

# A hyperiid amphipod acts as a trophic link between a scyphozoan medusa and juvenile Chinook Salmon

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## ABSTRACT

Gelatinous zooplankton (GZ) can impact productivity of marine ecosystems through competition with small pelagic fish and predation on early life history stages of species from multiple trophic levels. Nevertheless, GZ do not always represent 'trophic dead ends.' Some predators directly consume GZ, and many species host parasitoids which in turn are prey for other organisms. We characterized trophic relationships between the fried-egg jellyfish *Phacellophora camtschatica*, its hyperiid amphipod parasite (*Hyperia medusarum*), and juvenile Chinook Salmon *Oncorhynchus tshawytscha* in the Salish Sea. *Hyperia medusarum* occurred in 29–47% of Chinook Salmon stomachs over 3 years and were observed in high abundance on *P. camtschatica* medusae (mean = 428 individuals per medusa). Light and transmission electron microscopy confirmed the presence of morphologically similar nematocysts in the foreguts of *H. medusarum* from both medusae and Chinook Salmon stomachs. Occurrence of *H. medusarum* in Chinook Salmon diets was also positively related to an index of *P. camtschatica* abundance. Chinook Salmon stomachs contained almost exclusively mature female *H. medusarum* while males and juveniles were common on medusae. Size and sex ratio differences between hyperiids in Chinook Salmon diets and on medusae could reflect predator selectivity or sex and/or life-stage specific differences in *H. medusarum* behavior. Our results support previous speculation that GZ abundance may facilitate predation on hyperiids by Pacific Salmon. Hyperiid-mediated energy flow from GZ to fish is not limited to medusa-associated fish species and should be considered in studies of marine food webs.

## 1. Introduction

Gelatinous zooplankton (GZ) include scyphozoan and hydrozoan medusae, siphonophores, ctenophores and salps. The role of GZ in marine ecosystems has received considerable recent attention given regional increases in abundance (e.g., Link and Ford, 2006; Lynam et al., 2006) and suggestions that GZ are experiencing a global increase (e.g. Richardson et al., 2009). The validity of evidence for a global increase has also been called into question (Sanz-Martín et al., 2016), as many GZ populations are stable, fluctuating, or decreasing in abundance (Brotz et al., 2012; Condon et al., 2013). Overall, there is a growing awareness of the ecological importance of GZ in marine ecosystems (e.g. Brodeur et al., 2016). Many GZ species consume zooplankton, fish eggs, and ichthyoplankton. An increase in GZ biomass can therefore result in a direct reduction in fish production through predation on eggs and larvae, as well as cause an indirect effect through competition (Båmstedt, 1990; Purcell, 1990). It has been suggested that abundant GZ may also spatially exclude fish from access to prey during critical growth periods, leading to reduced survival (Chittenden et al.,

2017). Ecosystem and food web modelling studies have demonstrated that in certain ecosystems, seasonal blooms of GZ can result in an associated reduction of fish production (Brodeur et al., 2014; Ruzicka et al., 2016). The potential of GZ to rapidly achieve very high abundance may interact with anthropogenic factors including eutrophication, over-fishing, and non-native species introductions to fundamentally alter marine ecosystem function (e.g. Lancelot et al., 2002).

Despite their potential to reduce productivity of higher trophic levels through predation and competition, GZ are not necessarily 'trophic dead-ends' in marine ecosystems. Direct consumption of GZ has been documented across several taxa including many fish species (reviewed by Arai, 2005). The dietary importance of GZ may at times be underestimated, as digestion rates for gelatinous prey are high (Arai et al., 2003). Gelatinous zooplankton can also provide refuge for juvenile fish, increasing survival during periods of elevated abundance (Lynam and Brierley, 2007). Many GZ host crustacean hitchhikers, including larval decapods and hyperiid amphipods, which exhibit varying degrees of parasitism (Laval, 1980; Towanda and Thuesen, 2006). In fact, it has been suggested that all hyperiid amphipods may be obligate parasites of

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GZ during at least some stage of their life cycle (Laval, 1980). Hyperiid parasites may be consumed by GZ-associated fish (Mansueti, 1963; Riasco et al., 2012) or other predators, including seabirds (Harrison, 1984), thereby serving as a trophic link between GZ and higher trophic levels.

