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Dietary overlap and niche partitioning of sympatric harbour porpoises and Dall's porpoises in the Salish Sea

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ABSTRACT

Ecological theory regarding the coexistence of similar species predicts resource partitioning will arise through competition and lead to different ecological niches. The diets of harbour porpoises (*Phocoena phocoena*) and Dall's porpoises (*Phocoenoides dalli*) in the Salish Sea were investigated for evidence of resource partitioning between these ecologically similar species. Stomach contents of 36 harbour porpoises and 11 Dall's porpoises were analysed and ten and six fish taxa were identified in each, respectively. Pacific herring (*Clupea pallasi*) was important in the diet of both porpoise species and walleye pollock (*Theragra chalcogramma*) was second in importance in the Dall's porpoises. Pacific herring was estimated to contribute 60% to the total caloric intake of harbour porpoises. In addition to herring, Pacific hake (*Merluccius productus*), walleye pollock and a species of Pyschrolutidae were present in the diet of both porpoise species. Pianka's Index of niche overlap indicated substantial dietary overlap between the porpoise species based on measures of prey frequency of occurrence and prey percent numerical abundance. These results seem contrary to predictions from ecological theory. However, habitat and activity pattern differences between the two porpoise species exist and represent other dimensions of niche that likely contribute to resource partitioning in ways that were not strongly evident in stomach contents. Dall's porpoises, which prefer deeper water habitat in the Salish Sea than harbour porpoises, may feed more on walleye pollock which spawn in deep water. Dall's porpoises are also known to feed at night when lipid-rich mesopelagic prey such as Myctophidae and Bathylagidae, both present in the Dall's porpoise samples, migrate upwards from depths in excess of 200 m. In contrast shiner perch, present only in harbour porpoise samples, is a species associated with shallow nearshore habitats. Resource partitioning is also likely to occur in accordance with seasonal prey availability.

1. Introduction

Ecological theory states that similar species that co-occur in an area and have similar diets will be in competition with each other for existence (Gause, 1934). Prediction from this theory is that such species will have evolved mechanisms to reduce competition to allow co-existence (Schoener, 1974). The harbour porpoise (*Phocoena phocoena*) and the Dall's porpoise (*Phocoenoides dalli*) are two ecologically similar species that inhabit the Salish Sea (Keple, 2002; Hall, 2004, 2011). The Salish Sea includes the Strait of Georgia, a semi-enclosed sea on the west coast of Canada, and Juan de Fuca Strait to the south, which connects to the Pacific Ocean. The Strait of Georgia is a productive marine ecosystem driven by freshwater inputs from the Fraser River and by tidal and wind-driven mixing of deep nutrient rich waters from Juan de Fuca Strait (Thomson, 1981).

Harbour porpoises occupy shallow bays, estuaries, harbours, and sounds throughout temperate and subarctic waters of the northern hemisphere (Gaskin, 1992; Laake et al., 1998; Raum-Suryan and Harvey, 1998; Carretta et al., 2001). The Dall's porpoise occurs pelagically across the North Pacific but also inhabits nearshore areas of the Pacific, such as the Salish Sea, that are characterized by wide straits, deep open ended channels with strong currents or deep canyons where waters are 180 m or more in depth (McTaggart-Cowan, 1944; Jefferson, 1988).

Both species feed on schooling fish and cephalopods and appear to have similar diets. World-wide, harbour porpoises feed on a variety of fish and cephalopods, including Atlantic herring (*Clupea harengus*), Atlantic hake (*Merluccius bilinearis*), Atlantic cod (*Gadus morhua*), whiting (*Merlangius merlangus*), sandeels (Ammodytidae), Pacific herring (*Clupea pallasi*), smelt (Osmeridae), gadids (Gadidae) and opalescent squid (*Loligo opalescens*) (Wilke and Kenyon, 1952; Gearin et al., 1994; Recchia and Read, 1989; Santos and Pierce, 2003; Sveegaard et al., 2012). Dall's porpoises are also known to feed on Pacific hake (*Merluccius productus*), Pacific herring, northern anchovy (*Engraulis mordax*), lanternfish (Myctophidae) and opalescent squid (Morejohn, 1979; Jefferson, 1988).

The co-occurrence of harbour porpoises and Dall's porpoises in the Salish Sea and general similarities in their diets globally leads

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to a prediction about the existence of competition between these two species for prey. Ecologically similar species can co-exist when foragers partition the available resources and maintain different ecological niches. Such niche separation can involve some or all niche dimensions such as foraging in different areas, occupying different habitats, foraging at different times, or using different foraging tactics (Schoener, 1974; Pianka, 1976; Wilson, 2010).

