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Seabed Biodiversity Shifts Identify Climate Regimes: The 2011 Climate Regime Shift and Associated Cascades

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Abstract

Using search programs for a long-term SCUBA taxonomic database (3865 dives) for Strait of Georgia seabed sites, 1077 taxa were screened to select rare or highly abundant taxa and to present the data according to climate regime categories. Ocean Niño Index (ONI) climate regime shifts are defined here as the year of the end of the first La Niña closely paired with an El Niño by ≤ 2 months separation, where anomalies for both El Niño and La Niña exceed 1.0 on the ONI scale. For both rare and abundant taxa, patterns of increased or decreased abundance frequently correspond to years defining climate regimes. Cascading effects of climate regime shifts may occur via changes in community composition. The sea star wasting disease (SSWD) syndrome eliminated urchin predators so that urchins have decreased abundance of a kelp species that is nursery habitat for spot prawns. We conclude that 2011 was a climate regime shift. This 2011 regime shift coincided with loss of 11 seabed species in the Strait of Georgia, none of them at their southern range extreme.

Keywords: climate regime shift, seabed biodiversity, 2011 regime shift, sea star wasting, urchin barren, prawn nursery, cascade effects

1. Introduction

Monitoring of biodiversity may sometimes reflect human impacts on ecosystems, but analysis of biodiversity needs to account for naturally occurring trends as well. In the analysis of Strait of Georgia seabed biodiversity [1], climate regimes shifts were characterized by change in overall biodiversity during different regimes defined from the literature as starting in 1977, 1989 and 2001 (with the data presentation running from 1967 through 2010). It has been posited that seabed biotic changes indicated that a new climate regime had started in 2011 [2],

although, to our knowledge, no published physical oceanographic data exist to demonstrate such a regime shift. Here we present a precise logical definition for using Ocean Niño Index (ONI) data [3] to define start-year for regime shifts based on the end of pairings of strong El Niño and La Niña events. Biodiversity data presented according to those newly defined regimes support the designation of 2011 as the most recent climate regime shift. It is a positive sign that biodiversity trends relate to natural climate regimes.

Climate regime shifts have largely been modeled on the basis of physical oceanographic data, with different authorities sometimes indicating different start-years for a regime. For example, Ref. [4] determined 2001 to be the start of the millennial climate regime whereas Ref. [5] calculated that 1999 started that regime. Many investigations rely on the Pacific Decadal Oscillation (PDO) model [6] whereas the present manuscript relies on the Ocean Niño Index (ONI = ENSO, El Niño/Southern Oscillation index) [3].

In some cases, biodiversity may provide more accurate definition of climate regime shifts than do physical oceanographic data [7, 8]. Benthic biodiversity has been shown to shift in synchrony with climate regime shifts [1]. Echinoderms may be important indicators of these shifts, as they show extreme population fluctuations, with both large-scale recruitment events and catastrophic population declines [9]. A recent occurrence of extreme population fluctuations in echinoderms was the seastar wasting disease (SSWD) which decimated many seastar populations, notably of *Pycnopodia helianthoides* [10]. Such declines are often caused by disease outbreaks associated with climate cycles [11] and almost every previous occurrence of sea star wasting has been associated with warming waters [12–15].

Trophic cascades resulting from *Pycnopodia* wasting disease can affect kelp beds through release of herbivore populations of green urchin *Strongylocentrotus droebachiensis* from predation [16]. Green urchins are a main prey item for sunflower stars [17] and urchin abundance can increase rapidly in the absence of predators [18]. The intensity and geographic extent of previous echinoderm mortality events have recently been eclipsed by a sea star wasting disease (SSWD) mass mortality event encompassing most of the west coast of North America [19]. While the disease is associated with a densovirus in *Pycnopodia helianthoides* [10], no previous evidence relates the outbreak to climate cycles. In Howe Sound, British Columbia, high urchin abundance is linked to a decline in the sea colander kelp *Neogagarum fimbriatum* [16]. The decline in kelp beds could in turn have cascading effects for organisms that depend on kelp for structural cover or other resources [16], and in particular, may affect spot prawns (*Pandalus platyceros*) that use the structure of *Neogagarum* as nursery habitat [20]. The recent documentation of cascade effects over a half decade encompassing the SSWD in Howe Sound [16] is here expanded to encompass long-term biodiversity and abundance trends for the green urchins and sunflower stars, using the database that has enabled previous correlations with climate regimes [1].

The present book chapter, like our preceding chapter [1], relies on biodiversity data for comparing successive potential climate regimes. Using the 2013 die-off of sunflower sea stars [10] as a natural experiment, we sought to provide a link between trophic cascades and climate regime shifts. Specifically, we used over 30 years of subtidal biodiversity monitoring [1] in

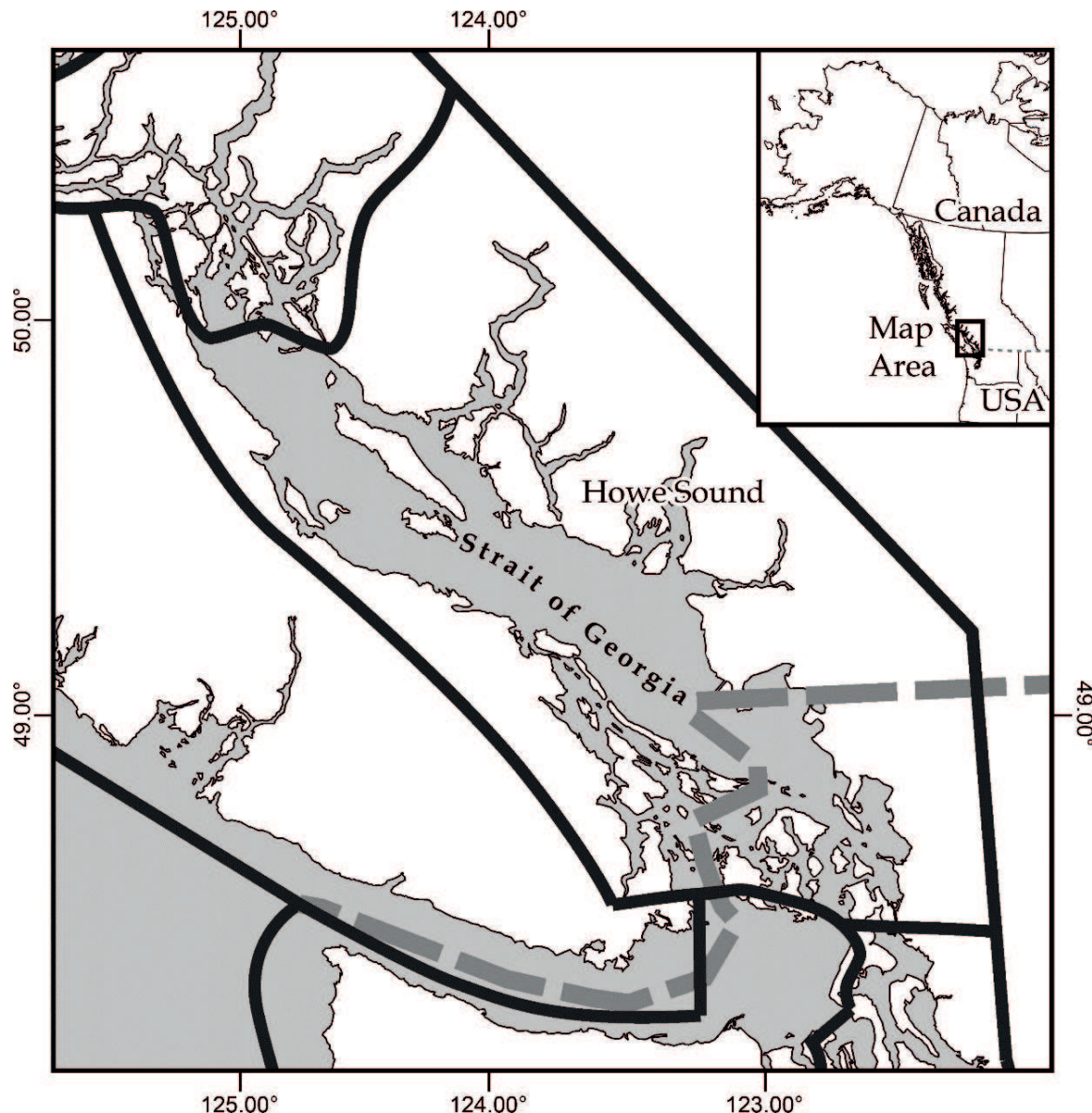


Figure 1. Boundaries [1] for taxonomy dive records for the Strait of Georgia region of British Columbia, Canada and a southeastern portion of the region inside the USA. Howe Sound is one adjoining water body discussed regarding trophic cascade effects.

