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Combining current and historical biodiversity surveys reveals order of magnitude greater richness in a British Columbia marine protected area

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Abstract
The value of biodiversity and of documented biodiversity surveys is well established. Extracting historical biodiversity data and synthesizing them with current data can provide a more comprehensive estimate of total diversity and guide future monitoring. We demonstrate the utility of compiling historical and recent biodiversity data to better characterize taxon richness and composition. Our focus is an otherwise unmonitored habitat in an unmonitored British Columbia provincial park, in a heavily impacted region of the Salish Sea that was designated a United Nation Biosphere Reserve in 2021. We conducted surveys and compiled historical records that together spanned three intertidal habitats and 43 years. From these combined data we report a total of 99 taxa, an order of magnitude increase over the number listed in the park's Master Plan. These include seven non-native species, of which four are newly reported here. Rarefaction, extrapolation, and multivariate dissimilarity analyses revealed the roles of methods and habitat types in contributing to differences in taxon richness and composition among surveys. This data compilation illustrates many of the challenges and opportunities in aligning and assembling independent space-time snapshots of alpha (i.e., local) diversity to better understand the gamma (i.e., regional) diversity of a marine protected area and provides the foundational data needed to design effective future monitoring at molecular to ecosystem scales.

Key words: Biodiversity monitoring; British Columbia; cobble beach; historical data; invasive species; marine protected area; Porteau Cove Provincial Park; riprap; UN Biosphere Region

Introduction
The benefits of assembling biodiversity inventories and monitoring changes in species composition are well established (e.g., Lindenmayer *et al.* 2012). Nevertheless, the amount of consistent, widely available diversity-monitoring data remains limited (Lindenmayer and Likens 2010; Hortal *et al.* 2015; Pendleton *et al.* 2019), and in marine systems new taxa continue to be discovered (Costello *et al.* 2010; Bucklin *et al.* 2016; Chenuil *et al.* 2019). While future data collection will continue to add to our knowledge of diversity, compiling historical data can also contribute to current estimates and inform future planning (Bates *et al.* 2009; Sloan and Bartier 2009; Stevens *et al.* 2014; Mannino *et al.* 2020). However, unless such data are part of a stringent long-term study, historical data from a given location typically consist of an assemblage of alpha (local) diversity snapshots reflecting different times, sites, and methods. The challenge is to glean from such data whatever knowledge one can of the gamma (regional) diversity of an area (Mushet *et al.* 2019).

The goal of our study is to demonstrate the utility of combining historical and recent biodiversity data to characterize the intertidal biodiversity of a provincial park in British Columbia (BC). British Columbia has the greatest reported biodiversity of Canada's provinces and territories (Austin *et al.* 2008), but a provincial audit revealed major gaps in biodiversity knowledge (OAG 2013). British Columbia Parks is North America's largest regional park system, smaller only than Parks Canada and the United States National Parks Service (BC Parks 2017). Its long-term ecological monitoring (LTEM) program established in 2011 spans five biomes, including the intertidal zone (Wright and Stevens 2012).

Within the BC Parks system, Porteau Cove Provincial Park (PCPP; Figure 1) is ripe for an intertidal

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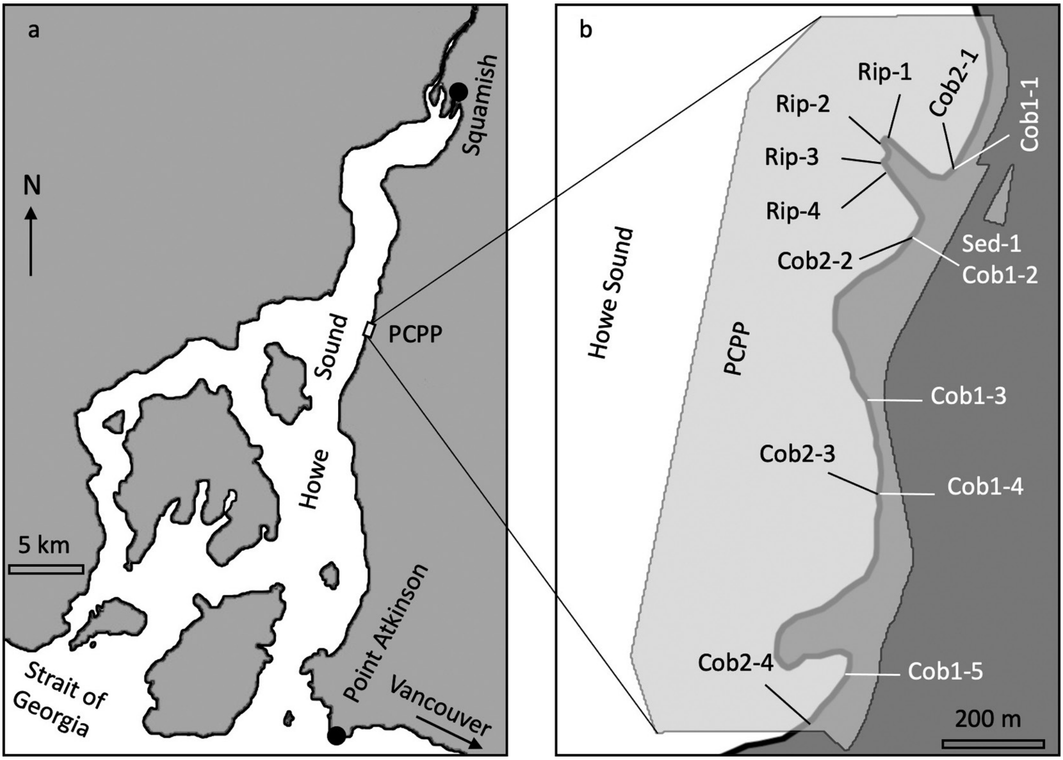

