Effect of temperature on the functional response and foraging behavior of the sand shrimp *Crangon septemspinosa* preying on juvenile winter flounder *Pseudopleuronectes americanus*

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ABSTRACT: Predator-prey dynamics between the sand shrimp *Crangon septemspinosa* and juvenile winter flounder *Pseudopleuronectes americanus* were examined in laboratory experiments to assess the joint effects of varying prey density and temperature on shrimp foraging behavior and flounder mortality. The functional response of shrimp to 6 densities of flounder was determined at 2 temperatures (10 and 16°C). The behavioral mechanisms underlying the shrimp's functional response were quantified with visual observations and compared to the foraging parameters predicted by continuous-time functional response models. Shrimp consumption rates increased significantly with increasing flounder density, irrespective of water temperature. At low flounder densities, however, significantly more flounder were consumed at 16°C than at 10°C. Analysis of proportional mortality of flounder across prey density and general functional response models revealed a sigmoidal, Type III functional response at 10°C, and a hyperbolic, Type II functional response at 16°C. Model parameter estimates and visual observations of shrimp foraging behavior suggest that the variable functional responses at different temperatures are the result of cold temperatures decreasing predator activity at low flounder densities, and conversely, shrimp maintaining high attack rates at low flounder densities when exposed to warm temperatures. These findings indicate that shrimp are capable of driving flounder populations to local extinction during warm water conditions. The recent warming trend experienced in northwest Atlantic estuaries, and its impact on trophic dynamics, may therefore explain the failure of the winter flounder stocks to recover in these areas.

KEY WORDS: *Crangon septemspinosa* · *Pseudopleuronectes americanus* · Sand shrimp · Winter flounder · Functional response · Foraging behavior · Predation

INTRODUCTION

The relationship between the consumption rate of a predator and the density of its prey is known as the predator's functional response. The type of functional response demonstrated by a predator provides insight into the behavioral mechanisms underlying predator-prey dynamics, and hence, may explain oscillations in prey populations, or the local extinction or persistence of certain prey (Murdoch & Oaten 1975). Quantitative examination of a predator's functional response is therefore a useful method for identifying the importance of predation in maintaining community structure and regulating prey populations (Abrams et al. 1990).

Functional responses have been classified into 3 general forms (Holling 1959, Hassell 1978). The Type I functional response is initially density-independent as consumption rates increase linearly with increasing prey density until reaching a plateau at satiation. Satiation occurs when a predator cannot handle prey any faster, at which point ingestion remains constant, despite increasing prey density, and prey mortality becomes inversely density-dependent (Hassell 1978). The Type II functional response is hyperbolic and inversely density-dependent as consumption rates rise at a decelerating rate to an upper asymptote, reflecting increased costs or constraints associated with higher ingestion rates (Hassell 1978). The Type III functional

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response is sigmoidal, demonstrating an initial density-dependent acceleration of ingestion at low to moderate prey densities until passing an inflection point, beyond which consumption increases at a decelerating rate, much as in the Type II functional response (Hassell 1978).

Distinguishing among functional responses is important because of their very different contributions to prey population stability (Hassell et al. 1977). In the Type II response, for example, the risk of mortality increases with decreasing prey density, whereas in the Type III response, there is change from an increasing to decreasing risk of mortality as prey density declines below a threshold level (Hassell 1978). The threshold level, quantitatively defined as the inflection point of the sigmoidal Type III response curve, results from decreased predator efficiency in the detection or capture of prey as prey density decreases (Hassell 1978). This, in turn, may be caused by a lack of reinforcement of learned predator searching behavior owing to a low rate of prey encounters at low prey densities (Real 1979), reduction in foraging activity in unrewarding circumstances (Taylor 1984), and predators switching to alternative sources of food when a given prey is scarce (Murdoch 1969, Wennhage 2002). Consequently, the Type III functional response stabilizes predator-prey dynamics via a relative refuge at low prey densities (Lipcius & Hines 1986, Eggleston et al. 1992).

Changes in abiotic and biotic factors can significantly alter the functional response of a predator. For example, previous research has documented that predator-prey dynamics are influenced by: relative spatial and temporal distribution of predators and prey (de Lafontaine & Leggett 1987); habitat heterogeneity (Lipcius & Hines 1986); dissolved oxygen (Sandberg 1997, Taylor & Eggleston 2000); predator learning (Landenberger 1968) and aggregation (Mansour & Lipcius 1991, Taylor & Eggleston 2000); and predator and prey size (Eggleston 1990a). An additional factor that influences the intensity or nature of a predator's functional response is temperature (Eggleston 1990b). Particularly in coastal-estuarine systems, oscillations in water temperature can affect predator-prey interactions by changing the spatial and temporal abundance patterns of both predator and prey. The predatory sand shrimp *Crangon septemspinosa*, for example, demonstrates a seasonal migration to deeper waters in the fall, when shallower estuarine waters decrease in temperature (Haefner 1979). The increase in water temperature during the spring then initiates a return migration of shrimp back to shallow water (Haefner 1979). The absence and reappearance of this voracious predator in shallow estuarine habitats, in response to changing water temperature, may affect the structure

and species composition of the benthic community (Wilcox & Jeffries 1974, Pihl & Rosenberg 1984, Bonsdorff et al. 1995).

The varying physiological responses by predators and prey to changing water temperature can enhance or impede predation efficiency. Increased water temperature, for instance, could be beneficial to a predator if the primary effect were to accelerate its level of metabolism, and thus enhance foraging activity. In a study examining the foraging efforts of the blue crab *Callinectes sapidus* on juvenile oysters *Crassostrea virginica*, Eggleston (1990b) observed an intensification of crab predation on oysters with increasing water temperature. Increased water temperature resulted in a greater persistence time and attack success-rate for the blue crab, shifting its functional response from a stabilizing, Type III response to a destabilizing, Type II response. Similarly, Beisner et al. (1997a,b) established that increasing water temperature led to a destabilization of the population dynamics of the invertebrate carnivore *Mesostoma ehrenbergii* and its prey *Daphnia pulex*, which ultimately resulted in the local extinction of *Daphnia* at higher temperatures.

Increased levels of water temperature can also have a detrimental effect on predation efficiency. For example, increased water temperature could accelerate the metabolism of prey species, which in turn increases their activity, mobility, and escape capability, thus decreasing vulnerability to predation. Enhanced prey metabolic rates are also likely to increase growth rates, and thus minimize the time during which animals remain susceptible to size-selective predation (Parker 1971, Post & Evans 1989). Because the physiology and behavior of estuarine predators and prey varies to such a large extent in response to changes in water temperature, fluctuations can lead to either increased or decreased prey capture, thereby affecting predators' functional responses and, ultimately, food-web dynamics. Despite mounting evidence for variable functional responses as a consequence of different biotic and physical conditions, few experiments have tested temperature impacts on predator-prey relationships in marine and estuarine systems.

The purpose of the following investigation was to determine the impact of increasing water temperature on a key estuarine predator-prey interaction between the sand shrimp *Crangon septemspinosa* and juvenile winter flounder *Pseudopleuronectes americanus*. The specific objectives were (1) to describe the foraging behavior of shrimp preying on varying densities of juvenile flounder; (2) to determine whether the predator's functional response and underlying behavioral mechanisms are temperature-dependent; and (3) to compare empirically derived foraging parameters with those predicted by functional response models.

PREDATOR-PREY SYSTEM

The sand shrimp *Crangon septemspinosa* Say (Arthropoda: Crustacea: Crangonidae) is a common estuarine decapod distributed along the northwestern Atlantic coast from Newfoundland to eastern Florida (Price 1962, Haefner 1979). Serving both as epibenthic predators and prey, sand shrimp are critical to energy transfer across trophic levels within estuarine ecosystems (Wilcox & Jeffries 1974, Haefner 1979). Aptly defined as omnivorous, sand shrimp are typically nocturnal predators, but will take preferred foods during daylight hours (Wilcox & Jeffries 1974, Haefner 1979). They feed primarily upon mollusks, arthropods, annelids, and detrital matter, but also upon fish (Wilcox & Jeffries 1974, Bertram & Leggett 1994, Witting & Able 1995).

Winter flounder *Pseudopleuronectes americanus* Walbaum (Vertebrata: Osteichthyes: Pleuronectidae) is a medium-sized (maximum 45 cm standard length), pleuronectid flatfish inhabiting estuaries and the continental shelf of the northwestern Atlantic (Collette & Klein-MacPhee 2002). Spawning of demersal eggs occurs in estuaries during the winter and early spring (Pearcy 1962). After hatching, the larvae are pelagic for approximately 60 d (Chambers & Leggett 1987), but the duration of this period can vary significantly depending on temperature (Laurence 1975). At metamorphosis, the left eye of the pelagic larva moves to the right side of the head, dense pigmentation develops, and the body flattens as the flounder assumes a benthic existence (Pearcy 1962). The small size of recently settled winter flounder (ca. 8 to 9 mm; Collette & Klein-MacPhee 2002) and their relatively weak swimming and burying capabilities makes this species particularly vulnerable to a host of crustacean and demersal fish predators (Witting & Able 1995, Manderson et al. 1999, 2000, Fairchild & Howell 2000). The result is intense predator-induced mortality, and thus, possible year-class determination at the post-settlement stage (Edwards & Steele 1968, Lockwood 1980, Van der Veer & Bergman 1987).