Howe Sound (**Figure 1**) to identify population trends consistent with a trophic cascade following the loss of an upper level predator [21]. We anticipated that the sea star die-off would coincide with an increase in green urchins and a decline in kelp, and indirectly to a decline in spot prawns via loss of kelp as nursery habitat. We compared the timing of abundance fluctuations and climate regime shifts, as defined by Ocean Niño Index (ONI). We present population data that suggest a correlation between fluctuations in *Pycnopus* populations and climate regime shifts, and discuss the etiology of SSWD. This discussion is based on the premise that 2011 was a climate regime shift [2].

2. Methods

Ocean Niño Index climate events are defined here as starting in the year of the end of the first La Niña closely paired with an El Niño by ≤ 2 months separation, where anomalies for both El Niño and La Niña exceed 1.0 on the ONI scale for 5 months or longer (available from tinyurl.com/ENSONOAA). By that definition, the starting points of climate regime shifts from the literature get changed to earlier years in some cases; 1974 rather than 1977 and 1999 rather than 2001. Since the 1989 regime shift involved only the pairing of one La Niña after a strong El Niño, it remains starting at 1989. The regime shift of 2011 [2] is designated for the end of the first of two consecutive La Niñas paired with a strong El Niño.

Using search programs for a long-term SCUBA taxonomic database (3865 dives) for Strait of Georgia seabed sites [22], 1077 taxa were screened to select 171 rare or highly abundant taxa and to present the data according to climate regime periods as defined above. The majority of taxa was more uniformly abundant through the survey period and obscured any trends visible from scanning just the 171 species. We present taxon data in tabular form so that relations of biodiversity data to Ocean Niño event-based regime shifts can be visualized.

We used these biodiversity surveys to compare the abundance of sunflower stars and green urchins in Howe Sound through time, the same survey methods used for the long-term database. Surveys were conducted on SCUBA using the roving diver technique at depths from 7 to 30 m between 1984 and 2016. The relative abundance of each species observed during a dive was estimated visually and grouped into a numerical category: none = 0; few ≤ 10 ; some ≤ 25 ; many ≤ 50 ; very many ≤ 100 ; abundant ≤ 1000 ; very abundant = thousands. To calculate annual averages, maximum values for each category were used (3000 for “very abundant”). Subsequent to SSWD and the green urchin explosion, observations of *Neoagarum fimbriatum* abundance and spot prawn nursery settlement have enabled interpretation of cascade effects that relate to climate regimes.

Geographic locations of dives within the Strait of Georgia (**Figure 1**) shifted through the years and research priorities may have influenced the abundance averages for some years. Many of the species, however, were not the focus of special dive searches and were listed in dive summary taxon records as a matter of routine, so that most abundance records can be taken as derived by standard methods. In recent years, focus on location and abundance of *Neoagarum* versus green sea urchins *Strongylocentrotus droebachiensis* in Howe Sound has required careful interpretation.

Spot prawn abundance was quantified by monitoring spot prawn nursery settlement [20]. Using settlement records, each site was scored as urchin barren or not, based on whether *Neoagarum* was present. At sites lacking records of urchins or *Neoagarum*, juvenile prawn counts greater than zero were assumed not to be an urchin barren. However, zero counts for prawns did not indicate an urchin barren, as zero counts frequently occur in dense *Neoagarum* [20].

3. Results

Most of the 1077 taxa were present during all climate regimes in the Strait of Georgia, documented in 3865 dives. When aligned with climate regime event-years, 171 selected rare and abundant species showed correspondence to the Ocean Niño events (**Table 1**). Only rare taxa were undetected during entire regimes. For the most abundant taxa, patterns of increased or decreased abundance correspond to the years defining climate regimes, suggesting the possibility that causal relations may one day be determined. Abundance data for the 171 selected species are in **Table 1** for the entire Strait of Georgia region, including Howe Sound. An asterisk indicates trace abundance.

Among the Orchophyta the *Desmarestia* (acidic) species occur irregularly but are of note in recent years since 1999. *Neogarum* jumped in abundance during the 1999 regime, whereas a search anomaly with regard to study of widespread urchin barrens and kelp recovery resulted in anomalously high abundance estimates for this kelp during 2014–2017. Limiting a data compilation to first dives at each site yielded different results, with *Neogarum* absent (urchin barrens) at over half of all sites for 2014–2017. Among the Rhodophyta there were seven genera (*Porphyra*, *Hildenbrandia*, *Clathromorphum*, *Callophyllis*, *Mazzella*, *Constantina* and *Opuntia*) that peaked during the 1999 regime. Note that seaweed dive identification had not advanced prior to the 1989 regime.

Among the Porifera, *Leucosolenia* and *Adocia* were mainly abundant during the 1999 regime, whereas *Pachychalina* and *Myxilla* were abundant in both the 1989 and 1999 regimes. *Plocamia* was abundant mainly in the 1974 and 1989 regimes, in contrast to *Cliona*, for example, which occurred throughout all years.

In the Cnidaria, *Cribrinopsis* was highest in abundance during the 1999 regime; few have been seen in recent years. *Peachia* was also most abundant during the 1999 regime. Similarly, *Pachycerianthus* was abundant during the 1999 regime, declining during the 2011 regime; *Ptilosarcus* was also most abundant during the 1999 regime. *Halipterus* was absent during the 1989 regime, abundant during the 1999 regime, then dropped out again in 2014. *Stylantheca* was also steady in abundance until 2014. The jellies *Cyanea*, *Aurelia*, *Aequorea* and various hydromedusae were especially abundant during the 1999 regime, as was the case for ctenophores.

Rare species of nemerteans were absent in the 2011 regime, as with sipunculid worms and some annelid worms. An exception is *Protula pacifica*, which was least abundant during the 1989 regime. Bryozoans were either lower in abundance or absent in the 2011 regime. The same was true for Brachiopoda.

In the Mollusca many species were reduced in abundance (some absent) in the 2011 regime. An exception is the very obvious species *Pododesmus machroschisma*, which was higher in abundance during the 1999 regime, but still remained abundant in the 2011 regime, typical for many common species not included in this table for which abundance does not fluctuate in any pattern discernable with regime shifts. Distinction of *Mopalia* spp. among ten different species was not achieved until 1996, yet the abundance of these species dropped in the 1999 and 2011 regimes. The common and obvious species *Ceratostoma foliatum* is typical of these

Year	1984	1985	1986	1987	1988	1989	1990	1991	1992	1993	1994	1995	1996	1997	1998	1999	2000	2001	2002	2003	2004	2005	2006	2007	2008	2009	2010	2011	2012	2013	2014	2015	2016	2017			
No. dives per year	51	71	67	55	52	52	58	59	56	109	120	101	122	121	115	110	97	93	112	138	126	136	188	98	191	123	104	83	102	155	93	166	130	69			
Ochrophyta																																					
<i>Desmarestia</i> spp.	.	.	15	*	.	30	50	.	1	21	35	13	11	8	8	*	1	3	37	19	23	18	2	*	4	*	3	47			
<i>Neogagarum fimbriatum</i>	.	.	1	.	.	.	17	*	.	19	34	71	48	70	39	210	248	265	123	188	117	116	101	112	88	145	66	38	29	64	119	214	168	283			
Rhodophyta																																					
<i>Porphyra</i> spp.	*	.	.	1	22	23	20	9	1	1	1	21	6	11	30	3	1	*	*	1	1	*			
<i>Hildenbrandia</i> spp.	20	36	25	20	130	171	143	162	239	204	54	76	137	206	194	176	123	14	28	7	40	46	5			
<i>Clathromorphum</i> etc.	*	18	9	9	20	48	11	12	79	236	88	181	127	44	104	57	84	69	145	83	95	60	35	20	54	73	8			
<i>Callophyllis</i> spp.	*	.	1	31	24	29	20	10	3	4	11	19	27	13	5	4	2	1	1	1	11	1			
<i>Mazzaella splendens</i>	*	.	*	*	1	*	3	1	23	1	1	1	2	2	2	5	3	.	1	1	*	*	1	1	.			
<i>Constantinea simplex</i>	*	.	*	*	*	2	2	1	9	10	1	1	1	2	1	*	1	*	1	*	*	.	.			
<i>Opuntiella californica</i>	.	.	1	9	.	*	1	*	*	11	3	13	3	2	3	1	1	1	4	3	1	1	1	*	1	1	*	*			
Porifera																																					
<i>Leucosolenia eleanor</i>	.	*	1	*	1	1	*	15	*	*	*	1	2	2			
<i>Craniella villosa</i>	*	3	78	40	2	4	7	9	24	13	24	32	12	9	*	29	3	1	10	9	2	3	6	2	4	27	1	2	11	*	.	*	*	.			
<i>Cliona californiana</i>	.	3	23	*	.	.	3	2	23	14	11	6	4	11	7	8	24	26	19	47	17	27	21	31	43	56	26	29	27	8	36	7	15	8			
<i>Hamaxinella amphispicula</i>	.	*	*	*	10	1	*	*	*	*	1	2	13	2	2	3	4	1	1	1	1	1	1	1	1	*	1	*	.	2		
<i>Pachychalina</i> spp.	1	21	18	57	40	19	14	11	1	10	11	84	33	46	15	.	22	.	*	*		
<i>Adocia</i> sp.	.	.	1	8	*	.	19	2	2	2	2	2	1	8	6	1	3	4	.	1	10	1	.	*	*	.		
<i>Plocamia karykina</i>	.	.	15	18	.	1	53	51	3	11	11	11	8	1	*	*	*	*	*	*	*	*		
<i>Myxilla incrustans</i>	*	*	*	1	1	20	34	9	9	1	2	12	63	1	17	2	2	1	4	3	3	1	*	*	*	*	*	1	1		

