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North Atlantic right whales, *Eubalaena glacialis*, exposed to paralytic shellfish poisoning (PSP) toxins via a zooplankton vector, *Calanus finmarchicus*

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Abstract

The seriously endangered north Atlantic right whale (*Eubalaena glacialis*) is regularly exposed to the neurotoxins responsible for paralytic shellfish poisoning (PSP) through feeding on contaminated zooplankton acting as a vector of these dinoflagellate toxins. This chronic exposure occurs during several months each summer while the whales are present on their late summer feeding ground in Grand Manan Basin in the lower Bay of Fundy. Based on estimated ingestion rates, we suggest that these toxins could affect respiratory capabilities, feeding behavior, and ultimately the reproductive condition of the whale population.
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Keywords: Right whale; *Eubalaena*; Dinoflagellate; *Alexandrium*; Zooplankton; *Calanus*; PSP toxin

1. Introduction

The north Atlantic right whale (*Eubalaena glacialis*) is seriously endangered with fewer than 300 individuals remaining (Knowlton et al., 1994). A switch from a slowly recovering population in the 1980s to a declining one in the 1990s appears to be due to recent increased mortality (Fujiwara and Caswell, 2001) from ship collisions and entanglement with fishing gear (Knowlton and Kraus, 2001). However, lower population growth rates and significantly less blubber thickness of north Atlantic right whales in comparison with south Atlantic right whales off Argentina and South Africa (Best et al., 2001; Cooke et al., 2001; IWC, 2001; Moore et al., 2001) suggest that environmental factors such as toxic chemical exposure and inadequate nutrition may affect survival or reproductive success. One group of toxic chemicals, organochlorines, are not bioaccumulated to levels that are hazardous (Weisbrod et al., 2000) and are thus not likely to be the cause of the poor condition of northern right whales. Another possibility would be through the effects of biotoxins. In New England waters, humpback whales have been killed by eating Atlantic mackerel which contained the potent tetrahydropurine neurotoxins responsible for paralytic shellfish

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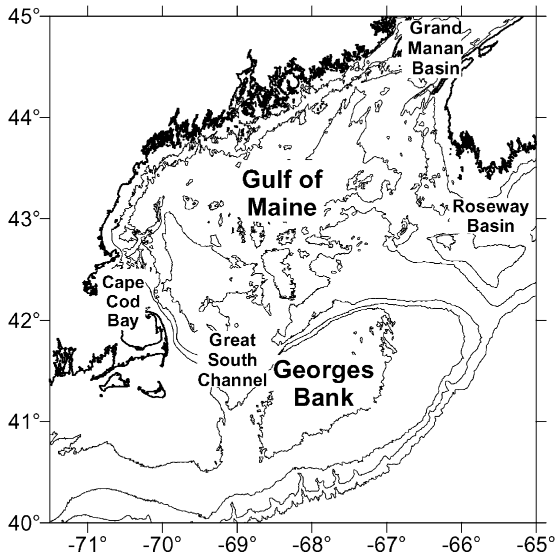

Fig. 1. The continental shelf region off northeastern United States and southeastern Canada showing right whale feeding habitats referred in the text. Isobaths shown are 50, 100, 200 and 1000 m.

poisoning (PSP) (Geraci et al., 1989). In the Gulf of Maine, these toxins are produced by the dinoflagellate *Alexandrium fundyense* and related species, and presumably were obtained by the mackerel through ingestion of contaminated zooplankton. In higher mammals, exposure to PSP toxins, comprising about two dozen naturally occurring derivatives of saxitoxin (STX), can cause neuropathology (including muscle paralysis) by blocking sodium-channel activity associated with neuro-muscular co-ordination. Ingestion of these toxins by right whales could affect respiratory capabilities, feeding behavior, and ultimately the reproductive condition of the whale population.

