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Authors: Mann, Roger, Powell, Eric N., and Munroe, Daphne M.

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THE CASE OF THE ‘MISSING’ ARCTIC BIVALVES AND THE WALRUS: THE BIGGEST [OVERLOOKED] CLAM FISHERY ON THE PLANET

ROGER MANN,^{1*} ERIC N. POWELL² AND DAPHNE M. MUNROE³

¹Virginia Institute of Marine Science, William & Mary, Rt. 1208 Greate Road, Gloucester Point, VA 23062-1346; ²Gulf Coast Research Laboratory, University of Southern Mississippi, 703 East Beach Drive, Ocean Springs, MS 39564; ³Haskin Shellfish Research Laboratory, Rutgers University, 6959 Miller Ave., Port Norris, NJ 08349

ABSTRACT Bivalve molluscs represent a significant proportion of the diet of both Atlantic and Pacific walrus (*Odobenus rosmarus* and *Odobenus rosmarus divergens*, respectively) and are pivotal to benthic–pelagic coupling and carbonate cycling in the Arctic oceans. The latter is of particular relevance in a period of seasonal ice retreat, freshwater release into associated surface waters, decreasing water pH, and possible undersaturation of Arctic waters with respect to aragonite. Using population estimates and predation rates for the walruses on bivalve molluscs, a conservative estimate of bivalve consumption in the regions of active walruses foraging is $2.0\text{--}3.0 \times 10^6$ tonnes y^{-1} —a tonnage comparable to the landings for the largest U.S. commercial fishery, the walleye pollock fishery in the eastern Bering Sea. Predation loss to other apex predators such as bearded seals is discounted. Using production:biomass ratios comparable to other high-latitude bivalves, a conservative estimate of bivalve standing stock required to support walrus populations is $0.4\text{--}3.0 \times 10^7$ tonnes. Whereas predominant clam prey species exhibit longevity in the 30+ y range, sampled populations in the Bering and Chukchi seas are dominated by small, often less than 1.0 cm individuals. Large clams are rare to absent in samples, suggesting either rapid turnover of the population with high predation balanced by high recruitment and/or a bias in sampling that discounts larger, more sparse individuals. Walrus grazing contributes up to $4.0\text{--}6.0 \times 10^6$ tonnes y^{-1} of carbonate to buffering of near-surface sediments in Arctic regions. Accurate estimates of bivalve biomass and, thereby, the carbonate budget of Arctic shelf clam species, are critical to understanding the stability of associated continental shelf communities with continued warming of these high-latitude systems and their associated tendency toward aragonite undersaturation.

KEY WORDS: walrus, *Odobenus rosmarus divergens*, *Odobenus rosmarus rosmarus*, bivalves, carbonate budget, P:B ratio

THE “MISSING” MOLLUSCS OF THE ARCTIC: EVIDENCE OF EXISTENCE

In Northern Hemisphere estuaries and coastal bays, the carbonate producers are typically oysters (genus *Crassostrea*, less so *Saccostrea* and *Ostrea*) or mussels (Mytilidae) as epifaunal reef-forming representatives (and arguably the dominant form where they have not been extirpated by human activity), often supplemented in sedimentary plains by Venerids (e.g., *Mercenaria*, *Saxidomus*, and *Tapes*) and Cardiids (e.g., *Cardium*, *Cerastoderma*, and *Clinocardium*). On the continental shelves of the Northern Hemisphere in the subtidal through 100-m realm, the Mactrids (*Spisula*, *Tresus*, and *Mactra*) are among the largest and most abundant nonsymbiont bearing forms. These genera, plus *Arctica islandica*, dominate the north-temperate to boreal shelves of both the North Pacific and North Atlantic margins. The proverbial missing piece in the Northern Hemisphere shelf inventory is the identification of large infaunal bivalves on the Arctic shelf.

The opinion is proffered that large, long-lived bivalves are present in the Arctic shelf ecosystem, and in extraordinary, but unknown, numbers. Supporting evidence is provided in the food demand of Pacific and Atlantic walrus populations [*Odobenus rosmarus divergens* (Illiger, 1815) and *Odobenus rosmarus rosmarus* (Linnaeus, 1758), respectively]. Clams are the most common dietary item for the walruses (Fay 1982, Ray et al. 2006, NAAMCO 2017). Using walrus population estimates and quantitative dietary data, conservative estimates are developed of bivalve consumption and bivalve standing stock on the

Arctic shelf, with a consideration of the role of walrus predation on carbonate cycling in these extensive, relatively shallow shelf waters.