Year	1984	1985	1986	1987	1988	1989	1990	1991	1992	1993	1994	1995	1996	1997	1998	1999	2000	2001	2002	2003	2004	2005	2006	2007	2008	2009	2010	2011	2012	2013	2014	2015	2016	2017			
No. dives per year	51	71	67	55	52	52	58	59	56	109	120	101	122	121	115	110	97	93	112	138	126	136	188	98	191	123	104	83	102	155	93	166	130	69			
Cnidaria																																					
<i>Metridium farcimen</i>	*	5	221	76	1	78	59	221	310	313	126	58	88	46	35	127	219	123	119	168	285	362	153	442	470	401	373	263	149	82	78	93	143	101			
<i>Cribrinopsis fernaldi</i>	1	4	21	*	.	*	1	1	4	2	1	1	1	2	2	2	5	16	3	5	11	10	1	1	3	7	1	1	1	1	*	*	*				
<i>Peachia quinquecapitata</i>	*	*	24	*	*	.	1	4	*	*				
<i>Pachycerianthus fimbriatus</i>	20	6	21	1	1	20	4	17	5	22	22	3	20	2	24	41	78	75	100	184	162	95	84	102	73	104	151	110	32	35	13	13	24	6			
<i>Balanophyllia elegans</i>	1	75	213	365	59	232	296	224	321	244	122	50	47	37	49	88	183	54	53	95	124	86	114	267	392	409	226	204	95	57	4	40	60	18			
<i>Caryophyllia alaskensis</i>	1	1	10	3	1	1	11	11	12	2	3	1	10	5	2	1	*	1	2	1	1	3	1	*	1	*			
<i>Ptilosarcus gurneyi</i>	*	3	48	*	2	*	2	2	4	3	3	3	2	*	4	14	14	15	22	11	31	6	7	37	17	9	8	4	2	2	1	3	2	1			
<i>Halipterus willemoesi</i>	*	*	*	*	*	*	8	1	*	1	*	.	*	*	40	*			
<i>Stylantheca papillosa</i>	.	2	167	55	.	20	20	36	4	33	71	73	27	18	1	20	33	11	38	8	*	22	1	1	13	62	4	13	11	7	.	1	1	.			
<i>Aglaophenia</i> spp.	*	57	18	*	.	19	1	.	*	12	10	2	8	8	10	28	22	*	1	1	*	*	6	1	9	3	*	.	1	*	.	.	*	.			
<i>Garveia annulata</i>	.	1	20	.	*	.	1	18	54	6	27	11	2	*	1	1	53	*	*	*	*	1	*	.	9	66	*	1	*	*	.	.	1	.			
<i>Lafoea dumosa</i>	1	*	*	.	*	.	.	1	*	.	2	5	2	2	24	3	3	3	29	18	11	5	3	*	1	.	1	.	2			
<i>Cyanea capillata</i>	*	*	1	*	.	.	*	*	*	*	*	*	*	*	*	1	1	*	*	2	2	*	1	1	1	9	*	*	*	2	*	*	*	*			
<i>Aurelia labiata</i>	.	15	45	.	.	.	*	.	*	1	*	10	26	*	1	82	13	33	10	23	35	1	3	67	42	31	28	*	*	2	*	*	1	1			
<i>Aequorea</i> spp.	.	3	93	55	.	.	*	1	1	31	10	42	*	*	19	77	13	1	3	17	29	11	32	70	140	148	112	5	2	5	2	1	2	4			
<i>Polyorchis penicillatus</i>	.	*	.	.	*	*	*	*	.	.	*	.	.	*	*	*	.	1	*			
<i>Clytia gregaria</i>	.	*	182	91	*	.	1	*	18	14	37	12	*	*	1	30	22	34	21	23	1	1	*	1	3	4	.	*	1	.	1	*	*	*			
<i>Eutonina indicans</i>	*	*	*	11	*	43	46	8	1	8	5	1	3	2	1	1	.	19	1	.	*	.			
<i>Sarsia</i> spp.	.	*	1	*	*	*	*	1	1	1	*	*	*	1	.	*	*			
<i>Nanomia bijuga</i>	.	*	1	.	.	.	*	.	*	*	*	*	*	1	1	1	*	1	1	23	*	1	*	2	*	9	1	1	1	*	*	.	*	1			

Year	1984	1985	1986	1987	1988	1989	1990	1991	1992	1993	1994	1995	1996	1997	1998	1999	2000	2001	2002	2003	2004	2005	2006	2007	2008	2009	2010	2011	2012	2013	2014	2015	2016	2017	
No. dives per year	51	71	67	55	52	52	58	59	56	109	120	101	122	121	115	110	97	93	112	138	126	136	188	98	191	123	104	83	102	155	93	166	130	69	
Ctenophora																																			
<i>Pleurobrachia bachei</i>	.	100	124	.	.	*	*	17	.	112	52	1	2	2	12	85	43	33	56	3	2	17	7	11	1	5	1	3	12	*	3	*	2	*	
<i>Bolinopsis infundibulum</i>	.	.	2	.	*	.	.	.	*	28	8	.	1	*	9	38	12	12	3	46	17	2	1	1	57	47	31	1	1	1	1	*	1	*	
Nemertea																																			
<i>Quasitetrastemma nigrifrons</i>	*	.	.	.	*	*	*	.	.	1	.	*	.	.	.	*	
<i>Cerebratulus californiensis</i>	.	.	.	*	.	*	*	.	.	*	.	.	*	.	.	.	1	*	.	*	
Sipuncula																																			
<i>Golfingia vulgaris</i>	*	.	*	*	.	.	.	*	*	*	*	*	*	*	*	*	*	.	*	*	
Annelida																																			
<i>Amblyosyllis</i> sp.	1	*	*	*	
<i>Tomopteris septentrionalis</i>	*	*	*	9	*	*	.	*	
<i>Ophiodromus pugettensis</i>	1	*	*	.	.	*	
<i>Harmothoe extenuata</i>	*	.	*	.	.	.	*
<i>Apomatus</i> spp.	.	5	2	.	.	.	*	*	1	3	2	1	1	1	2	2	1	3	1	*	1	1	*	*	*	*	*	*	1	*	1	*	*	*	
<i>Protula pacifica</i>	20	3	5	*	.	*	.	.	.	2	1	*	*	.	*	2	3	8	2	3	4	3	4	2	5	6	3	2	2	5	1	2	1	1	
<i>Pectinaria granulata</i>	*	*	*	.	*	.	*
<i>Sabellaria cementarium</i>	.	*	1	.	.	.	*	1	*	9	1	*	.	.	*	*	.	.	18	1	
Bryozoa																																			
<i>Lichenopora</i> spp.	*	12	12	9	8	9	*	*	*	*	.	1	1	*	2	*	1	1	.	