Right whales can be found in Grand Manan Basin in the lower Bay of Fundy (Fig. 1) during the late summer (Kraus et al., 1982; Winn et al., 1986) where they feed on the lipid rich, older stages of the large copepod *Calanus finmarchicus* (Murison and Gaskin, 1989; Woodley and Gaskin, 1996). This copepod species is known to graze on blooms of *A. fundyense* (Turriff et al., 1995; Teegarden, 1999) which regularly occur in Grand Manan Basin during the summer (Martin and White, 1988; Townsend et al., 2001). Although toxin assimilation in copepods is quite inefficient, high body burdens of PSP toxins may be accumulated during natural or simulated blooms (Teegarden et al., 1996). Here, we provide evidence for chronic exposure of north Atlantic right whales to PSP toxins from feeding directly on contaminated *C. finmarchicus*. Our results are based on observations of *A. fundyense* abundance, zooplankton toxicity and abundance, and right whale feeding behavior during cruises to Grand Manan Basin in late July 2001 and August 2001.

2. Methods

2.1. Phytoplankton and zooplankton sampling

Sampling was conducted during a NOAA Ship *Albatross IV* cruise (AL0108) from 23 July 2001 to 3 August 2001. *A. fundyense* surface samples were collected with a 20 l bucket, concentrated with a 20 μm mesh net, and counted immediately. Zooplankton were sampled with a 1 m^2 MOCNESS (0.15 mm mesh nets) at stations near feeding right whales and at two 24-h anchor stations. Prior to each MOCNESS tow, vertical casts were conducted with an optical plankton counter (OPC, Focal Technologies; Herman, 1988, 1992). The OPC, which measured the vertical distribution of particles between 0.25 and 20 mm, provided estimates of *C. finmarchicus* fifth copepodids (C5) using a calibration equation developed from comparisons with net samples (Baumgartner, 2002). Five contiguous depth strata were typically sampled with the MOCNESS and the size of each stratum was selected after examining the results of the preceding OPC casts. At the two anchor stations, MOCNESS samples were collected every 6 or 12 h.

2.2. Toxin analysis

Immediately after the MOCNESS net was retrieved, groups of 100 *C. finmarchicus* C5, the dominant taxon, were placed into vials and frozen (−20 °C) and the remaining sample preserved in 4% buffered formaldehyde for later enumeration. The frozen zooplankton samples were processed and analysed for the complete spectrum of PSP toxins by high-performance liquid chromatography with fluorescence detection (HPLC-FD) (Teegarden et al., 1996; Parkhill and Cembella, 1999). After extraction in 0.1 M acetic acid by ultrasonication (30 s at 25 W;

50% pulse duty cycle) and centrifuge–filtration of the suspension through a 0.45 μm membrane (Millipore Ultrafree-MC, Bedford, MA), duplicate injections of 20 μl of extract were compared with external toxin standards (PSP-1C) provided by the Certified Reference Material Program (CRMP) of the Institute for Marine Biosciences, NRC, Halifax, Canada. Toxin concentrations (μmol/l) were converted by the formula given in Parkhill and Cembella (1999) to toxicity units (in saxitoxin equivalents [STXeq.] per copepod).

The presence of specific PSP toxin analogues was confirmed by subsequent analysis of the copepod filtrate by hydrophilic-interaction liquid chromatography with detection by tandem mass spectrometry (HILIC-MS/MS) (Quilliam et al., 2001). The analyses were performed on an Agilent (Palo Alto, CA) HP1090 LC system with detection by a Perkin-Elmer SCIEX (Concord, Ont., Canada) API-III+ triple quadrupole mass spectrometer equipped with an ion-spray source. Qualitative analyses were carried out in positive ion mode by both full scan and selected reaction monitoring (SRM).

2.3. Right whale ingestion rates

Ingestion rates of copepods by right whales are based on (1) estimated in situ feeding rates from observations during a cruise immediately following AL0108 (Baumgartner, 2002), and (2) an assumption of a fixed weight-specific feeding rate. Weight-specific ingestion rates of PSP toxins were determined from these copepod ingestion rates, observed copepod toxicity and a right whale weight of 40,000 kg (Kenney et al., 1986).