In the Northeast Pacific, variability and declines in the marine survival of economically and ecologically important Pacific salmon (genus *Oncorhynchus*) have focused attention on the trophic ecology of juvenile salmon, including interactions with GZ (e.g. Schabetsberger et al., 2003; Chittenden et al., 2017). Negative effects of GZ on salmon have been documented in the California Current, where high abundance of a large scyphozoan medusa (*Chrysaora fuscescens*) is associated with reduced stomach fullness of juvenile Chinook *Oncorhynchus tshawytscha* and Coho Salmon *O. kisutch* at a local scale, and lower population productivity at an interannual scale (Ruzicka et al., 2016). Conversely, Schabetsberger et al. (2003) suggested that juvenile Chinook and Coho Salmon may target large aggregations of GZ in order to feed on associated hyperiid parasites. Increased GZ abundance has also been hypothesized to contribute to a recent increase in productivity of a Sockeye Salmon *O. nerka* stock which specializes on hyperiid amphipods during early marine residence (Beamish et al., 2016). Nevertheless, to our knowledge no hyperiid-mediated trophic link between GZ and juvenile Pacific salmon has yet been characterized.

In the course of research to understand depressed survival of juvenile Chinook and Coho Salmon in the Salish Sea (a complex estuarine system consisting of the Strait of Georgia and Strait of Juan de Fuca, British Columbia; and Puget Sound, Washington; Fig. 1), we frequently observed the hyperiid amphipod *Hyperia medusarum* in the diets of juvenile (first ocean summer) Chinook Salmon in the Southern Gulf Islands (inset; Fig. 1). We also frequently observed fried-egg jellyfish *Phacellophora camtschatica* in our study area. These large, conspicuous scyphozoan medusae were host to large numbers of *H. medusarum*. A previous stable isotope-based investigation of this association in Puget Sound suggested that *H. medusarum* derive the majority of their nutrition from their host (Towanda and Thuesen, 2006). We investigated the possibility that *H. medusarum* represents a trophic link between fried-egg jellyfish and juvenile Chinook Salmon.

## 2. Methods

### 2.1. Sample collection and processing

Seven *Phacellophora camtschatica* medusae were collected in Sansum Narrows, British Columbia, Canada (48.772° N 123.558° W, Fig. 1) in September 2015. Medusae were guided into a bucket using a fine-mesh dipnet; care was taken to avoid dislodging hyperiids. To assess abundance, size, and sex ratio of associated hyperiids, six medusae were immediately placed in plastic bags on ice for no more than 8 h before being frozen for up to one month. Medusae were thawed over 24 h and dissected into manageable sections. Hyperiids were removed individually with forceps, and liquid associated with medusae was passed through a 1 mm mesh sieve to collect small individuals. Hyperiids were then preserved in 10% formalin in seawater. All preserved *Hyperia medusarum* were examined using a stereomicroscope to determine size, sex and maturity. Cephalothorax length was measured using Olympus cellSens imaging software. Cephalothorax length was measured rather than total length because preserved amphipods showed varying degrees of urosome flexion. Adults were distinguished from juveniles based on the development of mature sexual characteristics: elongated A1 antennae in males and oostegites and/or egg clutches in females. Juveniles were separated and sexed based on segmented, but underdeveloped antennae (males) and a lack of segmented antennae (females). Oral arm tissue and *H. medusarum* from the seventh *P. camtschatica* were flash frozen in the field in liquid nitrogen and stored at  $-80^{\circ}\text{C}$  for subsequent transmission electron microscopy (TEM) analysis (see below).

Chinook Salmon (*Oncorhynchus tshawytscha*) in their first ocean summer were sampled in August–October 2014 (N = 79), July–October 2015 (N = 360), and August to October 2016 (N = 761) in the Southern Gulf Islands region of the Salish Sea (Fig. 1). Fish were captured individually by microtrolling, a non-lethal method of depth-stratified hook and line sampling (Duguid and Juanes, 2017). Up to 12 hooks were deployed simultaneously at depths between 2 m and 34 m for short, timed fishing events (~8 min). Upon gear recovery, catch and/or fouling (weed, jellyfish tentacles, etc.) were recorded for each hook. *Phacellophora camtschatica* were the only light-coloured medusae with long tentacles and oral arms observed in the study area, and hooks which were fouled with white gelatinous material were assumed to have encountered this species.