FIGURE 1. a. Porteau Cove Provincial Park (PCPP) in Howe Sound, British Columbia, Canada. b. Location of four intertidal biodiversity surveys: Sed, sediment survey from Levings and McDaniel (1976); Cob1-x, cobble-beach survey from Birch *et al.* (1990); Cob2-x, cobble-beach survey and Rip-x, riprap survey from our study.

biodiversity assessment. Neither the park nor its intertidal habitat types are currently included in BC Parks' LTEM program (BC Parks 2015). The park is situated in a region with an extensive history of industrial contamination and commercial exploitation (Bard 1998; Bright *et al.* 1999; Levings *et al.* 2004; Zis *et al.* 2004; Wilson *et al.* 2005), with myriad active and proposed conservation and development initiatives (Marliave and Challenger 2009; Ocean Wise Research Institute 2020; DFO 2022), and with a 2021 designation as the Átl'ka7tsem/Howe Sound United Nations Biosphere Reserve (UNESCO 2021). As the park contains one of the few accessible beaches in this Biosphere Reserve, its biotic inventory can help inform the region's management plan development. Further, while the park's Master Plan lists only eight intertidal species (BC Parks 1990), our personal observations indicated there were more.

Methods

Study area

Porteau Cove Provincial Park (49°33′N, 123°14′W) is located in southern coastal BC, Canada (Figure 1a). It is on the eastern side of Howe Sound, an estuarine fjord of the northern Salish Sea ~43 km long, with mid-sound surface salinities of ~15 ppt and a tidal amplitude averaging 3.2 m in a mixed semi-diurnal regime (Thomson 1981). Established in 1981, PCPP consists of a ~1.5 km strip of coastline with 4 ha of terrestrial forest and 56 ha of marine habitat. The shoreline is a gently sloping cobble-gravel-sand beach extending out ~100 m at low tide (4–20% grade; Birch *et al.* 1990; Figure S1). A tidal level of 1.0 m or lower (relative to the tidal datum of Lower Low Water Large Tide, LLWLT) provides access to the majority of its intertidal area (see Figure 2 for interannual variation in lower low tide levels). The park receives over 0.6 million day and overnight visitors annually (BC Parks 2018); anchoring, fishing, harvesting, and collecting are prohibited.

Our methods and taxonomy

We conducted two intertidal biodiversity surveys in PCPP: one on shallow-sloping cobble-gravel-sand beach that constitutes most of the park's intertidal habitat (hereafter: cobble) and one on the steep boulder riprap that surrounds the decommissioned ferry pier

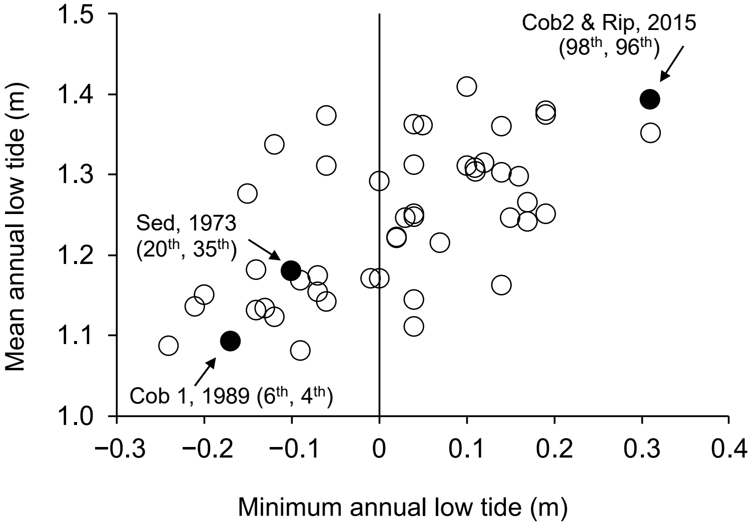

FIGURE 2. Annual minimum and annual mean daily lower low tides (m > LLWLT [Lower Low Water Large Tide]) recorded from 1970 to 2018 near Porteau Cove Provincial Park (PCPP), British Columbia, Canada. Solid points indicate the three years in which four intertidal biodiversity surveys were conducted at PCPP. Values in parentheses are percentile values for the (minimum, mean) low tides that year, out of the $n = 49$ years shown. Vertical line indicates chart datum, LLWLT. Data retrieved from Fisheries and Oceans Canada Tidal Inventory Data Station at Point Atkinson, the nearest station to PCPP (station no. 7795; 49.34°N, 123.25°W; DFO 2015).