Right whales were tagged with suction-cup mounted, recoverable, time-depth recorders (TDR; Wildlife Computers Inc.) in Grand Manan Basin during a NOAA Ship *Delaware II* cruise (DE0108) from 7–31 August 2001 (Baumgartner, 2002). These tags were attached to right whales from a 7.5 m rigid-hulled inflatable boat (RHIB) using a 9 m telescoping pole. The TDR measured pressure at a port exposed to the seawater and logged the corresponding depth of the tag at a resolution of 2 m once every second. The tagged whales were tracked visually and via radio and acoustic transmitters incorporated in the tag. Precise diving and resurfacing locations were obtained from the RHIB using a global positioning system (GPS) device. Shortly after obtaining a resurfacing location after a long dive, a vertical cast was conducted with an OPC at this same location from the NOAA Ship *Delaware II*. The abundance of *C. finmarchicus* C5 was estimated from these OPC data in 4 m depth strata. After detachment from the whale, the positively buoyant tag was recovered from the water and the archived data were downloaded. Successful attachment durations were between 1.1 and 2.0 h. Presumed feeding dives were characterized by a rapid descent, remarkable fidelity to a narrow depth strata for 4.7–13.6 min (median = 9.4 min) and a rapid ascent back to the surface.

Ingestion of *C. finmarchicus* C5 for feeding dives was estimated as the product of the filtration efficiency of right whale baleen, the mouth area, the swimming speed, the concentration of *C. finmarchicus* C5 available to the whale and the time at depth (excluding descent and ascent periods). We assumed filtration efficiency for *C. finmarchicus* C5 to be 100% and the mouth area to be 1.21 m^2 (Mayo et al., 2001). Swimming speeds were estimated from the diving and resurfacing positions, but these are likely underestimates of the true swimming speeds since right whales may not always feed along straight paths at depth (Mayo and Marx, 1990; Nowacek, personal communication). Therefore, the swimming speed was assumed to be 1.5 m/s whenever the estimated speed was less than 1.5 m/s (Watkins and Schevill, 1976). Tagged right whales consistently dove to and foraged at the depth of maximum *C. finmarchicus* C5 abundance (Baumgartner, 2002), so the concentration of *C. finmarchicus* C5 available to the whale was assumed to be the maximum concentration in the water column observed by the OPC. Ingestion rates were computed as the total estimated ingestion for all observed feeding dives divided by the duration of the deployment period.

The second approach assumed that right whales eat 4% of their body weight per day (Sergeant, 1969). Assuming that the typical *C. finmarchicus* C5 individual contains 150 μg C (Durbin et al., 1995a), has a carbon content of 55% dry weight (R. Campbell, unpublished), and a water content of 84% (Bamstedt et al., 1986), the estimated wet weight is 1.7 mg. The ingestion rate of *C. finmarchicus* C5 is then estimated to be 9.41×10^8 copepods per day based on a right whale weight of 40,000 kg (Kenney et al., 1986).