Chinook Salmon stomach contents were sampled non-lethally by gastric lavage (Duguid and Juanes, 2017) and preserved in 5% formalin in seawater. In 2014 and 2016, the presence or absence of *H. medusarum* in each stomach was assessed based on visual inspection in the field or lab by a single experienced observer. In 2015, all stomach contents retained on a 1 mm sieve were identified to pre-defined taxonomic and life history-stage categories (species level for hyperiid amphipods) using a stereomicroscope. Intact prey items within each category were enumerated; where only fragments of an item were present, a count of one individual was assumed. Stomach contents were grouped by prey category, blotted on kimwipes to remove excess moisture, and weighed to the nearest 0.00001 g. Where very large numbers of small prey were present (8/325 samples), a subsample was examined, and the remainder of the sample was blotted and weighed in bulk. Weight proportions and counts for prey categories were assigned in proportion to results for the subsample.

All intact *H. medusarum* from Chinook Salmon stomachs in 2015 (n = 281) were scored for size, sex and maturity as described above for those obtained from *P. camtschatica*. A subsample of *H. medusarum* obtained from Chinook Salmon stomachs in August 2015 were flash frozen in the field in liquid nitrogen and stored at  $-80^{\circ}\text{C}$  for subsequent TEM analysis (see below).

### 2.2. Nematocyst presence

All *H. medusarum* with intact foreguts that were obtained from Chinook Salmon by gastric lavage in 2015 (n = 218) were evaluated for the presence of nematocysts. Hyperiid foreguts were excised under a stereomicroscope, smeared on a glass slide, and examined using a compound microscope at 20 to 40 times magnification. Nematocysts were identified based on their similarity in size and morphology to those described by Towanda and Thuesen (2006). To facilitate detailed comparison of nematocysts, we used TEM to compare samples from *P. camtschatica* oral arms, and from the foreguts of *H. medusarum* removed from stomachs of *O. tshawytscha* and oral arms of *P. camtschatica*. All samples used for TEM were live material flash frozen in liquid nitrogen. Presence of nematocysts was identified using light microscopy as described above, and where nematocysts were observed, the sample was fixed and prepared for standard Epon-based TEM following von Schalburg et al. (2013).

### 2.3. Data analysis

The sizes of *H. medusarum* collected from *P. camtschatica* were compared to those of individuals found in the gut contents of juvenile Chinook Salmon using a Mann-Whitney *U*-test. Differences in sex ratio and maturity of *H. medusarum* from medusae and salmon diets were compared using a Chi-square test for independence. To test for a link between abundance of *P. camtschatica* and frequency of predation on *H. medusarum* by juvenile *O. tshawytscha*, we related the daily proportion of hooks fouled with *P. camtschatica* to the presence or absence of *H. medusarum* in stomachs of *O. tshawytscha* captured by microtrolling from 2014 to 2016. To account for potential seasonal and interannual



**Fig. 1.** The Salish Sea (Strait of Georgia and Strait of Juan de Fuca, British Columbia and Puget Sound, Washington); dashed box within inset indicates sampling region for Chinook Salmon in August–October 2014, July–October 2015, and August–October 2016 and *Phacellophora camtschatica* and *Hyperia medusarum* in September 2015. Star indicates sampling location for *P. camtschatica*.

variability in prey availability, independent of *P. camtschatica* abundance, we also included year (categorical) and day-of-the-year (continuous) in our analysis. Data were filtered to include only sampling days on which all sampling took place within the same area (< 2.5 km radius) and at least 50 hooks were deployed (mean = 258; SD = 71);

97 days met these criteria. We fit a candidate set of generalized linear models (binomial family, logit-link), relating all possible combinations of the categorical variable “year” and continuous variables day-of-the-year “DOY” and proportion of hooks fouled with jellyfish “fouling”, to the presence (1) or absence (0) of *H. medusarum* in each Chinook



Salmon stomach. The model which best balanced fit and parsimony was selected using Akaike's Information Criterion (AIC).

### 3. Results

#### 3.1. Occurrence, size, sex and maturity of *H. medusarum*

The six fried-egg jellyfish *P. camtschatica* inventoried for parasite load ranged from 20 to 27 cm in bell diameter (mean = 23 cm) and hosted from 81 to 714 *H. medusarum* (mean = 428). Mean *H. medusarum* cephalothorax length was 3.40 mm (SD = 0.81 mm) with an approximately normal size frequency distribution (Fig. 2a and b).

