BULLETIN OF MARINE SCIENCE, 72(3): 629–638, 2003

FIELD EVIDENCE OF KRILL GRAZING ON THE TOXIC DIATOM GENUS *PSEUDO-NITZSCHIA* IN MONTEREY BAY, CALIFORNIA

Sibel Bargu and Mary W. Silver

ABSTRACT

Both the interactions between toxic phytoplankton and their grazers, and the transport of these toxins through the food chain are relatively poorly understood. Recently, species of the diatom *Pseudo-nitzschia* have been found to produce the neurotoxin domoic acid, which has caused detrimental effects to higher trophic levels in the food web. One of the key potential vectors for the toxin is the euphausiids (krill). To determine whether krill feed in nature on local species of *Pseudo-nitzschia*, we compared diatoms in the water to those in the gut of three species of euphausiids in July 1998 during a *P. pseudodelicatissima* bloom and in the gut of one species of euphausiid in August 2000 during a *P. australis* bloom in Monterey Bay, California. Our findings show that *Pseudo-nitzschia* was the most abundant diatom in water samples at both times and was also the dominant food in krill. Our findings show that *Pseudo-nitzschia* was the most abundant diatom in water samples at both times and was also the dominant food in krill, though these diatoms were more common in the diet of resident than in transient species of krill. Thus we demonstrate that krill may be a critical vector in the transmission of domoic acid to organisms at higher trophic levels, including squid, seabirds, and whales, since these predators normally consume krill in Monterey Bay.

Krill (euphausiids) play a major role in the pelagic food web of the world's oceans, being both important zooplankton grazers on diatoms as well as valuable food for a variety of higher organisms such as planktivorous fish, squid, marine birds and baleen whales (Nemoto, 1972; Morejohn et al., 1978; Mauchline, 1980; Ainley et al., 1996; Schoenherr, 1991). Since krill are capable of directly feeding on phytoplankton, they can form a direct link between primary producers and their relatively large pelagic predators.

Recently species of the diatom *Pseudo-nitzschia* that produce domoic acid (DA), a neurotoxic amino acid, have been shown to be responsible for deaths of higher trophic level organisms, including humans (Wright et al., 1989). Monterey Bay hosted major DA poisoning events in 1991, 1998 and 2000, with deaths of hundreds of seabirds, and sea lions. In each case, *Pseudo-nitzschia australis* was believed to be the toxin source, and filter feeding anchovies the likely vector of DA to birds and sea lions (Fritz et al., 1992; Work et al., 1993; Lefebvre et al., 1999; Scholin et al., 2000). Anchovies are not the only potential DA vectors in Monterey Bay, because zooplankton may also be key consumers of phytoplankton. While the link between zooplankton and toxic algae has been confirmed by studies of zooplankton grazing on toxic dinoflagellates (e.g., White, 1981a; Ives, 1987; Uye and Takamatsu, 1990; Turriff et al., 1995; Bagoien et al., 1996; Teegarden and Cembella, 1996; Shaw et al., 1997; Turner and Tester, 1997; Turner et al., 2000; Tester et al., 2000), similar attention has not been focused on toxin transfer between toxic diatoms and their zooplankton grazers. Copepods have been found to accumulate domoic acid in earlier lab studies (Windust, 1992; Tester et al., 2001; Lincoln et al., 2001); however, there appears to be no previous study establishing a krill trophic linkage in any DA poisoning event in the field (Bargu et al., 2002, 2003), although herbivorous krill have

been shown to consume and thus potentially transmit toxins from a dinoflagellate that produces paralytic shellfish poisons (McClatchie, 1988).

The food preference of euphausiids (krill) depends on the availability and the quality of food, as well as the developmental stage of the animals (Mauchline, 1980; Opalinski et al., 1997). To define the role of krill in toxin transfer, it is necessary to know their position in the food web and their response to toxic food species. Krill are opportunistic omnivores, capable of both catching small zooplankton, such as copepods, and filtering water for phytoplankton (Ohman, 1994; Price et al., 1988). They can feed on phytoplankton directly, depending upon the availability and size of these food items. During regular spring and fall blooms in Monterey Bay, *Pseudo-nitzschia* is one of the dominant phytoplankton. Under such conditions, *Pseudo-nitzschia* may be heavily grazed by krill.

It is not yet known whether krill are killed by domoic acid, refrain from feeding on *Pseudo-nitzschia*, or whether they can transfer the toxin through the food web. The primary purpose of this research was, therefore, to determine whether krill feed on *Pseudo-nitzschia* species. Thus, the food items from krill digestive tracts were compared with phytoplankton populations in water samples from which krill were collected in Monterey Bay during blooms of *P. pseudodelicatissima* (a non-toxic species) and *P. australis* (a toxic species).