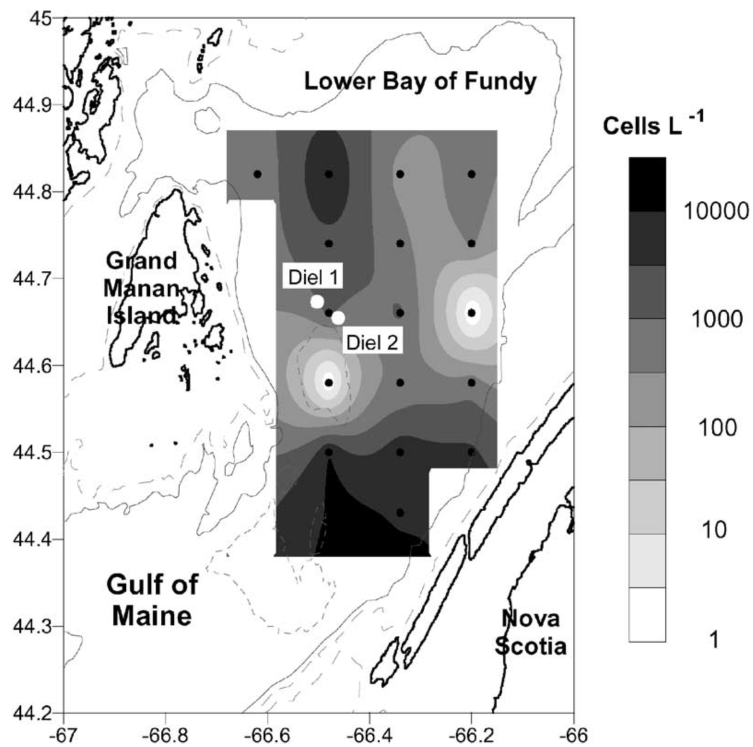

Fig. 2. Surface concentrations of *Alexandrium fundyense* in Grand Manan Basin during 25–26 July 2001. Concentrations are $\log_{10}$ cells/l.

3. Results

A bloom of *A. fundyense* was present in Grand Manan Basin during the cruise (23 July 2001 to 3 August 2001) at cell concentrations of up to 10,400 per liter (Fig. 2). The dominant zooplankter was the copepod *C. finmarchicus*, primarily as stage C5. At two 24-h anchor stations in the right whale feeding area where repeated MOCNESS casts were made, C5 individuals comprised an average of 79 and 94%, respectively, of the *C. finmarchicus* population. At the first anchor station (Diel 1), two *C. finmarchicus* populations were present: (1) an actively feeding and growing surface population comprised of primarily C5, but also containing some C4 and adult females, that was undergoing diel vertical migration, and (2) a deep population of non-migrating C5 individuals between 100 and 180 m, presumably in diapause (Fig. 3). Within the migrating population, C4 and C5 only appeared to be migrating within the upper part of the water column and did not move down into the diapausing layer during the day, while the adult females were migrating through the whole water column. In contrast, at the second anchor station (Diel 2), most of the population consisted of non-migrating deep dwelling C5. This deep population typically formed a dense layer near the top of a bottom mixed-layer (Fig. 4; Baumgartner, 2002).

Both surface and deep populations of *C. finmarchicus* contained substantial PSP toxin levels when converted to toxicity units (ng STXeq.). Overall mean toxicity of surface (0–60 m) and deep (75–200 m) C5 individuals was 0.87 ng STXeq. per copepod, (100 individuals per sample, $n = 28$, S.D. $= 0.33$, range $= 0.27$–1.59) and 0.41 ng STXeq. per copepod, ($n = 31$, S.D. $= 0.18$, range $= 0.09$–0.73), respectively. There were day–night differences in the mean toxicity of the surface C5 copepodites but not among copepods collected at depth. In the two diel studies, daytime toxicity of surface animals was 0.95 and 0.24 ng STXeq. per copepod while night-time values were 1.51 and