Predation by the sand shrimp has been implicated as one of the most significant sources of mortality for recently settled winter flounder (Witting & Able 1995). In an analysis of size-dependent mortality of juvenile winter flounder through *Crangon septemspinosa* predation, Witting & Able (1995) demonstrated that susceptibility of juvenile flounder to predation by sand shrimp decreases dramatically with increasing flounder size. Specifically, winter flounder susceptibility to shrimp predation reaches a maximum precisely at the time of initial settlement, when fish (ca. 8 to 10 mm total length, TL) are completing several aspects of morphological and ecological metamorphoses. This susceptibility to predation then gradually decreases after settlement until a complete refuge from *C. septemspinosa* predation is attained at sizes greater than 24 mm TL (Witting & Able 1995).

Further evidence supporting the hypothesis that *Crangon septemspinosa* is a significant regulator of juvenile winter flounder abundance comes from the strikingly similar morphology and behavior between the sand shrimp and a European congener, the brown shrimp *C. crangon*. Extensive field and laboratory research has implicated the brown shrimp as a significant source of density-dependent mortality for young-of-the-year plaice *Pleuronectes platessa* and flounder *Platichthys flesus* during and shortly after the flatfish settle on tidal flats in the western Wadden Sea (Van der Veer & Bergman 1987, Van der Veer et al. 1991). The observed density-dependent mortality was caused by a combined effect of a functional and numerical response of *C. crangon* to fluctuations in plaice and flounder density (Van der Veer & Bergman 1987, Van der Veer et al. 1991). Moreover, the occurrence of this intense predation on juvenile flatfish was strongly correlated with prey body size, whereby shrimp-induced density-dependent mortality ended in late spring, when flatfish populations achieved a mean size of approximately 30 mm (Van der Veer & Bergman 1987). The behavioral basis of this predator-prey size relationship between *C. crangon* and *P. platessa* was attributed to the superior escape capabilities of larger fish once captured by potential shrimp predators (Gibson et al. 1995).

Previous research has contributed little toward explaining the effects of prey density on predator-prey dynamics between the sand shrimp and juvenile winter flounder. Such analysis of the predator's functional response, coupled with empirically derived foraging parameters, may identify the behavioral mechanisms and overall effect shrimp have in regulating recently settled winter flounder populations. Quantifying a predator's functional response is a powerful method for examining predator-prey dynamics under varying environmental conditions, such as climatic fluctuations and subsequent oscillations in water temperature. Currently, the effect of increased water temperature on the predator-prey relationship between the sand shrimp and juvenile winter flounder is unknown. Investigating these effects is increasingly important given the anticipated impact of global warming on marine and estuarine systems (Schuurmans 1995).

MATERIALS AND METHODS

Collection and maintenance of experimental organisms. Juvenile winter flounder were either raised from broodstock that were collected by otter trawl from

Narragansett Bay (Rhode Island, USA) or provided by Llennoco Inc. (Chatham, MA, USA). Adult flounder, constituting the broodstock, were transferred and maintained in laboratory tanks supplied with running seawater at ambient temperature and salinity (approximately 4 to 6°C and 30 to 32 ppt). Eggs and larval fish were obtained using techniques described by Klein-MacPhee et al. (1982). All young-of-the-year flounder were maintained in 39 l aquaria that were immersed in an ambient temperature flow-through seawater bath (6 to 12°C), and fed wild plankton consisting primarily of copepod nauplii, rotifers, and polychaete larvae. Prior to experiments, flounder were measured to the nearest mm with calipers. Only those fish measuring 8 to 22 mm total length (TL) were used in laboratory feeding and filming experiments. Experimental flounder body sizes constitute the range in which flounder are vulnerable to sand shrimp predation (Witting & Able 1995).

Adult *Crangon septemspinosa* were collected with beam trawls from the Niantic River (Connecticut, USA). Shrimp were then transferred to the laboratory, where they were maintained in large flow-through tanks and fed frozen clam ad libitum each day. Only adult shrimp measuring 45 to 65 mm TL from the tip of the antennal scale to the end of the telson were used during this investigation. This size class dominates northern-temperate estuaries during late spring and early summer (Price 1962, Haefner 1979), and shrimp of this size have been observed to readily consume juvenile winter flounder (Witting & Able 1995).

Experimental procedure and design. To evaluate predator responses to prey density and water temperature, 6 densities of juvenile winter flounder (1, 3, 5, 10, 15, and 20 fish per tank; 4.47, 13.4, 22.4, 44.7, 67.1, and 89.4 fish m^{-2}) were exposed to predatory *Crangon septemspinosa* (3 shrimp per tank; 13.4 shrimp m^{-2}). The densities of fish used in this experiment include and exceed the range of densities of winter flounder observed in field populations (Meise et al. 1999, Sogard et al. 2001, Curran & Able 2002). Experimental flounder densities were chosen, however, to ensure encounters between predators and prey were sufficiently frequent for statistical comparisons across treatments, and to maintain consistency with previous investigations that examined crangonid shrimp predation on juvenile flatfish (Van der Veer & Bergman 1987, Bertram & Leggett 1994, Witting & Able 1995). Shrimp densities in this study represent a moderate range found in northern-temperate estuaries (Price 1962).

Eleven cylindrical (55.9 cm high, 53.3 cm diameter, 69.4 l volume) polyethylene tanks were filled with 4 cm of clean sand (grain size = 0.2 mm). The sediment chosen for this experiment was similar to that used in previous studies that examined the impact of juvenile

winter flounder body-size on sand shrimp predation rates (Witting & Able 1995). Each experimental container was also filled with 50 cm of overlying seawater and equipped with an air stone to provide aeration and water circulation. Experimental containers were part of a larger flow-through, re-circulating system in which water temperature was maintained at desired levels by thermostatic control (±0.2°C). Two water temperatures were implemented in this experiment: 10.0 and 16.0°C. Experimental temperatures represent (1) late spring to early summer average temperature found in northern-temperate estuaries (10.0°C) (DNC 2003); and (2) higher temperatures simulating anomalous warm years (DNC 2003) and possible future conditions resulting from anthropogenic impacts on global climate (16.0°C) (Schuurmans 1995). Laboratory photoperiod was maintained at late spring and early summer levels (light:dark, 14:10 h).

Prior to introducing winter flounder into experimental tanks, they were measured and placed in rectangular plastic vessels that contained excess quantities of wild plankton. These vessels were floated on individual experimental tanks for 24 h, allowing for a starvation period for shrimp already residing in the tanks (to standardize hunger levels for predators across varying treatments), and a feeding period for the flounder in the plastic vessels. Following the starvation period for shrimp and feeding period for flounder, flounder were visually examined to ensure all fish were adequately fed, after which they were carefully introduced into their respective experimental tank. Five to ten 24 h trials were conducted for each treatment. During each set of replicate trials, 2 tanks were left without shrimp to serve as controls for mortality due to factors other than predation. In the controls, all winter flounder were retrieved from experimental tanks after 24 h. Therefore, missing flounder at the conclusion of a feeding trial were due to shrimp predation. Prey mortality was quantified by counting surviving flounder and subtracting these values from initial prey density.

Analyses of consumption and proportional mortality rates. Consumption (no. fish eaten 24 h^{-1}) and proportional mortality rates (no. fish eaten fish density^{-1} 24 h^{-1}) of flounder were analyzed with a 2-way ANOVA model using prey density and water temperature as fixed factors. The natural log of (x + 1) and the arcsin square-root transformations were used for consumption rate and proportional mortality rate data, respectively, when variances were heteroscedastic. When data transformations were unsuccessful in achieving homoscedasticity, hypotheses were rejected at α-values lower than the p-values of Levene's test for homogeneity of variance (Underwood 1981). Mean consumption and proportional mortality of flounder

across 6 levels of prey density and 2 levels of water temperature were contrasted with a 2-way ANOVA model and Ryan-Einot-Gabriel-Welsch (Ryan's *Q*) multiple comparison tests (Day & Quinn 1989).

The ability to distinguish among functional responses may be difficult when analyses rely on predator consumption rates. The shape of the proportional mortality curves as a function of prey density, however, provides an accurate and quantitative definition of the form of functional response (Lipcius & Hines 1986, Eggleston et al. 1992). Therefore, initial determination of the type of functional response (Types I, II, or III) was based on the results generated from the Ryan's *Q* multiple comparison test of proportional mortality rates subsequent to the ANOVA. For example, a pattern of non-significant proportional mortality rates across prey densities is indicative of a density-independent Type I functional response. Conversely, a pattern with significantly higher proportional mortality rates at low prey densities characterizes a Type II functional response, whereas a pattern of significantly lower proportional mortality at low prey densities defines a Type III functional response (Hassell 1978).

Analyses of general functional response models. The general functional response model derived by Real (1977, 1979):

$$N_a = \frac{K \times N_t^\beta}{X + N_t^\beta} \qquad (1)$$

provides an explicit statistical test of the form of the functional response (Hassell 1978, Lipcius & Hines 1986). In this form, N_a is the number of prey eaten, K is the maximum feeding rate (i.e. satiation) estimated directly from observed data ($K = 3$ flounder eaten shrimp^{-1} 24 h^{-1}), N_t is initial prey density, X is the density of prey at which $N_a = 0.5 K$, and β is the parameter associated with the form of the functional response curve.