Year	1984	1985	1986	1987	1988	1989	1990	1991	1992	1993	1994	1995	1996	1997	1998	1999	2000	2001	2002	2003	2004	2005	2006	2007	2008	2009	2010	2011	2012	2013	2014	2015	2016	2017				
No. dives per year	51	71	67	55	52	52	58	59	56	109	120	101	122	121	115	110	97	93	112	138	126	136	188	98	191	123	104	83	102	155	93	166	130	69				
<i>Disporella separata</i>	1	*	1	1	*	1	.	*	1	1	*	*	1	1	2	*	*	1	2	.	.	*				
<i>Eurystomella bilabiata</i>	*	.	*	.	.	1	21	6				
<i>Bowerbankia</i> sp.	8	9	1	.	.	*	.	.	*				
<i>Diaperoforma californica</i>	.	15	78	291	58	21	125	1	291	51	113	23	58	9	35	65	33	1	28	8	9	26	19	29	63	51	15	2	1	1	*	1	1	.				
Brachiopoda																																						
<i>Laqueus vancouverensis</i>	.	31	52	21	19	2	106	21	11	26	16	5	5	1	3	24	4	6	3	3	2	9	2	1	2	1	1	2	2	*	1	1	1	1				
<i>Terebratulina unguicula</i>	.	.	*	.	.	.	52	.	.	2	.	60	*	*	.	1	15	3	10	1	10	8	6	1	16	*	1	2	*	*	.	6	*	.				
Mollusca																																						
<i>Tonicella lineata</i>	.	5	37	39	.	1	20	7	24	27	21	26	5	3	11	9	27	23	10	21	22	5	10	13	34	29	15	24	9	9	5	6	5	2				
<i>Mopalia lignosa</i>	*	*	.	.	*	*	*	1	2	1	*	*	*	*	*	3	1	2	*	*	.	*	*	1	1				
<i>Mopalia hindsii</i>	*	1	1	*	*	*	1	*	*	*	2	2	1	*	*	1	1	3	2				
<i>Mopalia spectabilis</i>	*	1	1	2	1	1	*	1	1	*	*	*	1	*	*	*	.	*	.	*	*				
<i>Mopalia</i> sp.	.	3	22	20	.	2	2	18	20	15	8	12	1	1	*	1	1	1	1	1	*	1	*	*	*	.	*	*	.	*	*	*	*	*				
<i>Lepidozonia mertensii</i>	*	.	2	3	4	3	1	1	1	3	3	5	1	2	2	9	3	3	5	4	5	2	1	1	*	2	2	2				
<i>Lepidozonia trifida</i>	*	1	*	*	1	1	2	2	1	1	1	2	3	2	*	2	1	*	*	*	*	*	2				
<i>Dendrochiton flectens</i>	*	*	*	*	.	*			
<i>Chlamys</i> sp.	20	59	34	1	1	2	55	288	234	58	80	43	43	19	18	12	26	37	110	18	58	12	5	7	21	7	15	4	4	2	3	2	12	7				
<i>Pododesmus macrochisma</i>	.	45	36	1	*	1	3	1	22	14	4	12	35	45	11	14	119	72	149	75	146	130	31	163	99	92	133	82	57	6	52	50	20	66				
<i>Kellia suborbicularis</i>	1	1	.	*	*	.	*	*	.	*	*	*	*	*	*	*	.	*				
<i>Saxidomus gigantea</i>	1	1	.	*	16	*	1	1	6	9	12	3	2	1	1	*	1	1				

Year	1984	1985	1986	1987	1988	1989	1990	1991	1992	1993	1994	1995	1996	1997	1998	1999	2000	2001	2002	2003	2004	2005	2006	2007	2008	2009	2010	2011	2012	2013	2014	2015	2016	2017	
No. dives per year	51	71	67	55	52	52	58	59	56	109	120	101	122	121	115	110	97	93	112	138	126	136	188	98	191	123	104	83	102	155	93	166	130	69	
<i>Humilaria kennerleyi</i>	.	*	*	.	.	*	*	.	*	*	*	*	*	.	*	*	*	*	.	*	.	*	1	3	2	2	1	1	*	*	*	.	*	*	
<i>Acmaea mitra</i>	.	2	49	1	1	1	1	1	21	3	3	13	11	1	9	2	43	3	3	2	2	1	1	1	2	4	2	3	1	1	.	*	*	.	
<i>Cryptobranchia concentrica</i>	1	1	*	*	*	*	2	12	6	*	*	*	*	*	*	*	1	1	
<i>Crepidula adunca</i>	.	*	*	.	.	.	*	17	.	1	2	1	*	8	*	9	*	*	.	*	*	1	.	*	*	*	
<i>Crepidula nummaria</i>	*	1	*	.	*	*	*	*	*	
<i>Crepipatella dorsata</i>	1	.	*	*	*	
<i>Ceratostoma foliatum</i>	.	18	7	1	1	1	3	4	24	7	22	14	12	2	2	41	7	9	17	5	5	11	4	5	10	22	19	12	4	5	3	4	14	6	
<i>Ocinebrina lurida</i>	.	1	47	40	.	1	2	18	3	11	4	1	2	1	*	9	1	1	*	*	1	9	1	*	1	2	3	1	*	1	.	.	1	.	
<i>Alia carinata</i>	.	14	1	18	.	.	17	.	.	1	17	11	9	.	*	*	*	.	*	1	
<i>Epitonium indianorum</i>	.	*	*	*	*	*	*	.	*	.	*	*	*	*	*	*	.	.	*	*	*	*	*
<i>Calliostoma ligatum</i>	.	16	81	74	*	1	53	35	97	15	43	27	4	2	10	31	57	25	14	12	5	11	8	2	13	10	1	4	2	3	36	3	3	1	
<i>Calliostoma annulatum</i>	*	.	2	*	.	*	*	*	.	1	*	*	*	*	*	.	.	*	*	*	.	*	.	.	*	*	*
<i>Calliostoma variegatum</i>	*	.	*	.	*	*	*	*	1	1	*	*	*	*	*	*	.	.	*	.	*	.	*	*	.	
<i>Calliostoma canaliculatum</i>	*	*	*
<i>Margarites pupillus</i>	1	15	34	.	.	.	52	34	72	2	1	21	1	9	1	*	12	*	.	1	1	*	*	*	1	*	10	*	.	.	.	1	.	*	
<i>Trichotropsis cancellata</i>	59	*	5	19	.	*	2	2	5	32	11	13	10	1	1	2	4	1	2	8	*	2	2	1	*	*	*	*	1	1	*	1	1	*	
<i>Rictaxis punctocaelatus</i>	.	*	9	1	*	*	*	*
<i>Aglaja diomedea</i>	*	*	*
<i>Aglaja ocelligera</i>	.	1	1	.	*	2	*	*	8	9	*	.	*	*	.	*	*	.	*

Year	1984	1985	1986	1987	1988	1989	1990	1991	1992	1993	1994	1995	1996	1997	1998	1999	2000	2001	2002	2003	2004	2005	2006	2007	2008	2009	2010	2011	2012	2013	2014	2015	2016	2017
No. dives per year	51	71	67	55	52	52	58	59	56	109	120	101	122	121	115	110	97	93	112	138	126	136	188	98	191	123	104	83	102	155	93	166	130	69
<i>Phyllaplysia taylori</i>	.	57	15	*	1	.	.	1	.	.	11	1	*	.	24
<i>Berthella californica</i>	.	1	1	*	.	*	*	3	1	*	*	*	*	12	1	1	*	*	*	*	*	.	*	*	.	*	*	*	*	*
<i>Cadlina luteomarginata</i>	.	3	8	2	1	1	4	5	3	4	6	4	3	3	2	4	3	4	4	4	4	3	6	8	7	7	7	5	3	5	3	1	1	*
<i>Rostanga pulchra</i>	.	*	*	*	.	.	.	1	.	*	*	*	*	*	*	.	*	.	*	*	*
<i>Triopha catalinae</i>	.	1	2	*	*	*	1	1	*	2	*	2	1	*	1	*	2	1	*	*	*	*	*	*	*	*	*	.	*	*	*	*	*	*
<i>Dirona albolineata</i>	1	16	4	*	*	*	1	*	6	11	2	2	1	1	1	1	3	3	2	2	1	*	*	4	9	16	5	2	2	1	2	1	*	*
<i>Dirona pellucida</i>	.	.	*	*	*	.	*	*	*	1	*	*	*	*	*	*	*	3	1	1	2	*	*	*	*	*	*	*	.
<i>Janolus fuscus</i>	.	14	31	*	.	*	52	1	2	1	1	*	*	*	*	1	1	1	*	1	1	*	.	*	*	*	*	*	1	*	*	.	*	*
<i>Janolus gelidus</i>	*	*	*	*	*	*	*	.	.	*
<i>Hermisenda crassicornis</i>	.	2	108	74	*	*	17	3	1	4	5	11	10	*	1	1	14	1	10	2	25	8	12	14	13	49	1	2	11	2	2	*	24	2
<i>Flabellina verrucosa</i>	.	.	*	.	.	.	1	34	.	13	29	12	*	9	*	2	32	11	*	1	*	*	*	*	17	6	2	.	*	1	.	*	*	*
Arthropoda																																		
<i>Heptacarpus kincaidi</i>	.	1	4	.	.	*	*	.	.	*	*	*	*	*	1	1	2	2	1	1	2	1	1	*	1	1	1	*	*	1	.	*	1	.
<i>Heptacarpus tridens</i>	*	.	*	1	10	1	1	*	*	*	*	*	1	1	1	*	*	*	7	*	*	1	1
<i>Heptacarpus tenuissimus</i>	*	*	.	.	*	1	1	*	.	.	*	*	*	*	.	.	*	*	.	.	*	.	.
<i>Heptacarpus sitchensis</i>	*	*	*	*	*	*
<i>Hippolyte clarki</i>	.	.	*	.	19	.	.	51	.	2	1	*	.	.	.	*	*	*	.	.	.	7	*	.	.	*
<i>Pandalus danae</i>	59	5	52	55	1	1	122	3	91	90	40	35	59	19	11	32	27	51	62	56	78	23	84	111	86	108	96	59	13	18	32	44	27	22
<i>Pandalus stenolepis</i>	20	*	*	*	1	*	1	1	*	2	10	1	10	10	20	4	24	15	2	1	2	42	3	5	12	3	14	4	1	2	.	2	3	2
<i>Lopholithodes mandtii</i>	.	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	1	*	*	*	*	*	1	1	1	*	*	*	*	*	1	*
<i>Cryptolithodes typicus</i>	1	*	*	*	*	*	*	*	*	*	*	*	*	1	*	1	1	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*