(Figure S1a,b), during low tides in June–July 2015. For each survey, we selected four similar sites separated by at least 100 m (cobble [Cob]) or 10 m (riprap [Rip]; Figure 1b). Tidal elevations are reported as metres above chart datum, LLWLT, with reference to the nearest Fisheries and Oceans Canada Tidal Inventory Data Station (Point Atkinson, station no. 7795; 49.34°N, 123.25°W; DFO 2015). (Tide heights average 2.3 cm higher in Squamish than at Point Atkinson [± 1 SD = 2.4, $n = 2027$, based on three months in 2006 when data were recorded at both stations]; PCPP is located between the two [Figure 1a].)

At each site, we established six transect lines parallel to shore evenly spaced between the upper biotic limit (barnacles on cobble; algae on riprap) and the waterline at low tide (Table 1). Along each transect, we placed a 25×25 cm quadrat randomly in each 1/10th transect block, with a minimum distance between quadrats (cobble 0.5 m; riprap 0.25 m). Of the six cobble transects at each site, we pooled and designated the upper two as high, the middle two as mid, and the lower two as low, giving each of these three intertidal zones 20 quadrats per site. The three riprap transects at each site were designated high, mid, and low, each with 10 quadrats. In each quadrat, we recorded all epifauna and epiflora visible to the naked eye on the surface, and from underneath the uppermost layer (cobble) or under rocks that could easily be lifted with one hand (riprap).

The cobble beach was tightly compacted and not amenable to digging for infaunal sampling. However, after noting abundant empty shells of the non-native Purple Mahogany or Purple Varnish Clam (*Nuttallia obscurata* (Reeve, 1857)) near site Cob2-1 (Figure 1b), we sampled the more loosely-packed sandy beach immediately to the north (Figure S1c) for live clams by digging two to three holes, each 30×25 cm and 30 cm deep, at 10 m intervals along a 70 m transect line running down the shore from the high-water mark.

We identified organisms in the field to the lowest taxonomic level possible (Cox *et al.* 2017; Gerwing *et al.* 2020). Taxa that can reliably be identified only using genetic techniques were identified to morphospecies (Bay Mussel as *Mytilus* "*trossulus*", per Wonham [2004]; Sitka and Checkered Periwinkle as *Littorina* "*sitkana*" and *Littorina* "*scutulata*", per Hohenlohe [2004]) or genus (e.g., the dominant red alga *Mastocarpus* spp., per Le Gall and Saunders [2010]; very small limpets [<0.5 cm long], *Lottia* spp.). The majority of barnacles were Acorn Barnacle (*Balanus glandula* Darwin, 1854); subsequent analysis of collected specimens revealed that Crenate Barnacle (*Balanus crenatus* Bruguière, 1789) was present at lower tidal elevations but as these were not distinguished in the field, counts refer to *Balanus* spp.

Larger invertebrates were identified following Kozloff (1996) and Carlton (2007). Specimens were

TABLE 1. Quantitative methods for four intertidal biodiversity surveys at Porteau Cove Provincial Park, British Columbia, Canada: Sed (Levings and McDaniel 1976); Cob1 (Birch *et al.* 1990); Cob2 and Rip (our study). Taxa consisted of invertebrates, fishes, macroalgae, and vascular plants. Low tides, minimum tidal elevations during sampling are as archived at Point Atkinson tidal station. For Cob1, the predicted low tides of 0.1–0.2 m that informed the sampling design were 10–20 cm above the observed lows on the sampling days, i.e., lowest samples were likely collected even lower than the report indicated. Upper and Lower quadrats give mean elevations ±1 SD for *n* sites in m > LLWLT (tidal datum, Lower Low Water Large Tide). Quadrat min–max gives minimum and maximum quadrat elevations across entire survey. Transect orientation is vertical (perpendicular to shore) or horizontal (parallel to shore). *n* gives number of sites per survey / transects per site / quadrats per transect. Quadrats in Sed were dug 2 cm deep.

Source	Historical		Current	
Survey	Sed (sediment)	Cob1 (cobble)	Cob2 (cobble)	Rip (riprap)
Sampling dates	May 1973	Nov–Dec 1989	Jun–Jul 2015	Jun–Jul 2015
Time of day	Day	Night	Day	Day
Taxa	Invertebrates	All	All	All
Tidal elevations				
Low tides	0.9	−0.1–0.3	0.7–0.9	0.7–0.9
Upper quadrats	4.4	4.26 ± 0.29	3.6 ± 0.7	4.2 ± 0.1
Lower quadrats	1.0	0.49 ± 0.25	1.5 ± 0.5	1.7 ± 0.3
Quadrat min–max	1.0–4.4	0.1–4.7	1.1–3.9	1.4–4.4
Design				
Transect length (m)	~85	45–95	30	10
Transect orientation	Vertical	Vertical	Horizontal	Horizontal
n sites/transects/quadrats	1/1/8	5/1/7–9	4/6/10	4/3/10
Total quadrats	8	40	240	120
Quadrat size	25 × 25 cm	5 × 5 m	25 × 25 cm	25 × 25 cm
Total sampling area (m^2)	0.5	1000	15	7.5

collected for smaller invertebrates that could not readily be identified in the field (amphipods, isopods, polychaetes, small shrimp); these were returned to the lab, euthanized in 77% $MgCl_2$ for 1–4 h, fixed in 4% buffered formalin for 1–8 h, rinsed and stained with 0.5% Rose Bengal for 2–8 h, preserved in 80% ethanol, and identified by Biologica Environmental Services, Ltd. (Victoria, BC). The specimens were not archived. Gunnel and prickleback fishes (Pholidae and Stichaeidae) were enumerated in the field but were not identified further because we did not have a vertebrate research permit. Macroalgae were identified using Gabrielson *et al.* (2006).

