

# Feeding patterns and predation potential of scyphomedusae in a highly productive upwelling region

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**ABSTRACT:** We quantified diet and predation rates for large scyphomedusae from a coastal upwelling region. In the Northern California Current, early stages of euphausiids, gelatinous taxa, and cladocerans were particularly vulnerable to predation by *Chrysaora fuscescens*, *Aurelia labiata*, and *Phacellophora camtschatica*, whereas copepods were not. Moreover, *C. fuscescens* had the potential to deplete the standing stock of euphausiid eggs where predator and prey overlapped. During August 2002, *C. fuscescens* ingested an average 32.5% of the standing stock of euphausiid eggs each day at stations close to shore and north of Cape Blanco (42.9° N, 126.6° W) where maximum abundances of the medusae occurred. Ingestion of other vulnerable prey, such as other early stages of euphausiids and gelatinous taxa, reached 10 to 12% d<sup>-1</sup>. In contrast, we calculated the maximum removal rate of the standing stock of copepods to be <1% d<sup>-1</sup>. Given the importance of euphausiids to fish and other top predators, and the potential for changes in abundance and distribution of both predator and prey taxa with changes in climate, we suggest that gelatinous zooplankton abundance and predation impacts be incorporated within long-term studies and ecosystem models.

**KEY WORDS:** Gelatinous zooplankton · Coastal upwelling · Euphausiids · California Current · Scyphozoa · *Aurelia* · *Chrysaora* · *Phacellophora*

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## INTRODUCTION

Gelatinous zooplankton are ubiquitous in coastal ecosystems and can prey voraciously on co-occurring zooplankton and ichthyoplankton. Although the role of predators in influencing zooplankton community structure is well established for freshwater lakes (Brooks & Dodson 1965), top-down effects are more difficult to establish as a primary factor structuring marine ecosystems. Nevertheless, several studies have shown inverse relationships between medusae and their prey (e.g. Möller 1984, Behrends & Schneider 1995). Anthropogenic effects such as overfishing, eutrophication, introduction of alien species, and cli-

mate change may lead to shifts to 'jelly' dominated communities in some areas (Purcell et al. 1999, Mills 2001, Purcell 2005, Lynam et al. 2006). We need to consider both changes in populations and predation impact of gelatinous predators if we hope to understand or predict marine ecosystem dynamics fully.

Most of what we know about jellyfish predation comes from studies of relatively small medusae in semi-enclosed bays or estuaries, or under experimental conditions. Gut content analyses of larger individuals (Graham & Kroutil 2001, Purcell 2003, Uye & Shimauchi 2005) show that, like smaller medusae, larger forms can feed across a broad range of zooplankton, including copepods, other gelatinous taxa, meroplank-

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ton and fish eggs. Reports on predation impact by large medusae vary widely. In the Bering Sea, Brodeur et al. (2002) estimated that *Chrysaora melanaster* consumed one-third of the standing stock of zooplankton during the summer season. In subregions of Prince William Sound, Alaska, Purcell (2003) calculated predation by scyphomedusae on copepod standing stock to be at most 0.3% d<sup>-1</sup> and on larvaceans up to 7% d<sup>-1</sup>, although stations with the largest jellyfish aggregations were excluded from her analysis. Uye & Shimauchi (2005) reported the *Aurelia aurita* population in the Sea of Japan could consume 26% d<sup>-1</sup> of the available net zooplankton biomass.

This study quantifies diet and feeding rates for large medusae from a coastal upwelling region. These areas are known for exceptionally high seasonal productivity, and it has traditionally been assumed that most animal biomass is transferred through crustacean zooplankton and then fish via relatively direct trophic pathways. Nevertheless, gelatinous taxa, including large medusae, are consistently abundant in shelf regions of both the California Current (Shenker 1984, Suchman & Brodeur 2005) and Benguela upwelling systems (Sparks et al. 2001, Lynam et al. 2006), with the summertime biomass of *Chrysaora fuscescens* off the Oregon coast reaching 50 to 65 mg C m<sup>-3</sup>. Copepod biomass off Newport, Oregon in recent years has had summer peaks within the same order of magnitude (~15 to 50 mg C m<sup>-3</sup>, Peterson et al. 2006). Given the high biomass of medusae in upwelling regions and their prodigious feeding rates in other geographic areas, it is reasonable to suggest that predation by medusae in upwelling systems may significantly impact zooplankton populations.