Year	1984	1985	1986	1987	1988	1989	1990	1991	1992	1993	1994	1995	1996	1997	1998	1999	2000	2001	2002	2003	2004	2005	2006	2007	2008	2009	2010	2011	2012	2013	2014	2015	2016	2017			
No. dives per year	51	71	67	55	52	52	58	59	56	109	120	101	122	121	115	110	97	93	112	138	126	136	188	98	191	123	104	83	102	155	93	166	130	69			
<i>Pagurus beringanus</i>	.	16	37	21	1	20	36	4	22	32	6	12	3	10	11	3	14	4	4	4	5	4	11	21	58	57	17	8	3	24	3	3	2	1			
<i>Elassochirus tenuimanus</i>	.	.	*	.	.	.	1	.	1	1	1	*	*	*	1	1	*	1	*	1	1	*	1	*	1	2	1	2	*	1	*	*	1	*			
<i>Pagurus armatus</i>	.	1	3	1	.	.	1	.	.	1	1	1	3	2	9	1	2	2	1	1	*	*	*	*	*	1	*	*	*	.	.	*	*	*			
<i>Balanus glandula</i>	.	17	185	55	19	.	86	136	92	129	97	130	68	68	54	114	102	278	209	217	101	356	156	191	197	486	232	258	99	62	117	161	275	121			
<i>Balanus nubilus</i>	59	59	128	184	2	116	278	121	220	171	147	64	12	34	29	50	157	15	130	63	77	205	23	19	143	91	64	34	46	13	4	21	28	2			
<i>Semibalanus cariosus</i>	.	*	30	18	58	.	.	17	23	1	1	10	8	*	.	9	10	22			
Echinodermata																																					
<i>Pisaster ochraceus</i>	20	6	25	19	58	1	3	76	43	13	30	65	3	13	31	25	70	34	19	65	4	13	11	16	31	23	5	19	15	6	20	4	4	4			
<i>Pisaster brevispinus</i>	.	6	5	2	1	2	4	1	1	4	2	5	2	4	3	3	4	8	5	14	14	5	27	10	11	26	33	9	27	13	7	1	1	*			
<i>Evasterias troschelii</i>	.	31	25	3	*	1	4	3	3	5	13	16	3	45	107	48	111	6	14	4	3	4	10	32	15	13	9	11	7	7	74	12	25	6			
<i>Dermasterias imbricata</i>	*	32	8	1	19	*	3	21	9	4	7	16	6	4	2	6	7	8	9	5	14	4	22	11	16	21	12	15	10	10	19	14	18	8			
<i>Mediaster aequalis</i>	*	5	3	*	19	.	22	18	1	2	3	1	2	2	2	3	6	13	6	8	7	8	7	10	24	47	18	21	5	14	7	9	5	4			
<i>Pteraster tessellatus</i>	.	2	4	1	*	1	1	1	2	2	1	2	1	1	1	2	2	4	2	1	2	1	1	1	1	2	1	1	2	3	1	*	*	*			
<i>Henricia</i> spp.	.	20	24	22	2	2	4	2	4	8	6	4	5	3	2	3	7	6	6	6	7	7	5	3	6	6	5	4	14	7	15	10	5	2			
<i>Pycnopodia helianthoides</i>	*	4	44	4	7	5	23	6	5	34	8	16	15	15	7	27	45	84	114	143	110	262	32	25	45	57	48	61	25	38	8	1	*	1			
<i>Solaster dawsoni</i>	.	3	3	1	*	1	2	2	2	3	1	2	1	1	1	1	3	5	3	4	13	4	7	4	5	5	7	3	4	4	1	*	*	*			
<i>Solaster stimpsoni</i>	1	2	5	1	*	1	1	1	1	3	2	4	2	1	*	1	2	3	1	1	2	2	2	2	4	5	2	1	2	2	*	*	*	*			
<i>Ophiura luetkenii</i>	.	*	15	*	*	.	18	17	*	42	29	2	2	19	3	23	58	62	115	115	182	221	193	219	187	330	192	45	30	35	86	38	12	4			
<i>Florometra serratissima</i>	.	1	*	*	.	.	1	.	1	21	2	4	34	4	4	49	45	16	51	119	32	48	75	193	179	92	140	57	6	6	39	25	28	6			
<i>Mesocentrotus franciscanus</i>	*	61	160	383	96	58	228	123	72	84	46	37	72	13	13	37	200	82	116	37	36	56	56	129	237	308	326	238	95	21	5	22	52	3			

Year	1984	1985	1986	1987	1988	1989	1990	1991	1992	1993	1994	1995	1996	1997	1998	1999	2000	2001	2002	2003	2004	2005	2006	2007	2008	2009	2010	2011	2012	2013	2014	2015	2016	2017				
No. dives per year	51	71	67	55	52	52	58	59	56	109	120	101	122	121	115	110	97	93	112	138	126	136	188	98	191	123	104	83	102	155	93	166	130	69				
<i>Strongylocentrotus droebachiensis</i>	59	44	66	38	60	3	21	21	20	52	36	12	28	120	150	85	184	82	159	92	136	56	20	33	78	199	296	98	56	128	337	546	617	488				
<i>Apostichopus californicus</i>	.	7	13	3	1	1	9	6	10	10	5	17	8	9	7	12	10	20	16	29	37	39	19	52	65	62	35	40	22	20	12	21	16	16				
<i>Cucumaria miniata</i>	59	71	186	92	.	3	3	3	24	14	39	33	12	2	4	5	35	15	32	5	13	12	16	8	54	55	7	29	16	14	6	17	39	8				
<i>Eupentacta quinquesemita</i>	59	1	37	4	.	20	2	3	5	5	19	15	2	1	1	14	54	3	4	3	4	2	3	1	8	30	3	3	4	15	*	1	3	5				
<i>Psolus chitonoides</i>	.	30	68	20	.	1	4	1	1	38	30	55	12	9	2	24	38	62	49	19	21	3	10	7	10	14	9	8	3	4	3	5	15	9				
Urochordata																																						
<i>Corella willmeriana</i>	.	4	26	4	*	*	1	1	57	5	3	72	2	3	3	29	38	17	44	64	20	2	32	43	96	48	39	77	45	26	3	2	10	1				
<i>Ascidia paratropa</i>	.	6	5	*	*	*	2	2	1	2	1	1	*	*	*	*	1	1	1	*	*	*	*	*	*	*	*	*	*	*	*	*	*	.				
<i>Cnemidocarpa finmarkiensis</i>	20	4	4	2	1	1	20	2	3	6	4	3	3	3	1	13	4	15	6	22	62	16	10	47	40	12	17	24	7	9	8	13	16	10				
<i>Halocynthia aurantium</i>	*	15	3	*	.	*	52	.	*	2	1	2	2	12	2	3	25	15	14	4	13	5	2	1	2	2	2	3	3	5	4	3	25	2				
<i>Halocynthia igaboja</i>	.	3	4	*	*	*	1	3	*	22	3	2	1	3	14	4	16	51	15	50	61	9	3	2	2	1	3	2	2	5	1	4	4	2				
<i>Pyura haustor</i>	118	45	19	1	*	1	4	3	22	5	12	3	3	2	2	4	4	5	5	3	4	4	2	3	6	1	3	4	3	2	1	1	10	1				
<i>Styela gibbsii</i>	1	59	50	*	.	*	21	2	4	30	18	11	2	9	1	65	4	38	39	5	28	1	2	65	38	1	24	5	1	2	1	1	1	2				
<i>Boltenia villosa</i>	*	59	6	.	*	*	3	2	4	15	21	35	29	37	30	42	19	42	53	41	22	5	7	61	27	5	10	6	4	8	4	2	5	2				
<i>Metandrocarpa taylori</i>	.	20	183	184	1	19	210	20	204	133	33	86	29	19	19	58	97	35	12	31	2	17	29	13	36	37	3	4	14	1	1	1	1	*				
<i>Pycnoclavella stanleyi</i>	*	.	49	182	1	40	37	23	4	22	27	51	25	9	.	19	11	1	*	8	1	9	5	2	3	10	.	.	1					
<i>Cystodytes lobatus</i>	118	1	33	55	*	38	156	19	.	24	11	2	11	.	1	19	22	*	9	*	1	1	2	2	18	10	*	1	1	*	*	.	.					
<i>Aplidium californicum</i>	.	1	4	18	*	.	.	3	39	2	2	40	18	1	*	*	2	2	11	1	1	*	7	3	10	12	2	3	1	2	.	*	*	*				
<i>Didemnum carnulentum</i>	.	58	62	73	.	20	.	*	*	11	2	2	*	.	1	*	*	*	*	*	*	1	*	*	*	*				