*Hyperia medusarum* was a frequent prey item for juvenile Chinook Salmon (N = 1200, mean nose to fork length = 190 mm; range = 104–330 mm), occurring in 47%, 36% and 29% of Chinook Salmon diets sampled in 2014 (N = 79), 2015 (N = 360) and 2016 (N = 761) respectively. In quantitatively sampled Chinook Salmon diets in 2015 (N = 325), *Hyperia medusarum* was the fourth most commonly observed prey category after decapod megalopae, *Hyperoche medusarum* (another hyperiid amphipod), and decapod zoeae (Supplementary Material; Table S1). Overall, *Hyperia medusarum* represented 2.45% of the diet by mass in 2015; collectively hyperiid amphipods represented 8.49% of the diet by mass. For Chinook Salmon containing *H. medusarum* (N = 128), between 1 and 12 (mean = 2.6) individuals were present, representing an average of 20.46% of the diet by mass (range = < 1%–100%).

Mean cephalothorax length of *H. medusarum* from salmon diets in 2015 was 4.32 mm (SD = 0.68 mm; N = 281) with a strong skew towards larger individuals (Fig. 2c and d). *H. medusarum* in juvenile Chinook Salmon stomachs were significantly larger than those found on *P. camtschatica* (Mann-Whitney U-test;  $p < 0.0001$ ). Almost all *H. medusarum* consumed by juvenile Chinook Salmon were mature adults (98.2%) as compared to only 31.0% on *P. camtschatica*. (Table 1). The

majority (94.2%) of mature *H. medusarum* in diets of Chinook Salmon were female (Fig. 2c and d); this sex ratio (16.3:1) differed significantly from that of mature *H. medusarum* on *P. camtschatica* (1.8:1; Chi-squared test of independence;  $p < 0.0001$ ).

#### 3.2. TEM/Nematocyst presence

Transmission electron microscopy identified two nematocyst types which were present in both the oral arms of *P. camtschatica* (Fig. 3 a and d) and the foreguts of *H. medusarum* removed from *P. camtschatica* (Fig. 3 b and e). The first type was characterized by a thread of constant width coiled many times within the capsule (Fig. 3a–c) while the second type possessed a thicker proximal butt and tapering thread (Fig. 3d–f). These nematocysts were also consistent with those from the foreguts of *H. medusarum* in diets of juvenile Chinook Salmon (Fig. 3 c and f). Light microscopy revealed nematocysts in 87.2% (190/218) of foreguts excised from *H. medusarum* from Chinook Salmon stomachs.

#### 3.3. Presence of *P. camtschatica* and predation on *H. medusarum*

The daily proportion of hooks fouled with *P. camtschatica* “fouling” was the only variable retained in the best model predicting *H. medusarum* presence in the gut contents of juvenile Chinook Salmon (Table 2). Fouling by *P. camtschatica* was strongly and significantly (Beta = 11.49,  $P < 0.0001$ ) related to the log-odds of observing *H. medusarum* in juvenile Chinook Salmon gut contents.

### 4. Discussion

We identified nematocysts consistent with those from the oral arms of fried-egg jellyfish, *Phacellophora camtschatica*, in the foreguts of most (87.2%) *Hyperia medusarum* in juvenile Chinook Salmon stomachs. The log-odds of encountering *H. medusarum* in Chinook Salmon stomachs