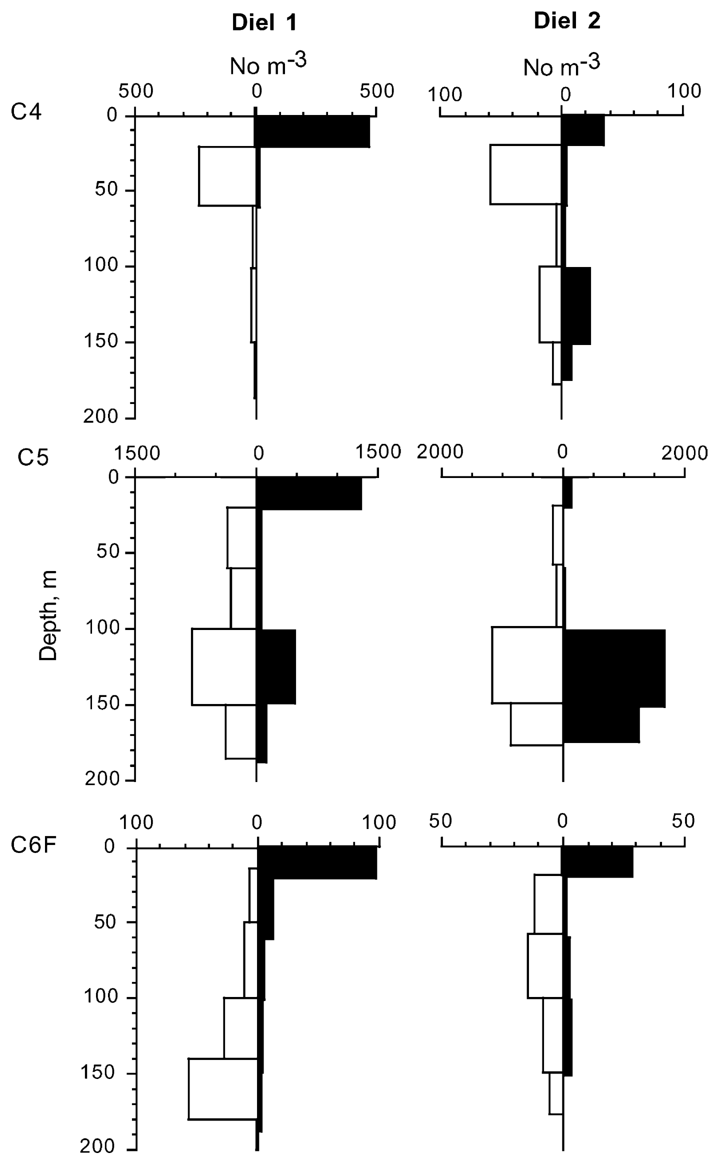

Fig. 3. Day and night *Calanus finmarchicus* C4, C5 and adult female abundance (per m^3) at two anchor stations in Grand Manan Basin during 29–30 July 2001 (Diel 1) and 31 July 2001 to 1 August 2001 (Diel 2). Data are from $1\,m^2$ MOCNESS samples. At each anchor station, a single night MOCNESS cast was made while the day data are the mean of 3 (Diel 1) and 2 (Diel 2) MOCNESS casts.

0.74 ng STXeq. per copepod, respectively, reflecting higher feeding rates at night. Molar composition profiles indicated a high proportion of potent carbamate derivatives, with neosaxitoxin, saxitoxin, and gonyautoxins contributing 40, 20, and 27%, respectively, to the toxin content of copepod tissues.

Right whales were present in Grand Manan Basin during the period of study and actively feeding at depth on thin dense layers of resting *C. finmarchicus* C5 populations (Fig. 4). The average concentrations of *C. finmarchicus* C5 encountered by tagged, feeding right whales ranged between 3020 and 11,900 copepods/m^3

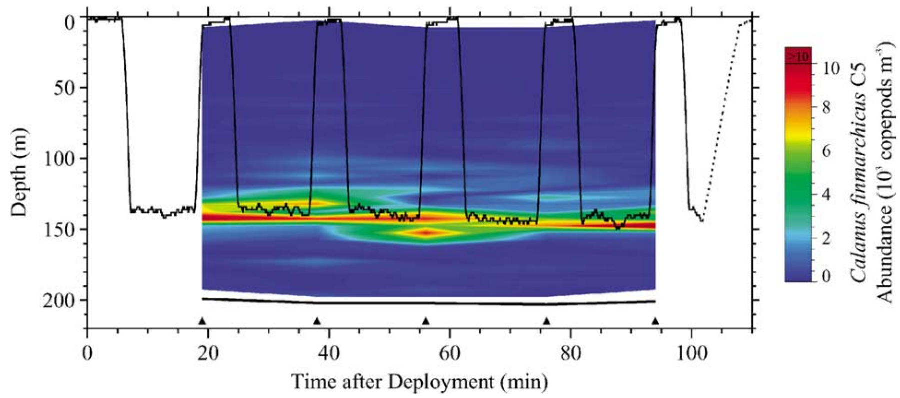

Fig. 4. Foraging behavior of a TDR-tagged right whale in Grand Manan Basin. The whale's dive profile is shown as a solid line and the vertical distribution of *Calanus finmarchicus* C5 along the whale's track is shown shaded in color. The triangles indicate the time at which a resurfacing was observed. A CTD/OPC cast was conducted at the location of each resurfacing shortly after the resurfacing occurred. The dotted line indicates the portion of the TDR record when the tag was detached from the whale. Data from Baumgartner (2002).