In this article we document predation patterns exhibited by large scyphomedusae that appear seasonally in the northern California Current. We present

diet data for 3 species (*Aurelia labiata*, *Chrysaora fuscescens*, and *Phacellophora camtschatica*) and calculate feeding rates in relation to prey densities for *C. fuscescens*. Finally, using abundances of *C. fuscescens* and other zooplankton species collected throughout a broad region of the northern California Current during August 2002, we use our estimates of feeding rates to predict predation potential of *C. fuscescens* on the standing stock of the most common zooplankton taxa.

## MATERIALS AND METHODS

**Gut contents of medusae.** During summer 2002 and 2003, we sampled 10 stations to collect 3 species of scyphomedusae (*Chrysaora fuscescens*, *Aurelia labiata*, and *Phacellophora camtschatica*) for gut content analysis or gut evacuation measurements. At the same time, we performed vertical net tows to assess the abundance and taxonomic composition of potential prey (Table 1, Fig. 1A).

Medusae were captured individually, either by divers (Stn 8, Fig. 1A) or from the deck of a research vessel (all other stations). At Stn 8, divers free-dove using a clear vinyl bag net on a pole to capture individual jellies, and while still under water, moved the jellyfish into individual plastic bags before removing them to the boat. Jellyfish near the surface were directly placed into bags. For other stations, we carefully dipped each medusa from the top 2 to 3 m of surface waters using a clear vinyl bag net with mesh bottom attached to a 4 m fiberglass extension pole. Those medusae analyzed for diet were preserved individually (immediately following capture) in a 2 l container using a 5% buffered formalin solution; those used in gut evacuation experiments were placed in 19 l buck-

Table 1. *Chrysaora fuscescens*, *Aurelia labiata*, *Phacellophora camtschatica*. Details for stations where scyphomedusae were collected for gut content analysis and summary of medusan size and gut contents. Stations are numbered in chronological order

Medusa species	Station	Collection date	Station location	Station depth (m)	N	Bell diameter (cm ± SD)	Prey ingested per medusa (N ± SD)	Zooplankton density (m <sup>-3</sup> ± SD)	
<i>Chrysaora fuscescens</i>	1	23 Jul 02	44.65°N, 124.18°W	62	5	17.4 ± 0.4	2896 ± 499	1605.2	
	2	23 Jul 02	44.65°N, 124.29°W	83	2	20.4 ± 5.0	2943 ± 1675	1712 ± 119	
	3	23 Jul 02	44.65°N, 124.41°W	92	1	15.3	2905	1535 ± 108	
	5	12 Aug 02	43.87°N, 124.22°W	60	7	19.0 ± 2.9	314 ± 185	2553 ± 51	
	7	17 Aug 02	44.00°N, 124.20°W	55	1	28.3	480	2925 ± 186	
	8	12 Sep 02	44.43°N, 124.12°W	26	6	20.1 ± 2.1	789 ± 437	36705 ± 343	
	9	24 Jul 03	44.65°N, 124.10°W	28	4	13.3 ± 6.0	262 ± 371	10566 ± 78	
	10	8 Aug 03	44.61°N, 124.12°W	30	5	18.5 ± 3.9	392 ± 258	9957 ± 80	
	Species total = 31								
	<i>Aurelia labiata</i>	4	5 Aug 02	41.90°N, 124.61°W	507	8	23.6 ± 3.1	1002 ± 783	1085 ± 151
<i>Phacellophora camtschatica</i>	6	13 Aug 02	42.69°N, 124.47°W	26	11	15.3 ± 4.1	95 ± 86	3794 ± 505	