Year	1984	1985	1986	1987	1988	1989	1990	1991	1992	1993	1994	1995	1996	1997	1998	1999	2000	2001	2002	2003	2004	2005	2006	2007	2008	2009	2010	2011	2012	2013	2014	2015	2016	2017
No. dives per year	51	71	67	55	52	52	58	59	56	109	120	101	122	121	115	110	97	93	112	138	126	136	188	98	191	123	104	83	102	155	93	166	130	69
<i>Didemnum/</i> <i>Trididemnum</i> complex	*	25	.	.	10	12	1	9	15	8	1	8	53	22	38	25	5	1	1	*	*	2	1
<i>Trididemnum alexi</i>	.	*	1	*	.	.	.	17	.	1	*	*	1	1	1	1	*	12	*	8	8	.	*	*	*	.	*	*	*
<i>Botryllus schlosseri</i>	*	*	.	.	.	1	2	9	8	*	.	.	13	*	*	1	*	*
<i>Botrylloides violaceus</i>	2	1	44	1	2	24	1	8	8	8	*	1	1	1	*	1	*	.
Chordata																																		
<i>Clupea pallasii</i>	.	85	149	36	.	*	.	.	*	*	*	*	*	*	*	*	*	*	*	22	*	8	17	1	1	*	*	50	2	1	.	38	1	43
<i>Engraulis mordax</i>	*	.	*	.	.	*	*	73	92	101
<i>Damalichthys vacca</i>	2	16	4	1	*	1	1	22	2	6	3	2	2	1	1	12	26	16	13	5	28	11	20	11	23	8	7	8	5	4	2	10	43	*
<i>Embiotoca lateralis</i>	3	17	7	37	1	4	75	8	9	34	29	4	4	2	1	14	21	9	24	8	32	18	20	48	39	15	14	40	40	17	4	12	27	19
<i>Cymatogaster</i> <i>aggregata</i>	63	87	35	2	58	1	73	120	110	23	37	53	11	44	2	58	88	38	31	19	75	140	136	3	14	12	3	33	5	4	66	160	133	89
<i>Sebastes caurinus</i>	60	66	32	7	4	7	41	23	10	21	14	16	14	5	3	14	21	55	9	28	56	74	43	65	67	96	137	68	42	13	8	20	18	4
<i>Sebastes maliger</i>	1	8	26	8	1	25	3	4	26	23	3	6	4	4	2	7	7	11	6	30	27	59	20	34	30	43	32	13	18	8	2	11	3	1
<i>Sebastes auriculatus</i>	.	*	*	*	*	*	*	*	.	.	*	*	*	*	.	*	*	3	28	4	12	5	3	10	1	3	*	2	*
<i>Sebastes flavidus</i>	*	*	1	.	.	*	.	*	1	.	1	*	*	1	1	1	*	*	1	*	1	2	2	1	*	*	.	*	9	*
<i>Sebastes emphaeus</i>	*	43	49	19	.	59	1	107	94	107	30	2	92	11	11	3	53	23	11	17	20	5	19	15	20	18	2	27	4	2	*	1	2	2
<i>Sebastes ruberrimus</i>	*	*	*	*	*	*	*	.	*	*	*	*	*	*	*	1	*	2	*	1	1	1	1	1	1	1	1	*	*	*	.	*	*	*
<i>Hexagrammos</i> <i>decagrammus</i>	*	5	12	22	*	*	4	7	6	8	6	6	5	6	2	6	10	16	12	10	9	10	9	9	15	27	30	14	19	8	4	4	2	*
<i>Hexagrammos stelleri</i>	.	*	*	1	*	1	1	*	*	1	1	1	*	*	*	*	1	2	*	*	*	*	3	*	1	1	*	*	1	1	2	*	*	*
<i>Ophiodon elongatus</i>	3	3	6	3	*	1	5	4	4	7	6	2	5	3	6	5	5	10	9	15	6	8	7	8	5	7	7	21	4	5	2	3	2	1
<i>Oxylebius pictus</i>	*	2	1	1	.	*	2	2	3	2	2	2	1	1	*	3	4	4	2	1	2	1	5	3	12	6	4	3	2	2	1	*	1	*

Year	1984	1985	1986	1987	1988	1989	1990	1991	1992	1993	1994	1995	1996	1997	1998	1999	2000	2001	2002	2003	2004	2005	2006	2007	2008	2009	2010	2011	2012	2013	2014	2015	2016	2017	
No. dives per year	51	71	67	55	52	52	58	59	56	109	120	101	122	121	115	110	97	93	112	138	126	136	188	98	191	123	104	83	102	155	93	166	130	69	
<i>Jordania zonope</i>	59	60	126	218	1	22	8	27	14	29	60	4	3	1	1	4	5	6	14	5	4	12	5	6	17	24	31	7	9	6	2	3	3	1	
<i>Radulinus taylori</i>	*	1	*	.	.	*	*	*	*	1	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	.	*	*	*	*	*	
<i>Chitonotus pugetensis</i>	3	43	*	1	.	.	*	.	.	1	2	2	1	10	*	*	1	1	*	*	*	*	*	1	*	1	1	*	*	.	*	.	*	*	
<i>Scorpaenichthys marmoratus</i>	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	.	*	*	*	*
<i>Hemilepidotus hemilepidotus</i>	.	*	*	*	*	*	*	*	*	1	1	1	*	1	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	.	
<i>Anoplagonus inermis</i>	.	.	*	.	*	*	.	*	*	
<i>Podothecus accipenserinus</i>	.	.	*	*	*	*	.	*	*	*	*	.	.	.	*	*	

An asterisk indicates trace abundance.
A period indicates zero abundance.

Table 1. Average abundance data for 171 selected seabed species in the Strait of Georgia. Shading indicates climate regimes.

common species, but it is included in the table owing to higher abundances during the 1989 and 1999 regimes. *Dendrochiton*, *Kellia*, *Crepidula* spp., *Crepidatella*, *Epitonium*, *Phyllaplysia* and *Rostanga* were gone in the 2011 regime, and *Calliostoma canaliculatum*, *Rictaxis punctocaelatus* and *Aglagia deometra* were gone in both the 1999 and 2011 regimes. *Flabellina verrucosa* has gone from high abundance during the 1989 and 1999 regimes to rarity in the 2011 regime.

Among the Arthropoda, the common shrimp *Pandalus danae* is included in the table as an example of a continuously abundant species, in contrast to *Pandalus stenolepis* with fluctuation up in abundance during the 1989 and 1999 regimes, then reduced abundance during the 2011 regime. Compare this to the stable, low abundance continuously evident for large lithode crabs. The large hermit crab *Pagurus beringanus* was high in abundance during most years, but has become less abundant in the last few years. The less common *Pagurus armatus* was elevated in abundance late in the 1989 regime and early in the 1999 regime, an abundance cycle not coincident with these designations for climate regime shifts. The *Balanus* species tend to be very abundant, but are less so during the 2011 regime. It should be commented that the abundance trend for *Semibalanus cariosus* reflects a shift in geographic location of diving effort from the more wave-exposed southern (USA) reaches of the Strait of Georgia; this species is absent from Howe Sound, for example.

Among Echinodermata, abundance of *Florometra serratissima* and *Ophiura luetkenii* increased only during the 1999 climate regime. *Mesocentrotus franciscanus* was high in abundance during the 1974, 1989 and 1999 regimes. Data on other echinoderms associated with cascade effects are reported below the following paragraphs on higher phyla.

Among the Urochordata, *Ascidia*, *Pyura*, *Metandrocarpus* and *Cystodytes* were high in abundance during the 1974 and 1989 regimes. These species have all become relatively rare in the 2011 climate regime. *Corella* and *Cnemidocarpa* were highest in abundance during the 1999 regime. *Trididemnum* and *Didemnum* spp. were abundant during the 1974, 1989 and 1999 regimes, but reduced in the 2011 regime. *Botryllus* and *Botrylloides* were high in abundance during the 1989 and 1999 regimes, then became rare in the 2011 regime.

In the Chordata, two southern species, the anchovy *Engraulis mordax* and the brown rockfish *Sebastes auriculatus* have become abundant in the Strait of Georgia during the 2011 climate regime. The live-bearing perches and most rockfishes are generally abundant, but *Sebastes maliger* and *Sebastes ruberrimus* became more abundant during the 1999 regime owing to observation of young fish from several successful reproductive year-classes during that decade [23]. The more rare fishes showed increases in different regimes, with *Chitonotus* most abundant during the 1974 and 1989 regimes and least abundant during the 2011 regime.