McLeod et al. (2014) and Higdon and Stewart (2018) provide a recent review of the biology, biogeography, and status of circumpolar walrus populations. Pacific walruses inhabit the Bering, Chukchi, and Laptev seas¹ (see Figure 1 in McLeod et al. 2014). Male Pacific walruses weigh up to 1,700 kg and reach 4 m in length. Female Pacific walruses weigh between 400 and 1,250 kg and reach 2.3–3.1 m in length. Age at sexual maturity for males and females is 8–10 y (NAAMCO 2017). Atlantic walruses inhabit coastal areas of northeastern Canada, Greenland, Arctic Norway including Svalbard, and Franz Josef Land, and have recently returned (early 2000s) to Novaya Zemlya (Kara Sea) in Russia.² Male Atlantic walruses weigh between 1,200 and 1,500 kg and approach 3 m in length. Female Atlantic walruses are smaller at 600–700 kg and 2.5 m in length.

¹The disputed status of the Laptev Sea population as a subspecies is examined by Lindqvist et al. (2009) using molecular and morphometric methods to assess the taxonomic status of *Odobenus r. laptevi* and to analyze the systematic and phylogeographic relationships between the three purported walrus subspecies. Lindqvist et al. recommend that *O. r. laptevi* be abandoned and the Laptev walrus instead be recognized as the westernmost population of the Pacific walrus *Odobenus r. divergens*. The Laptev population is a small population that was estimated at 4,000–5,000 animals according to Bychkov (1975, cited in Lowry 2015). Current abundance is unknown (Higdon & Stewart 2018).

²McLeod et al. (2014) report that exploitation of the Atlantic walrus in the 16th–18th century resulted in their extirpation from the Canadian Maritimes. The species has not inhabited areas south of 55°N for approximately 250 y.

*Corresponding author. E-mail: rmann@vims.edu

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Calves weigh 85 kg (Born et al. 1995). Atlantic walruses reach maturity at 5–12 y and produce one calf every 2–3 y thereafter. Both Pacific and Atlantic walruses have life expectancies of up to 40 y. Given the limited number of predators on adult walruses (e.g., polar bears and killer whales), natural mortality rates are low. Taylor and Udevitz (2014) provide an exploration of vital rates in the 1974 to 2006 period. Udevitz et al. (2013) note the possibility that as sea ice decreases and walruses must use land haul outs more frequently, consequent increased densities and population disturbance at haul-out locations have increased mortality in calves.

A series of Pacific walrus population estimates from aerial surveys have been made by joint U.S. and the former Soviet Union (now Russian) scientists since the implementation of the U.S. Marine Mammal Protection Act in 1972 and international agreements to limit hunting to subsistence levels for native peoples. The initial 1975 survey estimated the population size at 221,360. Additional surveys in 1980, 1985, and 1990 gave estimates of 246,360, 234,020, and 201,039, respectively. The 1990 estimate did not include part of the eastern Chukchi Sea, a region usually inhabited by walruses in more typical ice years, because ice was not present. A 2006 survey focusing on Pacific walruses, also not covering the entire range, estimated the population at 129,000, with a wide confidence interval of 55,000–550,000 animals (Speckman et al. 2011). The projected status of the Pacific walrus in the 21st century is increasingly fragile (Jay et al. 2011). Atlantic walrus population estimates are much more modest. NAAMCO (2017) states that the largest of the Atlantic stocks in Arctic Canada and West Greenland number approximately 20,000 individuals, sufficiently small to be listed as “vulnerable” and approaching “near threatened” on the global IUCN Red List (Kovacs 2016). The Svalbard population of Atlantic walruses remains small at 2,629 in August 2006 (Lydersen & Kovacs 2014). For the current estimation of Arctic-wide bivalve standing stock from walrus predation, a conservative collective population size of 200,000 adult walruses is assumed.

Walruses feed in depths less than 80 m (260 ft), but typically in 10–50 m (30–160 ft). Bornhold et al. (2005) describe foraging pits and narrow, sinuous furrows related to walrus feeding in depths less than 60 m on sandy seafloors in Bristol Bay, AK, and note the similarity to signatures found in the Bering and Chukchi seas. Walrus migration patterns, through swimming and riding ice flows, enable a wide annual geographic range of foraging (Higdon & Stewart 2018). Walruses rely on broken pack ice to gain access to feeding grounds (Fay 1982). Decreasing seasonal ice cover over much of the walrus feeding grounds will reduce access to productive offshore feeding grounds; however, walruses have been recorded in deeper waters as part of migration patterns and where feeding is not expected. For example, Atlantic walruses have been tracked across extensive open deep water. Dietz et al. (2014), for instance, reported that in 2005 to 2008, tagged walruses departed West Greenland in April and May and traversed an average distance of 338 km across the Davis Strait to southeastern Baffin Island over an average of 7 days. The combination of varying ice coverage, both seasonal and interannual, and migration thus confound estimation of absolute area subject to foraging.

