

AN ABSTRACT OF THE THESIS OF

Cara E. Fritz for the degree of Master of Science in Oceanography presented on April 2, 2002.

Title: A Seasonal Study of Sediment Reworking by *Neotrypaea californiensis* in Yaquina Bay, Oregon.

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Abstract approved \_\_\_\_\_

Robert A. Wheatcroft

A year-long field study was undertaken to investigate the influence of a number of physical and biological factors, specifically temperature, organic carbon content, and shrimp population dynamics on sediment reworking rates by the ghost shrimp *Neotrypaea californiensis*. Because of its role as a structuring agent in estuaries along the West Coast, it is important to understand the factors that impact shrimp reworking rates. At a site in the intertidal of Yaquina Bay, Oregon, measurements of sediment reworking (via direct entrapment of sediment ejected from burrows) were taken at monthly intervals over the course of a 15-month period. Abiotic (temperature, organic carbon content) and biotic parameters (shrimp size, density) were measured concurrently.

Rates of reworking normalized to shrimp biomass/m<sup>2</sup> varied over the year, with lows in the winter months and a peak in August. This pattern corresponds closely to temperature fluctuations. Although a deep subsurface deposit feeder, the close correspondence between reworking activity and temperature indicates that *Neotrypaea* is in close contact with conditions at the sediment surface. Taking into consideration the decrease in shrimp abundance over the year, the amount of sediment reworked over a given area ranged from 2.7 to 41.0 g dry sediment/hr/m<sup>2</sup>. The peak in overall reworking for this site was in early spring, which has implications for recruitment of benthic organisms. Observations on food

availability at feeding depths and sediment turnover rates, from direct entrapment and a heavy mineral tracer experiment, suggest that the ghost shrimp may obtain nutritional material using methods aside from ingesting particles that are subducted to depth.

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A Seasonal Study of Sediment Reworking by  
*Neotrypaea californiensis* in Yaquina Bay, Oregon

by  
Cara E. Fritz

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Dean of the Graduate School

I understand that my thesis will become part of the permanent collection of Oregon State University libraries. My signature below authorizes release of my thesis to any reader upon request.

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Cara E. Fritz, Author

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A SEASONAL STUDY OF SEDIMENT REWORKING BY  
*NEOTRYPAEA CALIFORNIENSIS* IN YAQUINA BAY, OREGON

INTRODUCTION

The ghost shrimp *Neotrypaea californiensis* (formerly *Callianassa californiensis* Dana; Manning and Felder, 1991) is one of the dominant macrofaunal species in intertidal and shallow subtidal habitats along the West Coast. As a burrowing, subsurface deposit feeder, the ghost shrimp modifies its physical habitat through extensive reworking of the sediment. This alteration and disruption of the environment in turn may affect the community composition of the surrounding infauna (e.g., Ronan, 1975; Posey, 1986a). Because of its role as an ecosystem engineer in the estuaries, it is important to understand the factors that influence the rates of sediment reworking by *Neotrypaea californiensis* (hereafter *Neotrypaea*). This year-long field study was undertaken to investigate the role of temperature, organic carbon content, and shrimp population dynamics on sediment reworking rates.

EFFECTS OF NEOTRYPAEA

The effects of *Neotrypaea* on the surrounding environment are well documented. In the process of burrowing and feeding, it deposits large amounts of sediment at its burrow openings, forming conspicuous mounds 5-10 cm high. The deposit consists of particles excavated at depth (50 cm or more) during burrow maintenance, sediment grains that have been processed during feeding (i.e., pseudofeces), and fecal pellets. The formation of surface mounds from subsurface sediment combined with high abundances (e.g., up to 500 shrimp/m<sup>2</sup>) results in

rapid overturning of the sediment (MacGinitie, 1934; Bird, 1982; Swinbanks and Luternauer, 1987). Bird (1982) found that several sediment characteristics were modified by *Neotrypaea*, including a decrease in organic carbon content, an increase in mean grain size, and more sorting (smaller range of particle size) in areas inhabited by *Neotrypaea*. Other impacts of thalassinidean shrimp bioturbation include transfer of nutrients to depth, increased bacterial abundances (Branch and Pringle, 1987), deeper oxic-anoxic boundary (Zeibis et al., 1996), higher water content of the sediment (Colin et al., 1986; Miller, 1984), and alterations of sediment transport through particle sorting and mound building (Suchanek, 1983).

Along with these physical and geochemical changes come alterations to the species composition of the infaunal community. In general, there is lower species diversity in areas of high density of *Neotrypaea* (Dumbauld, 1994). Bird (1982) observed that the abundances of several infaunal species, namely tube-dwelling polychaetes and tanaids, decreased as *Neotrypaea* densities increased. Ronan (1975) found evidence that *Neotrypaea* influences the abundance of phoronids, which were common in the Bodega Bay estuary only in areas that lacked *Neotrypaea*. In field experiments in which he transplanted phoronids to high-density *Neotrypaea* areas, Ronan observed large numbers of broken and disturbed tubes, suggesting that the mobile *Neotrypaea* disrupted the sessile phoronids. Posey (1986a) showed strong negative correlations between shrimp densities and the numbers of several infaunal organisms, including tube-dwelling, sedentary spionid polychaetes and tube-building amphipods. Like Ronan, Posey suggested that this was due to disruption of sessile organisms by the extensive activity of *Neotrypaea*. In field manipulations it has been observed that the removal of the ghost shrimp results in higher recruitment of the bivalve *Sanguinolaria nuttallii* (Peterson, 1977).

*Neotrypaea* has been the subject of much applied research because it is viewed as a pest by commercial oyster growers (Feldman et al., 2000). Extensive reworking activities by the shrimp may bury oyster spat and cause adult oysters to sink into the unconsolidated sediment, as well as clog the feeding structures of the suspension-feeding oysters (Dumbauld, 1994; DeWitt et al., 1997). Removal of the shrimp has been shown to increase the growth and survival of the Pacific oyster *Crassostrea gigas*. Since 1963, shrimp populations in estuaries of Washington State have been controlled by the application of the pesticide carbaryl to the sediments (Dumbauld, 1994). The use of carbaryl in Oregon estuaries was banned in 1984 due to concerns about toxicity to non-target species. By limiting the numbers of shrimp, Washington oyster growers obtain more abundant and healthier oysters. Thus, the rates of bioturbation by *Neotrypaea* have important management implications as well.

#### SEDIMENT REWORKING BY THALASSINIDEANS

Because of the conspicuous impact that thalassinidean shrimp have on the benthic environment, the rates of sediment expulsion have been studied in a number of species. Measured reworking rates can be quite high (Table 1). However, the various methods used to measure reworking make comparison between studies difficult (Rowden and Jones, 1993).

Table 1: Measured rates of sediment reworking by thalassinidean shrimp and several other conveyor-belt species from the literature.

Species	Location	g dry sed ind <sup>-1</sup> day <sup>-1</sup>	ml wet sed ind <sup>-1</sup> day <sup>-1</sup>	g dry sed m <sup>-2</sup> day <sup>-1</sup>	ml wet sed m <sup>-2</sup> day <sup>-1</sup>	Source
<i>Neotrypaea californiensis</i>	Yaquina Bay, OR	2.64		32.4-492.0		present study
<i>Neotrypaea californiensis</i>	Elkhorn Slough, CA		20-50			MacGinitie, 1934
<i>Neotrypaea californiensis</i>	Fraser Delta, B.C.	24	18			Swinbanks & Luternau.,1987
<i>Callianassa filholi</i>	Otago Harbor, New Zealand			263		Berkenbusch & Rowden,1999
<i>Callianassa</i> sp.	Discovery Bay, Jamaica				8600-10000	Aller and Dodge, 1974
<i>Callianassa</i> sp.	Discovery Bay, Jamaica				143-286	Aller and Dodge, 1974
<i>Callianassa</i> sp.	Great Pond Bay, St. Croix			3395		Roberts et al., 1981
<i>Callianassa</i> sp.	Great Pond Bay, St. Croix			819		Roberts et al., 1981
<i>Callianassa</i> sp.	Tague Bay, St. Croix			4		Suchanek, 1983
<i>Callianassa rathbunae</i>	Tague Bay, St. Croix			2590		Suchanek, 1983
<i>Callianassa</i> sp.	Enewetak Atoll				800	Suchanek and Colin, 1986
<i>Callianassa</i> sp.	Enewetak Atoll				56.0-240.1	Suchanek et al., 1986
<i>Callianassa kraussi</i>	South Africa				12140	Branch and Pringle, 1987
<i>Callianassa subterranea</i>	lab, North Sea			30.1		Rowden et al., 1998
<i>Callianassa subterranea</i>	Scottish sea lochs	1.53				Nickell et al., 1993
<i>Callianassa subterranea</i>	lab, North Sea			9.6		Witbaard & Duineveld, 1989
<i>Callianassa truncata</i>	Giglio, Italy				2000-3000	Zeibis et al., 1996
<i>Callianassa stebbingi</i>	Val Saline, Yugoslavia		25			Ott et al., 1976
<i>Callichirus armatus</i>	Tahiti lagoon	237				DeVaugelas et al., 1986
<i>Callichirus armatus</i>	Mataiva lagoon	71				DeVaugelas et al., 1986
<i>Scoloplos</i> sp.	lab, Lowes Cove, ME	0.064-0.112				Rice et al., 1986
<i>Clymenella torquata</i>	lab, Barnstable Harbor, MA		0.75			Rhoads and Stanley, 1965
<i>AxiotHELLa rubrocincta</i>	Tomales Bay, CA	5				Kudenov, 1982
<i>Arenicola marina</i>	Dutch Wadden Sea		11.0-12.8			Cadée, 1976

While these rates are impressive and demonstrate the ability of thalassinideans to impact their surrounding environment, most previous studies are limited to determining the rate of reworking. Few have looked at the factors affecting this sediment turnover, particularly how rates may change over the year. A study by Berkenbusch and Rowden (1999) on a New Zealand species, *C. filholi*, documented the importance of incorporating seasonal variations into estimates of reworking rates. Physical and biological variables such as shrimp size, bottom water temperature, and location on the tidal flat were found to influence sediment reworking in this species.

Sediment reworking by *Neotrypaea* is the result of burrowing and feeding activity. Therefore, a number of factors potentially could impact rates of reworking. For one, activity of marine invertebrates is typically correlated with temperature; consequently, sediment temperature may impact the rate of reworking in ghost shrimp. However, because *Neotrypaea* lives deep within the sediment, temperature fluctuations that occur at the surface may be reduced and consequently have little impact on shrimp activity over the course of the year.

The amount of food (e.g., organic carbon, sediment protein, chlorophyll *a*) available to ghost shrimp could also influence feeding rate and hence the reworking rate. The question of feeding rate of deposit-feeders has long been controversial. In their review, Lopez and Levinton (1987) discuss two current ideas- "optimal ingestion rate" and "compensatory feeding." Based on Taghon (1981), the former states that as food quality increases, feeding rate should also increase, as the reward per ingestion is higher. The latter theory, that ingestion rate decreases with increasing food quality, is also supported in the literature. For example, Cammen (1980) compiled a number of data sets and found that animals maintain a constant intake so that as quality increases, ingestion rate decreases. Reworking rate could therefore be inversely related to food availability, as sediment of low food quality would require the shrimp to process more of it.

Biological parameters such as shrimp size and abundance could also impact reworking rate. Specifically, high densities of shrimp have the potential to increase the rate of subduction of surface-derived food to depth, which would provide subsurface deposit feeders with higher quality organic material. Therefore, individual reworking rate per unit food would be lower within a dense population. A situation where it is advantageous to live at high densities would contrast to the more intuitive case of surface deposit feeders for which greater population densities tend to result in increased competition for food (Rice and Rhoads, 1989).

Alternatively, an increase in individual reworking rate with higher population densities is plausible. *Neotrypaea* burrows are impermanent structures and require upkeep (see SPECIES DESCRIPTION below). High population densities could result in more disruption and collapse of burrows. This disruption would require more burrow maintenance, so individual reworking rates would increase. Thus the influence of shrimp population densities on sediment reworking rates is uncertain.

Shrimp size may also influence the individual reworking rate. Because larger shrimp will likely have larger burrows and process more sediment for food, it would be expected that reworking rates would be higher for larger individuals. In a study that looked explicitly at shrimp size and rate of reworking, Berkenbusch and Rowden (1999) found a significant positive correspondence between the amount of sediment expelled and size of the shrimp.

## OBJECTIVES

This study was undertaken to investigate the influence and relative importance of temperature, food availability, and population characteristics (e.g., size and abundance) on the sediment reworking rates of *Neotrypaea* over the course of a

year. Understanding what drives ghost shrimp activity is important because changes in rates of sediment reworking will have major implications for the benthic environment of the estuary, including the physical and geochemical conditions of the tidal flat and its infaunal community composition.

## BACKGROUND

### YAQUINA ESTUARY

This research was conducted on Idaho Flat in Yaquina Bay, Oregon, located on the central Oregon coast (44° 37'N, 124° 3'W) (see Figure 1). The Yaquina River, which empties into the Bay, drains approximately 622 km<sup>2</sup> of the Coastal Range. The area of the Bay is 1,304 hectares and tidal influence extends 41.8 km inland from the mouth of the Bay (NOAA, 1988). Air temperatures along the Oregon coast are mild, averaging 10.2°C and ranging from 6.6°C (December average) to 14.2°C (August average) (Oregon Climate Service, 2002).

Dry summers and rainy winters characterize the region, with most of the precipitation occurring in November through January (monthly average over 250 mm). A comparison of the average monthly precipitation for the years 1961-1990 shows the marked variation in precipitation over the year. For example, the driest month, July, averages only 25 mm of rain, while in December the precipitation averages 299 mm (Oregon Climate Service, 2002). Maximum discharge of the Yaquina River is in December and January and consequently salinities are lowest during this period. Salinity ranges from 10 to 34‰, with the lowest salinities occurring only during times of heavy rain in winter months at low tide. For much of the year the Bay is a well-mixed estuary, with little salinity difference between surface and bottom waters (Kulm, 1965). Typical for the Pacific Northwest, tides in the area are of a mixed semi-diurnal type with a maximum tidal range of approximately 3.6 m during spring tides.

The wind regime can be separated into a winter condition and a summer condition, while the spring and fall are transitional times. Summer winds are typically strong from the N to NW, commonly reaching 25 knots at the late

afternoon peak of a daily cycle. In winter the average winds are lower velocity and S to SW, but this is the time when there are occasionally very strong winds (50+ knots is not unusual). The summer northerly breeze sets up upwelling conditions along the Oregon coast, resulting in cooler summer waters along the coast. This keeps the estuary waters at lower temperatures during the summer months than would be expected from insolation. Water temperature in the Bay is approximately 12°C throughout the year, but varies dramatically (e.g., from 6°C to 20°C) in the shallower areas (Collins, 1987; Davis, 1982).

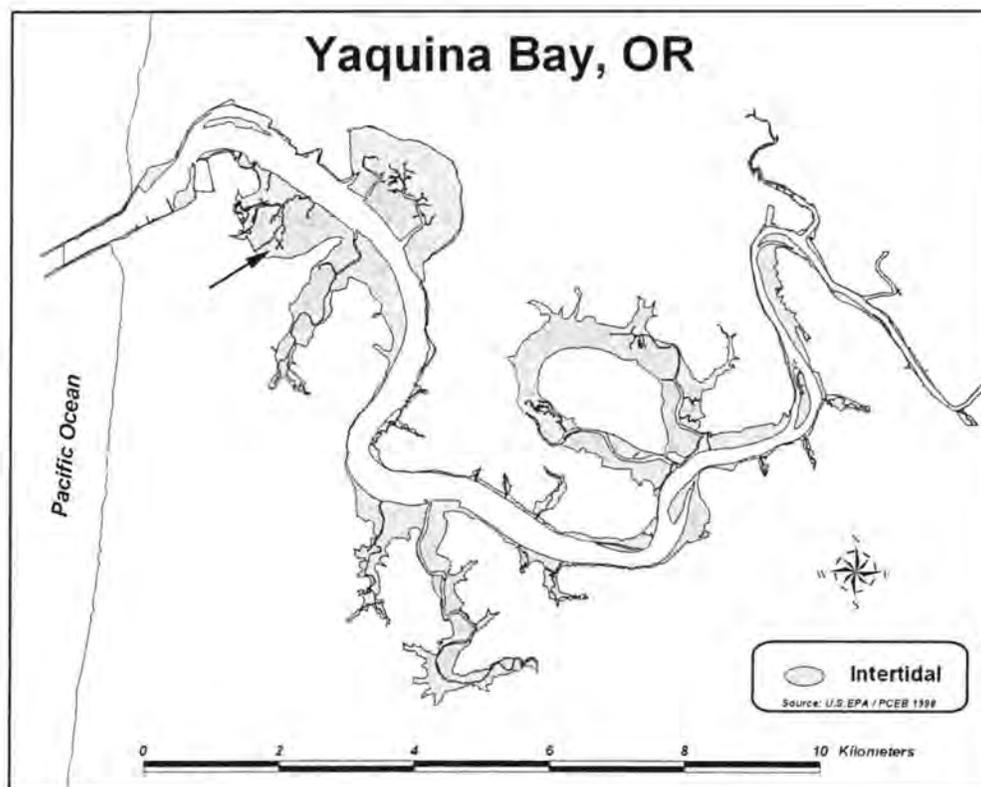


Figure 1: Location of study site in Yaquina Bay. X marks location on Idaho Flat.