Nomenclatures follow the online databases WoRMS (https://www.marinespecies.org/) for animals, AlgaeBase (https://www.algaebase.org) for macroalgae, and The Plant List (http://www.theplantlist.org/) for vascular plants, as of January 2021. Our surveys were conducted in 2015 as part of an unpublished undergraduate thesis (Gerstle 2016); however, we report the definitive methods and results here.

Historical surveys

To assemble a more comprehensive picture of the total intertidal biodiversity at PCPP, we compiled our two surveys with two historical surveys. The historical surveys are designated "Sed" (1973 sediment survey; Levings and McDaniel 1976) and "Cob1" (1989 cobble beach survey; Birch *et al.* 1990). Our two current surveys are designated "Cob2" (2015 cobble beach survey), and "Rip" (2015 riprap survey; Figure 1, Table 1). The Sed data were extracted from a government report that included PCPP as part of a larger Howe Sound survey. The Cob1 data were extracted from a consulting report that was unknown to PCPP staff or to us and surfaced only after our current study had been completed. The vertical extent of sampling differed across surveys because of the substantial interannual variation in low tide levels (Table 1, Figure 2). No specimens were vouchered from either historical survey.

We obtained additional qualitative records from Willems (2004) and by searching the GBIF (Global Biodiversity Information Facility) database for the latitude and longitude coordinates of PCPP (GBIF 2023). The GBIF search revealed only a few species that could be confirmed as having been found in the intertidal, and that had not already been reported in the four quantitative surveys above (see Table S1). A search of the online collection records at the Beaty Biodiversity Museum, the Royal British Columbia

Museum, and the Canadian Museum of Nature for the location keyword "Porteau" returned no additional records.

Data analysis

To summarize total taxon richness, we compiled a list of all quantitative and qualitative records across all four surveys, plus the additional sources (99 taxa; Tables 2, S1).

For quantitative analysis, we used only the quadrat data from the four quantitative surveys and counted only the distinctly identified taxa (84 taxa; Table S2); for example, unidentified limpets *Lottia* spp. were not counted as an additional taxon beyond the identified *Lottia* species.

To assess richness versus sampling effort in each survey, we used rarefaction and extrapolation analysis of frequency data using iNEXT version 2.0.17 in R version 3.3.3 for OSX (Gotelli and Colwell 2011; Chao *et al.* 2014; Hsieh *et al.* 2016). To examine the effects of smaller versus larger quadrats, we compared observed and estimated richness for a subset of Cob1 and Cob2 quadrats with matched taxonomic resolution and tidal elevation range, and with taxon accumulation data rescaled to the number of taxon occurrences rather than number of quadrats (see Gotelli and Colwell 2011). For this analysis we assigned the quadrats in Cob1 to the High, Mid, and Low elevation zones defined in Cob2, adding the zones Very High and Very Low for the Cob1 quadrats that fell above or below the Cob2 range.

To explore patterns in taxon composition, we followed Clarke (1993). Between-quadrat similarities were calculated using the Bray Curtis similarity index, on untransformed presence–absence data. Patterns of similarity were visualized using non-metric multidimensional scaling (nMDS) plots, and differences between surveys were evaluated using Analysis of Similarities (ANOSIM) routines. All multivariate analyses were performed in PRIMER (version 6, Primer-E).

Because the number of sites, transects, and quadrats, the size of quadrats, and the vertical intertidal elevation differed among surveys, it is not possible to meaningfully analyze differences in diversity over time. Instead, we report the magnitude of differences between surveys where they are notable, make selected methods-based comparisons where possible, and focus primarily on descriptive summary statistics calculated within each set of survey data.

Results

Taxon richness

In our two surveys we found 54 taxa, including 19 taxa newly reported from PCPP (Table 2). Combining these with the two historical surveys, we report a total of 99 distinctly identified intertidal taxa in the park (Tables 2, S1). In each survey, the estimated taxon richness was greater than the observed taxon richness, substantially so for Sed (154%), moderately so for Cob2 (15%) and Rip (13%), and only slightly for Cob1 (6%; Figure 3a,b, Table 3). Only in Cob1 was the sampling effort sufficient to sample an estimated ≥99% of taxa; the other three surveys were undersampled (Table 3).

Of the two cobble beach surveys, Cob1 reported a 63% greater observed richness and a 48% greater estimated richness than Cob2 (Table 3). To further explore this difference in richness, we examined the three main methodological differences between the two surveys. First, Cob1 extended one vertical metre lower into the intertidal than Cob2. Richness per quadrat increased nearly 4.5-fold from high to low elevation in Cob1 but did not vary over the narrower elevation range sampled in Cob2 (Figure 4a,b). This richness increase in Cob1 was due largely to the greater number of taxa found uniquely in the quadrats

TABLE 2. Number of taxa for each broad taxonomic grouping, total number of taxa, and number of non-native taxa reported from the intertidal zone at Porteau Cove Provincial Park (PCPP), British Columbia, Canada. The two historical surveys (Sed, Cob1) and our two surveys (Cob2, Rip) are characterized in Table 1. The number of Total and New taxa are given for our two surveys combined. "Other records" are qualitative reports of additional taxa from sources listed in Table S1. PCPP total is the number of distinct taxon records across all sources.