Our primary objective in this study is to examine the diet of harbour porpoises and Dall's porpoises in the Salish Sea from stomach contents of stranded animals to investigate resource partitioning. We predict that there will be differences in prey composition and sizes of prey items of the same species in the diet that will be indicators of resource partitioning. We also expect that by drawing upon life history and distribution information about prey species in the Salish Sea we will be able to make inferences about porpoise foraging habitat and foraging behaviour, two niche dimensions that can facilitate resource partitioning. Our secondary objective is to provide a better understanding of the contribution of these two species to community interactions and trophic dynamics in the Salish Sea.

2. Methods

2.1. Collection of samples

Thirty-six harbour porpoise and 11 Dall's porpoise stomach samples were obtained from stranded animals (1991–2010) (Tables 1 and 2). Stomachs and contents were collected and frozen for diet analysis. The study area includes the Strait of Georgia and Juan de Fuca Strait, which comprise the major part of the Salish Sea, as well as Johnstone Strait which connects to the Salish Sea in the north (Fig. 1).

2.2. Sample analysis

Stomachs were thawed and contents carefully rinsed through a series of sieves of which the finest was 500 μm. All diagnostic parts were retrieved and sorted by hand via visual inspection with the aid of a magnifying lens or a dissecting microscope. Fish bones were cleaned and dried. Cephalopod beaks were stored in 70% ethanol but were not identified to taxonomic level below class Cephalopoda. Polychaeta were not identified to taxonomic level below class. Fish prey remnants were identified based on diagnostic parts to the lowest taxonomic group. Otoliths were sorted by species and by quality (degree of erosion) into four classes (Table 3). Otoliths were measured using a Leica zoom lens dissecting microscope connected to a Leica DFC 320 camera. Image Pro Plus V 6.1.0.346 software was used to mark the edges of the otolith image and measure otolith length. A comprehensive list of all prey taxa identified in the diet of these porpoise species in the study area was made based on the results of this study and an earlier diet study (Walker et al., 1998).

2.3. Diet data analysis

Four measures were used to investigate diet composition of each porpoise species:

Table 1
Summary information for harbour porpoises collected in the study area.

Length (cm)	Weight (kg)	Sex	Age	Date	Location
U	U	U	U	October 15, 1991	Qualicum
134	U	F	U	December 22, 1998	Qualicum
143	37	F	A	May 2, 2001	Haro Strait
144	36	F	J	May 9, 2001	Race Rocks
110	20	F	J	September 2, 2001	Esquimalt Lagoon
166	50	F	A	May 1, 2004	Victoria – Ross Bay
U	U	M	U	May 3, 2004	Race Rocks
U	U	F	A	Spring, 2005	Juan de Fuca Strait/Strait of Georgia
127	U	M	A	May 5, 2005	Victoria
U	35	F	A	May 10, 2005	Oak Bay
127	38	M	A	May 14, 2005	Enterprise Channel
139	38	M	A	May 14, 2005	Victoria – Dallas Rd.
180	80	F	A	June 5, 2005	Saltspring Island
U	U	F	A	November 11, 2006	Comox
158	U	M	A	March 22, 2007	Whelis Bay
184	U	F	A	March 26, 2007	Whelis Bay
166	35	M	U	October 19, 2007	Campbell River
158	U	F	A	January 29, 2008	Tsawwassen
170	U	F	U	March 12, 2008	Esquimalt Lagoon
119	U	F	J	April 6, 2008	Esquimalt Lagoon
178	90	F	A	April 8, 2008	Esquimalt Lagoon
132	U	M	U	April 8, 2008	Delta
142	U	F	U	May 5, 2008	Maple Bay
U	U	F	U	May 17, 2008	Race Rocks
116	U	M	J	January 6, 2010	Miner's Bay, Mayne I
178	U	F	A	January 20, 2010	Albert Head
U	U	F	U	January 20, 2010	Albert Head
U	U	M	J	February 3, 2010	Albert Head
127	32	U	U	March 17, 2010	Trial Island
U	U	M	U	April 13, 2010	Race Rocks
145	U	M	A	May 7, 2010	Race Rocks
166	U	F	A	May 7, 2010	Albert Head
116	U	M	J	May 8, 2010	Samsun Narrows
173	U	U	A	May 10, 2010	Sooke Bluffs
174	U	F	A	May 11, 2010	Victoria – Clover Point
121	U	M	J	May 9, 2010	Witty's Lagoon

U = unknown, J = juvenile, A = adult.