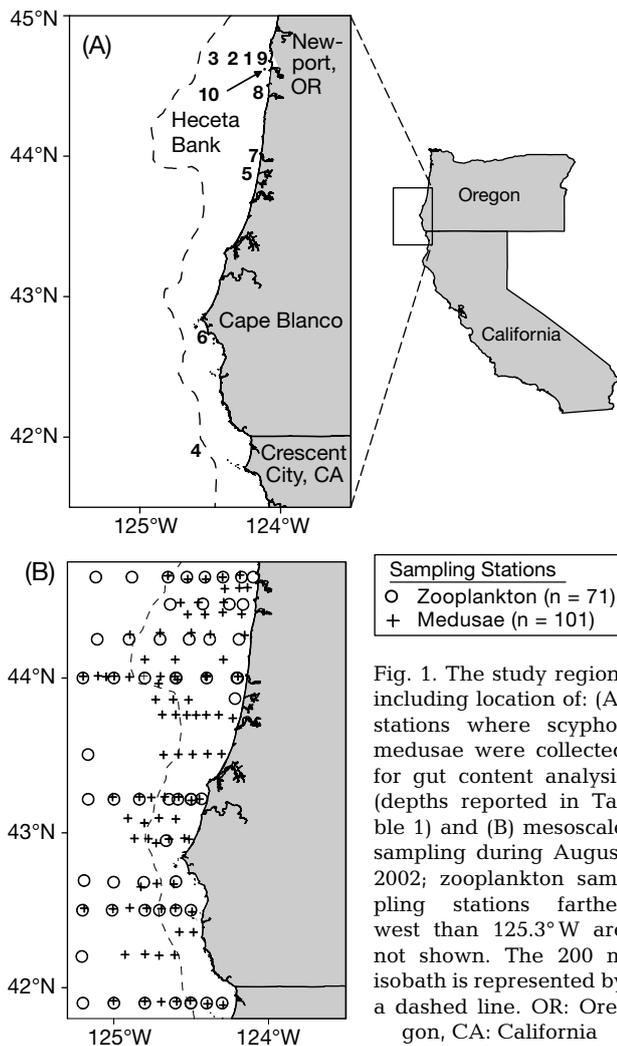


Fig. 1. The study region, including location of: (A) stations where scyphomedusae were collected for gut content analysis (depths reported in Table 1) and (B) mesoscale sampling during August 2002; zooplankton sampling stations farther west than 125.3°W are not shown. The 200 m isobath is represented by a dashed line. OR: Oregon, CA: California

ets containing filtered seawater for up to 6 h before they were preserved. In the laboratory (within 1 yr of preservation) we determined gut contents of medusae by identifying and counting zooplankton present in gastric cavities, oral arms, and surrounding formalin. An average of 2 d of laboratory time per medusa was required to enumerate all ingested prey.

When live medusae are preserved in formalin, they regurgitate a significant proportion of the prey in their gut pouch and oral arms (Fig. 2). Loss rates averaged 34.5 to 51% (by species). In order to obtain accurate data on gastric contents at time of collection and variability between individuals, each medusa was preserved in a separate container, and all surrounding fluid was examined during enumeration of prey.

We did not measure size of living medusae used for gut content analysis because extra handling could cause loss of prey. Since medusae shrink when preserved in formalin, we quantified shrinkage through

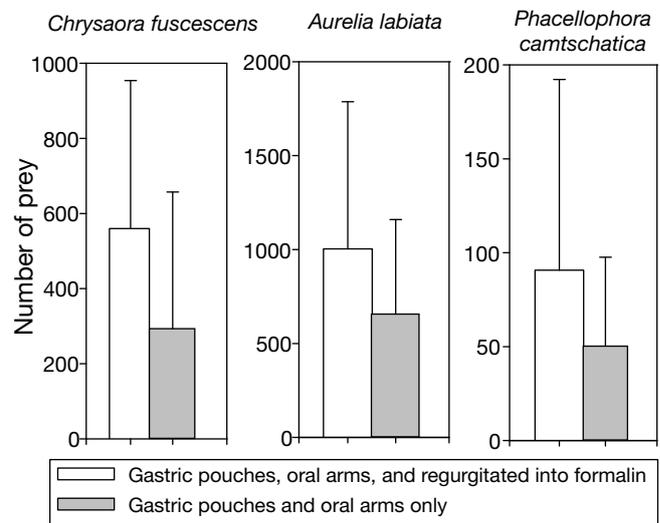


Fig. 2. *Chrysaora fuscescens*, *Aurelia labiata*, *Phacellophora camtschatica*. Difference between number of zooplankton recovered from gastric pouches and oral arms only, and number counted when zooplankton regurgitated into formalin preservative were included ( $p < 0.05$ , paired  $t$ -test for *C. fuscescens* and *A. labiata*, signed rank test for *P. camtschatica* where normality test failed). Number of medusae analyzed is available in Table 1. Values are means  $\pm$  SD

repeated measurements of bell diameters of 10 *Chrysaora fuscescens* individuals not used for gut content analysis; first measurements were on live specimens, followed by 8 weekly measurements of the same group preserved in formalin. We discontinued measurements after 2 mo since diameter decreased after 1 d and remained stable thereafter. We used average shrinkage ( $n = 10$ ) to estimate diameters of live medusae preserved for gut contents.

We sampled the zooplankton assemblage using a 50 cm diameter, 202  $\mu$ m mesh net towed vertically from 5 m above the sea floor to the surface ( $30 \text{ m min}^{-1}$ ); at Stn 4 (depth 507 m), we sampled the upper 100 m. Volumes of water filtered (5.3 to 23.2  $\text{m}^3$ ) were determined using readings from a calibrated TSK flowmeter. Zooplankton was preserved in 5% buffered formalin. At least two 1 ml piston pipette subsamples were counted for each tow to determine zooplankton abundance (279 to 1783 zooplankters counted per station).