($n = 13$, mean = 5742, S.D. = 2832). Estimated ingestion rates for the tagged whales averaged 4.61×10^8 copepods per day ($n = 13$, S.D. $= 2.81 \times 10^8$, range $= 7.4 \times 10^7$ to 1.08×10^9). Ingestion rates of PSP toxin by these whales were substantial when expressed in toxicity units. Based on a toxin content of 0.41 ng STXeq. per copepod (the toxicity of the deep copepods), the estimated PSP toxin ingestion rate averaged 4.73 μg STXeq./(kg right whale per day) (n = 13, S.D. = 2.88, range = 0.76–11.03). Alternatively, if right whales consume 4% of their body weight per day (Sergeant, 1969), then the PSP toxin ingestion rate would be 9.65 μg STXeq./(kg right whale per day).

4. Discussion and Conclusions

These results clearly demonstrate that right whales are ingesting substantial amounts of PSP toxin while feeding on *C. finmarchicus*, the dominant copepod in their late summer feeding ground in Grand Manan Basin. Because the blooms of *A. fundyense* are a regular occurrence during the summer in this region (Martin and White, 1988; Townsend et al., 2001; the present study) this exposure to PSP toxins is also likely to be a regular occurrence. The actual level of exposure will depend upon the toxin content of the zooplankton in addition to the total ingestion of zooplankton by right whales. In the present study, the right whales were feeding at depth, therefore their toxin intake was lower than it may have been if they had been feeding on the much more toxic surface copepods.

The differences in toxin content of the migrating and the deep, non-migrating populations of *C. finmarchicus* reflect differences in their physiological status. The migrating copepods were actively feeding at the surface at night and their toxin content will be influenced by their immediate feeding conditions, particularly the proportion as well as the total amount of toxic *A. fundyense* in their diet. The day–night differences in toxin content we observed (with higher toxin levels at night) presumably reflect the higher feeding rates of *C. finmarchicus* at night that have been observed elsewhere in the Gulf of Maine (Durbin et al., 1995b). Decreased daytime toxicity is the result of both evacuation of feces as well as fairly rapid short-term depuration processes (Teegarden, 1999). Laboratory studies show that metabolically active, feeding copepods typically accumulate an "equilibrium maximum" body burden within 48 h of initiating feeding on toxic *Alexandrium* spp., either as sole food or in mixed assemblages of phytoplankton; loss of these toxins is also rapid when ingestion of toxic cells ceases, with usually 90% removed within 48 h (Teegarden, 1999).

The toxin content of these feeding copepods was lower than levels observed in adult female *C. fin-*

marchicus feeding on relatively dense cultures of *A. fundyense* where values of 4 μg STXeq./g wet weight copepod tissue were observed (Turriff et al., 1995). Assuming a copepod wet weight of 1.7 mg, this corresponds to a value of approximately 7 ng STXeq. per copepod which is considerably higher than our night-time values of 1.5 and 0.74 ng STXeq. per copepod. Presumably, the potential exists for much higher values in the field if *A. fundyense* concentrations are sufficiently high.

The presence of significant levels of toxin in the deep non-migrating C5 was surprising. These copepods were observed to have no food in their guts and were presumably in, or entering, diapause when metabolic rates are reduced (Hirche, 1996). In the Gulf of Maine, *C. finmarchicus* undergoes an ontogenetic migration to depth during the summer and enters diapause (Durbin et al., 2000). Most of the population remains in diapause until the following December and January when they mature to the adult stage, return to the surface, and begin feeding and reproducing (Durbin et al., 1997, 2000). It is possible that the non-migrating copepods we observed at depth in Grand Manan Basin had just undergone their ontogenetic migration to depth and were entering diapause. Depuration rates will be lower in these diapausing copepods than actively growing individuals and we might expect toxin content to slowly decline with time. However, there is no information on this, and clearly experiments are needed to investigate retention rates of toxins by these resting copepods.