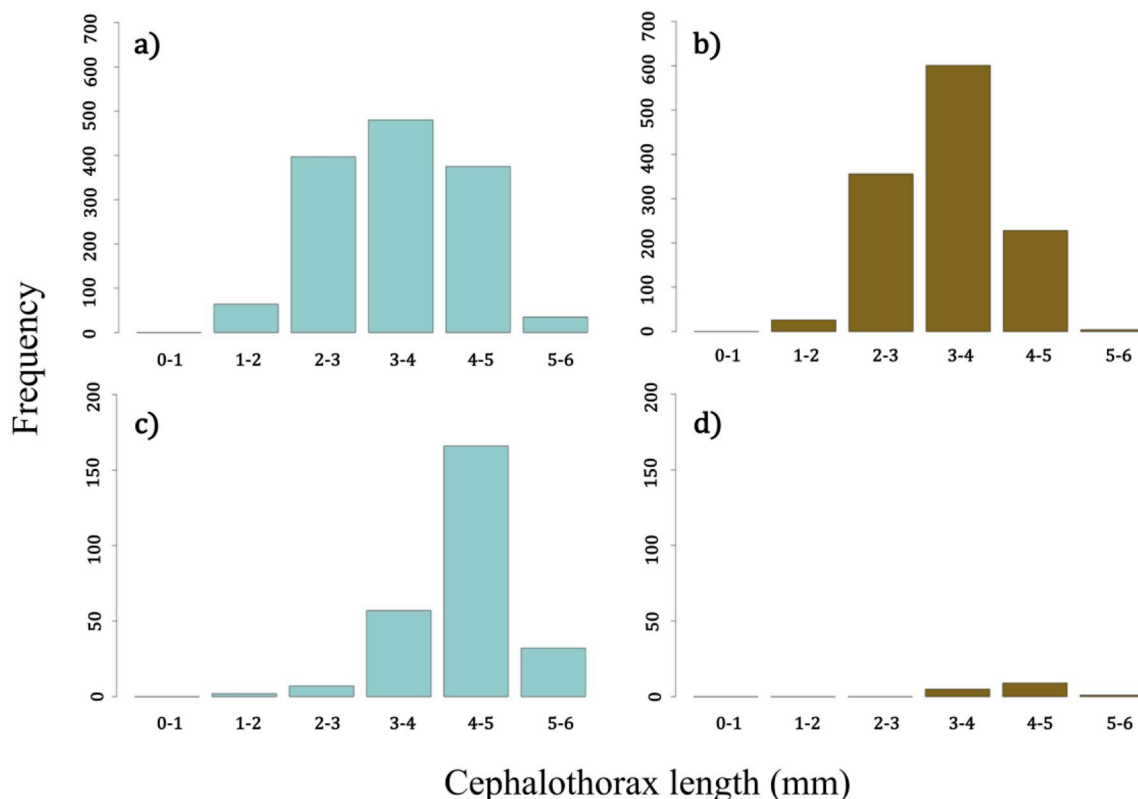


Fig. 2. Distribution of cephalothorax length of female (a and c) and male (b and d) *Hyperia medusarum* obtained from *Phacellophora camtschatica* (a and b) and from the stomach contents of juvenile *O. tshawytscha* (c and d).

**Table 1**Sex and maturity of *Hyperia medusarum* removed from the oral arms of *Phacellophora camtschatica* and the stomachs of juvenile *Oncorhynchus tshawytscha*.

| Source of <i>H. medusarum</i>             | Juvenile Males | Juvenile Females | Adult Males | Adult Females |
|---|----------------|------------------|-------------|---------------|
| Stomach of juvenile <i>O. tshawytscha</i> | 0              | 5                | 16          | 260           |
| Oral arms of <i>P. camtschatica</i>       | 935            | 854              | 278         | 498           |