Taxa	Surveys						Other records	PCPP total
	Historical		Our study					
	Sed	Cob1	Cob2	Rip	Total	New		
Invertebrates	36	34	36	24	44	16	3	75
Fishes	0	5	1	0	1	0	1	6
Macroalgae	0	11	8	7	8	3	1	15
Vascular plants	1	3	1	0	1	0	0	3
Total	37	53	46	31	54	19	4	99
Non-native	1	2	3	2	4	4	0	7

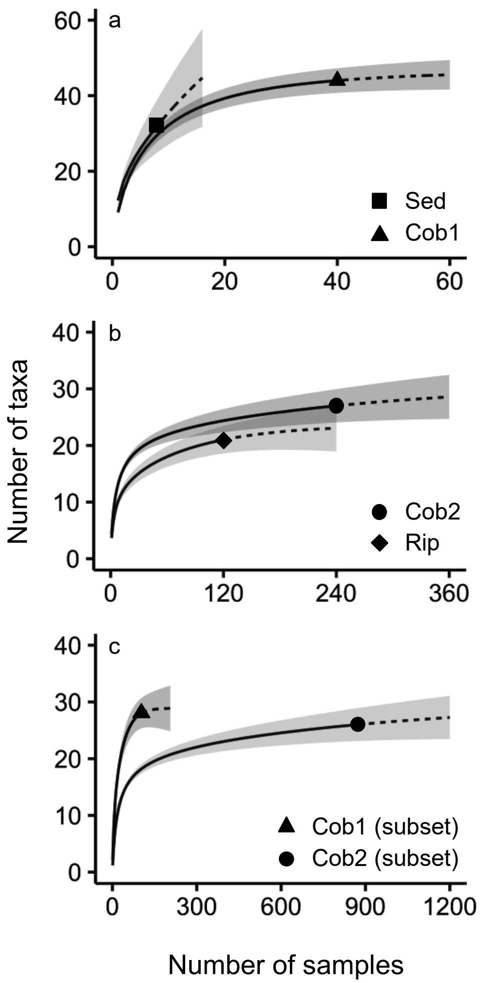

FIGURE 3. Observed intertidal taxon richness (points) with rarefaction (solid lines) and extrapolation (dashed lines) analyses showing estimated richness at Porteau Cove Provincial Park, British Columbia, Canada. a. Quadrat-based sampling in two historical surveys (Sediment [Sed] and Cobble 1 [Cob1]). b. Quadrat-based sampling in our survey of two habitats (Cobble 2 [Cob2] and Riprap [Rip]). c. Number of taxon occurrences for a matched subset of data from Cob1 and Cob2 with the same taxonomic resolution and tidal elevation range. Grey shading shows 95% CIs.

that fell below the range of Cob2 (Figure 4c versus d). Second, Cob1 used quadrats 16× larger than Cob2, sampling a total area 67× greater than Cob2. In the subset of data standardized for quadrat size, taxonomic resolution, and intertidal elevation however, the observed and estimated richness were similar between the two surveys, although observed richness saturated much faster in Cob1 than in Cob2 (Table 3, Figure 3c). Third, Cob1 sampled one site more than Cob2, but the additional site (Cob1-3; Figure 1) contributed only one taxon unique to that survey.

Taxon composition

For each survey, the similarity in taxon composition among quadrats was lowest for cobble beach (average Bray-Curtis similarity for Cob1 36.4%; Cob2 44.5%), moderate for Rip (54.4%), and highest for Sed (56.9%; Figure 5). In pairwise comparisons between surveys, taxon composition differed significantly for each survey pair: Rip and Sed were the least similar, whereas Rip and Cob2 were the most similar (Figure 5, Table 4). In all pairs except Rip and Cob2, the majority of taxa were not shared between surveys (Table 4).

The two dominant taxa in sediment were dipterans and oligochaetes, whereas those in cobble and riprap were barnacles and mussels (Figure S2). In the cobble surveys, greater numbers of lower intertidal taxa were found in Cob1 (sponge, anemone, flatworm, chiton, oyster, shrimp, nudibranch, seastar, kelp) than in Cob2 (Table S1, Figure S2). Of the eight species reported in the PCPP Master Plan (BC Parks 1990), six were found in one or more of the four surveys (Table S1). The other two, California Mussel (*Mytilus californianus* (Conrad, 1837)) and the orange nemertean *Tubulanus polymorphus* (Renier, 1804) (no common name), were not reported in any of the four surveys. The mussel would not be expected to be found in this habitat, and at small sizes could be mistaken for "*M. trossulus*". We have not seen it in 12 years of taking intertidal class field trips to this site (M.W. and C.B. pers. obs.) and exclude it from the list of reported species at PCPP (Table S1). The nemertean can be found in low-energy beach habitats (Kozloff 1983) and although we have not seen it here, it is so conspicuous that it would be impossible to mistake for anything else. We therefore leave this species in the inventory (Table S1).