**Gut evacuation experiments.** To determine digestion times for prey items eaten by *Chrysaora fuscescens*, we measured gut evacuation rates twice: (1) 24 July 2003 at Stn 9 (44.61°N, 124.12°W, surface temperature 7.5°C) and (2) 8 August 2003 at Stn 10 (44.65°N, 124.10°W, surface temperature 9.1°C) (Table 1, Fig. 1A). Medusae dipped from surface waters were either preserved immediately in buffered formalin (time = 0), or were placed in 19 l containers

filled with 80  $\mu\text{m}$ -filtered seawater and maintained in darkness at ambient temperature for 2 to 6 h. During Expt 1, *C. fuscescens* medusae were preserved after 0, 2, 4 and 6 h ( $n = 2$  for each interval, except  $n = 4$  at time = 0); medusae from Expt 2 were preserved after 2, 3, 4 and 6 h ( $n = 2$  for each interval, except  $n = 5$  at time = 0). Throughout, we monitored medusae to be sure they continued pulsing normally.

We estimated digestion time by prey category for each trial by calculating linear regressions of average number of prey present at time zero through the earliest time that prey type was largely absent (average number <20% than at time = 0) (similar to Purcell 2003). The average of the x-intercepts (time at prey = 0, from regression) of the 2 trials rounded to the nearest half hour was used as an estimate of digestion time.

We were careful to include only prey items that appeared to be digested by medusae in our analysis. Although bivalve veligers in Chesapeake Bay are able to survive ingestion by *Chrysaora quinquecirrha* by resisting digestion (Purcell et al. 1991), we saw bivalve and gastropod larvae in various stages of digestion in *Chrysaora fuscescens* gastric cavities. Therefore, we categorized these taxa as prey. In addition, the oral arms and gastric cavities of *C. fuscescens* and *Phacellophora camtschatica* were heavily parasitized by the amphipod *Hyperia medusarum* and occasionally by *Cancer* spp. megalopae. Since these taxa are known parasites of medusae, we excluded them from gut content analyses.

**Prey selection.** We used an electivity index ( $C$ ) to compare feeding patterns among prey taxa and predator species, as this type of calculation allowed us to compare stations with variable prey distributions and test whether apparent differences in prey vulnerability are statistically significant. For each medusa, we determined Pearre's ' $C$ ' (Pearre 1982) for the most common prey taxa:

$$C = (\chi^2/N)^{1/2}$$

where  $\chi^2$  tested for observed (in guts) versus expected (in environment) proportion of prey, and  $N$  = number of prey counted in gastric pouches + total number of zooplankton counted in subsamples of net tows. Values of ' $C$ ' span  $-1$  to  $1$  (with  $-1$  strongest selection against the prey type,  $0$  neutral, and  $1$  strongest selection for the prey type).

Counts of the numbers of zooplankton ingested (corrected for differences in digestion time among prey taxa; Sullivan et al. 1997) and zooplankton available in the environment (from counts of subsamples of net tows) were used to test for statistical significance using  $\chi^2$ . For *Aurelia labiata* and *Phacellophora camtschatica*, we assumed that the proportionate differences in digestion times for various prey taxa would be consistent with results from digestion experiments with

*Chrysaora fuscescens*. Other studies have shown that digestion time for a given prey type vary between predator species, but vary proportionately (Martinsen & Båmstedt 1999, Suchman & Sullivan 2000); therefore, we calculated prey selection indices, but not feeding rates, for *A. labiata* or *P. camtschatica* using digestion times for *C. fuscescens*.

**Feeding rates and daily ration.** We determined feeding rates by *Chrysaora fuscescens* on various zooplankton groups; we assumed that the 24 h feeding and digestion times for copepods were applicable to those crustacean taxa (including early stages of euphausiids) not present during gut evacuation measurements. Because medusae do not satiate at prey densities similar to or higher than those sampled during our study (Fancett & Jenkins 1988, Båmstedt et al. 1994, Titelman & Hansson 2006) and capture zooplankton based on prey vulnerability rather than active selection (Costello & Colin 1994), we assumed that (1) feeding rates would vary linearly across all zooplankton densities and (2) feeding rates on each prey category would be independent of densities of alternative prey. Therefore, for each *Chrysaora fuscescens* dissected, ingestion over 24 h was calculated as:

$$\text{Ingestion (no. prey d}^{-1}\text{)} = \frac{\text{[gut contents (no. prey)]}}{\text{digestion time (h)}} \times 24$$

We ran multiple linear regressions to estimate feeding by *Chrysaora fuscescens* across zooplankton densities and medusa sizes within the study region.