Tidal flats cover roughly 60% of Yaquina Bay (Percy et al., 1974). There is extensive seasonal macroalgae (primarily *Ulva* spp. and *Enteromorpha* spp.) in the intertidal areas. Growth begins in April and may cover 50% or more of an area during its peak in the summer months. Die-off occurs in late summer, and by December little macroalgae is found on the sediment surface. Other benthic flora includes diatoms (see McIntire and Overton, 1971; Amspoker, 1977) and regions of seagrass (*Zostera marina* and *Z. japonica*). Crandell (1967) provides a thorough look at a dominant meiofaunal group, harpacticoid copepods. The tube-building tanaid crustacean, *Leptochelia dubia*, is extremely abundant within the sediments of Yaquina Bay, reaching densities of  $3 \times 10^5 \text{ m}^{-2}$  (Krasnow, 1992). Other common macrofauna in this estuary include spionid polychaetes (Savidge, 1987), the suspension-feeding thalassinidean shrimp *Upogebia pugettensis* (see Griffen, 2002), and the subject of this study, the ghost shrimp *Neotrypaea*.

## SPECIES DESCRIPTION

Considering the cryptic lifestyle of the ghost shrimp, the species is remarkably well studied. *Neotrypaea* is a deep-burrowing deposit feeder, common in estuaries of the West Coast from Alaska to Baja California (MacGinitie, 1934). *Neotrypaea* beds are typically found in the mid- and high intertidal region. The shrimp are found at densities as high as 500 individuals  $\text{m}^{-2}$ , but such densities may be very localized, dropping off by a factor of 10 or more within 1-2 m (Posey, 1986). Although it has often been suggested that ghost shrimp prefer sandy sediments to muds (e.g. MacGinitie, 1934; Bird, 1982), no clear relationship between shrimp density and median grain size has been found (Bird, 1982; Swinbanks and Luternauer, 1987). Ghost shrimp are capable of surviving in a wide range of salinities, with significant mortality occurring only below 10‰

(Thompson and Pritchard, 1969). As an intertidal species, *Neotrypaea* is subject to long periods of exposure and appears to be quite tolerant to pore-water anoxia. Swinbanks and Luternauer (1987) observed *Neotrypaea* extending to the landward edge of a salt marsh, where the tidal flat may be exposed for up to 5 continuous days. McCrow (1972) found that *Neotrypaea* tended to be deeper in their burrows during low tide, a likely behavioral adaptation to avoid desiccation.

Burrows of the ghost shrimp form complex networks and may extend over 50 cm into the sediment (MacGinitie, 1934). The general structure of the burrow is Y-shaped, with two openings at the surface and horizontal side branches and bulbous turnaround chambers at depth (Griffis and Suchanek, 1991). The burrow wall is unlined and is therefore relatively impermanent. *Neotrypaea* spends a substantial portion of its time in burrow maintenance.

*Neotrypaea* has been observed burrowing and feeding when kept in the laboratory (e.g., MacGinitie, 1934; Posey, 1985). The shrimp uses its second and third pairs of legs as shovels in digging. Sediment is sifted for food using the hairs of the second and third legs; the maxillipeds then scrape the hairs and move particles to the mouth for ingestion (MacGinitie, 1934). The particles that are not ingested, along with sediment removed in the process of burrowing, are carried to within 1-3 cm of the surface and expelled from the burrow entrance by rapid movement of the pleopods (Posey, 1985). This ejection of sediment can be seen from the overlying water as a small jet of sediment and water (up to 3 cm high) coming from the burrow opening. This process results in a mound around the burrow opening, and it is this sediment that is captured in the direct entrapment procedure used in the study.

Although they are deep-burrowers, ghost shrimp spend a portion of their time near the sediment-water interface in this process of feeding and burrowing, as well as in mating, which makes them vulnerable to epibenthic predators (Posey, 1985; DeWitt et al., 1997). Posey (1986b) demonstrated that the lower boundary of

the shrimp beds during summer months is determined by predation by the staghorn sculpin, *Leptocottus armatus*. Caging experiments excluding the fish allowed the shrimp to extend into the lower intertidal. Additional predators of the ghost shrimp include other fish such as cutthroat trout, Chinook salmon, and sturgeon, Dungeness crabs, gulls, and gray whales (see references in DeWitt et al., 1997).

Adult ghost shrimp attain a maximum length of 9 cm and are estimated to live 4 to 5 years (Bird, 1982; Dumbauld et al., 1996). Sexual maturity occurs at 2 or 3 years and mature females are ovigerous April through August. The extended time during which ovigerous females are observed suggests that *Neotrypaea* has more than one brood each year, but in a detailed study in Willapa Bay, Washington, Dumbauld et al. (1996) found no evidence for multiple broods during the reproductive season. Eggs are brooded for 5 to 6 weeks and beginning in early summer the planktotrophic larvae are released into the estuarine water column and transported to nearshore waters on the ebbing tide (Johnson and Gonor, 1982). While in the coastal waters, the larvae progress through five zoeal stages (McCrow, 1972). Six to eight weeks later, during spring nocturnal flood tides, the postlarvae are returned to the estuary, ready for settlement (Johnson and Gonor, 1982). Settlement occurs during August through October (Dumbauld et al., 1996).

## SITE DESCRIPTION

As this was a temporal study, the sampling was conducted at a single site within the Bay to minimize spatial variation. The site is located to the south of Hatfield Marine Science Center on Idaho Flat (Figure 1). The sediment at this site is fine sand, with an average grain size of roughly 200  $\mu\text{m}$ . A 20 x 20-m area within the mid-intertidal was staked out. The area had a high density of shrimp, based on preliminary observations of burrow density. Additionally, a substantial

shell layer at roughly 50 cm within the sediment was observed and it was felt that this layer would provide a natural barrier to shrimp movement below this depth. The study area was then subdivided into 1-m<sup>2</sup> plots from which sampling plots were chosen randomly each month. To avoid sampling in a disturbed area, no plot was used that was adjacent to a plot that had been sampled within the previous 6 months.

## METHODS

To investigate what factors influence the reworking rate of *Neotrypaea*, a number of measurements were taken over the course of a week each month for a period of one year. The variables measured were individual reworking rate, organic carbon content, and shrimp size and abundance. Because the measurement of individual reworking rate required several hours on either side of high tide, the sampling dates for each month were chosen as a week during which high tide occurred close to mid-day. Sampling took place four times during a particular week, using the following methods.

### INDIVIDUAL REWORKING RATE

Individual reworking rate was measured using a direct entrapment method, similar to that of Berkenbusch and Rowden (1999). A plastic container (6.4-cm high by 10.2-cm square) was placed over a burrow opening to catch the sediment ejected. The container was constructed with a 1-cm diameter hole cut into the bottom and four heavy bolts forming the legs and anchors. Placement of the sampling container consisted of pushing the container's legs into the sediment until the hole of the container just touched the top of the mound and was directly over the burrow opening. Sediment that was ejected from the burrow during the sampling period was thus collected within the container.

The containers were in place for the time of submergence at the site (approximately 5 hr). The exact length of time was recorded each day. Containers were placed over burrow openings when there was sufficient water to cover the containers. Retrieval of the traps occurred prior to exposure (water depth of roughly 50 cm) and proceeded as follows. A spatula was inserted under the hole in

the container. After gently lifting the container out of the sediment, a cork was placed in the hole from below. Without removing the container from the water, a lid was placed on top, making the container watertight. Samples were immediately brought to the lab for analysis. In the lab, the contents of each container were gently rinsed with tap water on a 25- $\mu\text{m}$  sieve. Samples were then placed in a drying oven and weighed when dry.

For the sampling period of each month, five 1-m<sup>2</sup> plots were randomly selected within the site for sampling. Within each of the five plots, five containers were placed over haphazardly-chosen burrow openings. Sampling was conducted for four consecutive days each month, resulting in a maximum of 100 samples collected per month. However, weather conditions (e.g., strong winds, poor visibility) often limited the number of days during which sampling could be conducted. The total number of sediment containers collected for each month is summarized in Table 2. For five months of sampling, control containers were also sampled. Two types of controls were used. First, containers with holes in the bottom were placed on the sediment in the same manner as experimental traps, except they were not over a burrow opening. Second, containers were placed out that had no hole in the bottom, providing an estimate of the amount of material that might settle from the water column into the container. All controls were placed within a sixth randomly selected 1-m<sup>2</sup> plot within the site.

Table 2: Number of sampling days and number of direct entrapment containers sampled for each month of the study.

Month	Days of Sampling	Number of Samples
Oct 2000	4	95
Nov	0	0
Dec	2	50
Jan 2001	1	25
Feb	4	94
Mar	4	99
Apr	4	100
May	0	0
Jun	2	50
Jul	4	95
Aug	3	69
Sep	3	71
Oct	3	65
Nov	0	0
Dec	1	23

## SHRIMP POPULATION

On a fifth day of the sampling week, after all measurements of sediment reworking had been made, the five plots were sampled to provide estimates of shrimp density, size distribution, and number of burrow openings within the sampling area. This sampling was done at low tide.

Within each plot, the number of burrow openings within the 1-m<sup>2</sup> area was counted. Three cores of 21.5-cm diameter were inserted into the sediment to a depth of 50 cm (the approximate depth of the shell layer). The number of burrow openings within each core was recorded. The sediment within the core was then excavated by hand and placed in 18.9-L buckets to be transferred to the shore. When the tide came in, providing a water source, these sediment samples were passed through a 2-mm sieve. All *Neotrypaea* were collected, returned to the lab,

preserved in 5% formalin, and later transferred to 70% ethanol. The carapace length of each shrimp was measured using a dissecting scope at a subsequent date.

Data provided by Ted DeWitt of the USEPA (DeWitt, unpublished) were used to transform the carapace length measurements to shrimp biomass estimates. The regression equation of

$$\text{BIOMASS (g dry wt)} = 0.0001 \times [\text{CARAPACE LENGTH (mm)}]^{2.9228}$$

was used in these conversions ( $r^2 = 0.77$ ).

## ORGANIC CARBON CONTENT

The final sampling procedure for each month was coring to determine organic carbon content of the sediment. One small core (8-cm diameter x 40 cm) was taken at each of the 5 plots. Each of the cores was then divided into the following depth intervals: 0.5-cm intervals for the upper 2 cm, 1-cm intervals from 2-5 cm, and 5-cm intervals to the bottom of the core (30 cm). The bags of sediment were transferred to the lab and immediately frozen at -15°C. Cores from three of the plots for each sampling month were processed. From each core, three depth intervals (0-0.5, 4-5, and 25-30 cm) were selected to serve as representative samples of the surface, middle, and deep sediment, respectively. After acid treatment using vapor-phase HCl to remove inorganic carbon (Hedges and Stern, 1984), the dried and homogenized samples were run on a Carlo-Erba Model NA1500 CHN analyzer to determine weight-percent organic carbon and total nitrogen. Blanks were used and replicates were run for every fifth sample.

Additionally, to investigate another potential measurement of food, four sediment samples were analyzed by HPLC. Two surface samples from the summer (August) and two deep samples from February were chosen to represent the range of organic carbon measurements. Extraction of pigments was done using 100%

acetone (5 ml) added to the wet sediment sample (approximately 2 g) for 24 hr (Buffan-Dubau and Carman, 2000). An 80- $\mu$ l portion of the extract was then run on HPLC to determine the amount of chlorophyll *a*.

## OVERALL SUBDUCTION RATE

Whereas the above parameters were measured monthly from October 2000 to December 2001, measurements of overall subduction rate (i.e., the rate that sediment moves downward due to the excavation and feeding activities of *Neotrypaea*) were performed separately. To determine the rate of overall sediment subduction, a heavy mineral tracer, garnet sand, was used. Garnet sand is in the size range of the natural sediment, but approximately twice as dense, so it shows up as x-ray opaque sediment in x-radiographs. The garnet sand grain size was 180-230  $\mu$ m (sold as 60-80 mesh). Approximately 600 g of garnet sand was spread on each of six randomly selected 1-m<sup>2</sup> plots within the study site on August 24, 2001. During an incoming tide, with water depth at roughly 20 cm, the tracer was shaken from a container with a mesh top. The result was an evenly spread, thin, pink layer visible over each plot.

At three time intervals (18, 39, and 106 days), two of the six plots were cored using rectangular acrylic cores (40-cm high by 13-cm wide, thickness 2.2 cm). Three replicate cores were taken at each plot. These samples were brought back to the lab and x-rayed using a digital x-ray system to determine the depth to which the tracer was mixed. The garnet sand could be seen as a discrete layer of x-ray opaque sediment below the surface. The distance from the sediment-water interface to the top of the garnet sand layer was measured to the nearest 0.5 mm at three places in each core to obtain an average depth of the tracer.

## RESULTS

### INDIVIDUAL REWORKING RATE

Control data were taken over five months of the study (Figure 2). Although variable both from day to day (Figure 2A) and month to month (Figure 2B), the amount of sediment collected in control containers was low relative to the amount collected in the sampling containers. These controls show there was little material entering from the water column or being washed in through the hole in the bottom of the container. Additionally, the fact that there is little difference between controls with and without holes shows that the method of retrieving the traps had little effect on the contents of the container.

The data presented in Figure 3 are the average sediment expulsion rate for each month over the period of this study. This rate is the amount of sediment (g dry wt) expelled from a burrow opening per hour over the time of submergence. Note these are averages of five samples per plot and five plots within the sampling site over one to four days. At times weather conditions prevented a complete round of sampling (Table 2). In general the expulsion rate follows a seasonal pattern of lower activity in the winter months and higher in the spring and summer. The average expulsion rate is 0.22 g dry sed/hr. Assuming 12 hours of submergence each day, on average 2.64 g dry sed/burrow are expelled daily.