Four non-native species newly reported from PCPP are Purple Mahogany Clam, Softshell Clam (*Mya arenaria* L., 1758), and amphipods *Ampithoe valida* (Smith, 1873) and *Monocorophium acherusicum* (Costa, 1853) (no common names). Including the previously reported Pacific Oyster (*Magallana* (= *Crassostrea*) *gigas* (Thunberg, 1793)), tanaid *Sinelobus* (= *Tanais*) *stanfordi* (Richardson, 1901) (no common name), and Japanese Wireweed (*Sargassum muticum* (Yendo) Fensholt), a total of seven non-native intertidal species are reported from the park (Tables 2, S1). Purple Mahogany Clam constituted 98.5% of the 451 clams collected from the sandy beach north of site Cob1-1, with a mean estimated density of 172/m^2 (± 1 SD 230, n = 8 intertidal elevations) and a maximum of 2147/m^2 in one upper intertidal sample.

TABLE 3. Observed and estimated taxon richness based on rarefaction and extrapolation analysis from four intertidal biodiversity surveys at Porteau Cove Provincial Park, British Columbia, Canada. Survey names as in Table 1. First four data columns show results for all taxa from all quadrats, with quadrat as sampling unit. Last two columns show results for subset of data adjusted to the same taxonomic resolution and tidal elevation range, with sampling unit rescaled to number of taxon occurrences. Estimated Samples, number of samples (quadrats or taxon occurrences) predicted to be required to sample 90%, 95%, or 99% of the estimated richness in each study; >2*n* indicates analysis was truncated at twice the number of original samples.

Survey	Historical		Current		Matched data subset	
	Sed	Cob1	Cob2	Rip	Cob1	Cob2
Sampling unit	Quadrat	Quadrat	Quadrat	Quadrat	Occurrence	Occurrence
Observed						
Taxon richness	32	44	27	21	28	26
Total quadrats	8	40	240	120	28	240
Mean taxa/quadrat	12.3	9.1	4.9	3.7	3.7	3.6
Taxon occurrences					103	871
Estimated						
Taxon richness	81	46	31	24	29	30
SE	43.7	2.9	5.3	3.5	1.5	5.3
Samples for 90%	>2*n*	28	302	130	67	1122
Samples for 95%	>2*n*	41	461	187	87	1727
Samples for 99%	>2*n*	75	>2*n*	>2*n*	138	>2*n*

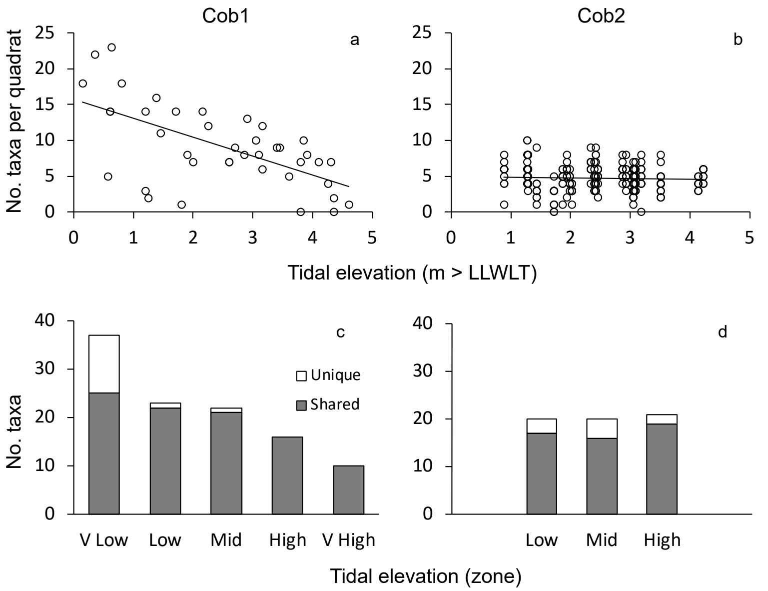

FIGURE 4. Intertidal taxon richness reported for Porteau Cove Provincial Park, British Columbia, Canada in cobble beach surveys Cob1 (a,c) and Cob2 (b,d). Number of taxa per quadrat versus intertidal elevation in m > LLWLT (Lower Low Water Large Tide) in a. $y = -2.6x + 15.7$, $r^2 = 0.38$ and b. $y = -0.10x + 5.0$; $r^2 < 0.01$). Total number of taxa per zone in c and d, distinguishing those taxa found uniquely in each zone (open) from those shared by two or more zones (shaded), within each survey.

Discussion

What is the intertidal diversity of PCPP?

Our compiled inventory of 99 intertidal taxa constitutes an over 12-fold increase above the eight taxa listed in the 30-year old PCPP Master Plan (BC Parks 1990) and provides the most complete picture of intertidal diversity from any location in Howe Sound to date.