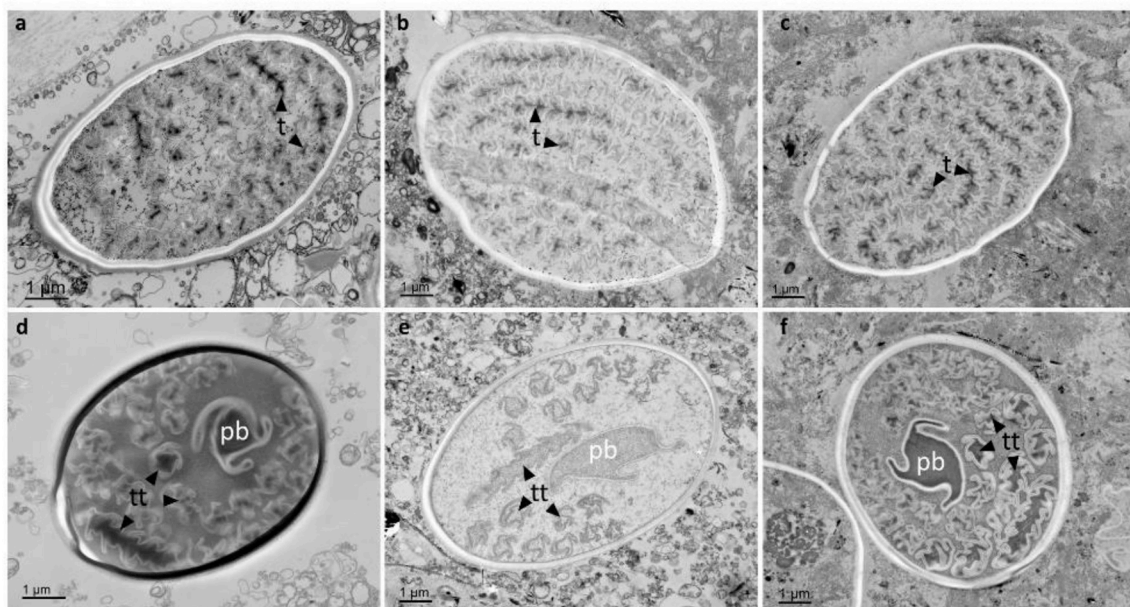
was also positively related to an index of *P. camtschatica* abundance. Together, this suggests that hyperiids consumed by Chinook Salmon had recently parasitized *P. camtschatica*. Previous stable isotope analyses have shown that *H. medusarum* residing on *P. camtschatica* derive the majority of their nutrition from their hosts (Towanda and Thuesen, 2006). We suggest that the consumption of these hyperiids by *Oncorhynchus tshawytscha* represents an energetic link between the jellyfish and juvenile salmon.

The circumstances of juvenile Chinook Salmon predation on *H. medusarum* remain uncertain. Predation on hyperiid parasites by fish which intimately associate with GZ as juveniles has been previously documented (Mansueti, 1963; Riascos et al., 2012). However, we are unaware of accounts of juvenile salmon associating closely with scyphozoan medusae, although Towanda and Thuesen (2006) reported observations of Chum Salmon *O. keta* biting pieces of the oral arms of *P. camtschatica*. Juvenile Chinook Salmon are highly active swimmers, and sustained association with medusae seems very unlikely. It is possible that juvenile Chinook Salmon are opportunistically plucking hyperiids from medusae, or that they are encountering hyperiids that have left their host for reproduction or some other purpose.

*H. medusarum* found in the gut contents of juvenile Chinook Salmon were almost exclusively (94.2%) mature females. This could reflect foraging selectivity when capturing hyperiids directly from medusae or from the water column. Planktivorous fish feed selectively on larger individuals within a prey field when prey abundance is high (Brooks and Dodson, 1965). For example, Baltic Herring *Clupea harengus* may be able to select gravid female copepods with conspicuous, lipid-rich egg clutches (Flinkman et al., 1992). Such selectivity would be consistent with evidence that salmon are visually-oriented, size-selective predators (Schabetsberger et al., 2003). Chinook Salmon predation on

primarily mature, female *H. medusarum* could also be a consequence of sex- and maturity-based differences in hyperiid behavior. Male hyperiids may leave their host to find mates, while females may leave to distribute their larvae among multiple new hosts (Laval, 1980; Dittrich, 1988). *Hyperia galba* in the coastal Northeast Atlantic may occupy alternative, possibly benthic, habitats during winter, when their scyphozoan medusa hosts are absent (Dittrich, 1988; Fleming et al., 2014). Female *H. medusarum* could be vulnerable to predation while migrating to such habitats. Towanda and Thuesen (2006) suggested that *H. medusarum* in the Salish Sea do not overwinter on the benthos, but rather as larvae and juveniles on smaller species of hydrozoan and scyphozoan medusae. Such behavior could also result in increased predation risk as it would require female *H. medusarum* to leave their host to demarsupiate larvae on these smaller medusae. Further sampling of both *H. medusarum* and their hosts across seasons is needed to reveal the true nature of these relationships.