The log-transformed general functional response model was analyzed by linear regression to estimate the slope parameter β. When $\beta = 0$, the number of prey eaten (N_a) is constant, thus signifying the saturated part of a Type I functional response. When $\beta = 1$, the curve rises at a decelerating rate to an asymptote (Type II functional response), or conversely, when $\beta > 1$ the curve is sigmoidal (Type III functional response) (Real 1979). Thus, a statistical test (standard *t*-test) of β is also a method for identifying the form of the functional response (Real 1979, Lipcius & Hines 1986).

Specific functional response modeling and parameter estimation. Continuous-time functional response models were used to estimate the basic behavioral components of predation (Holling 1959, Hassell 1978) (Table 1). Continuous-time models relate the number of encounters of a predator with prey (N_e), whether successful or not, to a function of prey density (N_t). Generally, the use of continuous-time models requires prey replacement throughout a feeding experiment. The assumption of prey replacement was relaxed, however, because continuous-time models often fit functional response data better than alternative models, irrespective of prey replacement (Lipcius & Hines 1986, Eggleston et al. 1992).

The parameters estimated by functional response models, which provide information on the behavioral mechanisms underlying predator-prey dynamics, are handling time and instantaneous attack rate (Table 1). Handling time (T_h) is defined as the time from the initial encounter of the predator with prey, through the capture and ingestion of prey, until searching by the predator resumes (Hassell 1978). Instantaneous attack rate (A') is a measure of encounter success with prey, and is quantified as the area a predator searches for prey per unit time (Hassell 1978). A non-linear least squares analysis was used to estimate T_h and A', and to fit daily consumption rates to the functional response model (Lipcius & Hines 1986, Eggleston et al. 1992) (Table 1). To compare instantaneous attack rates between models, A' was calculated for each density in the Type III model as:

$$A' = \frac{b \times N_t}{1 + c \times N_t} \qquad (2)$$

where *b* and *c* are parameter estimates (Hassell 1978).

The statistical fit of functional response models was examined with an *F*-test, employing the ratio of lack-

Table 1. Non-linear continuous-time functional response models

Model type	Eq.	Source
Type II	$N_e = \frac{A' \times T \times N_t}{1 + (A' \times T_h \times N_t)}$	Holling (1959)
Type III	$N_e = \frac{b \times T \times N_t^2}{1 + (c \times N_t) + (b \times T_h \times N_t^2)}$	Hassell (1978)

Symbol	Definition	Type
N_e	Number of prey encountered per predator	Variable
N_t	Initial prey density	Variable
T	Total time available for foraging (h)	Constant
T_h	Prey-handling time (h)	Parameter
A'	Instantaneous attack rate	Parameter
b, c	Replace A' to estimate variable search rate	Parameters

of-fit mean square to the pure-error mean square (Lipcius & Hines 1986, Colton 1987, Trexler et al. 1988, Eggleston et al. 1992). A significant *F*-ratio indicated a statistically inadequate fit of the data to a model. The criteria for determining a statistically valid functional response model were chosen according to Lipcius & Hines (1986) and Eggleston et al. (1992): (1) *F*-value of the non-linear regression is significant ($p < 0.05$); (2) lack-of-fit error is insignificant ($p > 0.05$); and (3) the response model has the lowest residual sum of squares.

Continuous-time functional response models may yield misleading estimates of predator handling time and attack rates when the non-linear curve is fit to consumption-rate data (Hassell 1978). Alternatively, continuous-time models should be constructed from predator-prey encounter rates (Hassell 1978). Shrimp foraging parameters, T_h and A', were reanalyzed *a posteriori* using non-linear least-squares analysis to fit continuous-time models to daily encounter rates between shrimp and flounder. Consumption rates measured during feeding experiments were recalculated as daily encounters according to empirical estimates of shrimp attack success, i.e. the proportion of attack encounters resulting in the consumption of a flounder (discussed in next section).

Behavioral observations. To gain perspective on the behavioral mechanisms underlying the predator-prey dynamics, and to allow for direct comparisons with functional response analyses, adult shrimp were observed feeding on juvenile flounder. To allow for such comparisons, experimental conditions for the observational study simulated those implemented during previous feeding experiments, with the exception that a sand substrate was not provided in order to facilitate visual observations. Similar behavioral studies of crangonid shrimp predation on post-settled flatfish have been conducted with experimental systems that lacked a substrate (Van der Veer & Bergman 1987, Ansell & Gibson 1993, Gibson et al. 1995). Moreover, *Crangon crangon* predation rates on juvenile plaice *Pleuronectes platessa* were unaffected by the presence or absence of sand (Ansell & Gibson 1993), indicating that sediments provide an inadequate refuge for newly settled flatfish because of their relatively poor burying capabilities (Gibson & Robb 1992, Phelan et al. 2001). In this study, interactions between shrimp and flounder were recorded with a monochrome video camera connected to a video recorder. Filming was performed continuously for 8 h under darkness, with illumination provided by infrared emitting diodes. Feeding observations performed under darkness simulated the sand shrimp's natural tendency for nocturnal foraging (Wilcox & Jeffries 1974). The experimental filming arena (4.0 cm high, 40.0 cm diameter) was immersed in

a temperature-controlled water bath (±1.0°C), where feeding behavior was examined at 10.0 and 16.0°C. Two densities of flounder (2 and 10 fish per tank; 15.9 and 79.6 fish m^{-2}) were exposed to 2 adult shrimp (15.9 shrimp m^{-2}) measuring 45 to 65 mm TL. Shrimp and flounder densities were chosen to maintain consistency across the functional response experiments and the observational studies, therefore allowing comparisons between observed behavior and those basic behavioral components estimated from functional response models.

Before the onset of any behavioral observations, shrimp and flounder were acclimated to the same experimental conditions implemented during the feeding trials. Shrimp were introduced into the filming arena at least 3 h before observations began. Subsequently, flounder measuring 8 to 22 mm TL were introduced into the filming arena at 18:00 h, after which filming began. Fifteen to 18 replicate 8 h filming episodes were performed for each treatment combination (10.0 or 16.0°C, and 2 or 10 fish per tank), from which the following behavioral observations were quantified (see Fig. 3):

(1) Random encounter rate between shrimp and flounder (E_R): the observed unintentional physical contact between shrimp and flounder that resulted in a noticeable reaction from predator and/or prey;

(2) Attack encounter rate between shrimp and flounder (E_A): the observed intentional physical contact between shrimp and flounder that resulted from a discernable predatory strike;

(3) Total encounter rate between shrimp and flounder (E_T): the estimated total number of random and attack encounter rates ($E_R + E_A$);

(4) Capture rate (C): the observed total number of attack encounters that resulted in shrimp seizing and maintaining initial control of a flounder;

(5) Successful encounter rate (E_S): the observed total number of captures that resulted in the consumption of a flounder;

(6) Attack success (S_A): the proportion of attack encounters resulting in the consumption of a flounder estimated from attack and successful encounter rates (E_S/E_A);

(7) Capture success (S_C): the proportion of captures resulting in the consumption of a flounder estimated from capture and successful encounter rates (E_S/C);

(8) Attack rate (A'): the area an individual shrimp searches per unit time calculated as the number of attack encounters standardized by flounder density (no. fish m^{-2}) and the area of the filming arena (m^2);

(9) Shrimp handling time (T_h): the observed time from the initial attack encounter between shrimp and flounder, through the capture and ingestion of prey, until searching by the predator resumes.

Separate visual observations were made to quantify shrimp activity levels (*a*) as a function of flounder density, temperature, and diel patterns. The protocol for the second filming experiment was the same as the previous, with the following exceptions: Filming was performed over a 24 h period (light:dark, 14:10 h), in which illumination was provided by overhead fluorescent tubes in combination with infrared emitting diodes. The second filming arena (18.0 cm high, 50.0 cm diameter) was filled with 4 cm of clean sand (grain size = 0.2 mm) and 12.5 cm of overlying seawater. The absence of a substrate may result in abnormal behavior of shrimp, particularly during daylight hours when shrimp prefer to bury (Ansell & Gibson 1993). Thus, with the addition of sand in the second filming experiment, a better estimate of daily shrimp activity was achieved. The filming arena was again immersed in a temperature-controlled water bath (±1.0°C), in which shrimp activity was examined at 10.0 and 16.0°C. Two densities of flounder (2 and 10 fish per tank; 10.2 and 50.9 fish m^{-2}) were exposed to 3 adult shrimp (15.3 shrimp m^{-2}) measuring 45 to 65 mm TL. Observations were recorded at 1 h intervals for a total of 6 h partitioned over a complete daily cycle. A total of 3 h of observation were performed under light and dark conditions for 1 daily cycle. Six to 10 replicates were performed for each treatment (i.e. prey density, temperature, and diel pattern). Shrimp activity levels (*a*) were quantified by laying a grid consisting of 50 × 50 mm squares (approximate body length of shrimp) over the video image of the filming arena and subsequently counting the number of times at least 50% of the shrimp's body entered a grid square. Shrimp were also filmed in the absence of flounder, thus serving as the control by measuring activity irrespective of available prey.