This apparent increase in richness results primarily from the Master Plan not having included all the

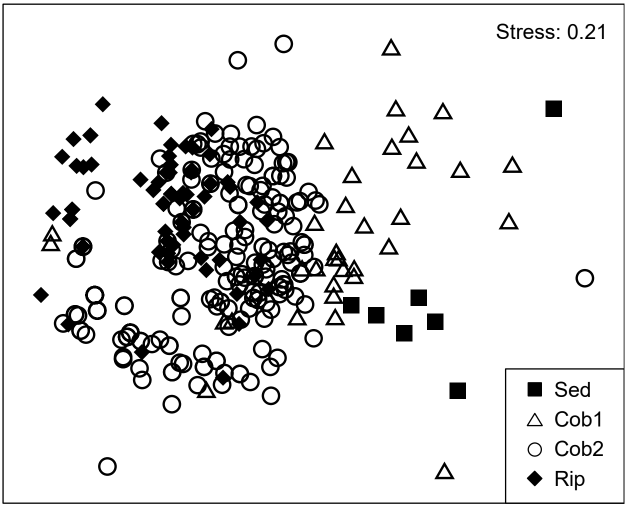

FIGURE 5. Non-metric multidimensional scaling ordination representing between-quadrat Bray-Curtis similarity based on per-sample taxon frequencies for four intertidal surveys at Porteau Cove Provincial Park, British Columbia, Canada.

TABLE 4. Multivariate taxon composition analyses for four intertidal biodiversity surveys at Porteau Cove Provincial Park, British Columbia, Canada. ANOSIM, Analysis of Similarities; % Dissimilarity, average percent dissimilarity between surveys, based on pairwise quadrat comparisons.

	ANOSIM		Number of taxa		% Dissimilarity
	R	*P*	Shared	Not shared	
Global comparison	0.28	<0.001			
Pairwise comparisons					
Rip-Sed	0.93	<0.001	6	41	83.1
Cob2-Sed	0.71	<0.001	6	47	81.5
Sed-Cob1	0.32	0.016	8	60	78.4
Rip-Cob1	0.72	<0.001	9	47	75.2
Cob2-Cob1	0.48	<0.001	14	43	73.6
Cob2-Rip	0.10	<0.001	16	16	57.2

taxa listed in the two historical surveys, and from the additional taxa we found in our surveys. It should not be construed necessarily as an increase in diversity over time, although it may reflect some species recolonization as the Sound continues to recover from historical contamination (Ocean Wise Research Institute 2020), and it includes new site records for four non-native species that are otherwise known from the region (Wonham and Carlton 2005). The most conspicuous of these, Purple Mahogany Clam, was readily visible as empty shells on the north side of the ferry pier. Its mean live density in the sandy beach to the north was similar to the mid-range of densities reported from other Salish Sea sites (Byers 2002; Dudas *et al.* 2007; Gordon *et al.* 2018). This is the one species we consider most likely to be a genuinely new colonizer in PCPP because the two historical surveys did not report it, and its large purple-interior shells make it difficult to miss. Overall, however, the data compiled here are too much of a habitat-and-methods mosaic to be read as a diversity timeline.

Our taxon inventory was compiled from quadrat-based surveys that, compared to other standard intertidal survey methods, are likely to sample the most taxon richness (Cox *et al.* 2017). Although our compilation represents an order of magnitude increase in known taxa at PCPP, it nevertheless underestimates the park's total intertidal richness. Particularly in sediment, rarefaction and extrapolation suggest that saturated sampling using the same methods would return over twice as many infaunal taxa. Even for more conspicuous taxa the records gleaned from iNaturalist via GBIF (Table S1) are testament to the additional species that can be reported by large numbers of natural historians who contribute observations outside the coverage of quantitative surveys. In addition, not all identifications were made to species level, and finer taxonomic resolution of cryptic taxa would likely reveal more species (e.g., Chenuil *et al.* 2019). Finally, additional richness would be recorded if the transient terrestrial and subtidal predators that frequent the intertidal at low or high tide were included (e.g., Northwestern Crow [*Corvus caurinus* Brehm, 1822] and Common Raccoon [*Procyon lotor* (L., 1758)]; Sunflower Sea Star [*Pycnopodia helianthoides* (Brandt, 1835)] and Pacific Octopus [*Enteroctopus dofleini* (Wülker, 1910)]; BC Parks 1990; Birch *et al.* 1990). (Sunflower Sea Star mortality from wasting syndrome has triggered a trophic cascade in Howe Sound [Schultz *et al.* 2016], and the species was recently assessed as Critically Endangered globally by the International Union for the Conservation of Nature due to population and range declines [Gravem *et al.* 2021].) Our inventory is, at the same time, slightly inflated by a few terrestrial insects and spiders that were visiting the intertidal from their supra-littoral habitat (e.g., Romanuk and Levings 2003).

The biotic composition and zonation observed at PCPP are consistent with those of a typical sheltered estuarine cobble shore in the Salish Sea (Kozloff 1983; Dethier and Schoch 2006). In Puget Sound, Washington, Dethier and Schoch (2006) reported 166 taxa from 45 sites with similar gravel/cobble habitat. The PCPP taxon count, which extended across a greater tidal elevation range, was 51% greater than that of the richest individual Puget Sound site but contained only 56% of the total richness of all Puget Sound sites. The number of reported non-native species at PCPP (n = 7) is less than 10% of the number reported from the Salish Sea region (Wonham and Carlton 2005). Although the surface salinity at PCPP is lower than full ocean salinity (Thomson 1981) and therefore less hospitable to some marine species, we expect that future sampling at PCPP and similar intertidal habitats in the region will reveal yet more native and non-native taxa in Howe Sound.

What is the value of compiling diversity studies?