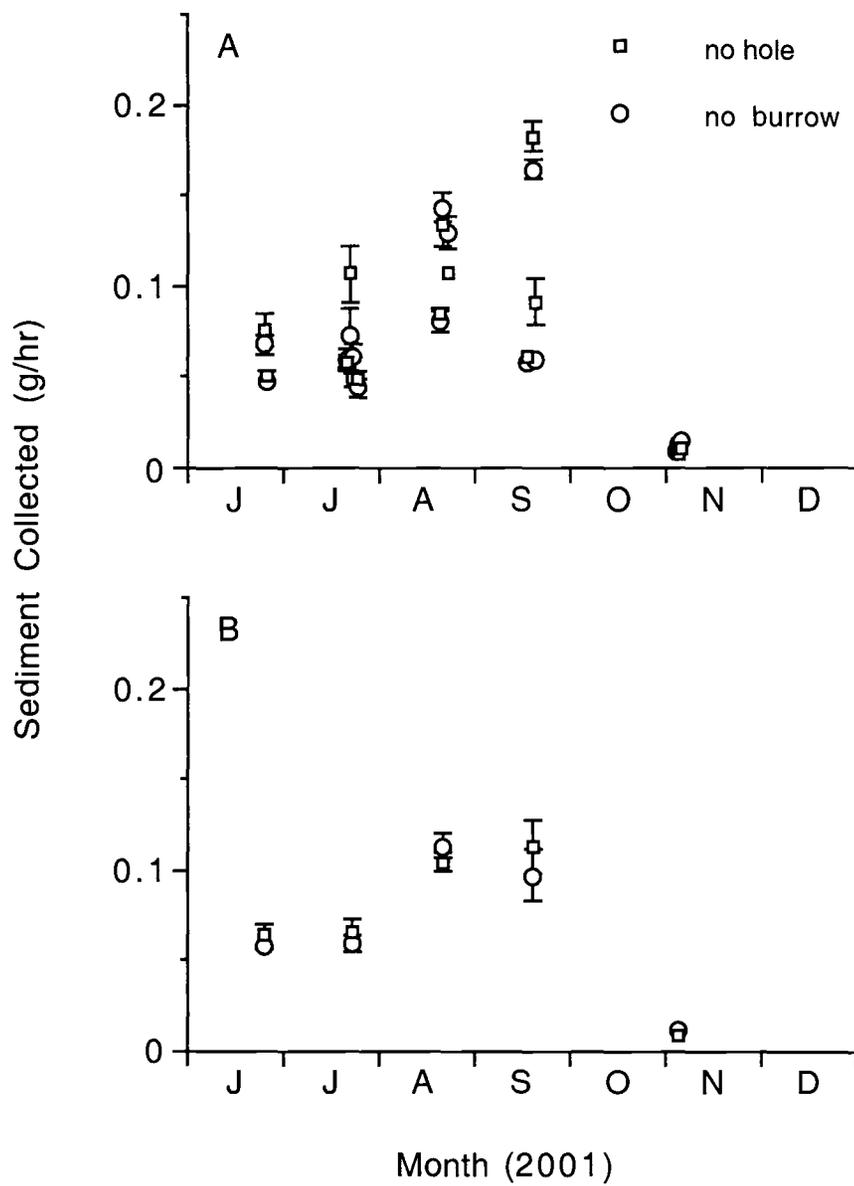


Figure 2: Dry weight of sediment collected (g/hr) for each of the days (A) and averages for the months (B) during which control samples were collected. Error bars indicate SE.

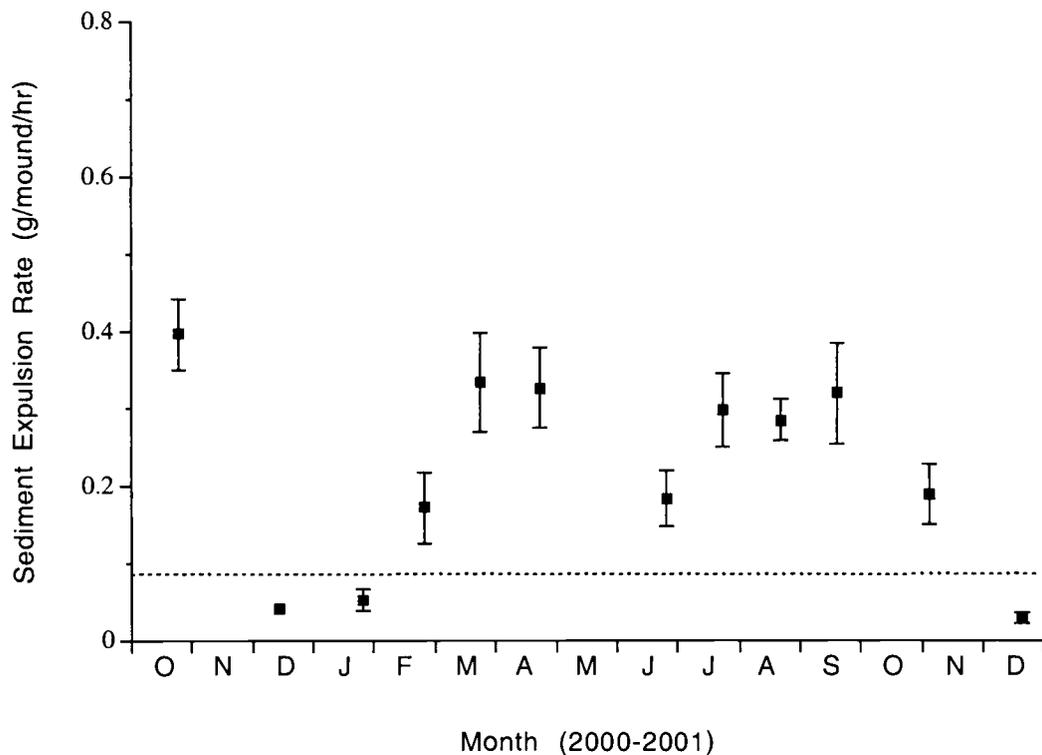


Figure 3: Sediment expulsion rate (g/mound/hr) for each sampling period. Dashed line indicates the average control (see Figure 2). Error bars indicate SE; refer to Table 2 for N.

Given the multiple temporal and spatial scales at which the sampling was conducted, it is possible to examine the sediment expulsion activity at various levels of detail. An important aspect of a seasonal study is determining whether the differences observed over the months are greater than the day-to-day variation within a given month. Except for the month of August when one day of particularly low shrimp activity was observed (one-way ANOVA,  $p = 0.003$ ), there were no significant differences between days within a given month (one-way ANOVA,  $p > 0.05$ ; see Figure 4). This is true for a single plot and for the entire site averaging the five plots. It is clear, however, that variability is high (Figure 4).

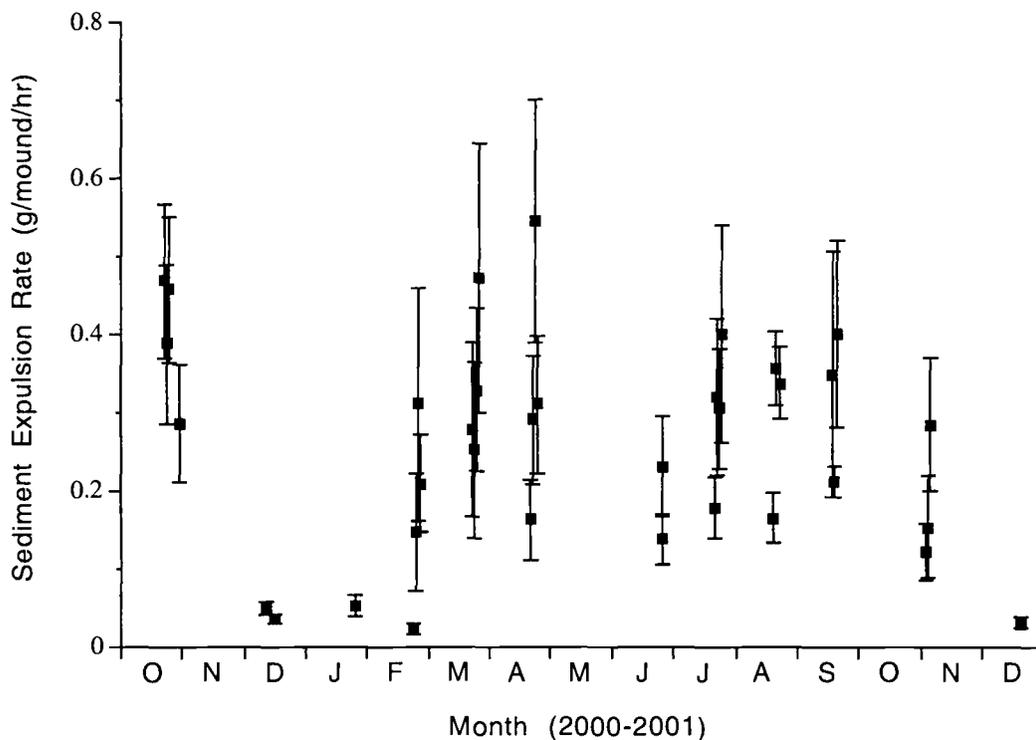


Figure 4: Sediment expulsion rate (g/mound/hr) for every sampling day averaged over five plots. Error bars represent SE.

In part this variability is due to differences among plots. There was a fair amount of spatial variability in expulsion rates within a given sampling month, and even within a single day. Figure 5 presents the sediment expulsion rates for each month, categorized by plot. It is clear that there are differences between plots, and these are significant for October and December 2000 and February, March, and April 2001 (one-way ANOVA,  $p < 0.05$ ). It appears that the spatial variability decreased in the summer and fall months.

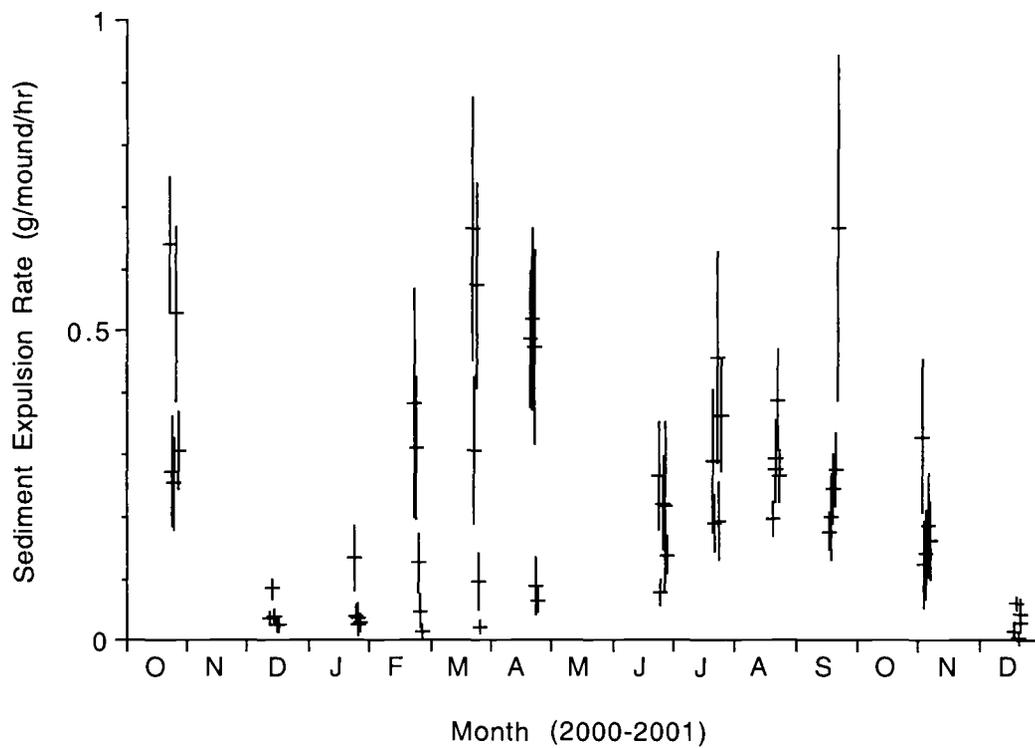


Figure 5: Sediment expulsion rate (g/mound/hr) for each month of sampling, averaged by plot. Five plots were sampled each month; data within each month are staggered slightly for graphing. Error bars represent SE.

### SHRIMP POPULATION

There was a substantial decrease in the density of *Neotrypaea* during the course of this study (Figure 6). At its extremes, the population at this site ranged from 241 shrimp/m<sup>2</sup> in December 2000 to 70 shrimp/m<sup>2</sup> in July 2001. Although no shrimp were collected in October 2000, observations of burrow densities suggest that the population density at the beginning of the study was comparable to that of December 2000.

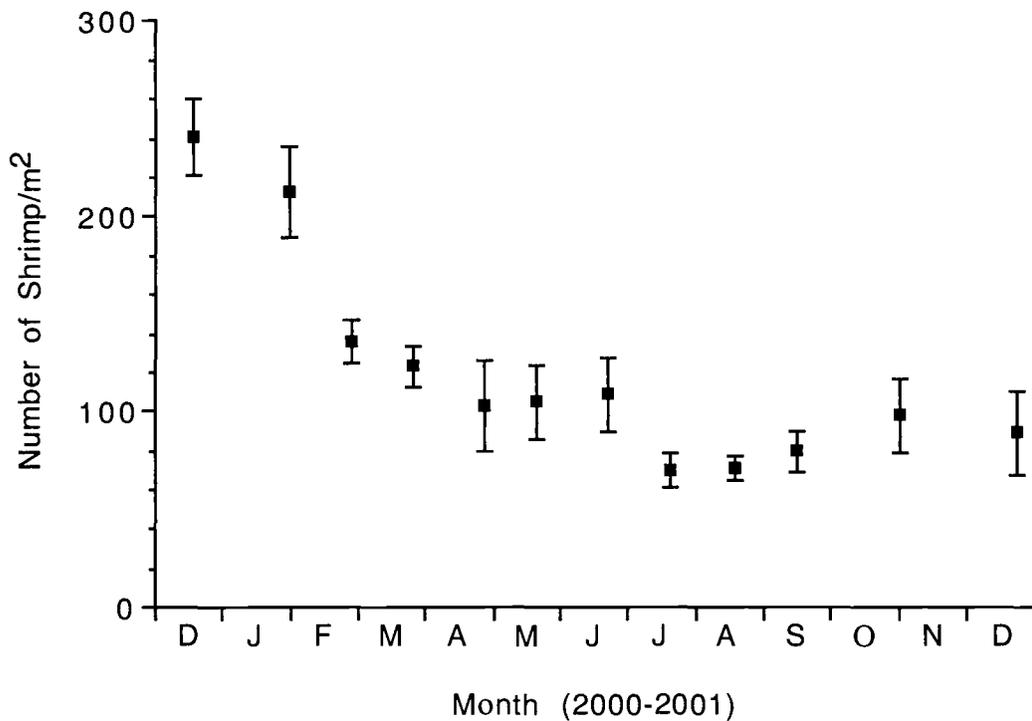


Figure 6: Number of shrimp per m<sup>2</sup> for each of the sampling months, with SE.

Because the population density in Figure 6 is an average of densities found at each of the five plots for a given month, it is also possible to examine the spatial variability of *Neotrypaea* at this site (Figure 7). No significant differences were observed among the plots within a month, with the exception of June and December 2001 (one-way ANOVA,  $p = 0.003$  and  $p = 0.013$ , respectively). During June, the plot lowest in the intertidal had a significantly lower density than the other four plots.

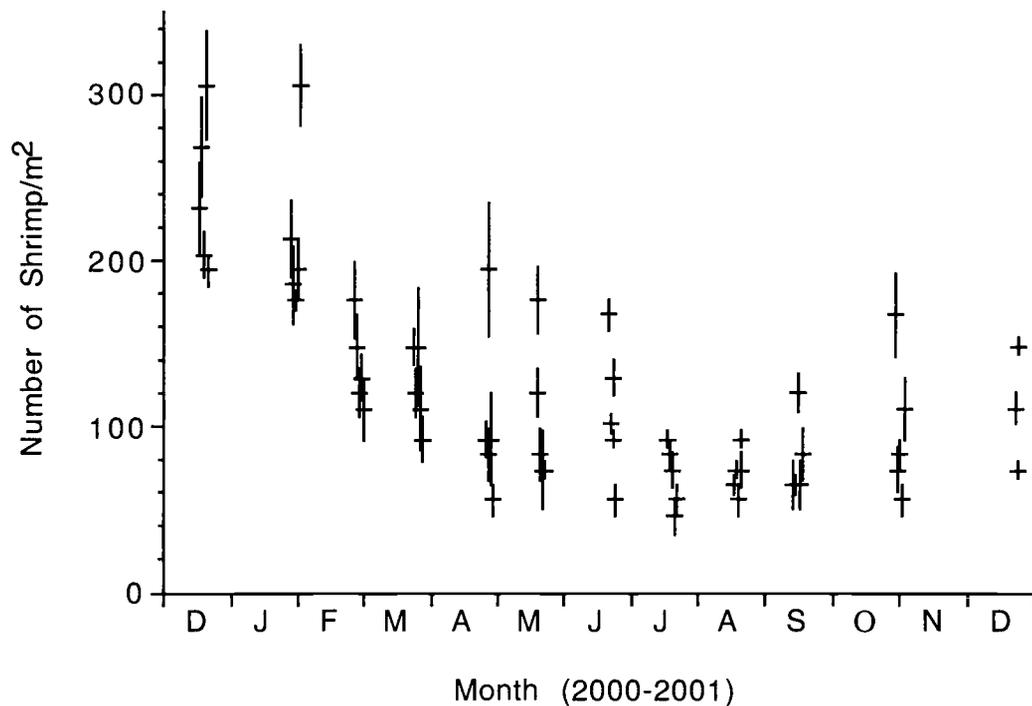


Figure 7: Number of shrimp per  $m^2$  for each month of sampling, averaged by plot. Five plots were sampled each month; data within each month are staggered slightly for graphing. Error bars represent SE.