What do walruses eat? Although authors have reported walruses to eat fish, holothurians, polychaetes, brachiopods, and even birds (Fisher & Stewart 1997, Higdon & Stewart

2018), a general consensus is that clams and gastropods form most of the diet under normal foraging (Fay 1982, Fisher & Stewart 1997, Ray et al. 2006, Sheffield & Grebmeier 2009, Noren et al. 2012, NAAMCO 2017). Fisher and Stewart (1997) examined stomach contents of Atlantic walruses taken by Inuit hunters in July 1987 and 1988 ($n = 105$) and September 1988 ($n = 2$). In July, 20 of 94 stomachs from immature and adult walruses contained greater than 5 g of food. Bivalves dominated the diet quantitatively—the clams *Mya truncata* (Linnaeus, 1758) and *Hiatella arctica* (Linnaeus, 1767) contributed 81.4% and 7.5% of the total gross energy, respectively, in the diet. Holothurians and the polychaete *Nereis* sp. contributed 3.5% and 2.8%, respectively, of the total. Male and female walrus diets were similar, except that females received a significantly ($P < 0.05$) greater percentage of gross energy from *H. arctica* than did males. Walruses less than 3 y old consumed mostly milk. September data suggested that walruses may feed more intensively in the fall; *M. truncata* remained the predominant prey, at 59.9% of total gross energy, with *Serripes groenlandicus* (Mohr, 1786), at 37.9%, replacing *H. arctica*, at 0.3%, as the second most important prey item. Sheffield and Grebmeier (2009) reviewed stomach content data for 798 Pacific walruses collected between 1952 and 1991 and considered the effect of digestion bias on results. Despite this acknowledged challenge, molluscs remained dominant food items, with bivalves predominating in Bering Sea collections and gastropods predominating in Chukchi Sea collections.

Noren et al. (2012) developed a bioenergetic model for estimating food requirements of female Pacific walruses. The model accounts for maintenance, growth, activity, molt, and reproduction. Estimated caloric requirements for nonreproductive females, 0–12 y old (65–810 kg), ranged from 16,359 to 68,960 kcal day $^{-1}$ (74–257 kcal $^{-1}$ kg $^{-1}$) for years when sea ice is readily available as a platform from which the walrus can forage. These values approximate to 7%–8% and 14%–19% of body mass per day for 5- to 12- and 2- to 4-y-old walrus, respectively. Noren et al. (2012) validate their estimates by comparison with earlier data from reports by Born et al. (2003), who made field observations of feeding free-ranging Atlantic walruses. Born et al. (2003) observed clam consumption rates of eight clams min $^{-1}$ of dive cycle, with a diet composition of 72% *Mya truncata*, 21% *Hiatella arctica*, and 7% *Serripes groenlandicus*. The dietary needs to serve the energetic requirements estimated by Noren et al. (2012) approximate to 3,200–5,960 clams day $^{-1}$, or 1168,000–2,175,400 clams y $^{-1}$!

For simplicity in the current estimation, the used maintenance ration is in the range of 8% body mass day $^{-1}$ for a 600 kg adult (48 kg day $^{-1}$, consistent with a nonlactating, nonpregnant female) through 7% day $^{-1}$ for a 1,250-kg adult (87.5 kg) that is rounded to 50–90 kg day $^{-1}$ for one walrus, or a range of 18,250–33,000 kg y $^{-1}$ walrus $^{-1}$. Assuming that 50% of the diet is bivalves provides a consumption rate of 9,125–16,500 kg clams y $^{-1}$ walrus $^{-1}$. A simple rounding to a low estimate of 10,000–15,000 kg clams y $^{-1}$ walrus $^{-1}$, a population of 200,000 walruses would consume $2.0\text{--}3.0 \times 10^9$ kg or $2.0\text{--}3.0 \times 10^6$ tonnes of clams each year. This is an extraordinary number and is comparable to the walleye or Alaskan pollock *Gadus chalcogrammus* (Pallas, 1814) catches from the eastern Bering Sea of $0.9\text{--}1.5 \times 10^6$ tonnes y $^{-1}$ for the 30-y period between 1970 and 2000 (Acuna & Kotwicki 2006)—pollock landings are the largest of any single fish species in the United States. For

comparison, the commercial landings of the surf clam *Spisula solidissima* in the mid-Atlantic and Georges Bank regions for the 10-y period between 2005 and 2015 varied in the range of $1.85\text{--}2.71 \times 10^4$ tonnes y^{-1} of meat (NEFSC 2017a). Landings for the ocean quahog *Arctica islandica* for the same location and period varied in the range of $1.36\text{--}1.63 \times 10^4$ tonnes y^{-1} of meat (NEFSC 2017b). Simply stated, annual walrus clam consumption is two orders of magnitude higher than surf clam or ocean quahog commercial landings.

