and 291 779 *Macomona* consumed (1.57% of the total estimated prey population).

Although foraging impacts average across the whole study plot were small, the impacts were highly spatially variable within the study site and related to prey density (Fig. 10). At prey densities below the threshold of 43.9 *Macomona* per 0.25 m^2, the area disturbed by rays averaged 27.8 m^2 (4.45%) per cell and about 950–1400 *Macomona* consumed (1.34%) per cell. The ray foraging impacts were disproportionately concentrated in cells with prey densities above the threshold density, with a maximum of a 1.9-fold increase in disturbance to about 80.6 m^2 (12.9%) per cell and a 2.61-fold increase in feeding to 5047 (3.86%) *Macomona* consumed per cell where polynomial fitted prey density increased only 0.189-fold to 52.2 *Macomona* per 0.25 m^2. The area of
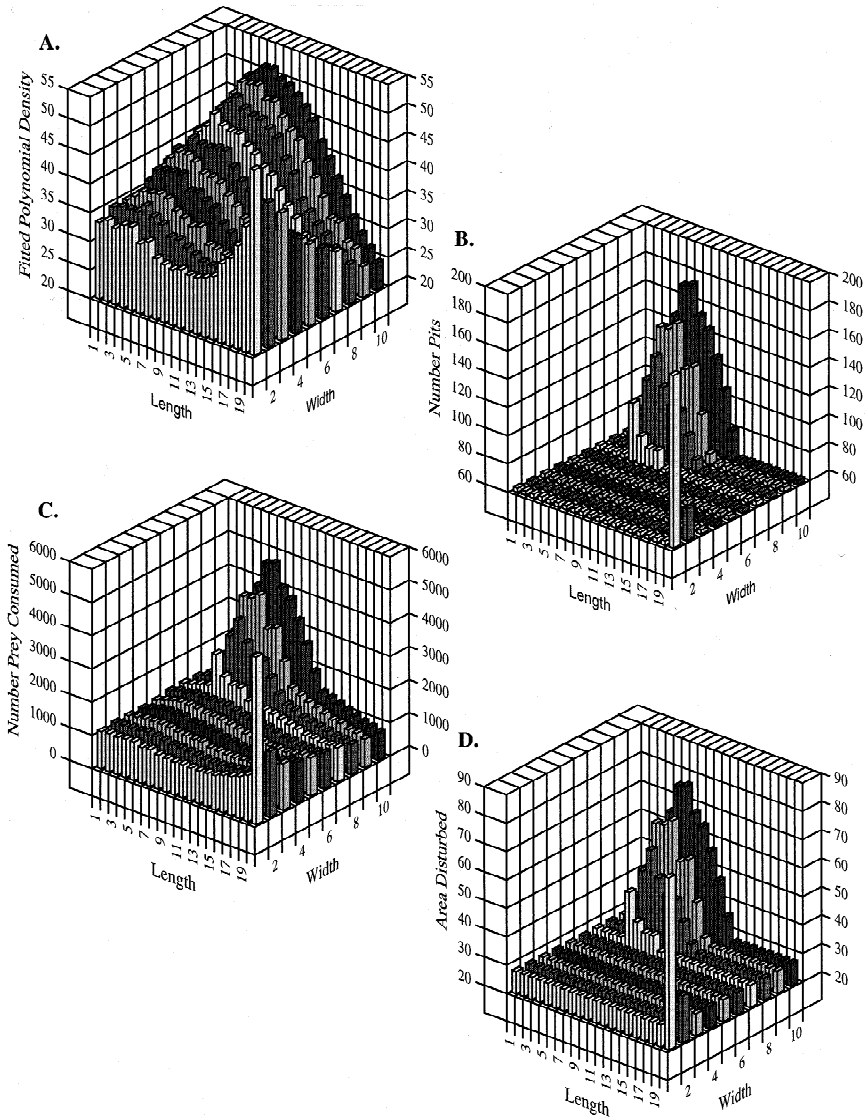
Fig. 10. Spatial distribution of prey (A), integrated number of ray pits (B), integrated number of bivalve prey consumed by eagle rays (C) and integrated area of ray pit disturbance (D) within the 250 m × 500 m study plot. The fitted polynomial density of *Macomona* was estimated from 0.25 m² quadrats sampled in each grid cell. Number of ray pits per grid cell, number of *Macomona* consumed per cell and area of sediment disturbed per cell were estimated from the nonlinear segmented model of ray pits versus bivalve density (see Fig. 8) integrated over the 31 day study period for each of the 200 cells of the grid.

markedly increased impact was concentrated in the areas of high prey abundance in the north-easterly quarter of the study site, and in a small area in the south-west corner of the site (Fig. 10).

4. Discussion

By repeatedly counting disturbance pits on a large plot of mapped prey density, we determined the density-dependent foraging response of a large marine predator on a New Zealand sandflat. Eagle rays foraging on infaunal bivalves at our study site exhibited a nonlinear response to prey density, in which ray foraging activity was low and independent of prey density at low *Macomona* densities, while foraging increased sharply above a threshold density of prey. While analysis of the response to bivalve density treated as a nominal (class, ANOVA-type) variable indicated that ray foraging rates increased significantly with prey density, our modelling approach of treating bivalve density as a ratio scale (continuous, regression-type) variable provided much more information about the nonlinear characteristics of the response. Both the nonlinear characteristic and the threshold of prey density were consistent features of the foraging response, although the levels and slope of the response varied temporally during the course of the season. At maximum prey densities measured in our study site, we did not detect a satiation of eagle ray foraging, which would have been reflected by a leveling off of pit formation at high *Macomona* densities.