Materials and Methods

Sampling.—Both water and krill samples were collected on July 13, 1998 from waters overlying the Monterey Submarine Canyon, approximately 13 km offshore from Moss Landing, California (121°59.28′W, 36°41.40′N) and on 24 August, 2000 from waters off Point Lobos, California (121°57.4′W, 36°31.3′N). Surface water samples were collected prior to towing a zooplankton net at 1 m depth. Phytoplankton samples were preserved in 10% Lugol (10% KI, 5% I_2 and 10% glacial acetic acid in 100 ml DI water) for cell counts and scanning electron microscopy (SEM). Another 15 to 30 ml of water were collected for cell enumeration using rRNA probes for August 2000 samples. For cellular DA determination, 500 ml water aliquots were filtered onto 25 mm GF/F filters (Whatman Inc., Clifton, New Jersey), and stored at −80 °C until being processed for analyses of particulate DA. Two ml of the filtrate was frozen at −80 °C for dissolved DA measurements. Domoic acid concentrations in the samples were analyzed using high performance liquid chromatography with fluorenylmethoxy carbonyl derivatization (HPLC-FMOC), as described by Pocklington et al. (1990).

Krill were obtained in near-surface hauls (0–100 m) at the same site on both occasions using a Bongo net equipped with 333 m mesh (Ocean Instruments Inc., San Diego, California). Specimens were placed in 5% buffered formalin for later gut content analysis. *Euphausia pacifica*, *Thysanoessa spinifera*, and *Nematoscelis difficilis* were available for qualitative gut observations in July 1998 and *E. pacifica* in August 2000. The gut contents were removed from the krill (n = 10 for each species) and gently discharged into scintillation vials. All the gut samples were preserved in 5% buffered formalin solution until being processed for SEM.

Toxic *Pseudo-nitzschia* Cell Counts.—Water column abundance of toxic *P. australis* was determined using whole cell hybridization with species-specific large subunit (LSU) rRNA-targeted fluorescent probes (Miller and Scholin, 1996). Fifteen to 30 ml aliquots of seawater were filtered onto 1.2 m isopore polycarbonate filters (Millipore) and preserved with a saline ethanol solution for at least one hour. After rinsing with hybridization buffer (Miller and Scholin, 1996), each sample was incubated with species specific probes for *P. australis*, *P. multiseries*, a positive eukaryote control probe and a negative control probe designed for *Alexandrium tamarense*. A third control consisted of sample with no probe added. After 1 h, filters were rinsed and placed on microscope

slides. Intact cells that retained the fluorescein labeled probe were then counted on a Zeiss Standard 18 compound microscope, equipped with epifluorescence (microscope illuminator 100, Zeiss Inc., with high pressure mercury lamp, 50 W). The entire area of each filter was counted. Results are given in cells per liter.

MICROSCOPY.—Cell counts for *Pseudo-nitzschia* and toxin measurements for domoic acid provided quantitative estimates for this study. To determine the cumulative abundance of all *Pseudo-nitzschia* species, counts were made from surface water samples using an inverted microscope on three replicates. On the light microscope, species of *Pseudo-nitzschia* can not be distinguished from each other and thus scanning electron microscopy (SEM) was needed to determine the proportions of individual species within the genus.

SEM methods for *Pseudo-nitzschia* identification in water and krill gut samples were slight modifications of methods from Miller and Scholin (1998). Water samples (10 ml) and krill gut contents were concentrated onto 1.2 μm pore size isopore polycarbonate membrane filters (Millipore). Salt was removed from samples by rinsing three times with 3 ml DI water under low vacuum pressure (150 mm Hg). To remove organic material, 2–3 drops of saturated $KMnO_4$ were added until the filters were covered (valves were closed) and allowed to digest for 5 min (water) or 15 min (krill gut contents). Next, 3 ml 12.1 N HCl was added to the water samples until the color became clear. Krill gut content samples were held for 30 min in 3 ml of 12.1 N HCl to complete the oxidation process. Samples were then gently vacuumed and rinsed three times with DI water. This process was repeated twice, and the filters removed from filter tubes and fixed to aluminum stubs. Filters were air dried in a dessicator for 24 h and then mounted onto SEM stubs with double-sided tape and sputter coated with gold palladium. All micrographs were taken with an ISI WB-6 electron microscope at 10 kV.