The aforementioned major dietary species for walrus, *Mya truncata*, *Hiatella arctica*, and *Serripes groenlandicus*, are all circumpolar in distribution (MacNeil 1964, Carey et al. 1984, Siford & Welch 1992, Sejr et al. 2002, Ambrose et al. 2006, Kilada et al. 2007, Carroll et al. 2009). All can demonstrate considerable longevity and large terminal size. Foster (1946) notes that *M. truncata* can reach 75 mm shell length (SL); the siphon is not enclosed when retracted and can more than double the clam length when extended. Kilada et al. (2007) estimated a maximum size of about 100 mm and age of about 30 y for *S. groenlandicus*. Sejr et al. (2002) reported extreme longevity, up to 126 y, for *H. arctica* with a maximum SL (von Bertalanffy L_∞) of 37 mm at approximately 35 y of age. Longevity is typically accompanied by rapid early growth transitioning to an extended period of mid to late life with little additional growth—the illustration in Figure 5 of Sejr et al. (2002) for *H. arctica* providing an excellent example. This growth pattern has implications for population-level production:biomass (P:B) ratios (see also Cusson & Bourget 2005). The P:B ratios provide a tool to relate standing stock and production. The P:B ratios for bivalves are typically higher where life spans are shorter (Zaika 1970) and during the early years of life for long-lived species. Dietary requirements of walruses have been estimated earlier. Production must exceed these needs. Can P:B ratios be used to estimate standing stock of bivalve prey species in the regions of walrus foraging? Note that this conservative approach discounts all other sources of mortality, so resultant estimates of standing stock will be biased low.

A summary of P:B ratios in bivalve populations is given in Table 1. The included habitats range from boreal lakes to high-energy beaches, intertidal mudflats, and high-latitude fjords. Although most examples are for populations with age structures limited to less than 10-y old, an extraordinary inclusion is that of Sejr et al. (2002) for *Hiatella arctica*. Production:biomass ratios vary between low values of 0.05 and 0.095 [*Mercenaria mercenaria* (Linnaeus, 1758) from Wassaw Sound USA and *H. arctica* from Greenland, respectively] and high values of greater than 2.5 [*Scrobicularia plana* (da Costa, 1778) and *Mya arenaria* (Linnaeus, 1758) from the United Kingdom and Nova Scotia, Canada, respectively]. Low values tend to be reflective of populations of old animals and higher latitudes, whereas high values tend to be reflective of younger animals, although there is considerable variation driven by local productivity. Of these reports, only a few share comparable annual temperature ranges, latitudes, and depths to the foraging range of walruses. The genus *Mya* is represented in both these P:B ratios and walrus diet reports, albeit for differing species. In addition, the aforementioned report by Petersen (1978) and Sejr et al. (2002) reports on *Serripes groenlandicus* (P:B = 0.1–0.13), *Hiatella byssifera* (Fabricius, 1780) (P:B = 0.15), *Mya truncata* (P:B = 0.15–0.17), and *Macoma calcarea* (Gmelin, 1791) (P:B = 0.16–0.33) from Disko Bay, West Greenland. Mid-latitude

populations of shallow water or intertidal populations of *Cerastoderma edule* (Linnaeus, 1758), *S. plana*, *M. mercenaria*, *Astarte borealis* (Schumacher, 1817), *M. arenaria*, and *Ruditapes philippinarum* (Adams & Reeve, 1850) provide examples with P:B ratios in the 0.2–0.5 range. Higher values of P:B ratios are typified by mostly short-lived species in productive habitats at lower latitudes. Brey and Clarke (1993, Figure 3) compare the logarithm of annual P:B ratio versus mean individual body mass for a suite of polar benthic invertebrate species, including both bivalves and gastropods, and note a general common regression with a negative slope of -0.219 , closely resembling the expected value as described by earlier investigators (Platt & Silvert 1981, Feldman & McMahon 1983, Calder 1985).