Measured behavioral observations from the first set of trails were standardized across the number of shrimp and flounder present during a trial. Results were then analyzed with a 2-way ANOVA using prey density and water temperature as fixed factors. Shrimp activity levels from the second set of trials were also standardized by shrimp and flounder numbers and analyzed with a 3-way ANOVA using prey density, water temperature, and diel pattern (light versus dark periods) as fixed factors. The natural log of (*x* + 1) transformation was used on behavior data when variances were heteroscedastic. When data transformations were unsuccessful in achieving homoscedasticity, hypotheses were rejected at α-values lower than the p-values of Levene's test for homogeneity of variance.

RESULTS

Analyses of consumption and proportional mortality rates

Shrimp consumption rates on flounder differed significantly with temperature and flounder density (Table 2). The interaction effect was significant, however, precluding contrasts across the main effects (Table 2). At the lowest flounder densities (1 and 3 fish per tank), significantly more flounder were consumed at warm temperatures (16°C) compared to cold temperatures (10°C) (Fig. 1a). Moreover, significantly more flounder were consumed as their density increased, irrespective of temperature (Fig. 1a).

Proportional mortality of flounder differed significantly with temperature, but not with flounder density main effect (Table 2). The interaction effect between temperature and flounder density was significant (Table 2), and was due to significantly lower proportional mortality at low flounder densities at 10°C (indicative of a Type III functional response), and significantly higher proportional mortality at low flounder densities at 16°C (indicative of a Type II functional response) (Fig. 1b). Specifically, at the lowest flounder densities (1 and 3 fish per tank), shrimp foraging under warm temperatures consumed 56 to 80% of the available flounder, whereas under cold temperatures only 0 to 9.4% of the flounder were eaten (Fig. 1b). Thus, as water temperatures increased from 10 to 16°C, shrimp foraging behavior was altered drastically such that it was no longer stabilizing to predator-prey dynamics at low prey densities. The functional response exhibited by shrimp predators feeding on juvenile winter flounder switched from a Type III to Type II functional response as water temperature increased.

Table 2. *Crangon septemspinosa* predation on *Pseudopleuronectes americanus*. Summary statistics for ANOVA of the effects of flounder density (1 to 20 fish per tank) and temperature (10 and 16°C) on shrimp consumption rates (no. fish eaten shrimp density^{-1} 24 h^{-1}) and flounder proportional mortality rates (no. fish eaten fish density^{-1} shrimp density^{-1} 24 h^{-1}). Natural log of (*x* + 1) and arcsin square-root transformations were performed on consumption rate and proportional mortality rate data, respectively

Source	SS	MS	df	*F*	p
Consumption rate					
Density	22.70	4.54	5	44.17	<0.0001
Temperature	2.10	2.10	1	20.43	<0.0001
Density × Temperature	1.81	0.36	5	3.51	<0.01
Error	7.30	0.10	71		
Proportional mortality rate					
Density	0.38	0.08	5	0.67	0.6508
Temperature	3.02	3.02	1	26.20	<0.0001
Density × Temperature	5.02	1.00	5	8.70	<0.0001
Error	8.20	0.12	71		

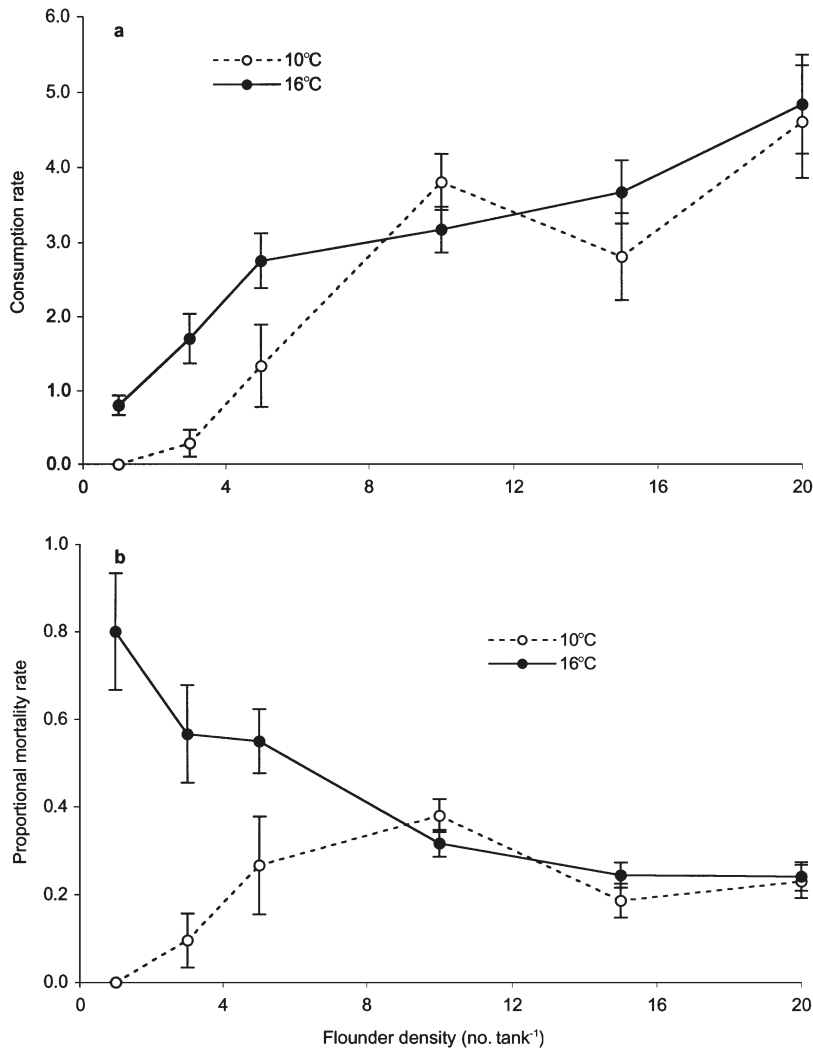Fig. 1. *Crangon septemspinosa* predation on *Pseudopleuronectes americanus*. (a) Shrimp consumption rates (no. fish eaten shrimp density^{-1} 24 h^{-1}), and (b) proportional mortality rates (no. fish eaten fish density^{-1} shrimp density^{-1} 24 h^{-1}) of flounder. Means (±1 SE) at each flounder density are plotted. See text for significant levels

Analyses of general functional response models

Statistical analyses of the general functional response model supported the results from the ANOVA of proportional mortality. The slope of the log-transformed general functional response model (β = 1.71) at 10°C was significantly different from 0 and 1, thus indicating a sigmoidal, (Type III) functional response (Table 3). Conversely, the functional response at 16°C was hyperbolic (Type II functional response), with β (=0.93) significantly different from 0 and 2, but not significantly different from 1 (Table 3). Thus, estimates of β verified that the functional response exhibited by shrimp feeding on flounder is temperature-dependent, with the Type III functional response most appropriate at 10°C, switching to a Type II response at 16°C.

Specific functional response modeling and parameter estimation

Both the Type II and Type III continuous-time functional response models adequately fit the consumption rate data at 10 and 16°C, as indicated by the significant *F*-value of the non-linear regression and non-significant lack-of-fit error for all models (Table 4). However, the Type II functional response model was more appropriate at 16 °C and the Type III model at 10 °C, based on the greater R^2 value of the non-linear regression and lower residual sum of squares (Table 4). Thus, statistical analyses of the continuous-time functional response model corroborated the results of the ANOVA of proportional mortality and the general functional response model.

Shrimp handling time per flounder (T_h) estimated from non-linear regression analysis was longer for predators foraging at 10°C as compared to 16°C (14.2 and 12.0 h, respectively) (Table 5). Shrimp instantaneous attack rates (A') increased at warmer temperatures, such that shrimp foraging at 10°C searched an average area of 0.037 ± 0.011 m^2 h^{-1}, and at 16°C the attack rate was 0.052 ± 0.011 m^2 h^{-1} (Table 5). Estimates of A' across 6 flounder densities (Type III functional response model only) indicated that shrimp attack rates decreased at an accelerated rate with decreasing prey density (Fig. 2). Thus, under more realistic flounder field densities (<10 flounder m^{-2}), differences in shrimp attack rates across temperatures are even more pronounced than initially stated (Table 5).