Although the abundance of *Neotrypaea* changed over the year, the size structure of the shrimp population within the study area remained stable. Based on a total of 768 shrimp collected over the year, there was little variation in average carapace length (CL) among the months (Figure 8). The average length was  $6.7 \pm 2.0$  (SD) mm. The size-frequency histograms for each month are presented in Figure 9. It is not possible to estimate a growth rate for the shrimp because the low numbers collected each month make it difficult to clearly identify cohorts. The histograms show that the smallest shrimp ( $CL < 4$  mm) did not appear until April, and fewer large shrimp ( $CL > 10$  mm) were collected in the summer months, but these differences had little effect on the average size for this population.

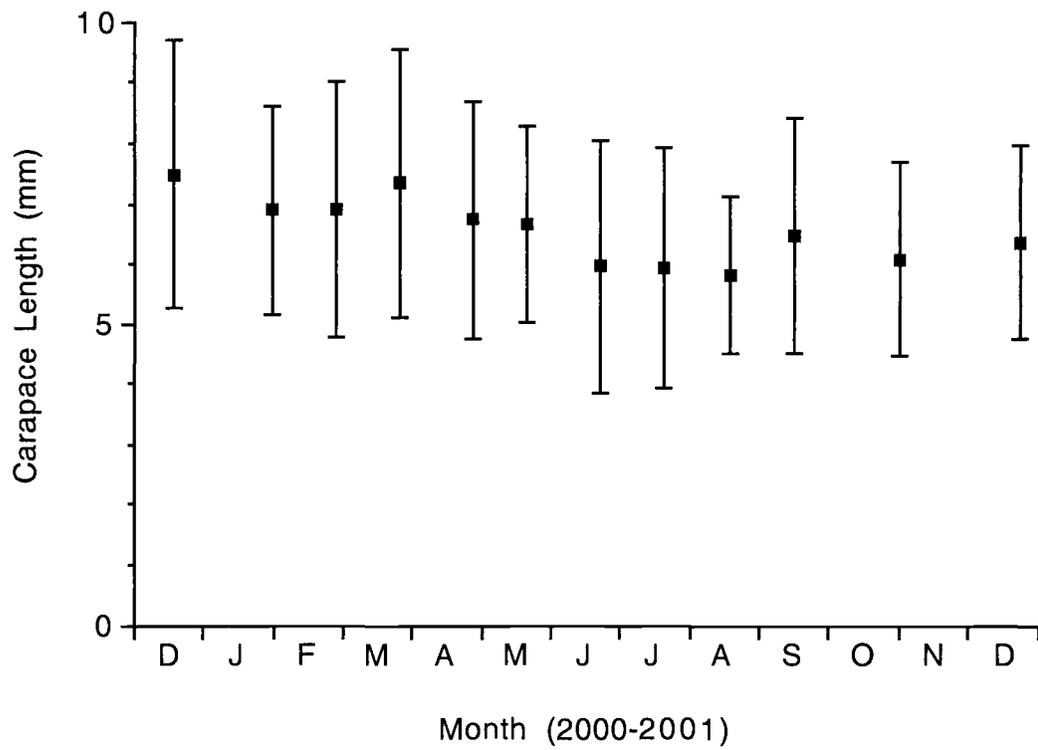


Figure 8: Carapace length of shrimp collected during each sampling period. Error bars represent SD.

Figure 9: Length-frequency histograms for the shrimp collected each month. Carapace length is in millimeters. Frequency is given as percent of total number. Total number of shrimp collected in the three cores at each of five plots is given as n. Note that in December 2001 only three plots were sampled.

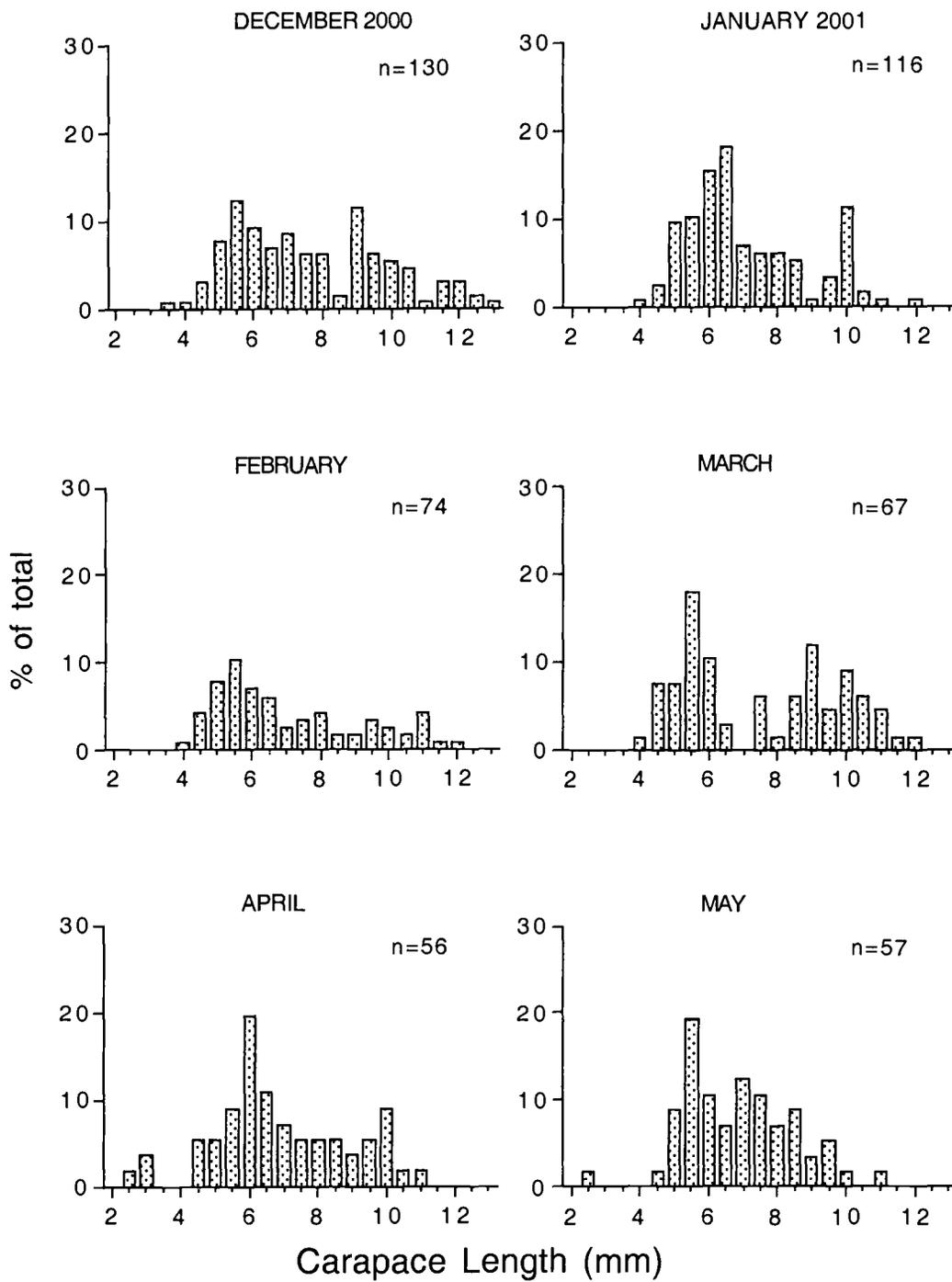


Figure 9

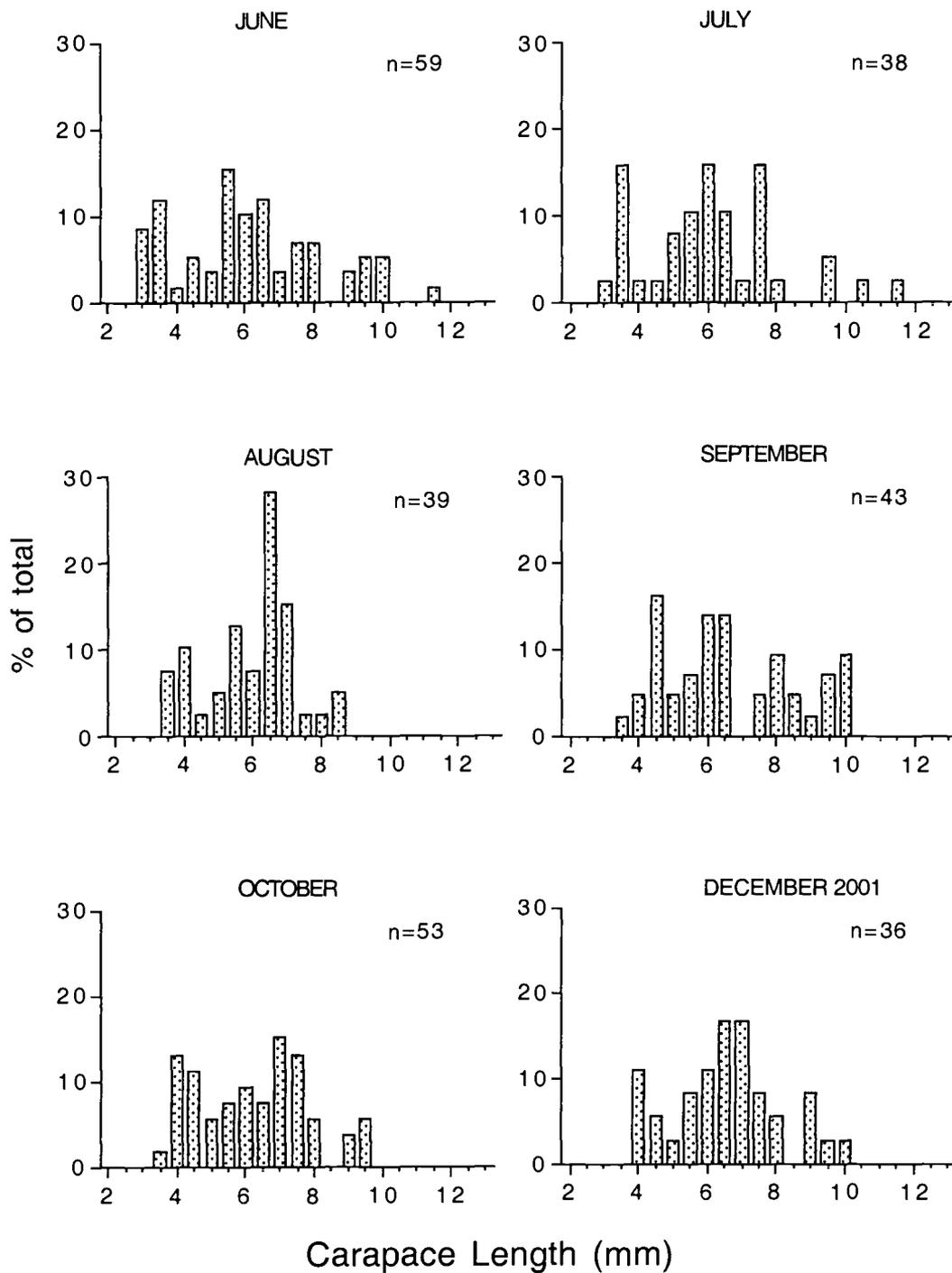


Figure 9 (continued)

To account for both numbers and size of the shrimp population, the overall biomass/m<sup>2</sup> was determined for each of the sampling months (Figure 10). Because the population size distribution showed little temporal variation, the pattern in biomass closely resembles that of density (cf. Figure 6). The variability in biomass/m<sup>2</sup> over the year encompassed an almost eight-fold difference between the extremes. The average biomass/m<sup>2</sup> for December 2000 was 10.8 g dry-weight/m<sup>2</sup> while that of August 2001 was only 1.4 g dry-weight/m<sup>2</sup>.

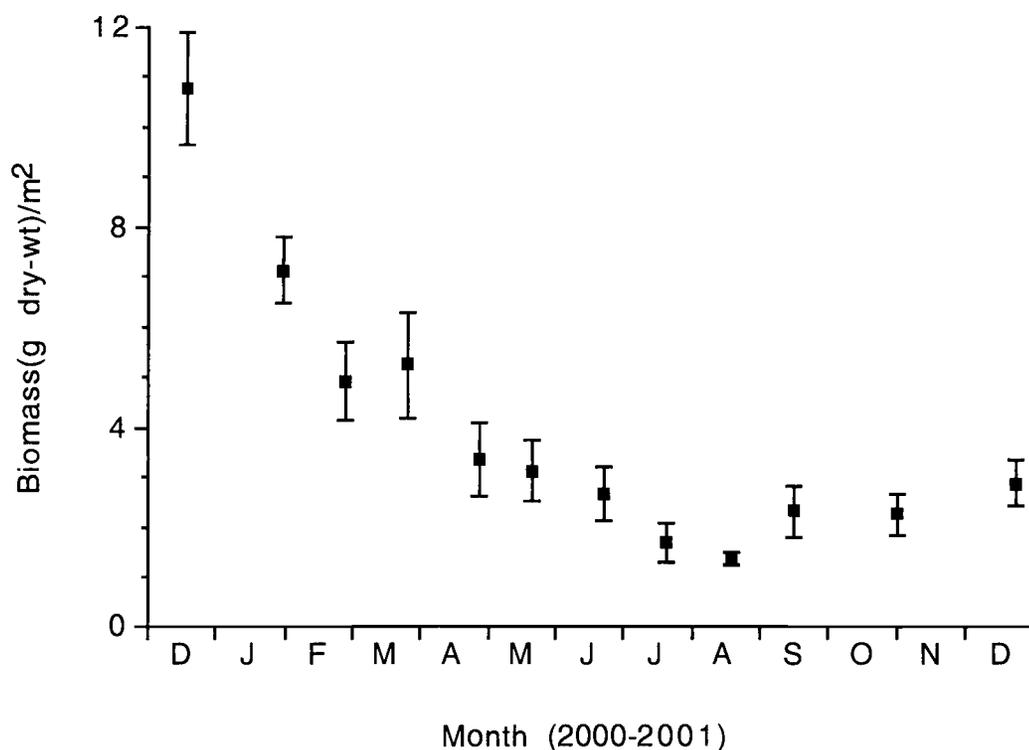


Figure 10: Average ( $\pm$ SE) biomass in g dry-weight/m<sup>2</sup> for each of the sampling months. See text for regression equation used to determine biomass from measured carapace lengths.

An additional measurement made along with the shrimp population estimates was the density of burrow openings. The number of burrow openings per shrimp proved to be quite variable (Figure 11). The winter months tended to have a lower burrow opening to shrimp ratio. The overall average is  $1.2 \pm 0.8$  (SD) burrow openings/shrimp.

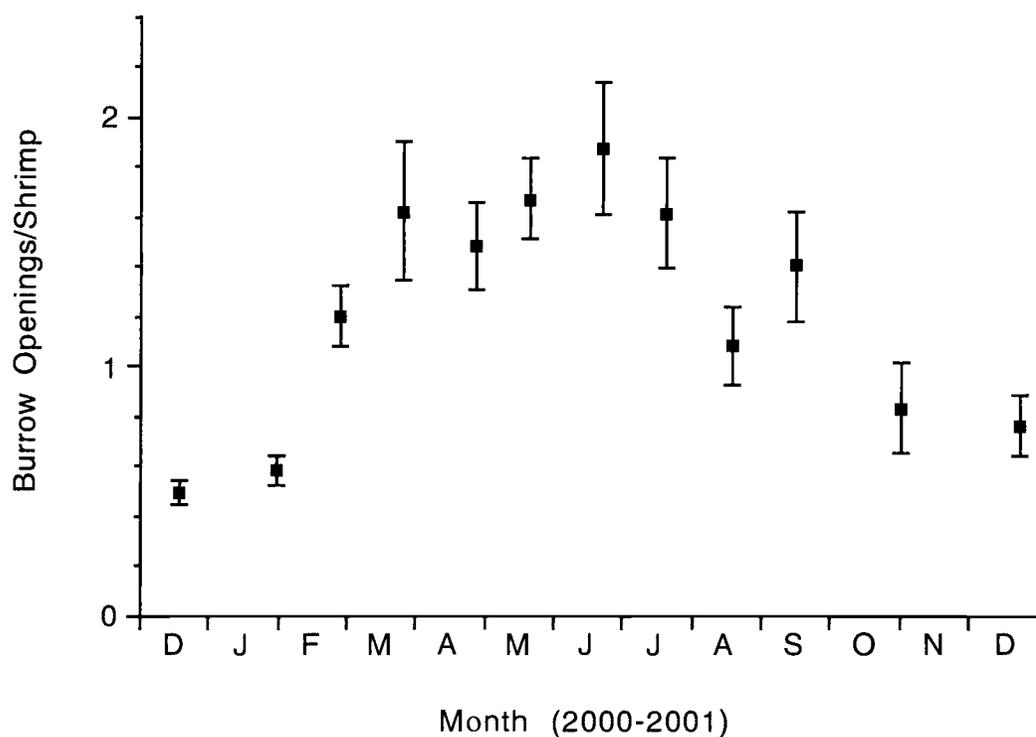


Figure 11: Number of burrow openings per shrimp for each of the sampling months. Error bars represent SE.