RESULTS

JULY 1998.—On July 13, 1998, cell densities of *Pseudo-nitzschia* (all species) in surface waters of Monterey Bay averaged 0.9×10^6 cells L^{-1}, indicating bloom conditions at the offshore sampling site. Domoic acid was not detected by HPLC-FMOC in particulate or dissolved samples from the site, suggesting the presence of non-toxic species of *Pseudo-nitzschia*. Light microscopy examination showed that diatoms were the dominant net plankton in the water, with *Pseudo-nitzschia* and *Chaetoceros* the most common genera. Scanning electron microscopy (SEM) was used to determine the species of *Pseudo-nitzschia*, and the taxonomic criteria used where these described in the literature (Hasle et al., 1996). SEM revealed that the pennate diatom *Pseudo-nitzschia pseudodelicatissima* was the overwhelmingly dominant species of *Pseudo-nitzschia* in the water (Fig. 1A–C), followed by species of *Chaetoceros* (Fig. 1-D1). Other small centric (Fig. 1-D2) and pennate diatoms, including two additional *Pseudo-nitzschia* species (*P. heimii*, *P fraudulenta*), also occurred in the samples at much lower numbers.

E. pacifica, *T. spinifera* and *N. difficilis*, the latter being an uncommon euphausiid for the area, occured abundantly in the zooplankton tow samples and all three were chosen for gut content analysis using SEM. All replicates of all three species of krill contained abundant frustules of *P. pseudodelicatissima* (Fig. 2A–E). Although all three species of krill contained *Pseudo-nitzschia*, there were differences in the relative abundance of this diatom genus among the three species of euphausiids. In all, *P. pseudodelicatissima* was the dominant, with *Chaetoceros* being the next most abundant diatom, and low numbers of other reportedly non-toxic *P. fraudulenta* and *P. heimii*. Diatoms, including *Pseudo-nitzschia*, were less abundant in *N. difficilis* (Fig. 2E) than in the other two euphausiid species (Figure 2A–D) and the frustules were also more frequently unbroken in *N. difficilis*.