In addition, for each medusa dissected, (1) carbon content (mg C) was calculated from its diameter using the conversions provided in Shenker (1985) and (2) daily carbon ingestion (mg C  $\text{d}^{-1}$ ) was determined by multiplying ingestion rate and carbon content of each type of prey (Table 2), adding all prey types.

**Mesoscale sampling of *Chrysaora fuscescens* and net zooplankton.** Abundances and distributions of medusae and zooplankton were determined from 31 July to 19 August 2002 in the shelf and shelf-break region between  $44.65^\circ\text{N}$  and  $41.90^\circ\text{N}$  (off Newport, OR, USA to Crescent City, CA, USA) (Fig. 1B). Scientists on board the FV 'Frosti' collected medusae and nekton at 101 stations by towing a Nordic 264 rope trawl in surface waters for 30 min (Suchman & Brodeur 2005). Net zooplankton were collected at 71 comparable stations on the RV 'New Horizon' as described previously. Contour maps summarizing abundance of *Chrysaora fuscescens* and copepods, early stages of euphausiids, and other gelatinous zooplankton in the region were generated using a Kriging interpolation algorithm in Surfer 8.0 (Golden Software, Inc.).

We estimated predation impact (fractional removal of standing stock  $\text{d}^{-1}$ ) of the *Chrysaora fuscescens* population at each station by multiplying the abundance of

Table 2. Values used for carbon content of zooplankton prey

Taxon	$\mu\text{g C}$	Source
Euphausiid eggs	3.2	Gómez-Gutiérrez (2003)
Euphausiid larvae	6	Ross (1982)
Calanoid copepods	5	Martinussen & Båmstedt (1995)
Cyclopoid copepods	1	Martinussen & Båmstedt (1995)
Molluscs	0.2	Martinussen & Båmstedt (1995)
Gelatinous taxa	2	Martinussen & Båmstedt (1995)
Polychaetes	4	Uye (1982)
Cladocerans	1	Martinussen & Båmstedt (1995)

*C. fuscescens* (from trawls) by feeding rate from linear regressions, given known zooplankton densities (from plankton net tows):

$$\text{Fraction zooplankton consumed d}^{-1} = (\text{medusae m}^{-3} \times \text{zooplankton medusa}^{-1} \text{ d}^{-1}) / \text{zooplankton m}^{-3}$$

For the stations where zooplankton counts were not available to pair with *C. fuscescens* abundance, zooplankton densities for target taxa were interpolated using the zooplankton contour map (30 stations).

## RESULTS

We grouped net zooplankton into categories: (1) euphausiid eggs, (2) euphausiid nauplii and calyptopes, (3) calanoid copepods (adult and copepodite stages), (4) cyclopoid copepods (adults and copepodites), (5) molluscs, (6) gelatinous taxa, (7) polychaetes, (8) cladocerans, and (9) 'other.' For digestion experiments and feeding rate regressions, all copepods were grouped together. Euphausiids were *Euphausia pacifica* and *Thysanoessa spinifera*, both broadcast spawners. Calanoid copepods included the genera *Acartia*, *Aetideus*, *Calanus*, *Candacia*, *Centropages*, *Clausocalanus*, *Eucalanus*, *Lucicutia*, *Metridia*, *Paracalanus*, *Pseudocalanus*, *Rhincalanus*, *Scolecithricella*, and *Tortanus*. Cyclopoids were primarily *Oithona*, but *Corycaeus* was also consumed. Molluscs were bivalve larvae, gastropod larvae, and pteropods. Polychaetes were primarily larvae of benthic taxa. Gelatinous taxa included primarily larvaceans but also ctenophores, hydromedusae, salps, doliolids, and siphonophores.

### Digestion experiments

Average gut evacuation time for various zooplankton groups ranged from 3 to 9 h (Fig. 3), with softer-bodied taxa disappearing from *Chrysaora fuscescens* gastric pouches and oral arms most quickly and molluscs least quickly. Gelatinous zooplankton averaged 3 h, polychaetes 4.5 h, copepods 6 h and molluscs 9 h.