The Chukchi Sea is considered to support a highly productive and diverse benthic community (Schonberg et al. 2014) that, in turn, supports higher-level megafauna. Similarly, the microbenthic assemblages in the northern Bering Sea are attributed to local high primary productivity and flux to the benthos (Grebmeier et al. 1988, 1989). McCormick-Ray et al. (2011) emphasized both the abundance and patchy distribution of small (<1.0 cm) bivalves on the Bering Sea shelf. The abundance of small-size classes suggests either rapid turnover of the population with high predation balanced by high recruitment and/or a bias in sampling that discounts larger, more-sparse individuals [compare the size distribution in McCormick-Ray et al. (2011) with maximum sizes for predominant food items as described earlier].

Reports describing abundance of large clams on Arctic shelves are not well ensconced in the literature—should they be? Descriptions of the benthic communities are a function of the gear used to sample them (Powell & Mann 2016, Powell et al. 2017). Is the latter problematic in the current context? Traditional grabs, widely used in studies of Arctic benthos, rarely if ever collect a large bivalve because of either the limitations of depth penetration of the gear or the area enclosed by the sample when the mean density of the target organisms approximates 1 m^{-2} at highest densities. Examples of the latter include swept area population estimates from stock assessment of the surf clam *Spisula solidissima* (Dillwyn, 1817) on the mid-Atlantic shelf of the United States (Weinberg 2005, Hennen et al. 2012), the Pacific geoduck *Panopea generosa* (A. A. Gould, 1850) (Goodwin & Pease 1989), and density estimates of $1\text{--}2\text{ m}^{-2}$ of *Mercenaria mercenaria* in exploited populations in Great South Bay, NY (Kraeuter et al. 2005). In a survey of the standing stock of *Spisula polynyma* [now *Mactromeris polynyma* (Stimpson, 1860)] along the southeastern Bering Sea, Hughes and Bourne (1981) estimated approximately 330,000 tonnes of biomass in the $6,800\text{ km}^2$ surveyed area, which translates to approximately 0.2 clams m^{-2} . To survey this high biomass, large-bodied but relatively sparse clam, Hughes and Bourne used a hydraulic dredge, the necessary gear type for a species like this (Powell & Mann 2016). In addition, some, large infaunal bivalves can dig deep into the sediments and close their valves [extreme examples include *Arctica* (Taylor 1976), *Tagelus* (Frey 1968), *Ensis* (Winter et al. 2012), and, in the current context, *Mya* (Zaklan & Ydenberg 1997)], thus escaping surface sampling. Large bivalves provide the extreme condition of biomass dominants that might be incorrectly underestimated based on ineffective sampling gear and/or sampling design. Standing stocks of walrus food species are thus likely to be underestimated by standard approaches.

If P:B ratios are used to estimate minimum standing stock required to support walrus feeding, then what P:B ratio should

TABLE 1.

Production:biomass (P:B) ratios for bivalve molluscs estimated from annual production (P) and standing stock (B) values unless otherwise stated.