A hyperiid-mediated trophic link from *P. camtschatica* to juvenile Chinook Salmon may be a recent phenomenon in the Salish Sea. The occurrence of *H. medusarum* in 29%–47% of juvenile Chinook Salmon diets from 2014 to 2016 contrasts with results of Argue et al. (1986) who did not report *H. medusarum* in the diets of Coho or Chinook Salmon sampled in the same region from March to September 1973 and July to October 1976 (occurrence of unidentified hyperiids in these samples was also negligible). Some evidence suggests that *P. camtschatica* has increased in abundance in the intervening period. These medusae were not recorded during Strait of Georgia dive surveys from the 1970s to 1994, but since then have been observed with increasing regularity (Andy Lamb, Pacific Marine Life Surveys Inc., unpubl. data). Reasons for this increase are unknown. Ecological interactions involving *P. camtschatica* are likely complex, as this species also preys



**Fig. 3.** TEM images of nematocysts observed in oral arms of *Phacellophora camtschatica* (a, d), in the foreguts of *Hyperia medusarum* removed from oral arms of *P. camtschatica* (b, e), and in the foreguts of *H. medusarum* removed from the stomach of juvenile *Oncorhynchus tshawytscha* (c, f). One type of nematocyst capsule contained an extensively-coiled thread (t) of constant width (a–c); the second nematocyst type (d–f) contained a tapering thread (tt) with an expanded proximal butt (pb).

**Table 2**

Log likelihood (LogL), regression statistics, and Akaike's information criterion (AIC) for candidate generalized linear models (binomial family, logit link) relating presence of *Hyperia medusarum* in the diets of juvenile *Oncorhynchus tshawytscha* to the categorical variable year and continuous variables day of the year "DOY" and daily proportion of sampling hooks fouled with *Phacelophora camtschatica* "fouling" (an index of *P. camtschatica* abundance). The best model (based on AIC) is indicated in bold.

| Model                | Intercept     | $\beta$ fouling | $\beta$ DOY | df       | LogL            | AIC           | $\Delta$ AIC | Weight       |
|----------------------|---------------|-----------------|-------------|----------|-----------------|---------------|--------------|--------------|
| <b>Fouling</b>       | <b>-0.979</b> | <b>11.49</b>    |             | <b>2</b> | <b>-736.912</b> | <b>1477.8</b> | <b>0.00</b>  | <b>0.436</b> |
| Fouling + DOY        | -1.869        | 12.60           | 0.003       | 3        | -736.245        | 1478.5        | 0.67         | 0.313        |
| Fouling + DOY + Year | -3.089        | 16.36           | 0.006       | 5        | -734.921        | 1479.8        | 2.02         | 0.159        |
| Fouling + Year       | -1.222        | 12.57           |             | 4        | -736.470        | 1480.9        | 3.12         | 0.092        |
| Year                 | -0.127        |                 |             | 3        | -744.373        | 1494.7        | 16.92        | 0.000        |
| DOY + Year           | 0.364         |                 | -0.002      | 4        | -744.141        | 1596.3        | 18.46        | 0.000        |
| null                 | -0.758        |                 |             | 1        | -751.488        | 1505.0        | 27.15        | 0.000        |
| DOY                  | -0.011        |                 | -0.003      | 2        | -750.894        | 1505.8        | 27.96        | 0.000        |

directly on other GZ (Strand and Hamner, 1988; Towanda and Thuesen, 2006). Abundance of *P. camtschatica* could therefore plausibly fluctuate with, and possibly control, that of other GZ. Improved understanding of hyperiid and GZ life-histories, their interactions, and the nutritional quality of hyperiids relative to other prey is required to understand the importance of trophic linkages between GZ, hyperiids and salmon in the Salish Sea.

Abundance of GZ species has increased in some marine systems (e.g. Link and Ford, 2006; Lynam et al., 2006), and a general trend of increasing abundance as a consequence of anthropogenic changes has been suggested (e.g. Richardson et al., 2009), although conclusive evidence for such a trend is lacking (Brotz et al., 2012; Condon et al., 2013; Sanz-Martín et al., 2016). What is certain is that GZ play an important role in marine food webs and should be considered in ecosystem monitoring efforts (Brodeur et al., 2016). Our results, while preliminary, support the hypothesis that predation on hyperiids by juvenile Pacific salmon may be related to GZ abundance (Schabetsberger et al., 2003; Beamish et al., 2016). Taken together with the results of Towanda and Thuesen (2006) they also suggest direct energy flow from a large scyphozoan medusa back to Chinook Salmon, an ecologically and economically valuable species in the Salish Sea. More work is clearly needed to understand both positive and negative effects of GZ on Pacific salmon productivity.

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## Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.ecss.2019.01.025>.

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