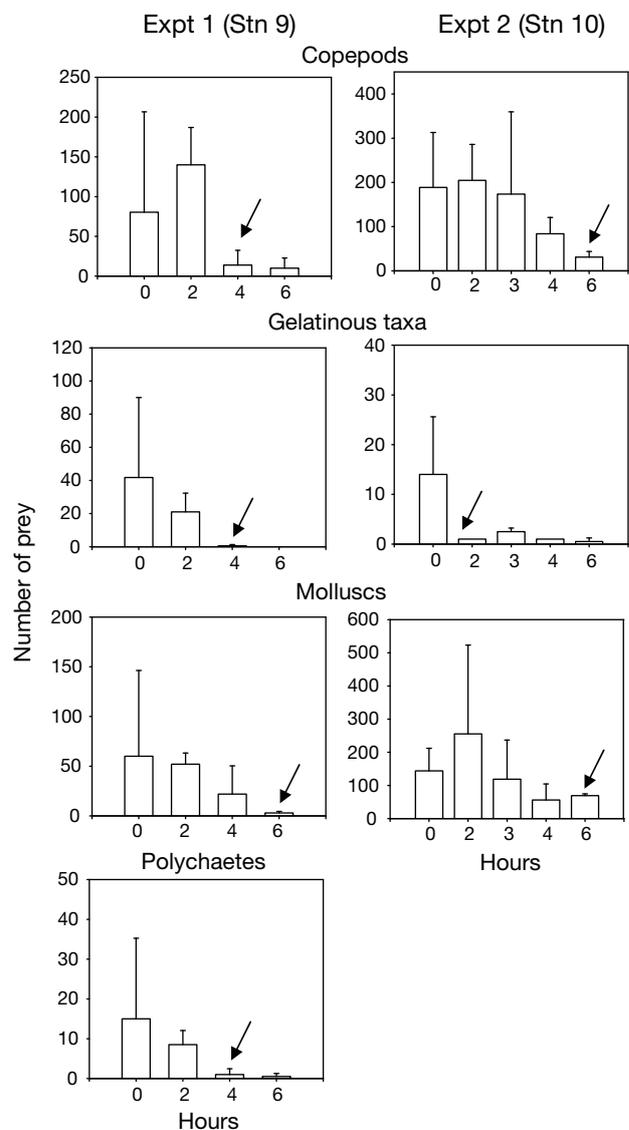


Fig. 3. *Chrysaora fuscescens*. Rate of disappearance of zooplankton from medusan guts, with full gut pouch at hour = 0. Medusae used in Expt 1 were collected from Stn 9 (surface temperature 7.5°C); those in Expt 2 were collected from Stn 10 (surface temperature 9.1°C). Arrows denote time used for linear regression with  $t = 0$  (with digestion time estimated where  $x = 0$ ). Scale differs for both axes among experiments and prey types. See Table 1 for stations. Values are means  $\pm$  SD

### Diet analysis

*Chrysaora fuscescens* individuals from 8 stations showed similar feeding habits, and in each case ingested zooplankton in proportions different from those available in the water column (Fig. 4). At all stations, calanoid copepods dominated the net zooplankton assemblage (42.7 to 78.0%), with cyclopoids also often abundant. At Stn 8, 'other' species was the

second most abundant group, comprising primarily copepod nauplii (29.4% of net zooplankton) and barnacle nauplii (7.4% of net zooplankton), though both of these were likely undersampled by the 202  $\mu\text{m}$  net. Copepods were not ingested in proportion to their abundance in the plankton. Instead, when euphausiid eggs (~400  $\mu\text{m}$ ) were present in the water column, even at relatively low densities (Stns 1, 2, 3, 5, and 7; 4.4 to 11.5% of total zooplankton), they were the largest component of the diet of *C. fuscescens* (32.8 to 91.5% of diet). When euphausiid eggs were absent,