Species	Location	P:B	Age (y)	SL max (mm)	Source
<i>Mercenaria mercenaria</i>	Wassaw Sound, GA	0.05	>7	—	Walker and Tenore (1984)
<i>Hiatella arctica</i>	Young Sound, NE Greenland	0.095	≤126	—	Sejr et al. (2002)
<i>Serripes groenlandicus</i>	Disko Bay, West Greenland	0.1–0.13	—	—	Petersen (1978)
<i>Modiolus demissus</i>	Georgia	0.11	≤7–8	—	Kuenzler (1961)
<i>M. mercenaria</i>	Little Tybee, GA	0.14	>7	—	Walker and Tenore (1984)
<i>Hiatella byssifera</i>	Disko Bay, West Greenland	0.15	—	—	Petersen (1978)
<i>Venerupis pullastra</i>	Norway	0.15	—	—	Johannessen (1973)
<i>Mya truncata</i>	Disko Bay, West Greenland	0.15–0.17	—	—	Petersen (1978)
<i>Macoma calcarea</i>	Disko Bay, West Greenland	0.16–0.33	—	—	Petersen (1978)
<i>M. mercenaria</i>	Southampton, England	0.17–0.52	—	—	Hibbert (1976)
<i>Cerastoderma edule</i>	Intertidal, Lynher estuary, Cornwall, England	0.2	—	41.6	Warwick and Price (1975)
<i>Scrobicularia plana</i>	Intertidal, Lynher estuary, Cornwall, England	0.2	—	—	Warwick and Price (1975)
<i>M. mercenaria</i>	North Cabbage Island, GA	0.23	≤7	—	Walker and Tenore (1984)
<i>Anodonta grandis simpsoniana</i>	Narrow Lake, Central Alberta, Canada	0.25	≤11	69	Hanson et al. (1988)
<i>Venerupis decussata</i>	Southampton, England	0.28–0.52	—	—	Hibbert (1976)
<i>Astarte borealis</i>	S.E Baltic Sea	0.41	≤8	21	Gusev and Rudinskaya (2014)
<i>Lissarca notorecadensis</i>	Weddell Sea Shelf, Antarctica	0.42–0.444	—	—	Brey and Hain (1992)
<i>Ruditapes philippinarum</i>	Intertidal, Arcachon Basin, SW France	0.44–0.92	—	—	Dang et al. (2010)
<i>Mya arenaria</i>	Intertidal, Lynher estuary, Cornwall, England	0.5	≤8	107	Warwick and Price (1975)
<i>Lissarca miliaris</i>	Signy Island, Antarctica	0.78	—	—	Richardson (1979)*
<i>Mytilus galloprovincialis</i>	Black Sea	0.91†	≤7–9	—	Zaika (1970)†
<i>Macoma balthica</i>	Grevelingen estuary, Netherlands	0.95	—	—	Wolff and de Wolff (1977)
<i>M. balthica</i>	Intertidal, Lynher estuary, Cornwall, England	0.95	≤7	—	Warwick and Price 1975
<i>Cardium edule</i>	Southampton, England	1	—	—	Hibbert (1976)
<i>Mytilus edulis</i>	Southampton, England	1	—	—	Hibbert (1976)
<i>Venerupis aurea</i>	Southampton, England	1.0–1.11	—	—	Hibbert (1976)
<i>Cerastoderma edule</i>	Southampton, England	1.1–2.61	—	—	Hibbert (1976)
<i>Donax serra</i>	High-energy beach, Namibia	1.167–1.589	—	82	Laudien et al. (2003)
<i>Cardium edule</i>	Grevelingen estuary, the Netherlands	1.5	—	—	Wolff and de Wolff (1977)
<i>M. balthica</i>	Nova Scotia, Canada	1.53	—	—	Burke and Mann (1974)
<i>Abra ovata</i>	Sea of Azov	1.6	≤3–4	—	Zaika (1970)‡
<i>Tellina tenuis</i>	Loch Ewe, Scotland	1.75	<5	—	Trevallion (1971)
<i>M. balthica</i>	Ythan Estuary, Scotland	2.07	—	—	Chambers and Milne (1975)
<i>Cardium edule</i>	Sea of Azov	2.24‡	≤5	—	Zaika (1970)
<i>Mytilaster lineatus</i>	Sea of Azov	2.25‡	≤3	—	Zaika (1970)
<i>S. plana</i>	Intertidal, Conwy Bay, Wales	2.5	≤4	—	Hughes (1970)
<i>M. arenaria</i>	Nova Scotia, Canada	2.54	—	—	Burke and Mann (1974)

Population age and maximum individual SL (mm) where available. *Cardium edule* and *Cerastoderma edule* are synonyms.

* Quoted in Brey and Clarke (1993).

† Estimated from daily production rates ×365.

‡ Based on 7 mo of production.

be applied? Based on the aforementioned, values in the range of 0.1–0.5 are reasonable. When applied to a consumption rate of $2.0\text{--}3.0 \times 10^6$ tonnes y^{-1} , a conservative estimate of required standing stock is $2.0\text{--}3.0 \times 10^7$ tonnes (at P:B = 0.1) to $0.4\text{--}1.5 \times 10^7$ tonnes (at P:B = 0.5). Again, these are extraordinary numbers. To place them in context, the commercially exploited surf clam *Spisula solidissima* and ocean quahog *Arctica islandica* (Linnaeus, 1767) stocks of the mid-Atlantic and Georges Bank region of the U.S. eastern continental shelf have standing stocks approximating to 1.0×10^6 tonnes (Hennen,

NEFSC, personal communication 2020) and 3.6×10^6 tonnes (NEFSC 2017b Figures 108, 109, 111), respectively.

BIVALVES AS CARBONATE RESERVOIRS ON THE ARCTIC CONTINENTAL SHELVES

Shell is released by walrus feeding. What are the implications of walrus feeding on bivalve prey for the regional carbonate budget? Table 2 summarizes shell:wet meat ratios for bivalves; ratios range between 1.08:1 and 4.2:1. Taking 2:1 as a working

TABLE 2.
Shell:meat wet weight ratios for bivalve molluscs.