Among the echinoderms that were generally high in abundance until later in the 2011 climate regime, many seastars (starfish) suffered the densoviral SSWD die-off [18]. *Pycnopodia helianthoides* had been very high in abundance during the 1999 climate regime, declining in the 2011 regime until the seastar wasting caused a drop-out of adults in 2013 (**Figure 2**). The annual averages depicted in **Figure 2** do not reveal the abrupt drop to nil that occurred in Sept/Oct 2013 in various locations of Howe Sound, spreading south to north (D.M. Gibbs, personal observations). Note that only juveniles of this species occur in the area today. In contrast, the modest abundance levels in sunflower sea stars for 1980–1999 and 2006–2008 represented an

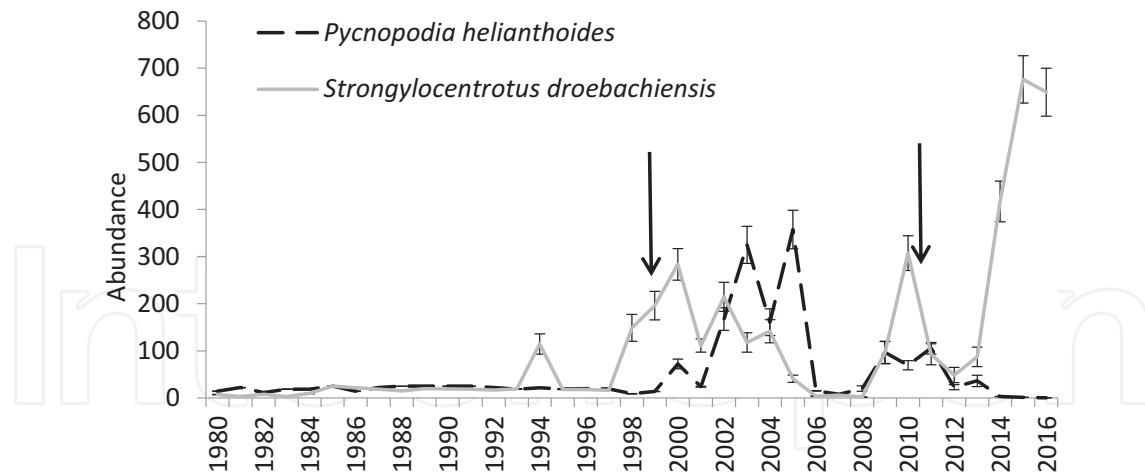


Figure 2. *Pycnopodia helianthoides* (black dashed line) and *Strongylocentrotus droebachiensis* (gray line) relative abundances in Howe Sound from 1980 to 2016. Bars represent two standard error. Vertical arrows indicate climate regime shifts.

adult population of high biomass with a relatively high predation capacity. As a result of loss of this predator, the urchin *Strongylocentrotus droebachiensis* has increased to unprecedented abundance in the last several years, with resulting urchin barrens that have greatly reduced seaweed abundance. In addition to this one seastar species dying-off, other seastar species like *Pteraster* and *Solaster* spp. are at trace abundance now.

The echinoderm population trends had cascade effects on seaweeds. An increase in urchin barrens since 2013 was evident in Howe Sound with 57% of surveyed sites recorded as urchin barrens in 2015 (**Figure 3**). The 3 years of 2014, 2015 and 2016 have seen very limited settlement of

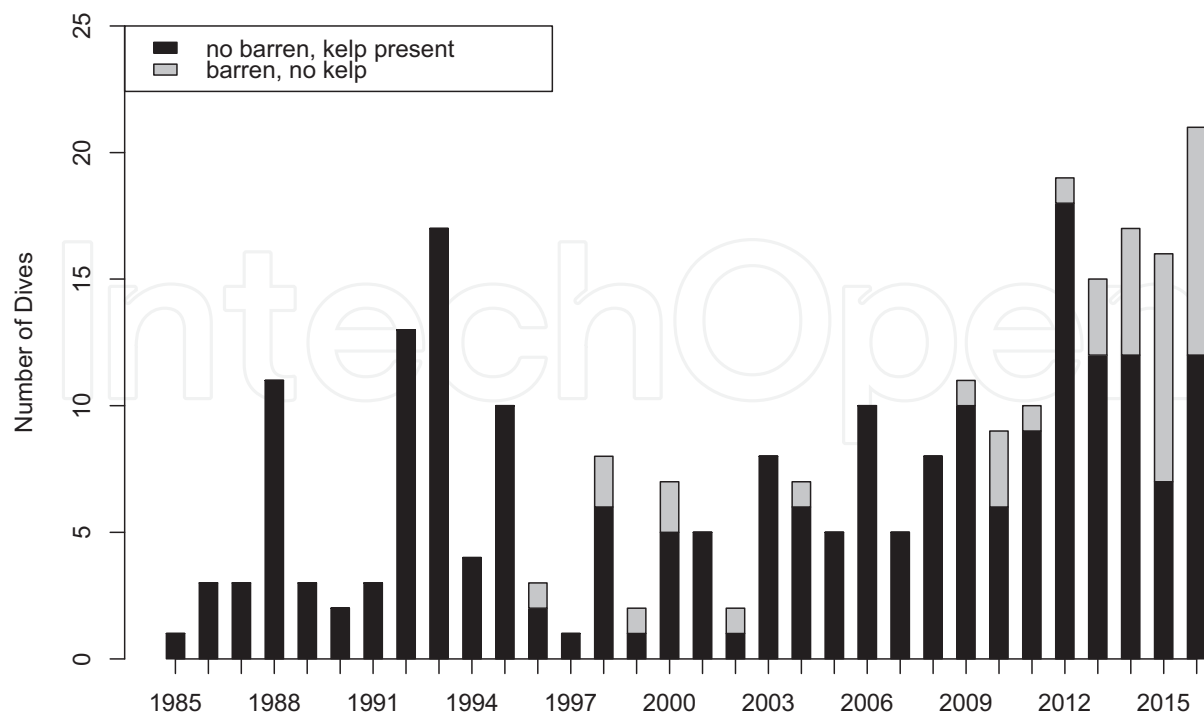


Figure 3. Proportion of juvenile prawn survey sites found to be urchin barrens, 1985–2016. Black bars indicate healthy *Neoagarum* kelp beds; gray bars indicate urchin barren (no kelp).

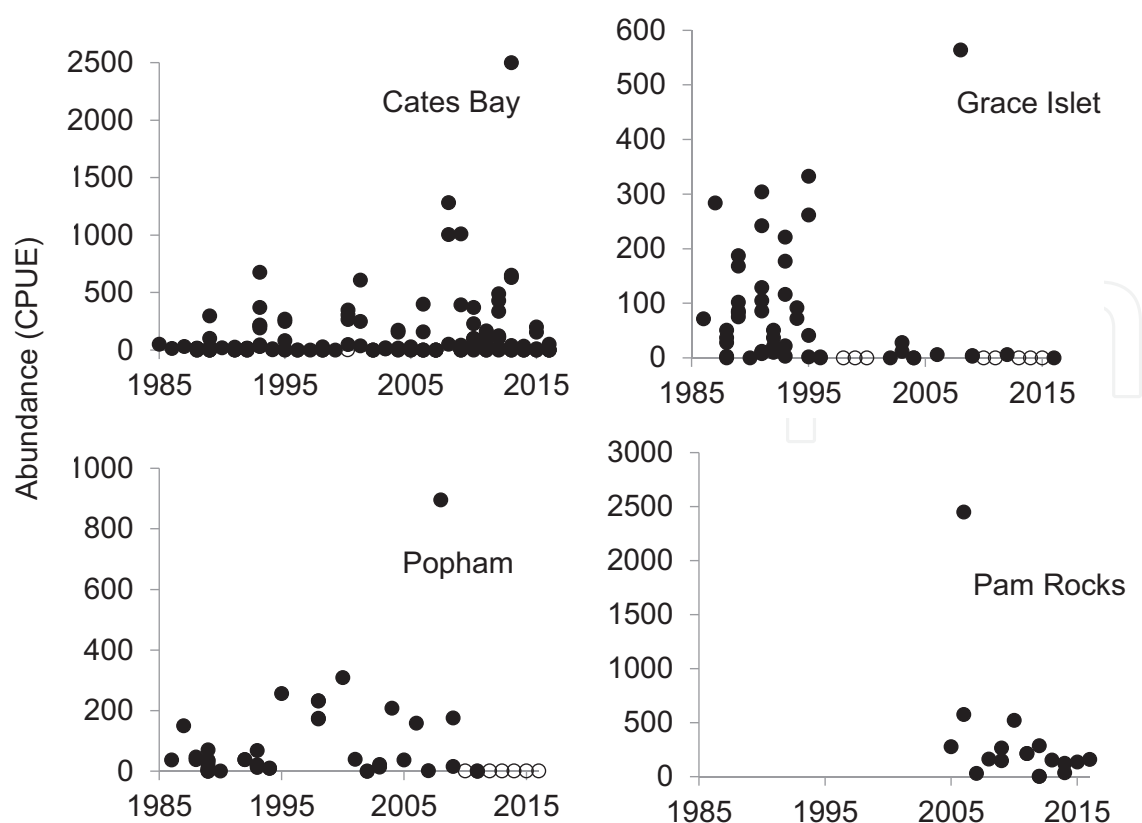


Figure 4. Juvenile *Pandalus platyceros* abundance in kelp beds from 1985 to 2016 at four reefs in Howe Sound, British Columbia. Open circles indicate years where reefs were an urchin barren; closed circles indicate presence of kelp bed (no urchin barren).

spot prawns in *Neogagarum* nursery habitat, despite modestly high settlement rates in the very few small patches of remaining *Neogagarum* in Howe Sound (**Figure 4**). Anecdotally, local prawn fisheries have contracted over the last 2 years, with reports of few small, young prawns in catches.