The proportion of shrimp attack encounters that resulted in the consumption of flounder was independent of water temperature and flounder density (discussed in following section). This proportion, defined as attack success (S_A), ranged between 0.09 and 0.22 (average = 0.16) during visual observations. Based on these empirical estimates, consumption rates were transformed to daily encounters between shrimp and flounder, assuming that the number of flounder eaten over the predation period (24 h) was 16% of the actual attack encounters. Subsequently, a non-linear least

Table 3. *Crangon septemspinosa* predation on *Pseudopleuronectes americanus*. Linear regression results of log-transformed general functional response models (Real 1977, 1979)

Feature	Temperature (°C)	
	10	16
Parameter estimates		
Intercept	−2.11	−1.05
Slope	1.71	0.93
Slope SE	0.16	0.13
Summary statistics		
Regression SS (df)	23.83 (1)	8.17 (1)
Residual SS (df)	7.21 (35)	6.90 (44)
F	116.62	52.11
p	<0.0001	<0.0001
R^2 (%)	76.8	54.2
Tests of hypotheses		
H_0: slope > 0	p < 0.0001	p < 0.0001
H_0: slope = 1	p < 0.0001	0.5892
H_0: slope < 2	0.0802	p < 0.0001

squares analysis was used to estimate T_h and A', and to fit daily encounters (N_e) to a Type III continuous-time model at 10°C and a Type II model at 16°C (Table 1). Because shrimp are nocturnal predators, the total time available for foraging (T) in the model was 10 h, representing the time in which shrimp were exposed to darkness. Regression estimates of shrimp handling time and instantaneous attack rates, derived from encounter rates, indicated that T_h was much lower, and A' was higher relative to parameters estimated from daily consumption rates (Table 5). Moreover, encounter-based estimates of instantaneous attack rates qualitatively corroborated previous results, whereby A' was lower at 10°C as compared to 16°C (Table 4). Conversely, shrimp handling time estimated from the encounter-based model was inconsistent with results from the consumption-based model, whereby T_h increased at higher temperatures (Table 5).

Behavioral observations

Shrimp random and total encounters (E_R and E_T) with flounder were not statistically different across temperature and flounder density (Table 6, Fig. 3a,b), and the interaction effects were not significant (Table 6). Shrimp attack encounters (E_A) differed significantly with temperature

but not with the flounder density main effect (Table 6, Fig. 3a,b). The temperature-density interaction effect was significant, whereby shrimp foraging on the low prey density attacked significantly more flounder at 16°C than at 10°C (Fig. 3a). Moreover, at low temperatures, shrimp attack encounters were significantly greater at the high flounder density than at the low density (Fig. 3a,b).

The number of flounder captured by shrimp (C) differed significantly with temperature, but not with flounder density main effect (Table 6, Fig. 3c,d). The interaction term was significant and was attributed to significantly more captures at 16°C than at 10°C, when shrimp were foraging at the low flounder density (Table 6, Fig. 3c). Moreover, when shrimp were exposed to 10°C, significantly more flounder were captured at high prey density than at the low density (Fig. 3c,d). The number of successful encounters (flounder consumed; E_S) was significantly greater at 16°C than at 10°C (Table 6, Fig. 3c,d). Shrimp successful encounters with flounder did not differ significantly across densities, and the interaction term was insignificant (Table 6, Fig. 3c,d).

Shrimp attack success (S_A), or the proportion of attacks resulting in the consumption of a flounder, did not

Table 4. *Crangon septemspinosa* predation on *Pseudopleuronectes americanus*. Summary statistics for non-linear continuous-time functional response models

Source	SS	MS	df	F	p	R^2 (%)
10°C						
Type II						82.5
Regression	23.81	11.90	2	82.65	<0.0001	
Residual	5.04	0.14	35			
Lack-of-fit	0.29	0.04	7	0.26	0.9654	
Pure error	4.76	0.16	30			
Total	28.85		37			
Type III						84.0
Regression	24.23	8.08	3	59.49	<0.0001	
Residual	4.62	0.14	34			
Lack-of-fit	0.22	0.03	7	0.21	0.9798	
Pure error	4.40	0.15	30			
Total	28.85		37			
16°C						
Type II						89.6
Regression	41.46	20.73	2	189.00	<0.0001	
Residual	4.83	0.11	44			
Lack-of-fit	0.06	0.01	7	0.07	0.9994	
Pure error	4.77	0.12	39			
Total	46.29		46			
Type III						89.0
Regression	41.22	13.74	3	116.55	<0.0001	
Residual	5.07	0.12	43			
Lack-of-fit	0.09	0.01	7	0.10	0.9980	
Pure error	4.98	0.13	39			
Total	46.29		46			

Table 5. *Crangon septemspinosa* predation on *Pseudopleuronectes americanus*. Estimated shrimp foraging parameters predicted from (consumption- and encounter-based) continuous-time functional response models and observed from behavioral inspection. Instantaneous attack rate (A') is the area a predator searches per unit time $(\text{m}^2\ \text{h}^{-1})$. At 10°C, predicted A' was calculated with Eq. (2) using b and c parameters generated from a Type III functional response model (Hassell 1978). Handling time (T_h) is the time (h) from the initial attack encounter between shrimp and flounder, through the capture and ingestion of prey, until searching by the predator resumed. Values are means (±1 SE)

Analysis	Temperature (°C)	Foraging parameters			
		A'	b	c	T_h
Predicted					
Consumption rate	10	0.04 ± 0.01	0.0012 ± 0.0005	0.0204 ± 0.0219	14.2 ± 0.92
	16	0.05 ± 0.01	–	–	12.0 ± 1.73
Encounter rate	10	0.31 ± 0.03	0.0680 ± 0.0745	0.7532 ± 0.8163	0.54 ± 0.43
	16	0.78 ± 0.16	–	–	0.80 ± 0.11
Observed	10	0.57 ± 0.14	–	–	0.57 ± 0.17
	16	1.00 ± 0.16	–	–	0.67 ± 0.13

differ significantly with temperature or flounder density (Table 6, Fig. 3e,f), and the interaction effect was insignificant (Table 6). Similarly, temperature did not significantly affect shrimp capture success (S_C) (Table 6, Fig. 3e,f). However, significantly more flounder were consumed per shrimp capture at the high prey density as compared to low density (Table 6, Fig. 3e,f).

Observed shrimp attack rates (A') differed significantly with temperature but not with the flounder density main effect (Table 6, Fig. 4a). The interaction term was significant (Table 6), and was attributed to significantly higher attack rates at 16°C than at 10°C, when shrimp were foraging at the low flounder density

Fig. 2. *Crangon septemspinosa* predation on *Pseudopleuronectes americanus*. Shrimp instantaneous attack rate (A'), i.e. area searched per unit time $(\text{m}^2\ 24\ \text{h}^{-1})$ across 6 flounder densities (no. fish m^{-2}) at 10°C. Predicted A' was calculated with Eq. (2) using b and c parameters generated from a Type III continuous-time functional response model (Hassell 1978)

(Fig. 4a). Moreover, when shrimp foraged at 10°C, attack rates were significantly greater at high prey density than at the low density (Fig. 4a). Thus, shrimp foraging at 16°C exhibited relatively constant attack rates across flounder density, whereas A' significantly decreased at the low flounder density when predators were exposed to cold temperatures (Fig. 4a). Observed shrimp attack rates, averaged across 2 levels of flounder density, were comparable to those values estimated by encounter-based functional response models, but were different from consumption-based models (Table 5).

The mean handling time (T_h) of an individual shrimp — initiated by attacking a flounder, followed by the capture and ingestion of the prey, and completed once searching by the predator resumed — did not differ significantly with temperature, and the temperature-density interaction effect was insignificant (Table 6, Fig. 4b). Predator handling time, however, differed significantly with flounder density, whereby T_h was significantly reduced at the high prey density (Table 6, Fig. 4b). Handling time predicted from consumption-based functional response models were substantially different from empirically derived values, whereby predicted T_h was approximately 18 to 25 times greater than estimates determined from visual observations (Table 5). Conversely, predicted T_h from encounter-based models was very similar to empirical estimates (Table 5). Thus, in this study, the encounter-based continuous-time functional response model (relative to the consumption-based model) gave the closest correspondence with empirically derived foraging parameters $(A'$ and $T_\text{h})$ (Table 5).

Daily shrimp activity levels (a) differed significantly with temperature and diel pattern, but not with flounder density (Table 7, Fig. 5). The number of shrimp movements was significantly greater at 16°C than at 10°C, and activity was significantly higher during dark periods as compared to light (Fig. 5).
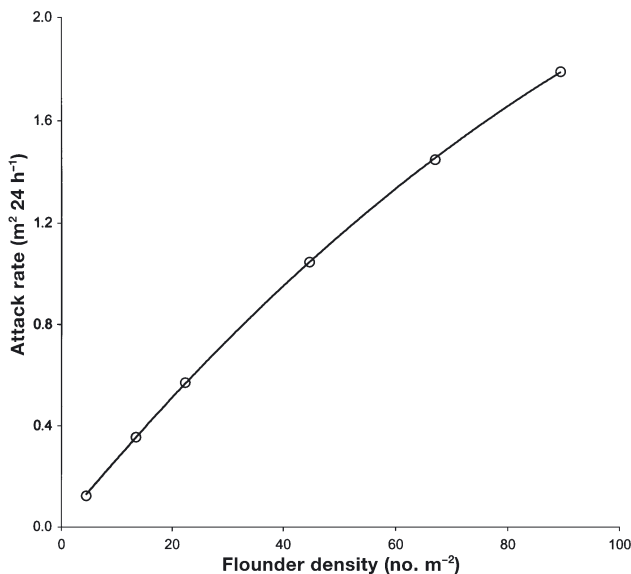
Table 6. *Crangon septemspinosa* predation on *Pseudopleuronectes americanus*. Summary statistics for ANOVA of the effects of flounder density (2 and 10 fish per tank) and temperature (10 and 16°C) on observed shrimp-foraging parameters. Natural log of $(x + 1)$ transformation was performed on data denoted by an asterisk (*)