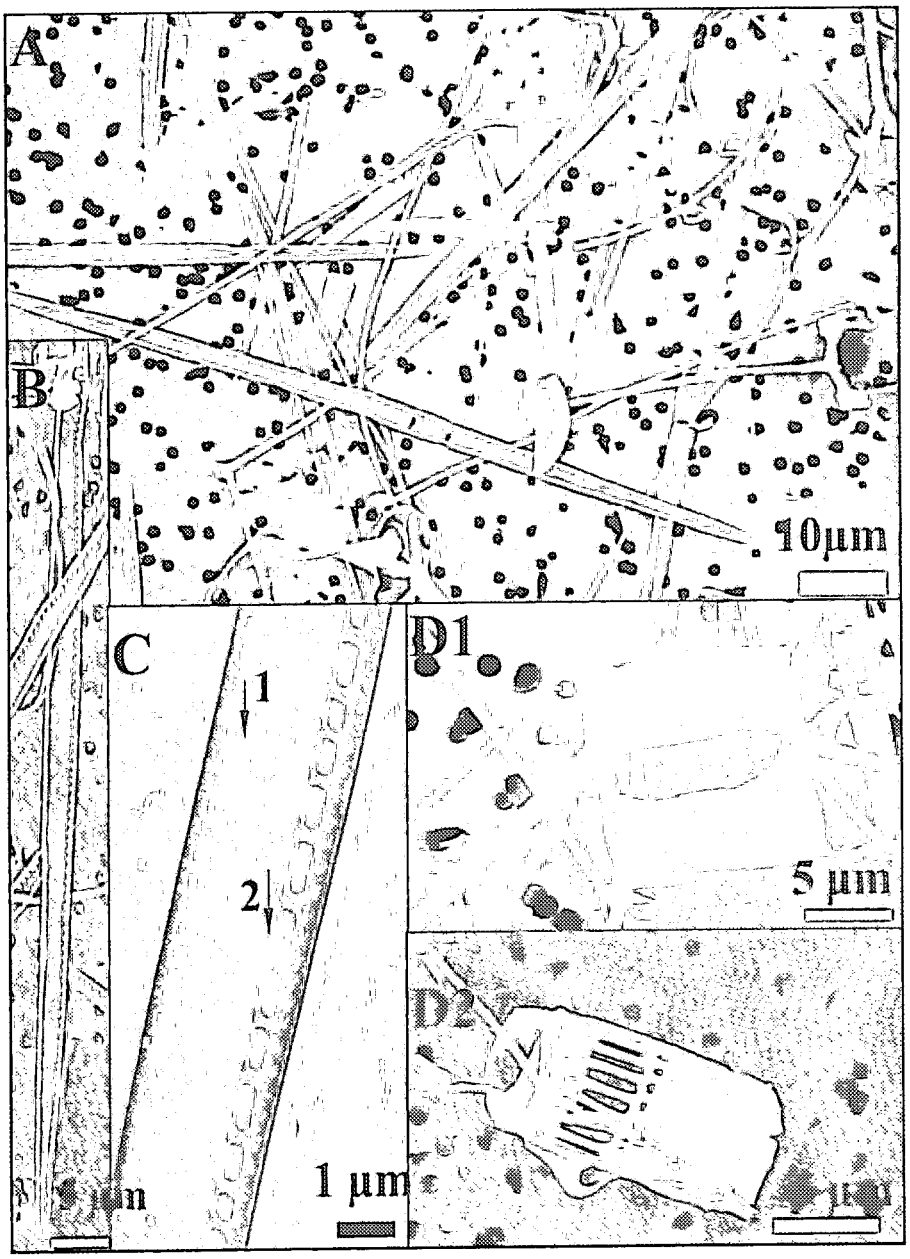

Figure 1. Scanning electron micrographs of phytoplankton samples. A. *Pseudo-nitzschia* spp. (mostly *P. pseudodelicatissima*); B. Complete valve of *P. pseudodelicatissima*; C. High magnification view of *P. pseudodelicatissima*, showing presence of single row of large poroids in the stria (arrow 1) and central interspace with central nodule (arrow 2). Other diatom species found in water: D1. *Chaetoceros* sp., and D2. *Skeletonema costatum*.

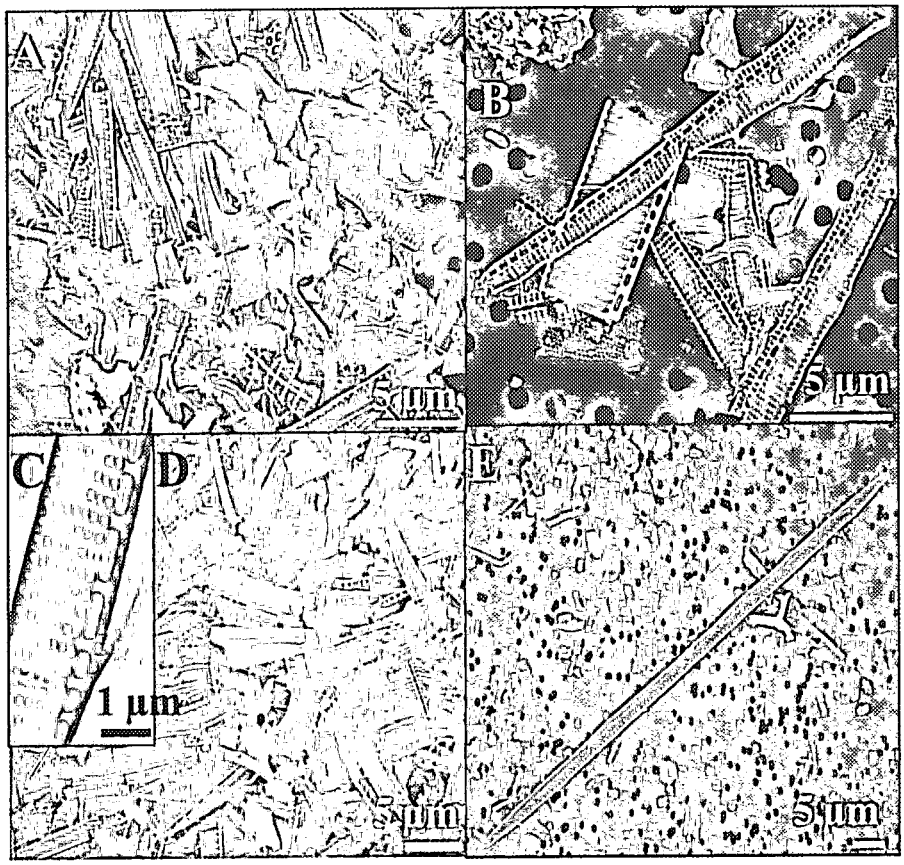

Figure 2. Scanning electron micrographs of krill gut contents taken from specimens collected on July 13,1998. A. *Euphausia pacifica* contents; B. Higher magnification view *of E. pacifica* content; C. *Thysanoessa spinifera* contents; D. Higher magnification view *of Pseudo-nitzschia pseudodelicatissima* valve from *T. spinifera*; E. *Nematoscelis difficilis* contents showing an intact frustule of *P. pseudodelicatissima*.

AUGUST 2000.—On August 24, 2000, as in the 1998 sample, cell densities of total *Pseudo-nitzschia* approached 10^6 cells L^{-1}, this time dominated by *P. australis,* as determined by species-specific LSU rRNA targeted fluorescent probes (Fig. 3A). Domoic acid averaged 24 pg $cell^{-1}$ in the particulate samples from the site, implicating *P. australis* as the source of the toxin. *E. pacifica* was the dominant euphausiid in the tow, with low numbers of *T. spinifera* but no *N. difficilis*. The digestive tracts of *E. pacifica* were dominated by *P. australis* (Fig. 3B,C).