Species	Size range	Location	Ratio	Source
<i>Cardium edule</i>	22–32 mm SL, 4–14 g live weight	Burny Inlet, South Wales	4.21	Hancock and Franklin (1972)
<i>Cerastoderma edule</i>	20–50 mm from regressions	Southampton, UK	4.16*†	Hibbert (1976)
<i>Donax vittatus</i>	28 mm "standard animal"	Kames Bay, Scotland	1.49	Ansell (1972)
<i>Macoma balthica</i>	6–20 mm SL from regression	Georgetown, ME	1.26–1.47*	Gilbert (1973)
<i>Tapes japonica</i>	6–10 g live weight	Cultured/experimental	1.1–2.57†	Mann (1979)
<i>Tellina tenuis</i>	6–22 mm, 15 mm "standard animal"	Kames Bay and Firemore Bay, Scotland	1.08	Ansell and Trevallion (1967)
<i>Venerupis aurea</i>	20–50 mm from regressions	Southampton, UK	2.22–4.04 *†	Hibbert (1976)

* Values calculated from regressions of weight versus length in source publications.

† Wet meat estimated from dry meat assuming 78% water content (Southworth and Mann, unpublished oyster data; also Ansell (1972) for *Donax vittatus*, range 75%–85%).

estimate, the aforementioned estimates of clam biomass consumed as wet tissue weight correspond to shell carbonate release rates on the order of $4.0\text{--}6.0 \times 10^6$ tonnes y^{-1} . This carbonate is either released into the buried carbonate pool or remobilized through dissolution. In either case, for a time, this carbonate must be an important contributor to buffering of near-surface sediments in the Arctic regions. Estimates of release of benthic carbonate are few in the literature. Smith (1972) reports loss of approximately 4.0×10^4 tonnes y^{-1} of biogenic carbonate from hard-bottom communities of coralline algae, bryozoan, molluscs, arthropods, and annelids in approximately 10^3 km^2 of the shallow shelf region off southern California. Lebrato et al. (2010) provided an estimate of global echinoderm carbonate production, from the shallows to the abyss, of approximately 10^9 tonnes y^{-1} . There are no comparable regional or global estimates for molluscan carbonate production.

What is the nature and dynamics of the bivalve carbonate reservoir? Although death assemblages commonly contain a range of small molluscs, these size classes (and species) often are poorly preserved (Cummins et al. 1986a, Callender & Powell 2000, Smith & Nelson 2003) and contribute disproportionately little carbonate in comparison with their abundance. Is this the case on the Arctic shelf? The importance of the larger bivalves in estuarine soft-bottoms and hard grounds in maintaining filter-feeder prominence in community dynamics is supported by a range of studies (Cloern 1982, Peterson 1984, Staff et al. 1985, Coco et al. 2006, Fulford et al. 2007, Smaal et al. 2019). In fact, the amensalism hypothesis³ developed to explain the dichotomy of filter-feeder versus deposit-feeder communities first promoted by Rhoads and Young (1970) and Young and Rhoads (1971) (see also modifications by Wildish 1977, Probert 1984) may be as much a dynamic of insufficient carbonate content to promote bivalve settlement as it is the inability of bivalves to feed in unstable sedimentary environments. Notably, many locales with well-documented seasonal sediment-transport cycles sustain significant bivalve populations (Anderson et al. 1981, Cummins et al. 1986c, Reise et al. 2008).

In estuaries, where taphonomic loss rates may be intense (Cummins et al. 1986b, Powell et al. 1989, Simon et al. 1994,

Waldbusser et al. 2011), high rates of carbonate production are essential to maintain a favorable sedimentary environment for early survival of juveniles; however, exceptions have been reported wherein high preservation occurs (Powell et al. 1992). Stability of the carbonate pool by the presence of large bivalves may not always be necessary, but is highly advantageous (Powell & Klinck 2007, Mann et al. 2009). Although high recruitment with short life expectancy can contribute substantially to the carbonate pool if maintained at high rates, such dynamics are at the mercy of failed year classes in a recruitment sequence. Small valves are thinner and susceptible to chemical degradation and physical breakage—residence time in the carbonate pool is short (e.g., Powell et al. 1984, 1986, Cummins et al. 1986a, Tomašových 2004). Life histories dominated by short life spans and variable recruitment proffer unstable carbonate pools with cascading impacts on the broader benthic invertebrate community. Carbonate loss rates within the sediment surface mixed layer may, however, demonstrate a rapid (disintegration) loss phase followed by a lower (sequestration) rate phase that maintains carbonate presence over extended time periods (Tomašových et al. 2014). The presence of long-lived species with large terminal size is the desired scenario (discussed for oysters by Mann & Powell 2007, Powell et al. 2012, Soniat et al. 2012); however, the reported abundance of small, presumably young individuals indicates a leaning toward a less-stable environment for continued recruitment.