The nonlinearity of response to variation in prey density indicates that a proportional aggregative response, as assumed by an Ideal Free Distribution (i.e. the number of foraging predators varying in direct proportion to the abundance of prey over the full range of prey density), does not apply to eagle rays foraging on infaunal bivalves, at least at low prey densities. Eagle rays appear to have a mechanism for assessing prey densities that allows them to ignore unprofitable areas of prey habitat. Density-independent formation of large pits across large areas of low prey density may indicate either that rays do test the substrate by excavating for prey resources or that rays responded to small scale patches of prey. However, the ampullary electroreceptors of rays probably allow them to detect feeding currents of infauna bivalves in complex and sophisticated ways without excavating the substrate (Murray, 1962; Kalmijn, 1971, 1974; Tricas, 1982; Montgomery, 1984a,b; Peters and Evers, 1985; New, 1991; Montgomery and Bodznick, 1994; Tricas et al., 1995), which could account for their consistent threshold of response to prey density.

The electrosensory capability of rays may confer considerable advantages in prey detection compared to some other common marine predators feeding on buried prey. Shorebirds use tactile senses of their bill, which can be affected by microhabitat features limiting penetration into the sediment (Mouritsen and Jensen, 1992; Piersma et al., 1995). Crabs may be intermediate between shorebirds and rays in capabilities of detection of infaunal prey, in that they utilize a combination of highly sensitive chemo-senses for prey detection at a distance (Pearson et al., 1979; Zimmer-Faust et al., 1996) and chemo-tactile senses within the substrate, which are also affected by sediment features (Arnold, 1994; Lipcius and Hines, 1986; Spronaugle and Lawton, 1990; Eggleston et al., 1992; Skilleter, 1994). At the highest prey densities we measured in our study, the aggregative response of eagle rays did not appear to produce interference or facilitation that altered prey removal rates, but we do not know the interaction between predator and prey densities. Presumably, at some extremely high level of aggregation, interference among individuals would occur; but at the maximal rates of pit formation

that we observed (about 55 pits per 707 m^2 per 4 days), eagle rays were still rather widely separated in our study site, especially compared to densities producing interference in shorebirds (Ens and Goss-Custard, 1984).

The spatial scale of the eagle ray foraging response can be deduced by comparing the estimators of prey abundance and our various manipulations of bivalve density. Rays did not target small patches of high density prey in the site, where we experimentally increased bivalve densities during parallel studies to our ray pit analysis: rays ignored 0.25 m^2 experimental patches of high density *Macomona* (Thrush et al., 1997b), as well as experimental patches of *Austrovenus* ranging in size from 0.25–9 m^2 (Whitlatch et al., 1997). The fitted polynomial density of *Macomona*, which smoothed the prey distribution on a scale >75 m, was the best predictor of the foraging response in the large plot compared to the two other estimators (Observed and Neighborhood densities), which represented prey distribution on smaller scales of 25–75 m. At the upper end of the scale of response, rays clearly distinguished prey patches within the 250 m×500 m study plot. Thus, eagle rays appear to forage on prey patches at a scale of 75–100 m. This scale for rays was intermediate between that of flat fish foraging at a scale of about 3 m (Whitlatch et al., 1997) and that of shorebirds foraging at a scale of kilometers (Cummings et al., 1997) on the Wiroa sandflat at the same time.

The nonlinearity of the response to prey density indicates ray predation had major consequences to the spatial distribution and stability of the *Macomona* population, as well as to sedimentary disturbance on the sandflat. This contrasts with the average impact of eagle ray foraging, which was relatively small, averaging about 1.6% of the *Macomona* population and 5.0% sediment disturbance across the study site over the month of study. This rate of disturbance is similar to rates of disturbance by dasyatid rays along the southeast coast of North America (Reidenauer and Thistle, 1981; Grant, 1983; Sherman et al., 1983). The spatial distribution of foraging activity was consistent over the time of our quantitative study, reflecting the apparent constancy in the distribution and density of large *Macomona*. However, in large patches with densities of *Macomona* about 0.19-fold greater than the threshold density, we estimated that ray foraging more than doubled, removing up to 4% of the prey population and disturbing up to 13% of the area during the study month, which would extrapolate to about 8–12% mortality and 26–39% disturbance over the course of the 2–3 month season. The disproportionate concentration of foraging impact at high densities of prey would have the effect of evening out prey distribution and stabilizing prey populations, which effectively gain a refuge from predation at low density (see also Eggleston et al., 1992; Piersma et al., 1993, 1995).

We are not aware of any other similar example of a nonlinear foraging response with a sharp threshold in prey density in marine ecosystems, perhaps because similar studies are limited. However, nonlinear foraging responses are likely to be very common (e.g., see Piersma et al., 1993, 1995). Empirical research on shorebirds (e.g., Goss-Custard et al., 1991; Piersma et al., 1993; Zwarts and Wanink, 1989) indicates that there are complex interactions among prey characteristics and distributions, and predator behavior. Similarly, analyses of crab foraging indicate important density-dependent shifts in predator behavior that are modified by habitat features (e.g., Lipcius and Hines, 1986; Eggleston, 1990; Eggleston et al., 1992). Theoretical considerations of the aggregative

response are needed to extend the stronger base of functional response theory to model the total, combined response more realistically (e.g., Holmgren, 1995; Tregenza, 1995). Our study of eagle rays, as well as the growing knowledge about shorebirds and crabs, indicates that predictive understanding of predator–prey interactions require more sophisticated, multi-factorial approaches incorporating temporal and spatial scaling into theory and field experiments alike.

Acknowledgements

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