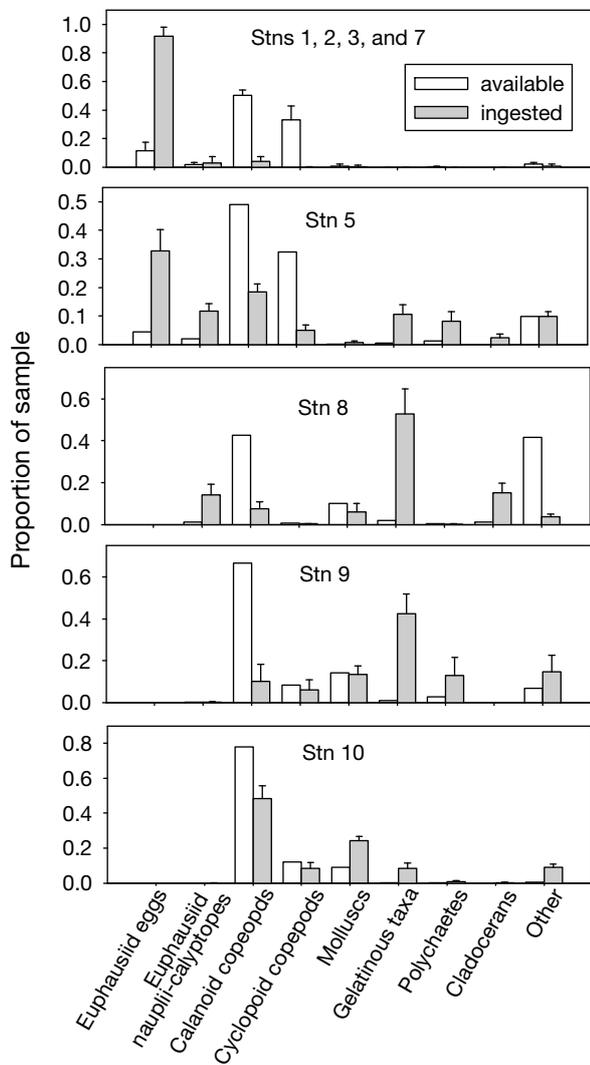


Fig. 4. *Chrysaora fuscescens*. Proportion of zooplankton available vs proportion ingested by medusae, by station. Ingested data have been corrected for differences in digestion time among prey types. Data from Stns 1, 2, 3, and 7 were aggregated as zooplankton prey fields were similar (SD represents variability among medusan gut contents or counts from plankton tows). Details on numbers of medusae analyzed and zooplankton densities are available in Table 1, as is the list of stations. Values are means  $\pm$  SD

gelatinous zooplankton were the prey type most consumed (Stns 8 and 9). Only at Stn 10, with no early stages of euphausiids and almost no gelatinous zooplankton available, were calanoid copepods the primary prey group ingested by *C. fuscescens*.

Results for *Phacellophora camtschatica* and *Aurelia labiata* were similar in that copepods, despite their availability in the plankton (70.1 to 73.8%), were not the primary prey ingested by medusae (Fig. 5). *Aurelia labiata* ingested mostly euphausiid eggs (7.8% in plankton, 61.6% ingested), and *P. camtschatica* ingested gelatinous taxa (11.1% in plankton, 65.9% ingested).

Applying a correction to gut contents to account for differences in digestion time among prey types refined, but did not alter, overall feeding patterns. At some stations, ingestion patterns were nearly identical with or without a digestion correction (<1% change for all prey types, Stns 1, 2, 3 and 7). Similarly, at all stations, proportion of euphausiid eggs and copepods changed little (maximum 6% change for euphausiid eggs and 4% for copepods). Fast digestion time for gelatinous zooplankton did increase the relative proportion of these animals in the diet of scyphomedusae in some cases, particularly at Stns 6, 8, and 9, where uncorrected diet had fewer gelatinous organisms (uncorrected diet: 24%, 18%, and 16% respectively) (Figs. 4 & 5). Even so, overall feeding pattern remained the same. Because this and other studies (e.g. Purcell 2003) have demonstrated relatively fast digestion times for soft-bodied taxa, the digestion correction should provide the most accurate view of feeding patterns.

When electivities for individual medusae were averaged (significant values of Pearre's 'C', by medusa;  $\chi^2$ ,  $p < 0.05$ ), general feeding patterns became clear

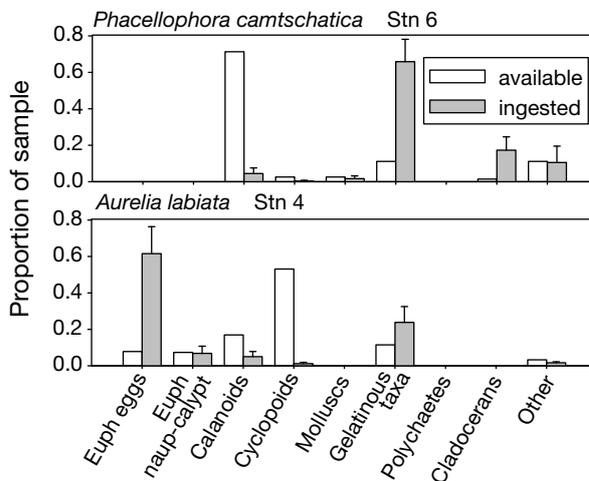


Fig. 5. *Phacellophora camtschatica*, *Aurelia labiata*. Proportion of zooplankton available vs ingested by medusae, by station. Details regarding number of medusae analyzed and zooplankton densities are available in Table 1, as is the list of stations. Values are means  $\pm$  SD