Source	Random* encounter (E_R)	Attack* encounter (E_A)	Total* encounter (E_T)	Capture* (C)	Success encounter (E_S)	Attack success (S_A)	Capture success (S_C)	Attack* rate (A')	Handling* time (T_h)
Density									
SS	0.08	2.01	0.11	0.06	0.04	0.01	0.65	0.31	30.76
MS	0.08	2.01	0.11	0.06	0.04	0.01	0.65	0.31	30.76
df	1	1	1	1	1	1	1	1	1
F	0.09	2.55	0.12	0.51	1.50	0.15	4.06	1.95	9.18
p	0.7703	0.1156	0.7260	0.4791	0.2253	0.7008	<0.05	0.1671	<0.005
Temperature									
SS	0.91	5.03	1.89	0.58	0.26	0.17	0.25	0.76	0.89
MS	0.91	5.03	1.89	0.58	0.26	0.17	0.25	0.76	0.89
df	1	1	1	1	1	1	1	1	1
F	1.02	6.36	2.08	4.59	9.35	2.18	1.58	4.73	0.27
p	0.3161	<0.05	0.1546	<0.05	<0.005	0.1455	0.2153	<0.05	0.6074
Density × Temperature									
SS	2.51	4.43	3.51	0.77	0.05	0.01	0.11	0.86	1.88
MS	2.51	4.43	3.51	0.77	0.05	0.01	0.11	0.86	1.88
df	1	1	1	1	1	1	1	1	1
F	2.82	5.61	3.85	6.03	1.67	0.08	0.68	5.41	0.56
p	0.980	<0.05	0.0541	<0.05	0.2013	0.7717	0.4119	<0.05	0.4559
Error									
SS	55.18	48.98	56.46	7.90	1.75	4.73	7.82	9.90	422.32
MS	0.89	0.79	0.91	0.13	0.03	0.08	0.16	0.16	3.35
df	62	62	62	62	62	60	49	62	126

DISCUSSION

Functional responses and underlying foraging behavior

This investigation quantified the effect of temperature on the predator-prey dynamics between the sand shrimp *Crangon septemspinosa* and juvenile winter flounder. Shrimp foraging at 10°C demonstrated a Type III functional response, whereby the prey density threshold for shrimp feeding on juvenile flounder occurred at approximately 16 fish m^{-2}. This high value is beyond natural densities of post-settled flatfish in field populations. Plaice *Pleuronectes platessa*, for example, achieve a peak settling density of 12 fish m^{-2} on tidal flats in the western Wadden Sea (Van der Veer & Bergman 1987), whereas winter flounder settle at densities of 0.5 to 4 flounder m^{-2} in various northwest Atlantic estuaries (Sogard et al. 2001, Curran & Able 2002, DNC 2003). Thus, the density-dependent portion of the Type III functional response curve exhibited by shrimp is projected to include the range of natural pop-

ulation densities of post-settled winter flounder. Predation by shrimp may, therefore, have a stabilizing effect on local populations of winter flounder, dampening temporal and spatial variations in juvenile flounder abundance (Wennhage 2002). Density-dependent mortality has been observed in other shrimp-flatfish predator-prey interactions. Van der Veer & Bergman (1987) and Van der Veer et al. (1991) established the importance of the brown shrimp *C. crangon* as a significant source of density-dependent mortality for recently settled plaice and flounder *Platichthys flesus*.

Table 7. *Crangon septemspinosa* predation on *Pseudopleuronectes americanus*. Summary statistics for ANOVA of the effects of flounder density (2 and 10 fish per tank), temperature (10 and 16°C), and diel pattern (day and night) on shrimp activity levels. Natural log of $(x + 1)$ transformation was performed on the data

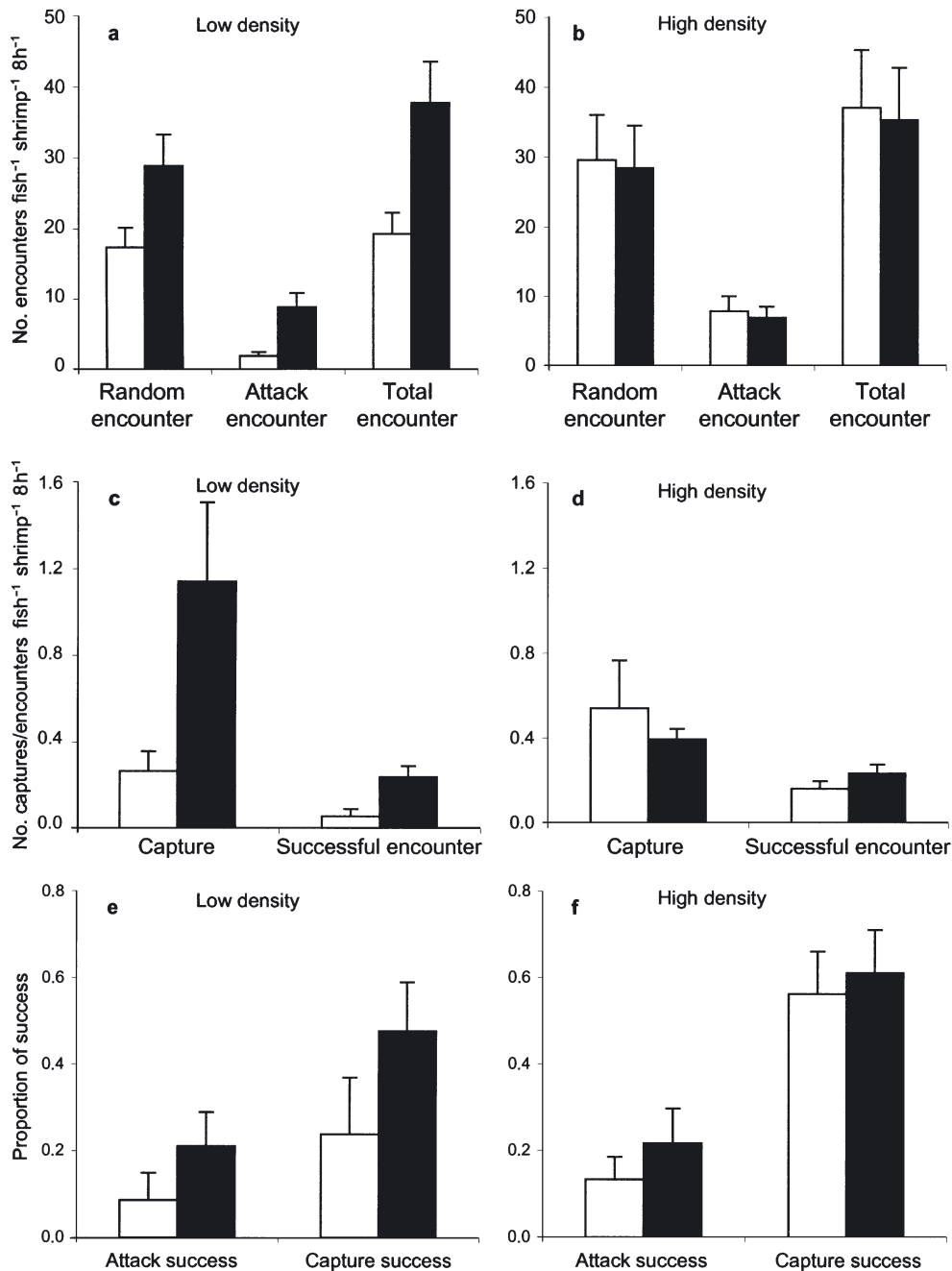| Source	SS	MS	df	F	p
Density	1.94	0.97	2	0.47	0.6262
Temperature	16.55	16.55	1	8.08	<0.01
Density × Temperature	1.53	0.77	2	0.37	0.6895
Diel pattern	43.26	43.26	1	21.10	<0.0001
Density × Diel pattern	3.59	1.79	2	0.88	0.4225
Temperature × Diel pattern	1.91	1.91	1	0.93	0.3384
Density × Temperature × Diel pattern	3.92	1.96	2	0.96	0.3906
Error	116.85	2.05	57		

Fig. 3. *Crangon septemspinosa* predation on *Pseudopleuronectes americanus*. Observed foraging behavior of shrimp as a function of temperature (10°C = white bars; 16°C = black bars) and flounder density (low density = 2 fish per tank; high density = 10 fish per tank). Values are means (±1 SE). See Table 5 for significant levels

The observed density-dependent mortality was caused by a Type III functional response by *C. crangon* (Wennhage 2002). Moreover, the functional response curve for shrimp was density-dependent in the range of 2 to 8 plaice m^{-2}, again indicating that crangonid shrimp have the capacity to regulate local flatfish populations (Wennhage 2002).