DISCUSSION

Our goal was to evaluate the potential role of krill as a toxin vector in Monterey Bay. To determine whether krill consume *Pseudo-nitzschia* in nature, including the domoic acid producing species, we compared diatom species in the water to those in krill digestive tracts in Monterey Bay. Results indicated that in July 1998, during a bloom of *P. pseudodelicatissima*, and in August 2000, during a bloom of *P. australis,* krill did, in-

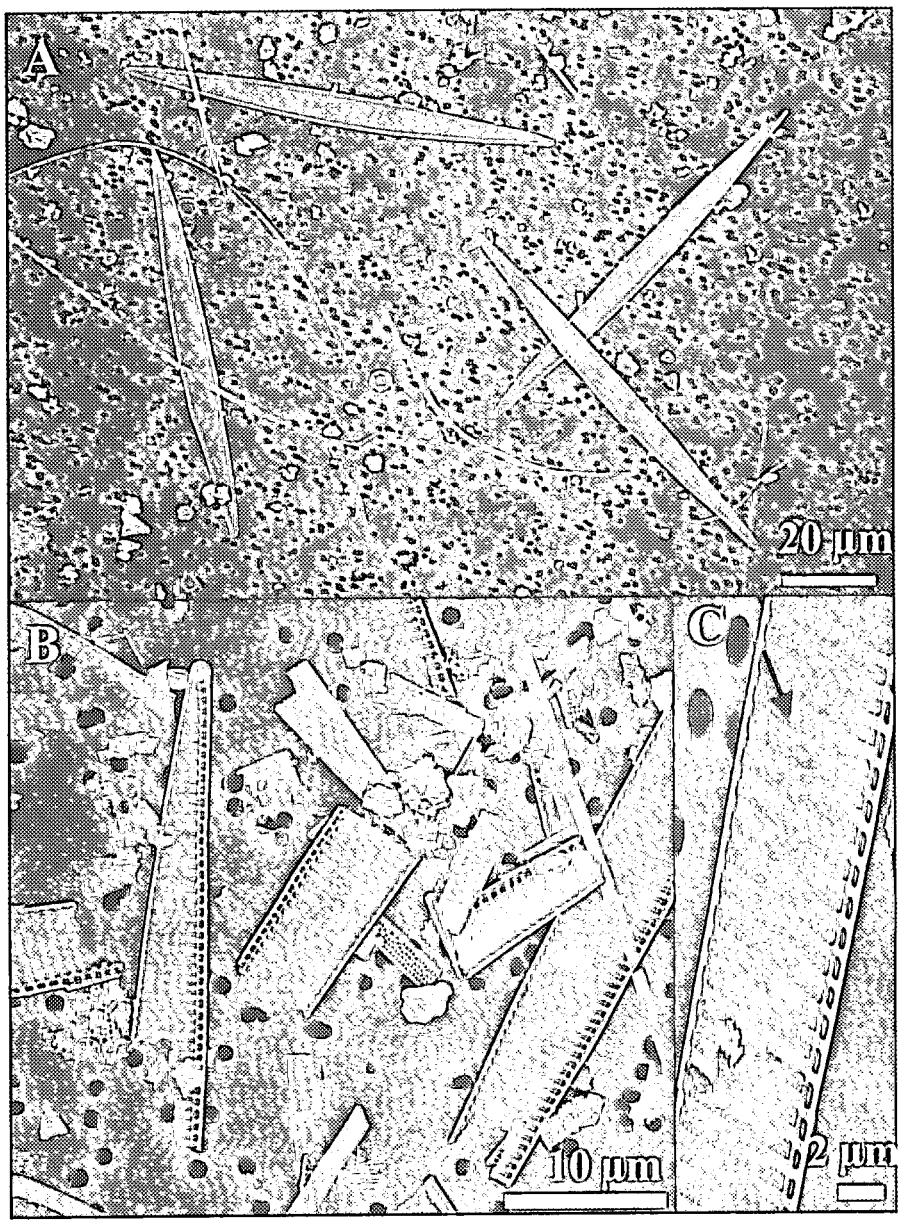

Figure 3. A. Scanning electron micrograph of water sample containing several *P. australis* frustules; B. Scanning electron micrograph of krill gut with *Pseudo-nitzschia australis* frustules; C. Higher magnification view of one of the frustules from B. An arrow indicates the presence of two rows of large poroids within the striae. A central nodulus is absent. Both krill and water samples were obtained during the August 2000 *P. australis* bloom event in Monterey Bay, California.

deed, feed primarily on *Pseudo-nitzschia*, the dominant diatom in Monterey Bay. In both events, the population density of both *P. pseudodelicatissima* and *P. australis* reached 10^6 cells L^{-1}, supplying an almost monospecific food source for organisms in the area.