#### ORGANIC CARBON CONTENT

The organic carbon content of the sediment was determined each month at three depth intervals: surface (0-0.5 cm), middle (4-5 cm), and deep (25-30 cm).

As is typical with sands, overall organic carbon content was very low, between 0.25 and 0.4 wt-%, except for a few surface samples collected in the summer that had values of almost 1% (Figure 12). The organic carbon content of the three depths are significantly different from each other (one-way ANOVA,  $p = 0.001$ ), with the surface samples usually showing the highest values. At depth within the sediment there is little seasonal variation in organic carbon content. This is true for the surface samples as well, with the exception of spikes in July and August.

There was even less variation in C:N ratios (Figure 13). The deep sediment is generally higher than the surface and middle samples, and this difference is significant (one-way ANOVA,  $p < 0.001$ ).

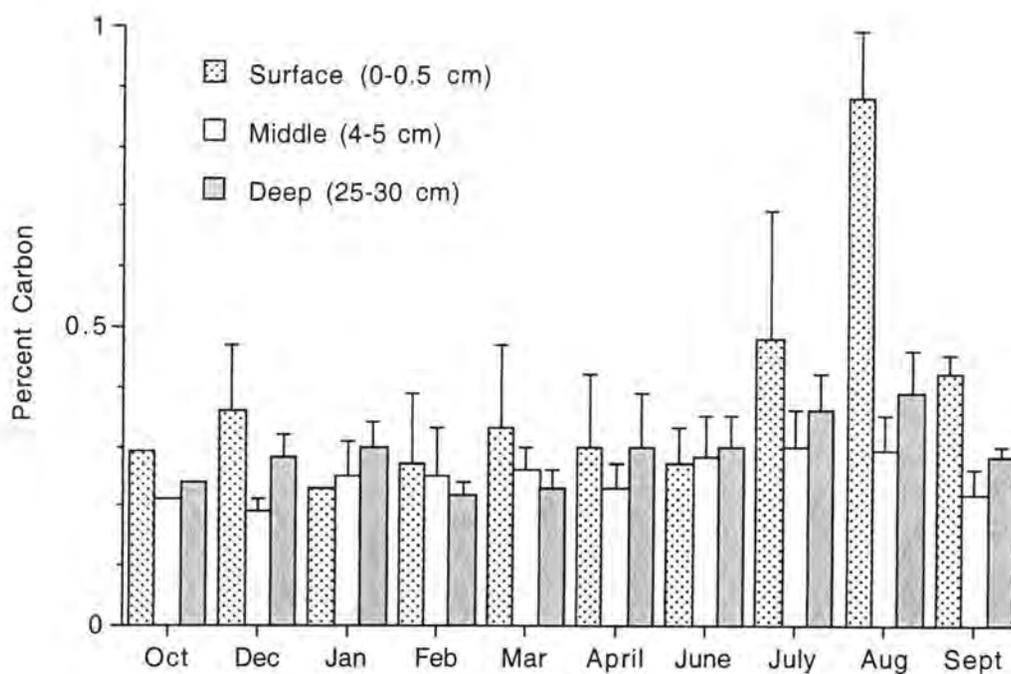


Figure 12: Weight percent organic carbon for each month, with SD. The three samples for each month represent three depths of the cores (0-0.5 cm, 4-5 cm, and 25-30 cm).

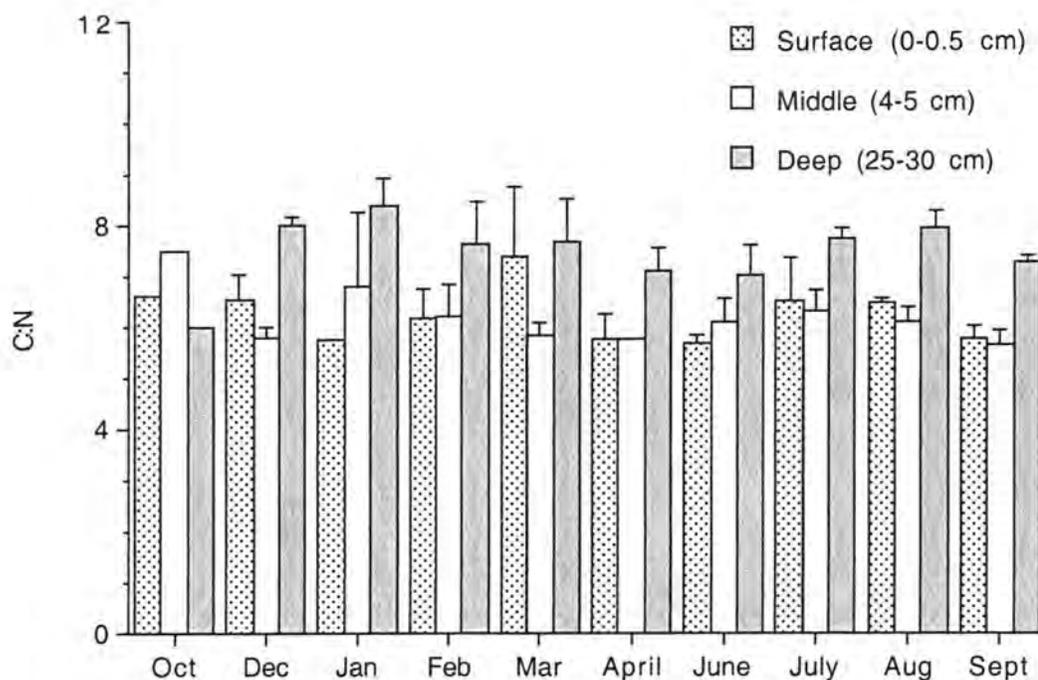


Figure 13: Organic carbon to total nitrogen atomic ratio, for cores taken during each of the sampling months, with SD. Depth intervals are the same as Fig. 12.

As another investigation into amount of nutritional material available in the sediment, four sediment samples were run on HPLC. The average amount of chlorophyll *a* in August at the surface was  $29.2 \mu\text{g chl } a/\text{g dry sediment}$ ; in February at 25-30 cm the average was  $2.1 \mu\text{g chl } a/\text{g dry sediment}$ . These samples represent the range seen in the organic carbon content.

#### OVERALL SUBDUCTION RATE

The overall sediment reworking rate can be examined using the individual reworking rates and shrimp abundance. Three calculations are presented here, in terms of shrimp biomass, shrimp numbers, and overall area. The first conversion is

seen in Figure 14A, in which the sediment expulsion rate was normalized to a rate per gram dry weight of shrimp/m<sup>2</sup>. There is a factor of 40 variation over the year, with the peak occurring in August and lowest values in the winter months of December through February. Alternatively, the expulsion rate can be given in terms of a sediment expulsion rate per shrimp/m<sup>2</sup>, which, because of the near constant size distribution of the shrimp population, results in a similar pattern (Figure 14B). A third conversion (Figure 14C), in terms of rate per area, peaks in the spring, with a high in March. Expulsion activity had increased from the low winter levels, while the shrimp abundance remained fairly high. Over the study, the rate per area ranged from 2.7 to 41.0 g dry sed/hr/m<sup>2</sup>.

Overall reworking rate may also be obtained from the tracer determination of sediment subduction rate. The heavy mineral tracer was evident in cores taken at each of the three coring times. Although not every core exhibited the tracer, in most cores the garnet sand was observed at a particular depth as a single layer. The discrete layer of x-ray opaque sediment made it fairly straightforward to estimate the subduction rate of the tracer (Figure 15). An example of an x-radiograph is provided in Figure 16, with a mean subduction depth of 1.8 cm.

Figure 14: Expulsion rate (g/hr) per total shrimp biomass (g dry wt/m<sup>2</sup>) (A), per total shrimp density (number of shrimp/m<sup>2</sup>) (B), and per area (g/hr/m<sup>2</sup>) (C) for each sampling period. Error bars represent SE.

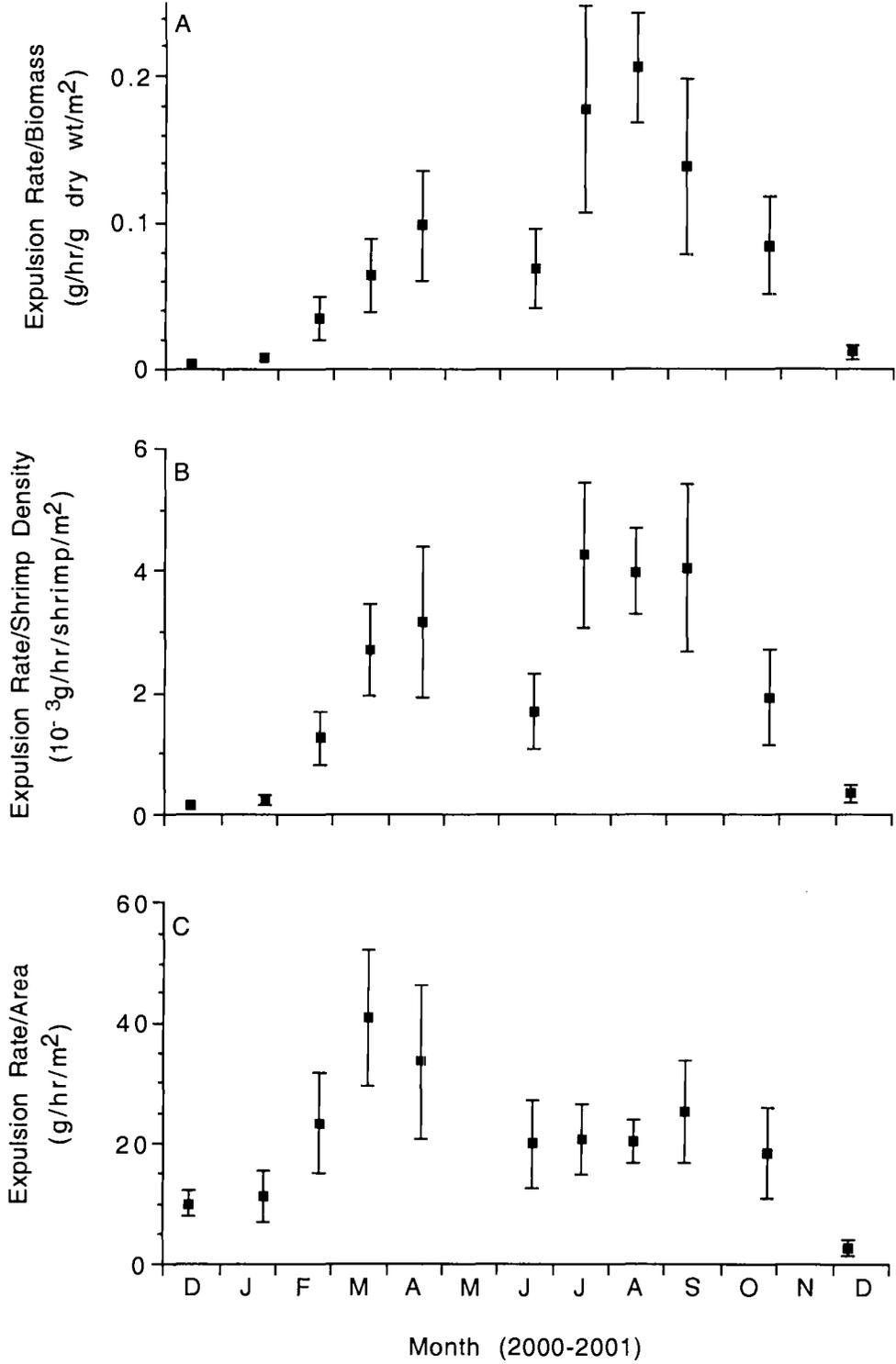


Figure 14

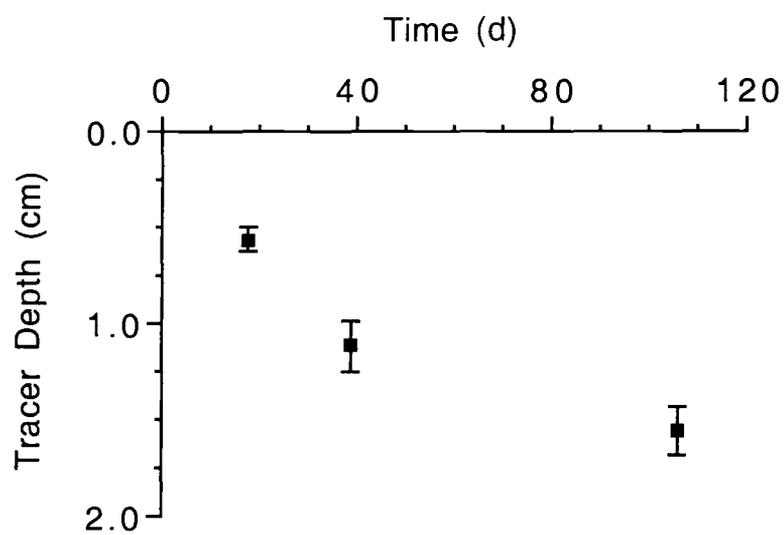


Figure 15: Depth (cm) of garnet sand tracer as measured from x-radiographs of cores taken at days 18, 39, and 106. Error bars represent SE.



Figure 16: X-radiograph of tracer subducted to a mean depth of 1.8 cm. Scale bars at left of core are spaced at 1-cm intervals.

## DISCUSSION

The "direct entrapment" method has been used by other researchers to estimate sediment reworking in thalassinideans (see review in Rowden and Jones, 1993). This method has the advantage of being non-destructive, with little obvious impact on the shrimp population. In contrast, using an alternative method called "leveling", which eliminates all mounds and measurements are made on newly produced mounds, may alter conditions for the shrimp within the burrow and consequently their activity levels. The flow of water increases in velocity as it moves over bedforms such as mounds, setting up pressure gradients that in turn may increase the flow of water through the burrows (Vogel, 1981). Elimination of mounds would tend to decrease this within-burrow water flow. Additionally, burrows may be filled in as the mounds are flattened, which would also alter the burrow environment and the behavior of the shrimp. Thus, the leveling technique likely results in an overestimate of reworking rate.

Using a tracer (e.g., dyed particles or a heavy mineral) to measure sediment reworking also causes little disturbance, but it measures overall sediment turnover. This measurement may be influenced by physical reworking and the contribution of sediment turnover by other fauna. (But see section on OVERALL SUBDUCTION RATE below, for the additional information provided by this method.) For these reasons, direct entrapment was chosen as the primary measurement of individual sediment reworking rate.

Control samples were collected during six months of this study and the results from these can be used as a check on the effectiveness of this sampling method. The amount of sediment collected in the controls was variable from day to day and month to month (Figure 2), but for most of the months the controls were low compared to a container into which sediment was expelled. The winter months were the exception; sediment expulsion rates during December 2000 and January

and December 2001 were within the range of controls (Figure 3) and therefore reworking rates during these times were approximately zero. As there is little difference between the controls with and without holes in the bottom, the procedure of collecting the container and placing a cork in the bottom had little effect on the contents.

Despite being the preferred method (Rowden and Jones, 1993), there are some problems inherent in direct entrapment. The most important arises because shrimp are infaunal organisms, which makes it difficult to know precisely their living arrangements at depth within the sediment. Direct entrapment collects all the sediment ejected from a single burrow opening. Scaling up from this measurement can only be done using assumptions about the number of mounds per shrimp. Because relying on burrow openings as representative of the shrimp population is inaccurate (for *Neotrypaea*: DeWitt et al., 1997; Dumbauld, 1994; Posey, 1985), this study included coring to obtain population estimates within each 1-m<sup>2</sup> area in which the reworking measurements were made.