The underlying mechanism controlling the predator-prey dynamics between *Crangon septemspinosa* and winter flounder is the behavioral response of shrimp to changes in temperature and prey density. Experimental observations indicated that shrimp foraging at 10°C on low prey densities had significantly lower attack encounters (E_A), attack rates (A'), and captures (C) of
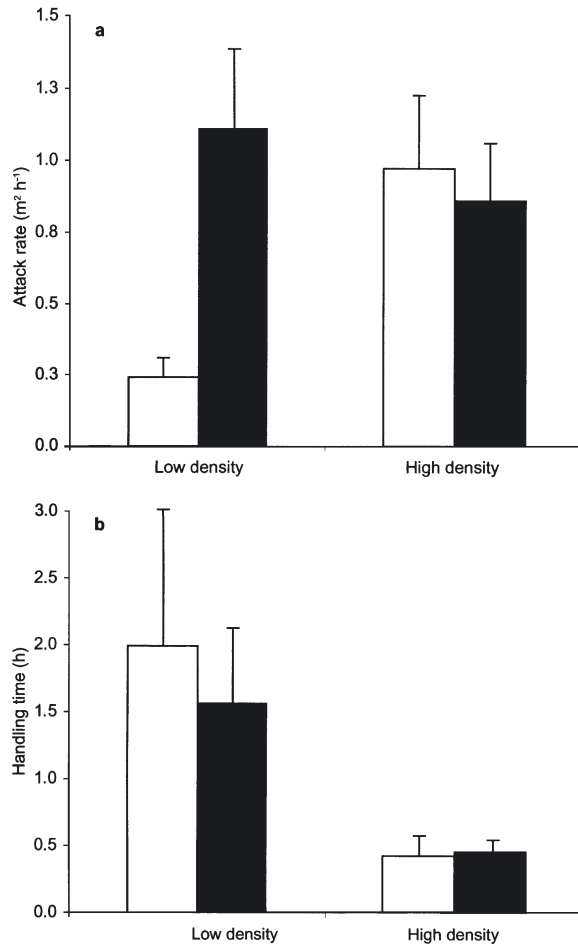
Fig. 4. *Crangon septemspinosa* predation on *Pseudopleuronectes americanus*. (a) Observed instantaneous attack rate, A', i.e. area searched per unit time ($m^2 h^{-1}$) of shrimp, and (b) handling time, T_h, i.e. time (h) from the initial attack encounter between shrimp and flounder, through the capture and ingestion of prey, until searching by the predator resumed. Foraging parameters are a function of temperature ($10°C$ = white bars; $16°C$ = black bars) and flounder density (low density = 2 fish per tank; high density = 10 fish per tank). Values are means (±1 SE). See Table 5 for significant levels

flounder. Shrimp activity levels (*a*) were also significantly lower at 10°C as compared to 16°C, irrespective of prey density. Consequently, shrimp foraging under cold-water conditions and low prey densities may lack reinforced learned searching behavior for juvenile flounder, thus causing the significant reduction in successful encounters (S_A) at 10°C. This regulatory mechanism is unlikely, however. During nocturnal foraging, shrimp rarely search actively for their prey, and encounters are mainly the consequence of random movements by both shrimp and flounder (Gibson et al. 1995). Encounters, and the subsequent capturing and ingestion of prey, are therefore strongly dependent upon the relative activity levels of shrimp and flounder.

In this investigation, the probability of a shrimp successfully consuming a flounder following an attack encounter or capture (attack and capture success; S_A and S_C) was independent of the number of encounters experienced throughout the duration of a trial, indicating that predatory learning is of minimal importance in this predator-prey interaction.

Water temperature is a critical determinant of metabolic rate, and thus influences an individual's foraging activity according to its current caloric and bioener-
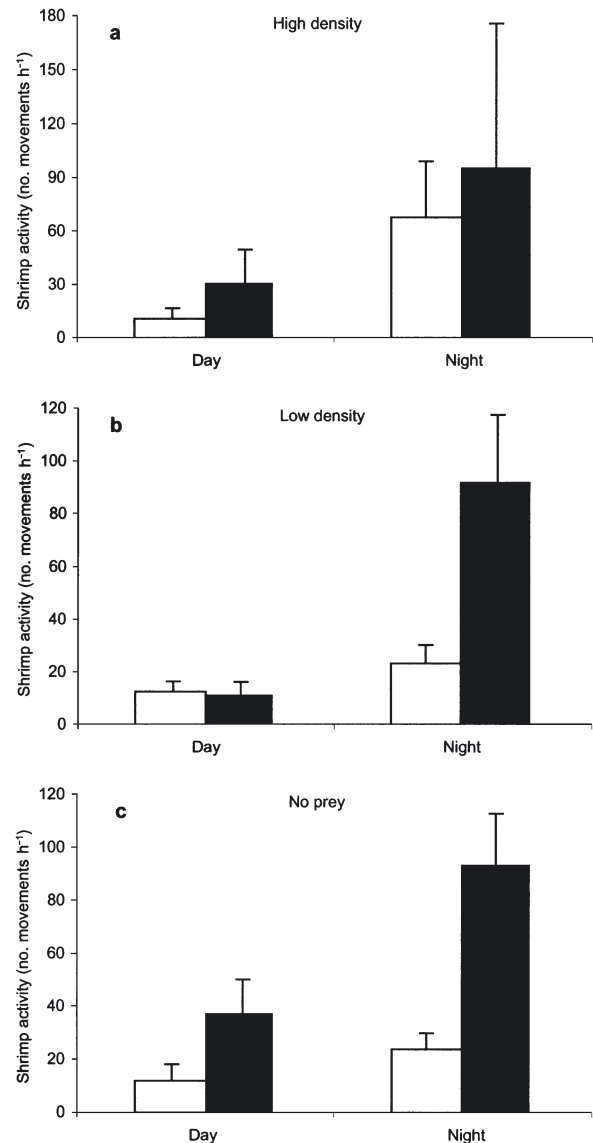

Fig. 5. *Crangon septemspinosa* predation on *Pseudopleuronectes americanus*. Observed activity levels, *a* (no. movements h^{-1}) of shrimp as a function of temperature ($10°C$ = white bars; $16°C$ = black bars), flounder density (a: high density = 10 fish per tank; b: low density = 2 fish per tank; c: no prey = 0 fish per tank), and diel pattern (day and night). Values are means (±1 SE). See Table 6 for significant levels

getic demands (Taylor & Peck in press). Shrimp in the presence of low flounder density and cold temperatures had decreased activity levels, probably to minimize the energy costs associated with foraging when reward rates were low. Conversely, high flounder densities elicited a feeding response in shrimp at 10°C, as indicated by greater activity levels and significant increases in attack encounters and captures of flounder. The change in foraging behavior at high prey density was attributed to shrimp being exposed to increased prey-induced mechanical and chemical stimuli, alerting the presence of juvenile winter flounder and a high reward situation. For the feeding behavior of shrimp, both tactile and chemical stimuli play a key role in mediating the various stages of feeding from initial excitation to sustained feeding (Pittet et al. 1996).

When water temperature was increased to 16°C, shrimp switched their foraging behavior to a destabilizing, Type II functional response, whereby juvenile flounder mortality became inversely density-dependent over all prey densities examined. Consequently, shrimp predation at 16°C was no longer stabilizing to the predator-prey dynamics, and precluded the low-density refuge afforded to flounder at 10°C. The predominant factor causing increased proportional mortality at low flounder numbers was shrimp maintaining high levels of activity (a) at reduced flounder densities and an overall increase in instantaneous attack rates (A') at warmer temperatures. The 2-fold increase in shrimp attack rates with increasing temperature (10 to 16°C) corresponds well with other reports of invertebrate foraging activity (Eggleston 1990b).

High levels of foraging activity at 16°C, even at low prey densities, may be the result of shrimp compensating for increased metabolic rates (Taylor & Peck in press). The energy devoted to metabolic processes for an individual is derived from the ingestion of available prey. Thus, the temperature-induced acceleration of metabolic rates increases foraging activity, as predators are physiologically required to increase consumption rates to meet greater bioenergetic demands (Bailey 1989). Warmer temperatures are also likely to increase the activity of prey species. Juvenile flounder, for example, increased their activity in response to elevated temperature. Consequently, increased flounder movement may cause more encounters with shrimp, which leads to even greater activity levels of the predator, and subsequently increases encounters further. This was evident by significantly more shrimp-attack encounters (E_A) and activity levels (a) observed at 16°C compared to 10°C at low flounder densities.

Shrimp handling time (T_h), estimated from continuous-time functional response models and visual observations, did not exhibit any consistent or significant

relationship with water temperature, and is therefore considered an unlikely mechanism underlying the variable functional responses observed at 10 and 16°C. Empirically derived estimates of handling time, however, suggest that T_h depends upon prey density. High prey density typically results in more prey consumed by an individual predator, which in turn leads to increased handling time as a predator approaches satiation (Hassell 1978). In contrast, the current investigation suggests that increased juvenile flounder numbers result in decreased shrimp handling time. The discrepancy between predicted effects of prey density on predator handling time and those estimated in this study are attributed to shrimp feeding at a rate below satiation during the observation period. The satiation level for an individual shrimp, determined graphically from the Type II and Type III functional response curves, occurred after approximately 3 flounder were consumed. During visual observations, the average number of flounder consumed per shrimp at the high prey density (10 flounder per tank) was 2.3 ± 0.4 at 16°C and 1.6 ± 0.3 at 10°C. Although shrimp were approaching satiation, the handling time at high flounder densities did not increase; instead T_h was reduced. The time required for shrimp to attack, capture and consume a flounder is probably comparable across temperature and prey density. However, the reduced handling time of shrimp at high flounder density may be caused by predators initiating search behavior sooner because of the increased abundance of prey. As previously discussed, increased flounder densities elicit a feeding response in shrimp. High flounder densities contribute to increased shrimp foraging activity, whereby shrimp devote less time to resting states after a predation event, consequently decreasing handling time.