Despite the long history of human impact in Howe Sound, primarily from acid mine drainage (Levings *et al.* 2004; Zis *et al.* 2004; Wilson *et al.* 2005), pulp and paper processing (Bard 1998; Bright *et al.* 1999), and fisheries and habitat modification (Marliave and Challenger 2009; Ocean Wise Research Institute 2020), there is a paucity of published intertidal diversity data from this region. Assembling historical taxonomic records can help us better understand current and future diversity patterns (Bates *et al.* 2009; Sloan and Bartier 2009; Stevens *et al.* 2014; Mannino *et al.* 2020) and inform future surveys at molecular, organismal, and ecosystem scales (e.g., Bucklin *et al.* 2016; Castelin *et al.* 2016; PISCO 2016).

Compiling these four intertidal surveys gives us insight into methodological and habitat effects on estimates of richness and composition at PCPP. Of the three habitats, cobble beach had the highest reported taxonomic richness and riprap the lowest (compared with Gittman *et al.* 2016). However, rarefaction and extrapolation estimates suggest that riprap richness might be similar to, and sediment richness might even exceed, that of cobble. Despite its small overall area within PCPP, riprap contributed four unique taxa to the overall richness.

Of the two cobble beach surveys, Cob1 reported more taxa than Cob2. It also sampled lower in the intertidal, used larger quadrats, and sampled one additional site. All three of these factors are well known to increase sample richness (Stephenson and Stephenson 1949; Gotelli and Colwell 2011; Chao *et al.* 2014). In this instance, it was the lower elevation that likely contributed the most to higher observed richness. Interannual variation in tidal amplitudes (Denny and Paine 1998) was such that unusually low tides exposed much more habitat in 1989 for Cob1, whereas unusually high low tides exposed much less in 2015 for Cob2. The Cob1 quadrats that fell below the reach of Cob2 contained the most unique taxa, and the majority of the total richness reported in Cob1. In contrast, larger quadrats in Cob1 appear to have had a lesser effect when quadrat size, taxonomic resolution, and intertidal elevation range were accounted for, and the additional site in Cob1 contributed only one additional taxon.

Finally, differing taxonomic expertise contributed to the composition differences among surveys, with a plethora of polychaetes in Sed, fish in Cob1, and amphipods (our study) identified based on available expertise. Overall, these composition differences illustrate the value of compiling alpha-diversity snapshots from multiple intertidal habitats to move toward a more comprehensive picture of the gamma diversity (Mushet *et al.* 2019) of a location, providing the organismal level ground-truthing required to design and implement future diversity monitoring (e.g., Castelin *et al.* 2016; Lobo *et al.* 2017).

This data compilation illustrates general challenges and opportunities in assembling historical data (e.g., Lindenmayer and Likens 2010; Hortal *et al.* 2015; Pendleton *et al.* 2019). All four PCPP surveys had limited original dissemination: Levings and McDaniel (1976) is a technical government report, Birch *et al.* (1990) is an unpublished consulting report, and the two surveys from our study were originally collected for an unpublished undergraduate thesis (Gerstle 2016). Neither of the historical studies was referenced in the PCPP Master Plan (BC Parks 1990), and the Birch *et al.* (1990) report was brought to our attention by parks staff only after our study was completed. A fifth survey conducted by Bard (1998) at multiple intertidal Howe Sound sites including Porteau Cove reported taxon numbers but not identities; one species from that study has since been identified in an unpublished thesis (Willems 2004).

A second major difficulty in such a data compilation is that voucher specimens were not archived by any of the four studies, including ours. This limitation can arise from lack of funding or institutional capacity or both, and hampers future confirmation of identifications. Digital vouchers in the form of photographs on iNaturalist (via GBIF) allowed us to confirm the identifications of several large and conspicuous species that added to the overall taxon list. The growing capacity to store and search digitized collection records will continue to make both physical and photographic vouchers easier to search and share (e.g., Pendleton *et al.* 2019; Hedrick *et al.* 2022), facilitating future biodiversity compilations.

Our compilation of current and historical surveys demonstrates the value of doing the detective work to obtain and analyze such hidden and scattered data: it makes available historical information, it substantially updates our diversity knowledge of a provincial park, it reports on a habitat otherwise uncatalogued in a provincial monitoring program, and it provides the foundational data needed to inform future monitoring at multiple ecological scales.

Author Contributions

Conceptualization: C.G. and M.W.; Methodology: C.G.; Investigation: C.G.; Supervision: M.W.; Data Curation: M.W.; Formal Analysis: M.W. and C.B.; Visualization: M.W. and C.B.; Writing – Original Draft: M.W., C.B., and C.G.; Writing – Review & Editing: M.W., C.B., and C.G.

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SUPPLEMENTARY MATERIALS:

FIGURE S1. Intertidal survey habitats at Porteau Cove Provincial Park, British Columbia.

FIGURE S2. Rank-order frequency curves for taxa found in four intertidal biodiversity surveys at Porteau Cove Provincial Park, British Columbia.

TABLE S1. Intertidal taxa found in four quantitative surveys or reported as qualitative text records in Porteau Cove Provincial Park, British Columbia.

TABLE S2. Compiled quadrat records of intertidal taxa from four quantitative intertidal surveys at Porteau Cove Provincial Park, British Columbia.