The number of burrow openings per shrimp was found to be highly variable (Figure 11). Adequate enumeration was hampered by a number of factors, including extensive macroalgae cover during the summer months and occasional physical reworking on particularly windy days that caused ripples to wipe out the mounds. However, the average estimate of 1.2 burrow openings/shrimp matches findings by Dumbauld (1994) working in Willapa Bay, Washington. These estimates are lower than densities found in British Columbia, where Swinbanks and Luternauer (1987) found 2.5 burrow openings/shrimp. The results from the winter months are much lower, which is likely due to physical disturbance of the holes, not movement of several shrimp into a single burrow.

Investigations into the burrow architecture of *Neotrypaea* have been made using resin casts and observations in laboratory "ant farm" aquaria. The general structure is a Y-shaped burrow, with several tiers of chambers and branches at

depth (Griffis and Suchanek, 1991). Griffis and Chavez (1988) found there were two openings per burrow in sands, while MacGinitie (1934) states that there were "two to several" openings. Mounds are formed at the excurrent opening, which is where the containers used for direct entrapment in this study were placed. In numerous burrow casts, Griffis and Chavez (1988) found only one shrimp per burrow.

Clearly, the issue of burrow openings/shrimp is complex. From March-July, the average number of burrows/shrimp is relatively constant around 1.7. During these months, counting burrow openings may be a viable way to approximate density when coring or other destructive and time-consuming methods are inappropriate. Whenever possible in this study, the number of shrimp collected from cores was used as a density estimator rather than the number of burrow openings. For instance, Figures 14A and 14B are based on the coring data, not on assumptions about burrow openings/shrimp. However, because there are no literature reports of multiple shrimp in a single burrow, and the average openings/shrimp was greater than one, it seems a reasonable assumption that the sediment captured in a container expelled from a burrow opening over one tidal cycle represents the activity of a single shrimp. The assumption of one shrimp per burrow was used when converting from direct entrapment measurements to overall subduction rates (see OVERALL SUBDUCTION RATE).

#### SEDIMENT EXPULSION RATES

The monthly average sediment expulsion rate for this study ranged over an order of magnitude from 0.03 to 0.33 g dry sediment/mound/hr. In general this rate is lower than other researchers have found for *Neotrypaea*. The earliest work on this subject by MacGinitie (1934), estimated a rate of 20-50 ml wet sediment/

individual/day. Studying a population in British Columbia, Swinbanks and Luternauer (1987) estimated  $24 \pm 12$  g dry sediment/individual/day. They used the leveling method, making measurements after a 25-hour period. It is important to note that the length of exposure, during which shrimp are much less active, averaged only 4.5 hours over the 25-hour sampling period at their experimental sites. This longer submergence time could result in greater reworking. MacGinitie did not describe his method of determining sediment expulsion, making comparisons to his findings problematic. Studies on other thalassinideans have generally found higher rates (see Table 1), but because few give information on shrimp size, it is difficult to compare the results found here to other species.

Turning now to the factors that may influence *Neotrypaea* reworking rates, the seasonal pattern of average sediment expulsion rate and temperature fluctuations in the sediment is similar (Figure 17). Tony D'Andrea at the USEPA provided the temperature data (D'Andrea, unpublished). Measurements were logged at approximately 20-minute intervals at a depth of 5 cm within the sediment. Minimum reworking rates were seen in the winter months of December through February, when temperatures were lowest. Reworking rate and temperature increased steadily into the summer months. There was a sharp decline in September for both temperature and reworking rates and this decrease continued until the end of the study in December. A regression of average expulsion rate and temperature shows a close correspondence ( $r^2 = 0.77$ ). This relationship suggests that temperature plays an important role in influencing sediment expulsion activity of *Neotrypaea*.

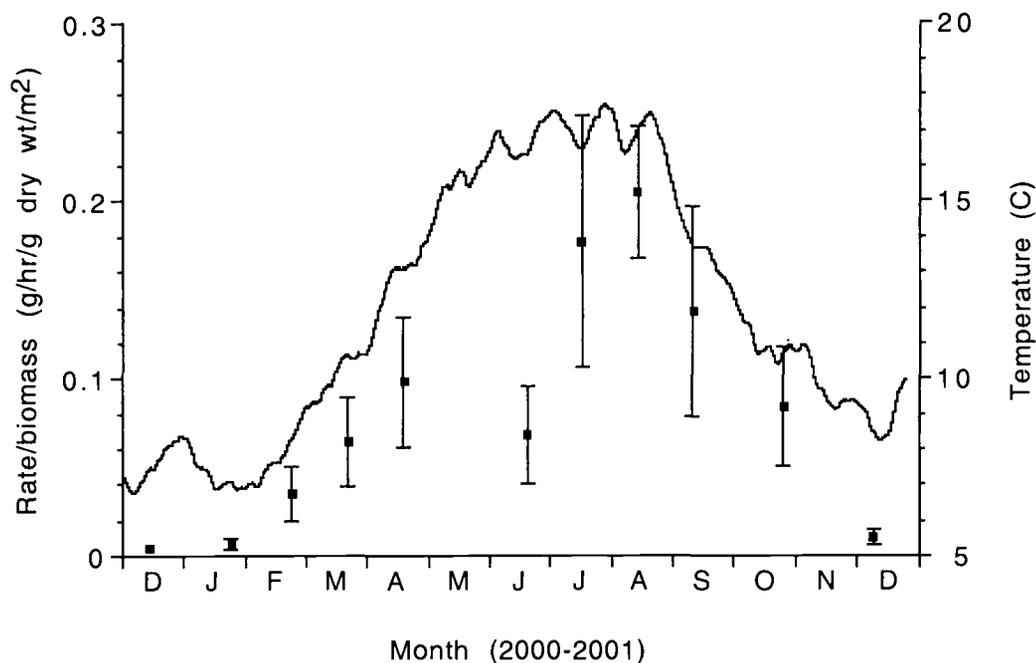


Figure 17: Sediment expulsion rate per biomass (g/hr/g dry wt/m<sup>2</sup>; see Figure 14A) and a 14-day running average of temperature (°C) at 5 cm below the sediment-water interface.

Other researchers have found that temperature may be a factor in sediment expulsion rate of thalassinidean shrimp. In *Neotrypaea*, Swinbanks and Luternauer (1987) compared rates during two time periods exhibiting a 4°C temperature difference (18 to 22°C) and observed higher rates at the higher temperature, although the difference was not statistically significant. The average reworking rate in July when temperatures were warmer was 23 wet ml sed/shrimp/day, while in September the average rate was 12 wet ml sed/shrimp/day. The limited data set of Swinbanks and Luternauer makes it difficult to compare directly to the present study.

In a seasonal study of reworking rates in a New Zealand species, *Callianassa filholi*, Berkenbusch and Rowden (1999) found that reworking rate was significantly related to seawater temperature over the course of a year. Seawater

temperature in the New Zealand study ranged from roughly 7 to 16.5°C, very similar to the variation recorded in Yaquina Bay (Figure 17). Berkenbusch and Rowden observed sediment expulsion rates from a minimum of 1.4 g dry sediment/day to a maximum of 54.1 g dry sediment/day, a factor of roughly 40. This agrees closely with the approximately 40x variation seen in Figure 17.

Lower activity of invertebrates during periods of cooler temperatures is a typical finding, but is not necessarily straightforward, given that *Neotrypaea* spends much of its time at depths of up to 50 cm within the sediment. Living at depth reduces the temperature fluctuations that shrimp are exposed to in an intertidal environment in a temperate estuary. For example, McCrow (1972) measured temperatures at three depths within Yaquina Bay sediment and found that over a complete tidal cycle during the summer, the temperature at 1-cm depth varied from 10 to 23°C. At 25 cm within the sediment, the range was from much less, roughly 13°C to 18°C. The temperature at 50 cm would be expected to fluctuate even less. These measurements, however, are of bulk sediment temperatures. *Neotrypaea* burrows are open at the sediment surface and are well irrigated with seawater. Therefore, temperature fluctuations within the burrow would likely be closer to that of the overlying seawater at high tide. Because no experimental field manipulation or laboratory work was done, the conclusions made here are necessarily correlative. Nonetheless, the strong relationship between bottom water temperature and *Neotrypaea* activity suggests that individuals may be in close contact with conditions at the surface.

Food concentration (e.g., percent organic carbon or chlorophyll *a*) could also potentially influence expulsion rates. Organic carbon content and C:N ratio were used in this study as a measurement of the amount of nutritional material available. As there was very little variation over the year in organic carbon content at depth (Figure 12), it is unlikely to be an important influence in reworking rate. This pattern is in contrast to other studies that suggested that high food

concentrations tend to decrease reworking rates. When observing a tropical callianassid, Suchanek (1983) noted the speed of sediment turnover and hypothesized that this was necessary given the low nutrient content of the sands. Nickell et al. (1995) suggested that differences in organic carbon content could partially account for the higher rates of sediment expulsion in areas of lower organic carbon for the thalassinidean *C. subterranea*. Similarly, Berkenbusch and Rowden (1999) hypothesized that the lower rates of reworking found further from the shore could be due to higher nutritional value of the sands that are covered with water for a longer time.

No study has looked specifically at the response of shrimp activity to increased food availability and it is an area that could benefit from some experimental studies. The difficulty in such studies is estimating the nutritional value of the sediments. Potential measurements of food in sediments include bulk organic carbon, chlorophyll *a*, protein, and bacteria concentrations (Lopez and Levinton, 1987). However, the amount of organic material that is available as food to deposit feeders cannot readily be assessed, much of it may be refractory material of little importance to the organisms (Mayer et al., 1986). This is particularly problematic in *Neotrypaea* because its feeding mode is not completely understood. General information on what *Neotrypaea* feeds on, data that could be obtained from detailed gut content analysis, is lacking. Additionally, there are no data on particle selectivity in *Neotrypaea* as there are for other thalassinideans (Stamhuis et al., 1998; Pinn et al., 1998).

The most notable aspect of the *Neotrypaea* population studied here was the dramatic decrease in density, and corresponding biomass, at this site. This decrease is not likely due to sampler avoidance. The shell layer at 50 cm probably prevented escape in the vertical direction by the shrimp. In addition, the population remained low into the winter of 2001, so it is not a case of more activity and better escape response in the summer months. The decrease in the population was not simply

due to mortality of older individuals because there was little change in the average size within the population. It is interesting to note that the decrease in *Neotrypaea* numbers observed here was accompanied by an increase in numbers of *Upogebia pugettensis* and *Abarenicola* sp. (personal observation). Although the cause of the *Neotrypaea* decrease remains unknown, changes in population abundance have been observed in other studies. For instance, Dumbauld (1994) observed an increase in density over the course of two years, from 153 to 285 shrimp/m<sup>2</sup>. Similarly, in Alsea Bay, Oregon, Bird (1982) found 5 times greater abundances of *Neotrypaea* during the second year of his study, which he attributed to high recruitment. The intertidal is a dynamic environment, which becomes apparent with detailed monthly sampling and that might otherwise be missed with short-term sampling.

A 2-mm sieve was used in this study, so it is likely that not every shrimp was collected; particularly the small, post-larvae shrimp may have been missed. However, because sediment reworking was the main interest in this investigation and the smallest individuals contribute little to these rates, it was determined that the greater number of cores that could be sieved using a 2-mm sieve outweighed the fact that the smallest shrimp would be missed.

The decline in numbers provided something of a natural experiment to examine another factor that potentially could influence reworking rate, that of a density-dependence in sediment expulsion. Referring to Figures 3 and 6, December 2000 was a time of high shrimp density and low reworking rates, while December 2001 also exhibited low reworking rates although populations were low. This pattern suggests that other factors are likely to be more influential than population density. Clearly there is room for closer investigation into this question.

## OVERALL SUBDUCTION RATE

Both individual reworking rate and shrimp abundance contribute to the overall subduction rate that is measured using the heavy mineral tracer. The two methods used in this study, direct entrapment and tracer, agree fairly well (Table 3). The tracer rate tends to be higher than that found by direct entrapment, but in general the two measurements are within a factor of 2. To convert between the two measurements it was assumed that the amount of sediment collected per mound represented the activity of one shrimp. (See Appendix 2 for full equation used in conversion from mm/day to g/burrow/shrimp.)

Table 3: Comparison of two methods of measuring sediment subduction rate, direct entrapment and garnet sand tracer, with SE.

Day	Direct Entrapment (g/burrow/hr)	Tracer (g/burrow/hr)
0-18	$0.30 \pm 0.03$	$0.60 \pm 0.12$
19-39	$0.30 \pm 0.06$	$0.41 \pm 0.15$
40-106	$0.17 \pm 0.04$	$0.11 \pm 0.05$

The decrease in the rate of subduction seen in the tracer cores (Figure 15) is reflected in the direct entrapment measurements (Figure 18) and is likely a consequence of lower temperatures in the late fall. Although the rate of tracer burial approaches zero it would be expected that with the rise in temperatures in the spring, the rate of subduction would increase as well. Conducting a tracer study over a greater portion of the year would be helpful in determining how well the

seasonal variations in shrimp activity are reflected in the overall subduction rate. The layer of tracer should continue being buried until reaching the level of shrimp activity.

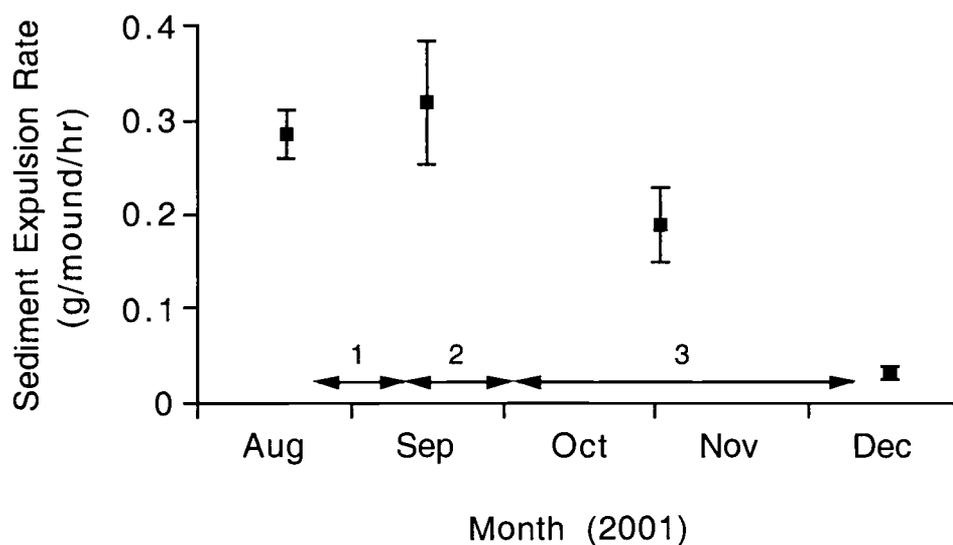


Figure 18: Sediment expulsion rate (g/burrow/hr) during the time of the garnet sand tracer experiment. The three arrows indicate the time periods of each of the three corings (after day 18, 39, and 106). Averages in sediment expulsion rate during the three periods are given in Table 3.

The subduction of the garnet sand as a single layer, rather than a gradual mixing of the tracer throughout the core, suggests there is little diffusive bioturbation occurring at this site. This is to be expected, as *Neotrypaea* is the dominant species in the habitat, with other infauna consisting primarily of small, shallow-dwelling species such as *Leptochelia dubia*.

Using the values of subduction rate obtained by the tracer method, it is possible to determine how rapidly surface material would reach a shrimp feeding at a depth of 30 cm. At the highest rate of 0.031 cm/day (cf. Figure 15), it would take

approximately 970 days (2.65 years) to reach the feeding depth, and this estimate does not include much of the seasonal variability. This subduction rate is much slower than that given by other researchers investigating *Neotrypaea*. MacGinitie (1934) estimated that turnover of the upper 30 cm occurred every 240 days, although he did not discuss his method of estimating reworking rate. Miller (1984) used MacGinitie's published rates combined with densities observed in Mugu Lagoon, CA to conclude that it would only take 36 days to mix to 30 cm. These rates are presumably based on measurements made at a single time period. As the present study and others (Berkenbusch and Rowden, 1999; Rowden and Jones, 1993) discuss, the variability in expulsion rates over the seasons must be considered. Other differences that may account for the discrepancies in these rates include the density of the population, the average shrimp size, and the warmer conditions found in the California estuaries where MacGinitie and Miller studied.