Switch-feeding behavior to alternative prey is a possible explanation for the sigmoidal, Type III functional response observed for crangonid shrimp feeding on flatfish (Wennhage 2002). In the analysis of *Crangon crangon* predation on newly settled plaice, Wennhage (2002) defined a Type III functional response for shrimp feeding on plaice, despite the presence of the alternative amphipod prey *Corophium volutator*. Wennhage (2002) attributed the shrimp's Type III response to switch-feeding behavior and a change in feeding strategy as plaice density decreased below a threshold level. Because of the high abundance of alternative prey species in the field, and the high prevalence of these prey items in the gut contents of shrimp, reduced foraging activity in unrewarding circumstances was dismissed as a plausible mechanism underlying *C. crangon* density-dependent feeding behavior (Wennhage 2002). Similar mechanisms could explain the predator-prey dynamics between *C.*

septemspinosa and juvenile winter flounder under field conditions. In this study, however, feeding trials did not include alternative prey, thus precluding possible switch-feeding behavior for shrimp. Further research is needed before one can explain the behavioral mechanism underlying the foraging responses of sand shrimp in the field, including: (1) quantifying the spatial and temporal abundance patterns of the predominant prey species of shrimp in the field; and (2) defining the feeding strategy of shrimp relative to its targeted prey.

The numerical response, the relationship between predator density and the abundance of their prey, is recognized as the second key component underlying predator-prey dynamics (the other component being the functional response) (Solomon 1949, Holling 1959). An explicit numerical response, or increase in predator numbers at high prey densities, resulting from *Crangon septemspinosa* reproduction and population growth, is an unlikely mechanism regulating juvenile winter flounder populations. The short time-period during which post-settled flounder are vulnerable to *C. septemspinosa* predation restricts newly hatched shrimp from preying on the same flounder year-class (Van der Veer & Bergman 1987, Witting & Able 1995), and it is unlikely that the extent to which shrimp population growth is dynamically linked to juvenile flounder is sufficient to impact subsequent flatfish settlement seasons.

A plausible mechanism resulting in a numerical response is that of predators congregating in areas of high prey density (i.e. aggregative response), and leaving those prey patches when the rate of prey capture falls below a threshold necessary to sustain constant foraging efforts (Mansour & Lipcius 1991). Aggregative responses have also been observed to promote agonistic interactions and mutual interference among crustacean predators, which adversely affected either their searching efficiency or feeding rates (Mansour & Lipcius 1991, Taylor & Eggleston 2000). The combination of predator aggregation and mutual interference may stabilize predator-prey dynamics by providing partial refuges for prey at low densities, and thus promote a feeding response curve that is sigmoidal (Hassell 1978, Mansour & Lipcius 1991). *Crangon crangon* was suggested to exhibit a numerical response to fluctuations in juvenile plaice density, which would partially explain the observed density-dependent mortality of post-settled flatfish (Van der Veer & Bergman 1987). Moreover, *C. crangon* was observed to attack conspecifics feeding on juvenile plaice in attempts to steal the prey (Gibson et al. 1995). In this study, mutual interference among *C. septemspinosa* feeding on juvenile winter flounder was minimal, and there was no evidence of physical

injury to shrimp following agonistic interactions with conspecifics (Mansour & Lipcius 1991, Taylor & Eggleston 2000). Moreover, shrimp densities chosen for feeding and filming trials (13.4 and 15.9 shrimp m^{-2}, respectively) represent levels at which maximum predation rates occur on post-settled flounder (Witting & Able 1995). The effect of mutual interference on the foraging behavior of shrimp was negligible, and therefore the primary mechanism defining the predator-prey dynamics between *C. septemspinosa* and juvenile winter flounder is the functional response.

Temperature effects on flounder population stability

The key finding in relation to predator-prey dynamics is that the type of functional response exhibited by *Crangon septemspinosa* can vary significantly as a consequence of temperature. Post-settled winter flounder benefit from a low-density refuge at 10°C due to the stabilizing and density-dependent, Type III functional response of predatory sand shrimp. Increasing water temperature to 16°C, however, destabilizes the predator-prey interaction as shrimp switch their feeding behavior to an inversely density-dependent, Type II response. Consequently, warmer temperatures preclude the low-density refuge for juvenile winter flounder, and thus shrimp have the capacity to drive prey populations to local extinction. It is not certain at what point between 10 and 16°C shrimp alter their feeding behavior, nor how abruptly this change occurs. In an analysis of the foraging behavior of *C. crangon*, Wennhage (2002) determined that shrimp feeding on juvenile plaice exhibited a Type III functional response within a temperature range of 12.6 to 15.6°C. This suggests that *C. septemspinosa* shifts its functional response abruptly from a Type III to a Type II response at 16°C. Further studies are needed, however, to quantify the foraging behavior and feeding strategy of sand shrimp within this critical temperature range.

The population abundance of winter flounder has declined precipitously in parts of its geographic range since 1979, and has yet to rebound from the last 24 yr of decline (Jeffries & Terceiro 1985, NEFSC 2003). The demise of winter flounder has been paralleled by a significant warming trend in many northwest Atlantic estuaries that are used by juvenile flounder as important nursery habitats (Keller & Klein-MacPhee 2000). This increase in water temperature is hypothesized to be a critical factor determining the survival of juvenile winter flounder in northern-temperate estuaries. The negative effect of increased temperature is imposed, not directly as a physiological mortality factor, but rather by altering predation pressure on the early life stages of winter flounder (Jeffries & Terceiro 1985). For

example, elevated temperatures can intensify predator-induced mortality of juvenile flounder by increasing the metabolism, and thus consumption rate, of benthic predators. In a study examining the mechanisms altering recruitment success of the North Sea plaice, Van der Veer et al. (1990) determined that juvenile plaice survival was highly dependent on water temperature. Those fish inhabiting estuaries with increased spring water temperature suffered greater predator-induced mortality from *Crangon crangon* than those inhabiting estuaries with lower spring water temperature. A similar phenomenon could occur in northwest Atlantic estuaries, in which elevated temperatures lead to intensified *C. septemspinosa* predation on juvenile winter flounder. Moreover, results from this investigation suggest that increasing temperature can drastically alter shrimp foraging behavior, leading to a destabilization of the predator-prey interaction with juvenile flounder.

Winter flounder are vulnerable to shrimp predation at initial settlement, when flounder are approximately 8 mm TL. This susceptibility to predation then gradually decreases after settlement until a complete refuge from shrimp predation is attained once flounder achieve a body size of 24 mm TL (Witting & Able 1995). The growth period through this size range (8 to 24 mm TL) represents the 'mortality window' for winter flounder — a period lasting several months and characterized by high predator-induced mortality. Temperatures throughout the mortality window have important consequences on winter flounder survival, including effects on flounder growth and shrimp predation intensity and foraging behavior.

Preferential survival occurs for faster-growing juvenile flounder because their exposure to the mortality window is limited. Reported growth estimates of juvenile winter flounder in northwest Atlantic estuaries range between 0.22 and 0.27 mm d^{-1} (Buckley & Caldarone 1990, Meise et al. 1999), and thus, newly settled flounder require 59 to 72 d to reach a size refuge from shrimp predation. Winter flounder settle at peak densities in early spring (April) when water temperatures are approximately 5°C. Growth through the mortality window then progresses for the next 2 to 2.5 mo, after which the mortality window concludes in early to mid-June, when temperatures are approximately 15 to 16°C. Thus, under typical temperature conditions, flounder progress through a mortality window in which they are exposed to compensatory density-dependent (Type III functional response) predation from shrimp. Shrimp may therefore have a stabilizing effect on flatfish abundances, allowing for flounder population persistence and ultimately supporting a strong year-class and successful recruitment into the adult population.

Elevated temperatures caused by anomalous warm years or anthropogenic impacts on global climate can have detrimental effects on winter flounder population stability. Post-settled winter flounder achieve maximum growth rates at approximately 14°C (Rose et al. 1996). At temperatures beyond the maximal growth for juvenile flounder, a disproportionate amount of energy is devoted to increased metabolism, thereby reducing energy for somatic growth (Rose et al. 1996). The advent of increased temperatures above optimal ranges, therefore, potentially reduces flounder growth, prolonging the mortality window and increasing predator-induced mortality. Moreover, the premature increase in seasonal temperature to 16°C while flounder are still vulnerable to shrimp predation (flounder < 24 mm TL) destabilizes the predator-prey interaction once shrimp switch their foraging behavior to a Type II functional response. Consequently, shrimp would have the ability to drive juvenile flounder populations to local extinction, and therefore contribute to a weak flounder year-class, and overall recruitment failure.

Water temperature is a key factor that alters the form of functional responses underlying predator-prey dynamics. Results from this study suggest that increases in water temperature exacerbate the predator-induced mortality of juvenile flounder and cause the destabilization of the predator-prey interaction with the sand shrimp *Crangon septemspinosa*. Thus, the recent warming trend experienced in northwest Atlantic estuaries, and its impact on trophic dynamics, may explain the failure of the winter flounder stocks to recover in these areas.

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