Likely, taphonomic rates are lower on continental shelves, although data are meager at present (Powell 1992, Flessa & Kowalewski 1994, Smith & Nelson 2003); thus, carbonate content is sustained in part by a benign taphonomic environment. All else being equal, taphonomic rates should rise in colder high-latitude waters based on the influence of temperature on carbonate saturation state and the expected effect of ocean acidification that is anticipated to further expose this sensitivity (Fabry et al. 2009, McClintock et al. 2009). Thus, high bivalve carbonate production may be critical to maintenance of habitat and community health in estuaries and north-temperate to Arctic environs: what large and long-lived bivalves are the major contributors to this carbonate resource?

The role of bivalve molluscs in providing ecosystem services, effecting bioturbation to facilitate elemental cycling, and modulating benthic–pelagic coupling is well documented (Loo & Rosenberg 1989, Gerritsen et al. 1994, Peterson et al. 2003,

³Amensalism is the interaction between two species wherein one of them, without being affected, impedes the growth and survival of the other.

Coen et al. 2007, Smaal et al. 2019). In tropical waters, coral reefs are the dominant reservoir of carbonate to neutralize acid production (Milliman 1974, Mallela & Perry 2007, Kleypas & Yates 2009, Burdige et al. 2010). In temperate to boreal waters, the major carbonate reservoirs are molluscan shells and to a lesser extent echinoderm tests (Chauvaud et al. 2000, Gutiérrez et al. 2003, Lebrato et al. 2010). Filter-feeding bivalves dominate this carbonate pool because most are primary consumers. In the geologically ephemeral estuarine regions of continental margins, carbonate production serves to build and maintain oyster reefs (Mann & Powell 2007, Powell & Klinck 2007, Mann et al. 2009, Powell et al. 2012). These are critical biological habitats that accrete in concert with sea level (Mann et al. 2009, Powell et al. 2012).

Appreciation of the role of molluscs as carbonate (alkalinity) reservoirs in the soft-bottom benthos has received less attention (Mann & Powell 2007, Powell & Klinck 2007, Powell et al. 2012, Waldbusser et al. 2013). As primary productivity falls to the benthos and decays, acids are formed. These are buffered by carbonate at the sediment–water interface or in near-interface sediments (Tribble 1993, Green & Aller 1998, Green et al. 2004, Perry & Taylor 2006). Lack of such buffering has been observed to impact the survival of *Mercenaria mercenaria* (Green et al. 2004), and the burrowing and post-settlement behavior of *Mya arenaria* (Clements et al. 2016) with obvious extension to other juvenile infauna. In most of the soft-sediment benthic habitats, carbonate production must balance taphonomic loss to maintain the chemical milieu of the near-surface sediments to sustain a filter-feeding component in the benthic community. The vast majority of marine invertebrates, including bivalve molluscs, have ciliated larvae that metamorphose at a maximum dimension of less than 1 mm—Reynolds numbers dictate that anything larger could not swim with cilia because of fluid dynamic restrictions of viscosity (Vogel 1994, McEdward 1995). Metamorphosing larvae have very high surface:volume ratios, making them susceptible to dissolution (Sanders 2003, Green et al. 2004, Miller et al. 2009). In addition, they are incapable of extensive osmoregulation. Thus, critical enzyme systems for

early post-metamorphosis are susceptible to environmental challenge if internal pH cannot be regulated within a narrow optimal “window.” As a result, buffering of the sediment–water interface is critical to successful metamorphosis and early juvenile survival at the individual organism level (Green et al. 2009, 2013) and the maintenance of diversity at the community level. The only widespread exception to this general scenario is lotic beaches where the “high-energy window” maintains a chemically benign environment (Ott & Machan 1971, Riedl 1972, Riedl & Machan 1972).

CONCLUSION

A disconnect exists between the molluscan biomass estimated from known benthic surveys and the feeding requirements of walruses. This suggests that either the food requirements of walruses are vastly overestimated, the diet of walruses is substantively misunderstood, or the benthic surveys vastly underestimate continental shelf molluscan biomass. The last is likely the case and is a primary obstacle worldwide in managing continental shelves and understanding the reorganization of benthic communities during a period of global warming. The walrus underscores a missing and very important piece of the benthic community puzzle that might substantively reshape the view of continental shelf soft-bottom benthic communities and the carbonate budgets associated with them, wherein carbonate sequestration rates may be occurring at rates much higher than presently appreciated.

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