Few studies have compared two methods of measuring reworking rate. As the review by Rowden and Jones (1993) discusses, there are several potential problems with making comparisons, including scaling up or down to arrive at the same units. In one study that explicitly looked at two methods, direct entrapment and leveling, Suchanek and Colin (1986) found that reworking rates were nearly twice as high using leveling than for direct entrapment. They attribute the higher rates found in leveling to chance selection of a particularly active area because the difference in the two measurements is not statistically significant, although it is more likely that the destruction of the mounds in the leveling process may cause an increase in shrimp activity as they rebuild the mounds. The results here show that the two non-destructive techniques are comparable, at least in an area where *Neotrypaea* is the primary bioturbator and physical reworking is limited.

## FEEDING MODE

The subduction rate results suggest that if *Neotrypaea*'s method of feeding is to ingest food at depth that has gradually been brought down from the surface by burial (i.e., it is a conveyor-belt species; Rhoads, 1974), then individuals are not closely tied to the seasonal variations that occur at the surface. Additionally, they must be feeding on very refractory material because what is left after months of degradation is of very low quality. This is reflected in the higher C:N ratio observed in the sediments from depth (cf. Figure 13).

The long turnover times and therefore low quality food suggests that *Neotrypaea* may be feeding on material other than, or in addition to, that found at depth. This has been proposed by a number of other researchers. Griffis and Chavez (1988), after close examination of burrow architecture and trophic mode-burrow morphology models, suggest that *Neotrypaea* is a generalist, feeding on both detritus and suspended particles, at least at the southern portion of its range. Another possible nutritional source for the shrimp is bacteria found within the sediment. It has been proposed that sediment reworking by *Neotrypaea* creates an environment that is favorable to growth of bacteria and thus the shrimp have an additional food resource (Miller, 1984). Recent investigation of optimal foraging in *Callinassa subterranea* by Stamhuis et al. (1998) suggests that thalassinidean shrimp may selectively ingest small sediment grains. As there is greater surface area per volume for small particles, ingesting smaller particles would be energetically more favorable, assuming equal amounts of organic material per area. These studies suggest that the shrimp work actively to improve their nutritional options and may not be limited to only the very refractory material that reaches them at depth.

Rice and Rhoads (1989) examined early diagenesis of organic matter and its consequences for subsurface deposit feeders. Their analysis suggests that below

the top few centimeters of sediment, very little of the particulate organic carbon is available to deposit feeders. They conclude that deposit feeders can only make use of labile organic material by rapid bioturbation, which would subduct surface material to feeding depth, or by regular physical disturbance, which would serve as an "injection mechanism" delivering high quality surface material to depth. In the absence of such subduction or injection, subsurface fauna must rely on organic material that is not surface derived (e.g., bacteria or dissolved organic carbon).

The results of studies on several subsurface deposit feeders have supported this general idea. Biologically-mediated subduction of surface particulate organic material appears to be the mechanism providing the nutritional material for the conveyor-belt, deposit-feeding, orbiniid polychaete *Scoloplos* spp. The maintenance of its patch density over the year was attributed to "population-level control of subduction of food resources" because higher density patches would subduct a greater proportion of the food material and this food would be of higher quality (Rice, 1986). Physical injection of surface-derived benthic diatoms was found to be the primary food source for a similar orbiniid polychaete, *Leitoscoloplos fragilis* (Bianchi, 1988). Although bioturbation by *L. fragilis* was negligible, sediment mixing by the high-energy environment of Cape Henlopen enabled the polychaete to feed on high quality material at depth. Clough and Lopez (1993) examined the head-down deposit feeding polychaete *Heteromastus filiformis*. They concluded that because of its high sulfide tolerance, this polychaete is able to feed on dissolved and particulate carbon sources, primarily bacterial-derived, that other deposit feeders are unable to use.

Although Rice and Rhoads' (1989) model gives two options, rapid bioturbation or regular physical disturbance, to provide labile organic material to subsurface deposit feeders, an experiment on another conveyor-belt species, *Clymenella torquata*, suggested that this polychaete uses an additional feeding mode, namely "hoeing," to feed on material that is deposited directly on the surface

before it has been degraded (Weinberg, 1988). In the study, natural detritus was added to the sediment surface and polychaete growth was measured after 30 and 80 days. Higher growth rates were observed after 30 days, a response too rapid to be accounted for by subduction of surface material to the feeding depth, which would take 100 days based on reworking rates.

The presence of fresh pieces of green macroalgae at depths of 20-50 cm within the sediment suggest that *Neotrypaea* may indeed use additional methods than simply deposit feeding on material that has been slowly subducted from the surface. Additionally, the HPLC data suggests that the amount of chlorophyll *a* found at depth is too high to be the result of subduction of material. Given published degradation rates ( $k = 0.1 \text{ day}^{-1}$ ) (Sun et al., 1993), the  $29.2 \mu\text{g chl } a/\text{g}$  dry sed found at the surface would be completely degraded to undetectable levels in approximately 70 days. The relatively high levels of chlorophyll found at depth within the sediment during the winter months ( $2.1 \mu\text{g chl } a/\text{g}$  dry sed at 30 cm in February) indicate that there must be other mechanisms of input of organic material. Laboratory or field manipulations on *Neotrypaea* such as those conducted on *Clymenella* would help to clarify this issue.

#### GENERALIZATIONS FROM THE TEMPORAL STUDY

When applying the findings in this study, it is important to remember that only one full year was covered by the sampling regime. Deviations from typical climate conditions could impact the activity of the shrimp in unknown ways. In fact, the period from October 2000 through December 2001 was much drier than a normal year. Table 4 presents a summary of Oregon Climate Service data for this time period compared to long-term averages. For the usually rainy months of

October through February, 594 mm of rain fell, only 50% of the 1961-1990 mean of 1189 mm.

The low level of precipitation is reflected in the discharge of the Yaquina River, which was significantly below normal for much of the year. River discharge was measured for the Yaquina River only for the period 1972-1991, but data for the nearby Alsea River are available up to the present. Examination of daily data from the two rivers for the years of 1989-1991 shows that the two are closely correlated. The regression equation of YAQUINA DISCHARGE = (0.204 x ALSEA DISCHARGE) - 0.064 ( $r^2 = 0.90$ ) allows for extrapolation of the river discharge to the period covered by this study (Figure 19). During the winter of 2000-2001, the Yaquina River discharge was at levels roughly one-third of average for much of the time.

Table 4: Newport climate data, temperature and rainfall, for the period covered by this study and the long-term average (1961-1990).

	Temp 2000 (°C)	Temp 2001 (°C)	Avg. (°C)	Precip 2000 (cm)	Precip 2001 (cm)	Avg. (cm)
Jan	7.29	8.68	6.96	37.1	11.4	27.2
Feb	8.86	7.22	7.85	28.4	11.2	20.3
Mar	8.00	8.76	8.16	12.4	16.8	20.8
Apr	10.34	12.67	8.96	8.9	13.5	12.2
May	12.09	11.53	10.93	9.9	5.6	8.9
Jun	13.46	12.87	12.92	8.9	7.9	6.9
Jul	14.74	14.08	14.18	1.3	1.0	2.5
Aug	14.68	15.09	14.51	0.3	4.6	3.3
Sep	14.96	13.49	13.98	4.3	1.8	6.6
Oct	11.91	11.05	11.74	11.4	12.7	13.7
Nov	8.18	10.36	9.12	10.7	32.3	27.7
Dec	8.94		7.04	14.7	33.8	30.0
Year	11.12	10.89	10.56	148.3	152.4	180.1

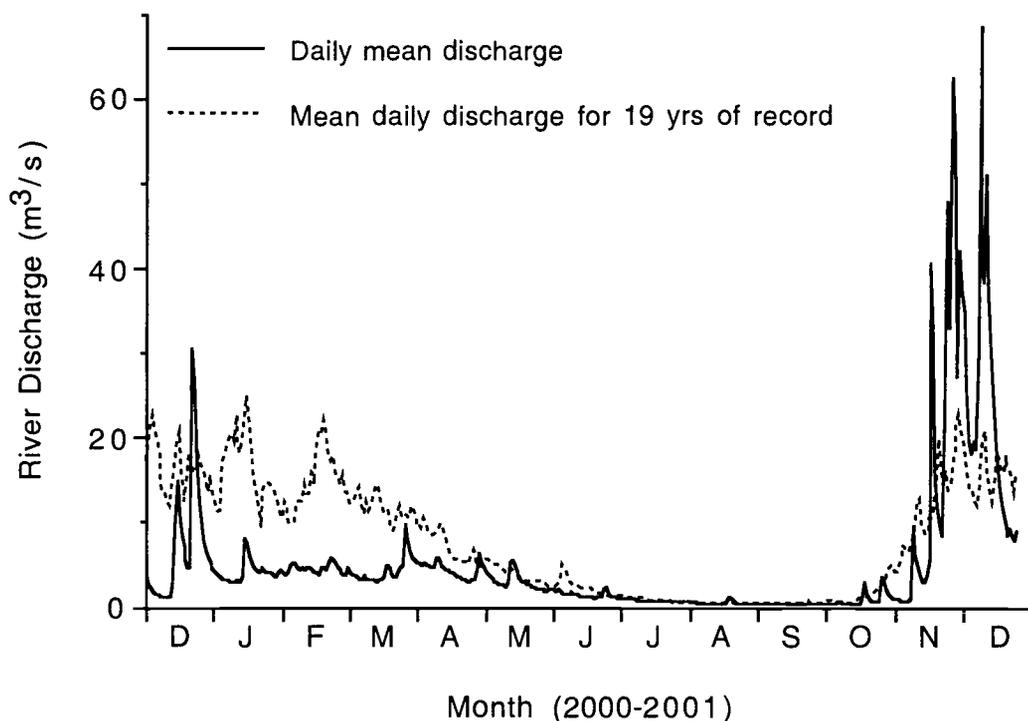


Figure 19: Yaquina River discharge (m<sup>3</sup>/s) for the period of this study obtained from a regression with Alsea River, compared to the 19-year observed average (1972-1991).

It is not clear what effects, if any, the low levels of precipitation may have had on the ecology of Yaquina Bay. Because *Neotrypaea* is tolerant to a wide salinity range (Posey, 1987), it seems unlikely that higher salinities (a consequence of low precipitation and river discharge) had any impact on the shrimp. There is anecdotal evidence suggesting that the amount and extent of macroalgae in the intertidal region were greater than recent years past.

While precipitation was significantly below average, temperatures over the study period were roughly average. Because there is a close correlation between

temperature and sediment reworking rates (cf. Figure 17), the reworking rates measured in this study are likely to be representative of an average year.

## IMPLICATIONS FOR THE YAQUINA BAY ESTUARY

*Neotrypaea* dominates extensive portions of the tidal flats of Yaquina Bay. This seasonal study was limited to a single 400-m<sup>2</sup> area in the intertidal to minimize the spatial variability. Because of this limitation, applying the findings to the Bay as a whole must be viewed with caution. Nevertheless, because *Neotrypaea* is a key structuring agent in the estuary, there are some important implications of the patterns observed in this study for understanding the intertidal ecology in Yaquina Bay.

Even with the decrease observed in population numbers, the average biomass of *Neotrypaea* at this site was 4.7 g dry wt/m<sup>2</sup>. Other areas of the estuary may maintain biomass higher than that, since the average shrimp size at this site was fairly small compared to maximum sizes attained by *Neotrypaea*. Clearly *Neotrypaea* is a significant portion of the infaunal biomass in Yaquina Bay.

The peak in sediment turnover, as given by rate/m<sup>2</sup>, occurred in the spring. This could affect the settling larvae of other species, namely the suspension-feeding mud shrimp, *Upogebia pugettensis*, which recruits in the spring (April-June) (Dumbauld et al., 1996). Several researchers have documented the division between areas populated by *Neotrypaea* and by *Upogebia*; particularly at their highest densities the two species are rarely found inhabiting the same area (DeWitt et al., 1997; Swinbanks and Luternauer, 1987). It is possible that the high rate of sediment reworking limits the ability of *Upogebia* to recruit in dense areas of *Neotrypaea*.

In soft-sediment research, there are several theories about how benthic organisms may influence the success of other species via modification of the sedimentary environment. These hypotheses include trophic-group amensalism (Rhoads and Young, 1970), adult-larval interactions (Woodin, 1976), and the mobility mode hypothesis (Brenchley, 1981).

Trophic-group amensalism states that suspension feeders have lower growth and survival in the presence of deposit feeders because the particle resuspension caused by bioturbation clogs the feeding parts of suspension feeders. Suspension feeders would therefore be limited to areas where there are few deposit feeders. This hypothesis suggests an amensalistic interaction, in which one group, the suspension feeders, is negatively impacted while the other, the deposit feeders, is unaffected.

Woodin put forth a competitive interaction hypothesis in adult-larval inhibition. Her work is particularly relevant when considering possible negative impacts of *Neotrypaea* reworking on recruitment of *Upogebia*. Woodin considered three discrete assemblages of infaunal organisms: burrowing deposit feeders, suspension feeders, and tube builders. She hypothesized that sharp boundaries of these assemblages may be explained by interactions of the established adults and the settling larvae. Specifically, deposit feeders inhibit recruitment by ingesting and/or disturbing recent recruits, suspension-feeders filter larvae out of the water, and the feeding and defecation of tube-builders inhibits recruitment.

Other modes of competitive interactions between *Neotrypaea* and infaunal organisms have been proposed. The mobility mode hypothesis states that the burrowing of mobile infauna negatively impacts sedentary species by disruption of the sediment. Tube building by sedentary species stabilizes the sediment, which in turn inhibits the activity of mobile species. Consequently, species of the two mobility modes will be segregated. Posey (1986a) showed strong negative correlations between shrimp densities and the numbers of several infaunal

organisms, including spionid polychaetes and amphipods. He suggested that this was due to disruption of sessile organisms by the extensive activity of *Neotrypaea*, giving support to the mobility mode of inhibition. Because he observed less shrimp activity in the winter months, Posey hypothesized that there would be less of a difference in faunal composition between areas of high and low ghost shrimp densities during the winter. Although some species appeared to follow this pattern, his data overall were inconclusive.

The present study shows that sediment reworking tends to follow a seasonal pattern. This would have important implications for the success of other species, whether through adult-larval interactions or a mobility mode of inhibition. Additionally, because reworking negatively impacts the commercial oyster through the burial of spat, sinking of adults into the unconsolidated sediment, and clogging of feeding structures, variations in shrimp activity could have implications for management of *Neotrypaea* populations in regions of oyster culture.

## FUTURE INVESTIGATIONS

Although this study investigated three factors influencing sediment reworking rates of *Neotrypaea*, there are several areas that would benefit from more extensive investigations. Ideally these studies would involve manipulative laboratory or field experiments that could establish a more definitive relationship between reworking rates and forcing parameters than the correlations observed here. In particular, the question of food availability and nutritional source for *Neotrypaea* remains unclear. Experiments that alter the availability of food, in the form of macroalgae or diatoms, and measure subsequent reworking rates would be valuable (and challenging). Particularly interesting would be to see if the nutritional sources vary over the year; gut content analyses would provide useful

information. Additionally, because of the limited spatial scope of this project, it would be helpful to look at sediment reworking in other areas of Yaquina Bay and/or other Pacific Northwest estuaries. The garnet sand tracer method requires less time and energy than the direct entrapment method and therefore could be useful in estimating overall reworking rates at several locations. This extended spatial coverage could help to elucidate other factors, such as population demography, tidal height location and duration of exposure, and salinity effects, that may be relevant to understanding sediment reworking by *Neotrypaea*.

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**APPENDICES**

## APPENDIX 1

Included in this appendix are the data collected over the course of this study for the direct entrapment measurements and the coring to determine shrimp population densities.

Table A1: Sediment expulsion rates (g/mound/hr), as measured by direct entrapment, for all months of the study.