4. Discussion

As previously suggested [6], it appears that marine life provide a refined method of designating climate regime shifts. The biodiversity data presented here also suggest that the modification of regime start-years from those suggested (1977, 1989, 2001) by previous literature [1] to the uniformly defined years presented here (1974, 1989, 1999, 2011) may provide a superior basis for predictions of seabed biodiversity changes with climate regime shifts. The present data correspond more closely to 1999 as a regime start rather than 2001, as was suggested in Ref. [4], which indicated 1988–1989 and 1998–1999 as climate regime shifts. Ref. [3] had indicated that 2000–2001 was the millennial regime shift.

Our data are not adequate for analysis of 1974 versus 1977 for the start of that earlier climate regime shift. Abundant analysis of oceanographic data [5, 6, 24] show that 1977 marked the change

to warmer sea surface temperatures in southern California following the 1972–1973 El Niño and the paired 1973–1974 La Niña. The analysis in [24], however, was based on biotic data from 1974 onwards, not considering what may have occurred during the 1972–1973 El Niño, so that it cannot be determined whether 1974 or 1977 was the actual tipping point. The winter of 1976–1977 was actually a weak El Niño following three consecutive La Niña winters. Both the mid-1970s and the turn of the millenium involved three consecutive La Niña winters, whereas 1988–1989 was a single La Niña event and 2010 was the start of two La Niña winters. The coincidence of taxon abundance increases with the end of the first rather than the third La Niña after the 1997–1998 El Niño suggested the rule adopted in this treatment of designating the start of a climate regime shift as the end of the close pairing of strong El Niño and La Niña events. Different taxon data may enable analysis of biodiversity shifts after 1974 versus 1977.

Extreme La Niña events are predicted to become more frequent under global warming [25, 26]. If biodiversity changes after climate regime shifts result from warming trends, then it would be expected that species would drop-out in the southern extremities of their geographic range [27]. Of the eleven species that could not be detected in the Strait of Georgia during the 2011 climate regime, not one of these species is characterized by being at the southern extreme of their distribution; indeed a few were at the north end of their range [28]. Thus, there is no signal of global warming in these data with respect to species drop-out. On the other hand, the increase of more southern fishes like anchovy and brown rockfish after 2011 coincides with aspects of warm sea surface waters since 2011. The very high taxon abundances notable for the 1999 climate regime occurred during a period characterized by three consecutive weak El Niños without intervening La Niñas. In contrast, the 2011 climate regime was characterized by the anomalous “warm blob” that appeared in 2013 [29], followed by the 19-month El Niño that peaked in winter 2015–2016 with 5 month maximum anomalies (ONI) averaging >2.0 , arguably the strongest such event yet recorded in terms of duration plus intensity.

This chapter uses ONI climate events rather than PDO, as mentioned. Ref. [30] examined the relation of zooplankton and salmon production with respect to climate-driven regime shifts. Particularly with respect to the Pacific Decadal Oscillation (PDO) [5], the analysis has been with regard to productivity and physical oceanography of the surface layers of the sea where salmon live; Ref. [5] found no relationship between Pacific salmon abundance and ONI indices. The present discussion, however, is of seabed biodiversity; the regime shifts defined from El Niño and La Niña pairings (Ocean Niño Index events) may be more relevant than PDO events to productivity and physical processes in deeper layers of the ocean. The seabed biodiversity trends discussed here do not coincide with Pacific Decadal Oscillation events the way they do with Ocean Niño Index events.

One of the possible impacts of an ONI climate regime shift can be cascade effects of the biodiversity shifts tabulated here (**Table 1**). Cascade effects may lag the timing of climate regime shifts. The reduction in sunflower stars and increase in green urchins following the 2013 SSWD was unprecedented. The increase in urchins after Sept. 2013 exceeds any previous abundance of green urchins recorded in our 1984–2016 database. The reduction of *Neogarrum* beds (**Figure 4**) following the urchin increase could lead to a further cascade effect. Since the spot prawn is a strict protandric hermaphrodite [20], two successive years of very low nursery

recruitment in absence of *Neoagarum* beds could result in a population in Howe Sound consisting of mostly females for the winter of 2017/2018. This would lead to expectation of very little successful fertilization of eggs, a negative feedback loop that would further exacerbate the limit to nursery settlement that results from low availability of *Neoagarum* kelp beds. The reduction in sunflower stars, however, started with the 2011 regime shift, then was exacerbated by the SSWD, with further cascades through urchins, kelp and prawns following.

The present data compilation is the first to reveal the full decade of extraordinary sunflower star abundance during the millennial climate regime of 1999–2011, as well as the drop in abundance coincident with the 2011 regime shift (**Figure 2**). That drop in abundance coincident with the paired La Niñas of 2010–2012 could have resulted from some loss of condition factor during the cool conditions that then were followed by the SSWD event of 2013. A SSWD event with *Pisaster* in Oregon correlated with cooler temperatures rather than warmer [31]. We must note that the continuing SSWD of other sea star species such as *Pisaster ochraceus* in 2014 has only resulted in up to 80% mortality in populations [31]. This contrasts to the reduction to nil abundance, as occurred in the present observations of *Pycnopodia helianthoides* in Howe Sound (**Figure 2**) and in 1978 with *Heliaster kubinji* in the Gulf of California [10]. Further, no discussion to date of proximate (SSWD) versus ultimate factors [31] has considered climate regime shifts as a possible ultimate factor.

5. Conclusion

Based on these results, together with data for Ocean Niño events as defined herein, we conclude that 2011 marked the most recent climate regime shift. The new climate regime is characterized by reduced abundance of numerous species, representing over 10% of all the seabed biota in this region. The 2011 regime shift was marked with eleven taxa dropping from detection as well as numerous taxa decreasing in abundance. There is no signal of global warming suggested by the absence of those eleven species, but the lowered abundance of other species and increase in warm water anchovies and brown rockfish may relate to overall temperature. The present suggestion is to define start-year for climate regimes based on the end of pairings of strong (anomalies >1.0) El Niño and La Niña events where ≤ 2 months separate such paired events. We are unable to assess the correct timing of the 1974 or 1977 regime shift owing to limited biodiversity data for that period, but our results support 1999 rather than 2001 as the start of the millennial climate regime.

It is noteworthy that the SSWD eliminated sunflower sea stars along much of the entire west coast of North America and is continuing in various localities today. Urchin abundance has similarly shifted along the coast, both from emergence of adults from seclusion and from reproductive success [16] so that kelp may go through a cycle of low abundance. Reliance of the spot prawn on *Neoagarum* as nursery habitat in the Howe Sound region [19] suggests that an ultimate cascade effect of the sea star wasting syndrome could be reduction of prawn abundance below levels supporting commercial harvest. This endpoint would give the best indication that urchin barrens really are significantly more prevalent than in any previous period, since urchin barrens always seem to occur at one or another small locality. Even with

the current level of citizen science focused on sea star wasting, many areas remain uninvestigated, so the fate of the prawn fishery in Howe Sound and Strait of Georgia waters will be an important indicator of ecosystem status from the standpoint of *Neogagarum* kelp beds.

Ref. [16] discusses the densovirus die-off of various seastar species in the Strait of Georgia that resulted in the very high sea urchin abundance evident for the last several years. This may have driven cascade effects that reduced seaweed abundance and associated fauna. It is not clear, however, that all the biodiversity changes associated with this 2011 climate regime shift relate to the seastar collapse. It seems more likely that the anomalous “warm blob” followed by a record El Niño event may have affected overall ecosystem processes. The determination of how global warming interacts with regular Ocean Niño Index events remains a foremost concern for future observations and analysis.

Although caveats about global warming always need acknowledgment, the principal finding in this book chapter of close correspondence of biodiversity shifts to naturally occurring climate regime shifts is a positive sign. Both increases and decreases in species abundance tend to coincide with climate regime shifts that have occurred regularly as a fundamental aspect of weather and climate on earth. Examination of long-term biodiversity databases should include comparisons to ONI climate regime cycles.

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