In the 1998 event, our data suggest that krill were grazing a non-toxic population of *P. pseudodelicatissima*, based on our DA analyses. There is, however, a possibility that a

small amount of the toxin may be produced by Monterey Bay clones of *P. pseudodelicatissima* (C. Scholin, pers. comm.). Low levels (up to 2.7 $\mu g\ L^{-1}$) of DA were found in October 1998 in Washington coastal waters dominated by *P. pseudodelicatissima,* with cell concentrations about $10^6\ L^{-1}$ (Trainer et al., 2000). In addition, it has been reported that *P. pseudodelicatissima* produces toxin in eastern Canada, Danish coastal waters, and the northern Gulf of Mexico (Martin et al., 1990; Lundholm et al., 1997; Pan et al., in press). Even though *P. pseudodelicatissima* was not (or was minimally) toxic in the present study, the ability of krill to graze these colonies in the field suggested that they may also consume the similarly sized and shaped toxic members of the same genus.

In the August 2000 bloom, *P. australis* numbers were $10^6\ L^{-1}$ and DA levels reached 24 $pg\ cell^{-1}$. Even though the *Pseudo-nitzschia* cells were highly toxic, krill consumed these diatoms. It is not known whether krill are affected by the toxin, but it is possible that they might avoid absorption of the toxin through the gut, or might have developed a detoxification mechanism. The ability of krill to consume toxic *P. australis* reveals a new vector for toxin transfer to krill predators, including squid, seabirds and baleen whales.

It is known that krill can also consume smaller zooplankton, including copepods, even in the presence of suitable phytoplankton (Ohman, 1994; Holm-Hansen and Huntley, 1984; Price et al., 1988). Copepods can be important prey, especially for those species of krill that show carnivorous feeding preferences. Since copepods can ingest toxic *Pseudo-nitzschia* (Windust, 1992; Tester et al., 2001), krill may also alternatively vector domoic acid by preying on copepods that are consuming toxic *Pseudo-nitzschia.*

The dominance of *Pseudo-nitzschia* in the stomachs of krill reflected the dominance of this phytoplankter in the water. Different species of krill, however, seemed to show slight differences in their food preference. While both *E. pacifica* and *T.spinifera* contained many fragments of both toxic and non-toxic species of *Pseudo-nitzschia* in their gut, *N. difficilis*, found only in 1998 sampling, contained fewer *Pseudo-nitzschia* and other diatoms in general. *N. difficilis* is not a common euphausiid in Monterey Bay and its presence here at latitudes more northerly than its normal range may have been linked to the El-Niño conditions at the time. This krill species, therefore, may be unfamiliar with common food species in the region, resulting in lower consumption rates. Similar results have been found by Turner and Tester (1989): the copepod *Centropages typicus*, which almost never co-occurs in nature with the more southerly *Gymnodinium breve*, did not ingest this toxic dinoflagellate. Alternatively, Mauchline (1980) indicates that *N. difficilis* has mouth appendages appropriate for a more carnivorous diet than the other two species. For whatever reason, *N. difficilis* may have been consuming more zooplankton than phytoplankton at the time of the 1998 *Pseudo-nitzschia* bloom in Monterey Bay.

Gut contents of animal prey are difficult to recognize in krill, because krill masticate or suck out the soft tissues of their prey, rejecting any exoskeleton. Furthermore, our SEM preparation methods would have digested organic material that might have provided clues to their prey's identity. Thus we could not determine the relative abundance of diatom vs zooplankton prey of krill in this study. However, most importantly, we found all three species of krill to consume *Pseudo-nitzschia* when this diatom is abundant. We could not make quantitative measurements of *Pseudo-nitzschia* from gut contents, because the diatom frustules were usually fragmented. However, among the frustules present, *P. pseudodelicatissima* and *P. australis* were the clear dominant in 1998 and 2000, respectively, as they were in the water. SEM was critical in identifying the mineralized algal walls, which are impossible to identify to the species level in this genus by light micros-

copy. Even the newer molecular probe methods are unsuitable for partially digested *Pseudo-nitzschia* from stomach contents, thus leaving SEM as the only practical method of determining species of *Pseudo-nitzschia* from stomach contents.

In summary, this study presents a first step in understanding the interaction between krill and the domoic acid-producing genus *Pseudo-nitzschia*, suggesting that krill may potentially vector domoic acid to higher trophic levels. Further research is necessary to determine whether DA affects krill themselves, and whether it is depurated rapidly or retained for sufficient time periods to contaminate higher level predators.

Acknowledgements

We thank B. B. Marinovic and C. Scholin for help with sample collections and advice. We also thank S. L. Coale for providing counts of *Pseudo-nitzschia* for the 2000 event. We thank to J. M. Krupp for help with the SEM. P. Tester and B. Steele provided insightful reviews of the manuscript. SEM costs were supported by Institute of Marine Sciences, University of California, Santa Cruz.

Literature Cited

Ainley, D.G., L. B. Spear and S. G. Allen. 1996. Variation in the diet of Cassin's auklet reveals spatial, seasonal and decadal occurrence patterns of euphausiids of California, USA. Mar. Ecol. Prog. Ser. 137(1): 1–10.