Plot	Replicate	10/24/00	10/25/00	10/26/00	10/31/00
1	A	0.2175	0.3923	1.0470	0.2539
1	B	0.8735	-	0.4212	1.1785
1	C	-	1.2196	1.7132	0.5675
1	D	1.1506	0.5283	0.2801	0.0217
1	E	0.2348	0.7111	0.5957	0.1123
2	A	0.6608	0.2326	1.0516	0.0158
2	B	0.3406	0.0340	0.0850	0.0536
2	C	0.0935	0.3481	0.0910	0.0090
2	D	0.2267	0.0291	0.0726	0.1616
2	E	0.1352	0.0113	1.5466	0.2664
3	A	0.1251	0.1724	0.3078	0.0102
3	B	0.5648	0.0285	0.3489	0.1085
3	C	-	0.3281	0.2881	0.0744
3	D	0.0493	0.2532	0.0288	0.2176
3	E	1.4883	0.1746	0.0122	0.2380
4	A	0.1101	0.5115	0.4377	0.9802
4	B	0.0890	0.0698	0.1312	0.0200
4	C	0.0948	0.5629	0.5018	0.2541
4	D	-	0.0420	0.4090	0.0653
4	E	1.4838	2.3065	0.5930	1.3761
5	A	0.9983	0.0175	-	0.3453
5	B	0.1849	0.0717	0.3212	0.1308
5	C	0.1322	0.2563	0.3473	0.1245
5	D	0.8148	0.5151	0.1313	0.0065
5	E	0.2141	0.4861	0.1888	0.5529

Table A1 (continued)

Plot	Replicate	12/13/00	12/17/00
1	A	0.0369	0.0118
1	B	0.0216	0.0130
1	C	0.0479	0.0222
1	D	0.0278	0.0537
1	E	0.0916	0.0203
2	A	0.0453	0.0602
2	B	0.1545	0.0371
2	C	0.0648	0.1128
2	D	0.0752	0.0284
2	E	0.1840	0.0705
3	A	0.0524	0.0317
3	B	0.0247	0.0658
3	C	0.0270	0.0171
3	D	0.0197	0.0251
3	E	0.0162	0.1154
4	A	0.0178	0.0145
4	B	0.0757	0.0125
4	C	0.0452	0.0279
4	D	0.0166	0.0114
4	E	0.0127	0.0224
5	A	0.0536	0.0125
5	B	0.0315	0.0247
5	C	0.0146	0.0188
5	D	0.0291	0.0189
5	E	0.0320	0.0269

Table A1 (continued)

Plot	Replicate	1/24/01
1	A	0.0430
1	B	0.2232
1	C	0.0780
1	D	0.0271
1	E	0.2910
2	A	0.0580
2	B	0.0277
2	C	0.0279
2	D	0.0900
2	E	0.0021
3	A	0.0092
3	B	0.0087
3	C	0.0854
3	D	0.0139
3	E	0.0077
4	A	0.0076
4	B	0.0181
4	C	0.0031
4	D	0.0099
4	E	0.1378
5	A	0.0634
5	B	0.0625
5	C	0.0065
5	D	0.0086
5	E	0.0096

Table A1 (continued)

Plot	Replicate	2/22/01	2/23/01	2/24/01	2/25/01
1	A	0.1707	0.0212	0.0129	0.3054
1	B	0.0091	0.0649	0.2295	0.2573
1	C	0.0149	0.0161	1.4274	-
1	D	0.0127	0.0140	0.0295	0.2312
1	E	0.0156	0.7012	3.3737	-
2	A	0.0057	1.7655	0.0131	-
2	B	0.0097	0.0277	0.2811	0.0404
2	C	0.0116	0.3171	0.0335	1.2207
2	D	-	0.0205	0.0367	0.2218
2	E	0.0213	0.0099	1.1247	0.4243
3	A	0.0140	0.0131	0.0585	0.2387
3	B	0.0104	0.3829	0.8649	0.2943
3	C	0.0093	0.2076	0.0191	0.1136
3	D	0.0101	0.0093	0.0668	-
3	E	0.0078	0.0175	0.0110	0.0319
4	A	0.0037	0.0088	0.0256	0.0259
4	B	0.0191	0.0066	0.0134	0.0606
4	C	0.0245	0.0061	0.0063	0.0663
4	D	0.0255	0.0449	0.0364	0.5252
4	E	0.0043	0.0029	0.0253	0.0191
5	A	0.0152	0.0059	0.0080	-
5	B	0.0317	0.0067	0.0088	0.0119
5	C	0.0348	0.0073	0.0186	0.0200
5	D	0.0329	0.0054	0.0092	0.0136
5	E	0.0186	0.0032	0.0079	0.0446

Table A1 (continued)

Plot	Replicate	3/22/01	3/23/01	3/24/01	3/26/01
1	A	0.0102	2.1105	0.2755	0.6550
1	B	0.1276	0.1137	0.6102	0.0356
1	C	0.4484	0.1637	0.5403	0.3037
1	D	0.1217	0.4100	0.2069	1.2995
1	E	0.7761	0.0231	1.0455	4.0296
2	A	1.8097	0.0124	0.3112	0.1319
2	B	0.0574	0.2647	0.2359	0.6604
2	C	0.7864	0.0206	0.0181	1.3884
2	D	0.0152	0.0203	0.0312	0.0077
2	E	0.0129	0.0000	0.0462	0.0176
3	A	0.5141	0.0237	0.5560	1.1800
3	B	2.0889	0.2451	1.9950	0.4860
3	C	0.0064	1.7629	1.6587	0.0124
3	D	0.0173	0.0072	0.1754	0.6789
3	E	0.0171	0.0128	0.0122	0.0303
4	A	0.0214	0.0215	0.0162	0.6254
4	B	0.0105	0.6828	0.2451	0.0494
4	C	0.0171	0.0133	0.0078	0.0329
4	D	0.0103	0.0130	0.0103	0.0132
4	E	0.0080	0.0101	0.0109	0.0801
5	A	0.0067	0.0110	0.0202	0.0194
5	B	0.0085	0.0192	0.0284	0.0139
5	C	0.0216	0.0323	0.1113	0.0101
5	D	0.0110	0.0135	0.0112	0.0202
5	E	0.0104	0.0150	0.0174	0.0336

Table A1 (continued)

Plot	Replicate	4/20/01	4/21/01	4/22/01	4/23/01
1	A	0.1937	0.2437	0.9398	0.7344
1	B	0.0988	0.2524	1.3234	0.0330
1	C	1.1497	0.1420	0.8935	0.9007
1	D	0.0256	1.3561	0.9231	0.0252
1	E	0.4105	0.0067	0.0191	0.0556
2	A	0.0163	0.2335	0.1569	0.0947
2	B	0.4397	0.9134	0.0464	0.0197
2	C	0.0651	0.8314	0.0086	0.5009
2	D	0.6024	0.8978	1.3649	1.5961
2	E	0.1888	0.0111	2.3695	0.0219
3	A	0.0279	0.0183	2.6882	0.1106
3	B	0.0807	0.0194	1.5870	0.2059
3	C	0.0241	0.0208	0.1193	0.2505
3	D	0.0354	0.6674	0.1350	0.6190
3	E	0.0619	1.1233	0.5607	1.1234
4	A	0.0309	0.0250	0.0060	0.0069
4	B	0.0336	0.0266	0.0980	0.0181
4	C	0.1528	0.0322	0.0059	0.0158
4	D	0.0691	0.0140	0.0802	0.0352
4	E	0.0834	0.0678	0.0073	0.9334
5	A	0.0729	0.0290	0.0122	0.0256
5	B	0.0118	0.0247	0.0958	0.0206
5	C	0.0546	0.1677	0.0076	0.0139
5	D	0.0561	0.0138	0.0054	0.0131
5	E	0.0666	0.1114	0.1433	0.3638

Table A1 (continued)

Plot	Replicate	6/23/01	6/24/01
1	A	0.0278	0.1927
1	B	0.0415	0.1450
1	C	0.6405	0.0808
1	D	0.0467	0.3889
1	E	0.2705	0.8147
2	A	0.0217	0.0819
2	B	0.0627	0.1014
2	C	0.0537	0.0505
2	D	0.0234	0.2448
2	E	0.0411	0.0947
3	A	0.0457	0.0380
3	B	0.1046	0.0372
3	C	0.3533	0.0314
3	D	0.3961	0.0449
3	E	0.4638	0.7024
4	A	0.0602	0.0490
4	B	0.0422	1.4360
4	C	0.0638	0.0514
4	D	0.0790	0.1246
4	E	0.0459	0.2179
5	A	0.1600	0.1089
5	B	0.0604	0.3715
5	C	0.0607	0.1089
5	D	0.2136	0.1150
5	E	0.0587	0.1189

Table A1 (continued)

Plot	Replicate	7/19/01	7/20/01	7/21/01	7/22/01
1	A	0.4316	0.0288	0.0417	0.0291
1	B	0.1334	2.2132	0.6233	0.1885
1	C	0.0802	0.3977	0.0596	0.0728
1	D	0.0468	0.0466	0.0733	0.2542
1	E	0.0607	0.0405	0.9134	0.0434
2	A	0.0325	0.1648	0.0551	0.2647
2	B	0.0538	0.0396	0.3534	0.0964
2	C	0.0572	0.0166	0.0808	0.6249
2	D	0.0281	0.2068	0.0712	0.4388
2	E	0.1741	0.6181	-	0.2272
3	A	0.0845	0.7313	0.1202	0.7847
3	B	0.0237	0.2575	0.0609	2.0842
3	C	0.3054	0.3884	0.0558	0.0384
3	D	0.5249	0.1686	-	2.7391
3	E	0.1717	0.0297	0.0814	0.0275
4	A	0.0566	0.0322	0.1040	0.1791
4	B	0.0556	0.9680	0.0346	0.1933
4	C	0.2573	0.0418	0.0495	0.0437
4	D	0.0831	0.0367	0.1891	0.1329
4	E	0.1163	0.2050	0.8888	-
5	A	0.4297	0.0423	0.3345	0.0714
5	B	0.8688	-	1.4083	0.0878
5	C	0.1028	0.0386	0.5331	0.2736
5	D	0.0927	0.8871	0.6667	-
5	E	0.1484	0.0453	0.2056	0.2854

Table A1 (continued)

Plot	Replicate	8/17/01	8/18/01	8/20/01
1	A	0.0720	0.1383	0.1487
1	B	0.1085	0.1296	0.1876
1	C	0.1241	0.1611	0.2987
1	D	0.2960	0.2562	0.4722
1	E	0.0900	0.1872	0.2777
2	A	0.0757	0.2279	0.2909
2	B	0.0934	0.2881	0.3831
2	C	0.1117	0.5431	-
2	D	0.0921	0.4609	0.2812
2	E	0.1433	0.1525	0.7153
3	A	0.1807	0.7468	0.6326
3	B	0.0846	0.1732	0.4683
3	C	0.1150	0.1692	-
3	D	0.1013	0.2644	0.1458
3	E	0.1083	0.6568	0.2612
4	A	0.0838	0.5127	0.1592
4	B	0.7780	1.0595	0.1537
4	C	0.2849	0.2821	0.2625
4	D	0.1773	0.2945	0.9543
4	E	0.1640	0.5596	0.0917
5	A	0.2098	0.1751	0.4373
5	B	-	-	0.4263
5	C	0.2066	0.3207	0.1320
5	D	-	0.2401	-
5	E	0.0752	0.5050	0.2040

Table A1 (continued)

Plot	Replicate	9/14/01	9/15/01	9/16/01
1	A	0.0687	0.2770	0.1839
1	B	0.0657	0.1413	0.4178
1	C	0.3429	0.1446	0.0968
1	D	-	0.1817	-
1	E	0.0530	0.1314	0.1891
2	A	-	0.1548	0.0918
2	B	0.0614	-	0.1508
2	C	0.0642	0.5490	0.0827
2	D	0.0397	0.1362	0.0878
2	E	0.9284	0.1756	0.0730
3	A	0.2230	0.1751	0.8845
3	B	0.0787	0.2584	0.1254
3	C	0.2589	0.2280	0.1433
3	D	0.0924	0.2169	0.0530
3	E	0.5415	0.2849	0.1148
4	A	0.3650	0.3874	0.2139
4	B	0.1861	0.1281	0.0887
4	C	0.2408	0.2081	1.0095
4	D	0.1005	0.1386	0.0728
4	E	0.3478	0.3387	0.2927
5	A	3.6484	0.1769	2.5980
5	B	0.0670	0.1545	0.0988
5	C	0.0641	0.1571	1.1928
5	D	0.0991	0.1618	1.0787
5	E	0.0514	0.1521	0.2618

Table A1 (continued)

Plot	Replicate	10/30/01	10/31/01	11/1/01
1	A	0.0132	-	1.5562
1	B	0.5132	0.6292	0.5155
1	C	0.0060	0.0047	0.1387
1	D	-	0.0064	0.0843
1	E	0.5395	0.0123	0.2632
2	A	-	-	0.0048
2	B	-	0.0464	0.8476
2	C	0.0904	-	0.0489
2	D	0.0316	0.0085	0.2486
2	E	0.0203	0.0088	0.0157
3	A	0.0328	0.2317	1.0330
3	B	0.0047	0.1162	0.0114
3	C	0.0365	0.0128	0.0101
3	D	0.0549	0.0177	0.4203
3	E	0.0449	0.0513	0.0075
4	A	0.0387	0.0510	0.0330
4	B	0.4114	1.2070	0.0170
4	C	0.1314	0.1027	-
4	D	0.1225	0.0150	0.0385
4	E	0.0065	0.0365	0.3950
5	A	0.1917	0.0145	0.1546
5	B	0.0044	-	0.0097
5	C	0.0098	0.0081	0.6634
5	D	0.2487	0.6313	-
5	E	-	0.0048	0.0114

Table A1 (continued)

Plot	Replicate	12/15/01
1	A	0.0092
1	B	0.0227
1	C	0.0189
1	D	0.0148
1	E	0.0062
2	A	0.0422
2	B	0.0809
2	C	0.0346
2	D	0.0917
2	E	0.0562
3	A	0.0031
3	B	0.0076
3	C	0.0074
3	D	0.0037
3	E	0.0096
4	A	0.0427
4	B	-
4	C	0.0302
4	D	0.0111
4	E	-
5	A	0.0043
5	B	0.0031
5	C	0.0932
5	D	0.1126
5	E	0.0040

Table A2: Total number of shrimp collected in 3 cores (21.5 cm diameter, to a depth of 50 cm) at each of 5 sampling plots.

Date	Plot	Number of Shrimp
12/20/00	1	25
	2	29
	3	22
	4	33
	5	21
1/30/01	1	23
	2	20
	3	19
	4	21
	5	33
2/28/01	1	19
	2	16
	3	13
	4	14
	5	12
3/28/01	1	16
	2	13
	3	16
	4	12
	5	10
4/30/01	1	10
	2	21
	3	9
	4	10
	5	6
5/24/01	1	19
	2	13
	3	9
	4	8
	5	8

Table A2 (continued)

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<u>Date</u>	<u>Plot</u>	<u>Number of Shrimp</u>
6/26/01	1	18
	2	11
	3	10
	4	14
	5	6
7/24/01	1	10
	2	9
	3	8
	4	5
	5	6
8/23/01	1	7
	2	8
	3	6
	4	10
	5	8
9/20/01	1	7
	2	7
	3	13
	4	7
	5	9
11/6/01	1	18
	2	8
	3	9
	4	6
	5	12
12/30/01	1	12
	2	12
	3	5
	4	no data
	5	no data

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## APPENDIX 2

The following calculations were done to convert between individual reworking rate from direct entrapment and overall reworking rate from the heavy mineral tracer. Bold units indicate measurements that were obtained from sampling.

Converting from tracer subduction rate (mm/day) to individual reworking rates (g/burrow/hr) for a 1-m<sup>2</sup> area:

$$\text{mm/day} \times 1 \text{ cm}/10 \text{ mm} \times (100\text{cm})^2/1 \text{ m}^2 \times 1 \text{ day}/12 \text{ hrs submerged} \times 1.835 \text{ g/cm}^3 \times \mathbf{1 \text{ m}^2/\text{no. of shrimp}} \times 1 \text{ shrimp}/1 \text{ burrow} = \text{g/burrow/hr}$$

Converting from individual reworking rate (g/burrow/hr) to subduction rate of tracer (mm/day) follows the reverse of the above equation.