The presence of toxin in the resting *C. finmarchicus* in Grand Manan Basin may also indicate that these copepods had previously been feeding at the surface in this region before descending rather than being advected in from outside and accumulating in the basin. A potential source region is the westward flowing current along the south of Nova Scotia carrying copepods from the Scotian Shelf. However, surveys in this current have shown *A. fundyense* to be absent (Townsend et al., 2001), which would preclude this option.

The estimated toxin ingestion rates of right whales in Grand Manan Basin are substantial and are similar to the estimated minimum lethal oral dose for humans of 7–16 μg STXeq./kg (Evans, 1972; Schantz et al., 1975). While there is no direct evidence of PSP toxin-related deaths of right whales, we suggest that during their prolonged summer feeding period in this region, they would be experiencing chronic exposure to PSP toxins. Such toxins are potent sodium-channel blockers in muscles and membranes and affect nerve function (Rao, 1993), thus they are likely to have both physiological and behavioral effects. Since PSP toxins are highly water soluble, they are readily absorbed through the gastrointestinal mucosa. They would not be retained in lipophilic tissues such as blubber, but would tend to be transferred from the digestive tract to physiologically active tissues supplied by circulating blood. Initial symptoms of PSP toxicity include parethesia and numbness and a weakening of muscles. In high doses, the PSP toxicity syndrome in mammals is characterized by respiratory difficulties, which may cause death in the absence of ventilatory support (Rao, 1993). These symptoms have led to the suggestion that after ingestion of PSP toxins, whales may lose control over peripheral heat-conserving mechanisms and respiratory capabilities (Geraci et al., 1989).

We suggest that although PSP toxins do not tend to bioaccumulate in most mammalian tissues, chronic effects of repeated PSP toxin exposure will be seen in measures of diving capabilities, including dive times, swimming speeds while at depth, and frequency of dives. Impaired diving capabilities in right whales would lead to reduced ingestion rates and may be a possible explanation for their poorer condition and reduced calving rates despite the high concentrations of *C. finmarchicus* in Grand Manan Basin. Possible evidence of such an effect comes from recent increases in calving intervals for right whales. Right whale occurrence in the lower Bay of Fundy has increased since the abandonment of the summertime Roseway Basin habitat on the Scotian Shelf during 1992–1993 (Kraus et al., 2001). From 1980 to 1993, calving intervals averaged 3.7 years, however, from 1993 to 1998, calving intervals increased significantly to 5.1 years (Kraus et al., 2001). There was no temporal trend in calving intervals prior to 1993 ($n = 87$, $r = 0.168$, $P = 0.12$; Kraus et al., 2001, Table 2), but calving intervals increased significantly at a rate of 4 months per year from 1993 to 1998 ($n = 38$, $r = 0.441$, $P = 0.0056$; Kraus et al., 2001, Table 2). These results suggest that abandonment of Roseway Basin and increased use of the lower Bay of Fundy has been accompanied by increasing calving intervals.

Other effects of toxin ingestion on "whale fitness" may be greater susceptibility to disease, reproductive failure, disruption of migration and mechanical damage (e.g. by collisions with ships or fouling in nets and other fishing gear). For example, recovery from dives during periods of PSP exposure would likely be longer than normal, and increased time at the surface would increase a whale's chances of being hit by a ship. In fact, Moore et al. (2001) indicate that right whales in Grand Manan Basin do indeed remain at the surface longer and take more breaths per surfacing than whales encountered in Cape Cod Bay. We suggest that these observations are related to PSP toxin exposure. The significance of ingested PSP toxins on the survival of right whales should not be underestimated. Few studies have been conducted on the effects of chronic exposure to PSP toxins or other sodium-channel blocking agents in higher mammals, and no previous data are available on the sub-lethal effects of PSP toxins in cetaceans. Nevertheless, our findings are the first to suggest that physiological impairment via exposure to high dosages of PSP toxins through the food chain may compromise the health of a population.

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