Bagoien, E., A. Miranda, B. Reguera and J. M. Franco. 1996. Effects of two paralytic shellfish toxin producing dinoflagellates on the pelagic harpacticoid copepod *Euterpina acutifrons*. Mar. Biol. 126: 361–369.

Bargu, S., C. L. Powell, S. L. Coale, M. Busman, G. J. Doucette and M. W. Silver. 2002. Krill: A potential vector for domoic acid in marine food webs. Mar. Ecol. Prog. Ser. 237: 209–216.

_____, B. marinovic, S. Mansergh and M. W. Silver. 2003. Feeding responses of krill to the toxin-producing diatom *Pseudo-nitzschia*. J. Exp. Mar. Biol. Ecol. 284: 87–104.

Fritz L, M. A. Quilliam, J. L. C. Wright, A. M. Beale and T. M. Work. 1992. An outbreak of domoic acid poisoning attributed to the pennate diatom *Pseudo-nitzschia australis*. J. Phycol. 28: 439–442.

Hasle, G. R. and E. E. Syvertsen. 1996. A review of *Pseudo-nitzschia*, with special reference to the Skagerrak, North Atlantic, and adjacent waters. Helgoländer Merres. 50: 131–175.

Holm-Hansen, O. and M. Huntley. 1984. Feeding requirements of krill in relation to food sources. J. Crust. Biol. 4: 156–173.

Ives, J. D. 1987. Possible mechanisms underlying copepod grazing responses to levels of toxicity in red tide dinoflagellates. J. Exp. Mar. Biol. Ecol. 112: 131–145.

Lefebvre, K. A., C. L. Powell, G. J. Doucette, P. D. R. Moeller, J. B. Silver, P. E. Miller, M. P. Hughes, S. Singaram, M. W. Silver and R. S. Tjeerdema. 1999. Detection of domoic acid in northern anchovies and California sea lions associated with an unusual mortality event. Nat. Toxins 7: 85–92.

Lincoln, J. A., J. T. Turner, S. S. Bates, C. Léger and D. A. Gauthier. 2001. Feeding, egg production, and egg hatching success of the copepods *Acartia tonsa* and *Temora longicornis* on diets of the toxic diatom *Pseudo-nitzschia multiseries* and the non-toxic diatom *Pseudo-nitzschia pungens*.Hydrobiologia 453/454: 107–120.

Lundholm, N., J. Skov, R. Pocklington and Ø. Moestrup. 1997. Studies on the marine planktonic diatom *Pseudo-nitzschia*. 2. Autecology of *P. pseudodelicatissima* based on isolated from Danish coastal waters. Phycologia 36: 381–388.

Mauchline, J. 1980. The biology of mysids and euphausiids. Adv. Mar. Biol. 18: 373–677.

Martin, J. L., K. Haya, L. E. Burridge and D. J. Wildish. 1990. *Nitzschia pseudodelicatissima* – a source of domoic acid in the Bay of Fundy, eastern Canada. Mar. Ecol. Prog. Ser. 67: 177–182.

Miller P.E and C. A. Scholin. 1996. Identification of cultured *Pseudo-nitzschia* (Bacillariphyceae) using species-specific LSU rRNA-targeted fluorescent probes. J Phycol. 32: 646-655.

_____ and _____. 1998. Identification and enumeration of cultured *Pseudo-nitzschia* using species-specific LSU rRNA-targeted fluorescent probes and filter based whole cell hybridization. J. Phycol. 34: 371–382.

Morejohn, G. V., J. T. Harvey and L. T. Krasnow. 1978. The importance of *Loligo opalescens* in the food web of marine vertebrates in Monterey Bay, California. Calif. Dept. Fish Game, Fish Bull. 169: 67–97.

Nemoto, T. 1972. History of research into the food and feeding of euphausiids. Proc. Roy. Soc. Edinburgh (Biology). 73: 259–265.

Ohman, M. D. 1994. Omnivory by *Euphausia pacifica*: the role of copepod prey. Mar. Ecol. Ser. 19: 125–131.

Opalinski, K. W., K. Maciejewska and L. V. Georgieva. 1997. Notes on food selection in the Antarctic krill, *Euphausia superba*. Polar Biol. 17: 350–357.

Pan, Y., M. L. Parsons, M. Busman, P. D. R. Moeller, Q. Dortch, C. L. Powell and G. J. Doucette. (in press). *Pseudo-nitzschia pseudodelicatissima* – a confirmed producer of domoic acid from the northern Gulf of Mexico. Mar. Ecol. Prog. Ser.

Pocklington, R., J. E. Milley, S. S. Bates, C. J. Bird, A. S. W. De Freitas and M. A. Quilliam. 1990. Trace determination of domoic acid in seawater and phytoplankton by high-performance liquid chromatography of the fluorenylmethoxycarbonyl (FMOC) derivative. Int. J. Environ. Anal. Chem. 38(3): 351–68.

Price, H. J., K. R. Boyd and C. M. Boyd. 1988. Omnivorous behavior of the Antarctic krill *Euphausia superba*. Mar. Biol. 97: 67–77.

Schoenherr, J. R. 1991. Blue whales feeding on high concentrations of euphausiids around Monterey Submarine Canyon. Can. J. Zool. 69: 583–594.

Scholin, C. A. and others. 2000. Mortality of sea lions along the central California coast linked to a toxic diatom bloom. Nature 403: 80–84.

Shaw, B. A., R. J. Andersen and P. J. Harrison. 1997. Feeding deterrent and toxicity effects of apofucoxanthinoids and phycotoxins on a marine copepod (*Tigriopus californicus*). Mar. Biol. 128: 273–280.

Teegarden, G. J. and A. D. Cembella. 1996. Grazing of toxic dinoflagellates, *Alexandrium* spp., by adult copepods of coastal Maine: Implications for the fate of paralytic shellfish toxins in marine food webs. J. Exp. Mar. Biol. Ecol. 196: 145–176.

Tester, P. A., J. T. Turner and D. Shea. 2000. Vectorial transport of toxins from the dinoflagellate *Gymnodinium breve* through copepods to fish. J. Plankton Res. 122(1): 47–61.

_____, Y. Pan and G. J. Doucette. 2001. Accumulation of domoic acid activity in copepeods. Pages 418–420 *in* G. M. Hallegraeff, S. E. Blackburn, C. J. Bolch and R. J. Lew, eds. Harmful algal blooms 2000. Proc. 9th Int'l. Conf. Harmful Algal Blooms, IOC-UNESCO, Paris 2001.

Trainer, V. L., N. G. Adams, J. C. Wekell and M. Lesoing. June 2000. Domoic acid production by *Pseudo-nitzschia pseudodelicatissima* off the central Washington coast is linked to record levels of toxin in razor clams. J. Shellfish Res. 19(1): 638.

Turner, J. T. and P. A. Tester. 1989. Zooplankton feeding ecology: copepod grazing during an expatriate res tide. *In* Cosper, E. M., Bricelj, V. M. and Carpenter E. J., eds. Coastal and Estuarine Studies, 35. Novel phytoplankton blooms. Causes and impacts of recurrent brown tides and other unusual blooms. Springer Verlag.

_____ and _____. 1997. Toxic marine phytoplankton, zooplankton grazers, and pelagic food webs. Limnol. Oceanogr. 42: 1203–1214.

_____, G. J. Doucette, C. L. Powell, D. M. Kulis, B. A. Keafer and D. M. Anderson. 2000. Accumulation of red tide toxins in larger size fractions of zooplankton assemblages from Massachusetts Bay, USA. Mar. Ecol. Prog. Ser. 203: 95–107.

Turriff, N., J. A. Runge and A. D. Cembella. 1995. Toxin accumulation and feeding behavior of the planktonic copepod *Calanus finmarchicus* to red-tide dinoflagellate *Alexandrium excavatum*. Mar. Biol. 123: 55–64.

Uye, S. and K. Takamatsu. 1990. Feeding interactions between planktonic copepods and red-tide flagellates from Japanese coastal waters. Mar. Ecol. Prog. Ser. 59: 97–107.

White, A. W. 1981. Marine zooplankton can accumulate and retain dinoflagellate toxins and cause fish kills. Limnol. Oceanogr. 26: 103–109.

Windust, A. 1992. The responses of bacteria, microalgae and zooplankton to the diatom, *Nitzschia pungens* f. *multiseries* and its toxic metabolite domoic acid. MS. Thesis, Dalhousie Univ. 107 p.

Work, T. M., A. M. Beale, L. Fritz, M. A. Quilliam, M. W. Silver, K. Buck and J. L. C. Wright. 1993. Domoic acid intoxication of brown pelicans and cormorants in Santa Cruz, California. Pages 643–649 *in* T. J. Smayda and Y. Shimizu, eds., Toxic Phytoplankton Blooms in the Sea. Elsevier, Amsterdam.

Wright, J. L. C. and others. 1989. Identification of domoic acid, a neuroexcitatory amino acid, in toxic mussels from eastern Prince Edward Island. Can. J. Chem. 67: 481–490.

DATE SUBMITTED: December 11, 2000. DATE ACCEPTED: June 22, 2001.

ADDRESS: *Department of Ocean Sciences, University of California, Santa Cruz, Earth and Marine Science Building, 1156 High Street, Santa Cruz, California, 95064.* CORRESPONDING AUTHOR: (S.B.) *E-mail: <sbargu@cats.ucsc.edu>.*