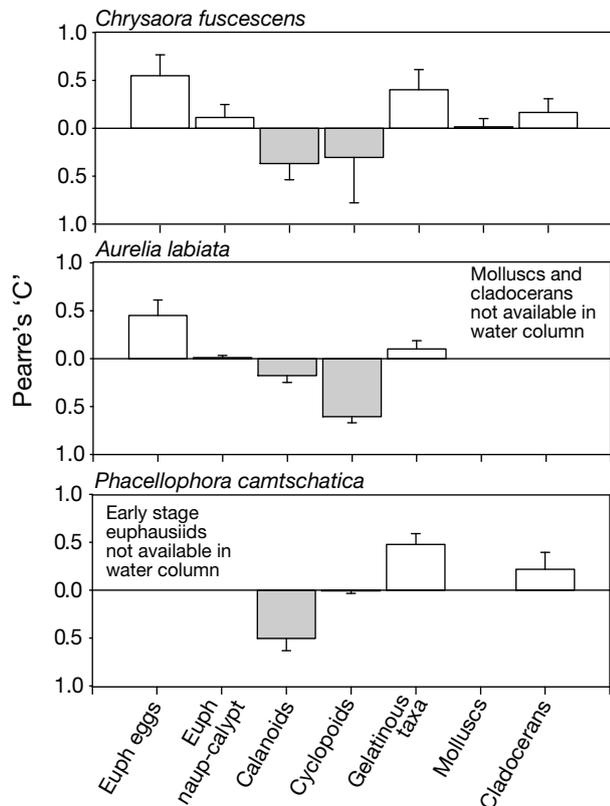


Fig. 6. *Chrysaora fuscescens*, *Aurelia labiata*, *Phacellophora camtschatica*. Feeding summarized by averaging significant electivity values ( $\chi^2$ ,  $p < 0.05$ ) of Pearre's 'C' for zooplankton prey categories, using 0 when 'C' was not significant (neutral selection). Pearre's 'C' ranges from  $-1$  to  $1$ , with positive values indicating selection for highly vulnerable prey and negative values selection against prey type. Sample sizes are available in Table 1. euph: euphausiid; naup calypt: nauplii-calyptopes. Values are means  $\pm$  SD

(Fig. 6). When euphausiid eggs and gelatinous taxa were present in the plankton, they were preferentially ingested by medusae. Cladocerans were also positively selected, but less strongly than euphausiid eggs or gelatinous taxa. Copepods were consistently negatively selected.

### Feeding rates and predation impact

We limited our analysis of feeding rate to *Chrysaora fuscescens* because it was the only species of medusa for which we had adequate data (number of individuals = 31, and number of stations = 8; Table 1). Zooplankton densities by station ranged from 1535 to 36705  $m^{-3}$ . Live bell diameters of *C. fuscescens* ranged from 10.6 to 28.3

cm, with averages of 13.3 to 28.3 cm per station. Preserved medusae were  $0.85 \pm 0.02$  (SD) of the live size. Numbers of prey ingested by each medusa ranged from 39 to 5329, with averages of 262 to 2943 medusa $^{-1}$  by station (Table 1).

Medusae dissected ingested an average of 1.3% of their carbon content  $d^{-1}$ , with no significant differences between average daily ration at stations with and without euphausiid eggs present as prey (Table 3).

To account for differential prey vulnerability, we separated zooplankton into groups for linear regressions: (1) euphausiid eggs, (2) other naupliar and calyptopes larval stages of euphausiids, (3) copepods, and (4) gelatinous zooplankton (Table 4). Feeding rates on copepods could not be estimated using linear regression ( $p > 0.05$ ). Regressions for other taxa, though significant, had adjusted  $r^2$  values of 0.70 at most, indicating high variability among individuals or unidentified covariates. Medusa diameter was never a

Table 3. *Chrysaora fuscescens*. Average carbon content of medusa and gastric contents, by station. Numbers of medusae dissected and prey counted available in Table 1, and carbon conversions in Table 2

Stn	mg C medusa $^{-1}$ ( $\pm$ SD)	mg C $d^{-1}$ ingested ( $\pm$ SD)	% C $d^{-1}$ ( $\pm$ SD)
1	1552 $\pm$ 860	38 $\pm$ 22	2.7 $\pm$ 0.9 <sup>a</sup>
2	1033 $\pm$ 73	41 $\pm$ 8	3.9 $\pm$ 0.4 <sup>a</sup>
3	672	37	5.6 <sup>a</sup>
5	1303 $\pm$ 490	5 $\pm$ 3	0.4 $\pm$ 0.2 <sup>a</sup>
7	2906	6	0.2 <sup>a</sup>
8	1490 $\pm$ 368	10 $\pm$ 6	0.6 $\pm$ 0.3
9	1084 $\pm$ 860	4 $\pm$ 4	0.4 $\pm$ 0.04
10	1226 $\pm$ 671	4 $\pm$ 3	0.4 $\pm$ 0.2
	All medusae		1.3 $\pm$ 1.5
	Euphausiid eggs present		1.9 $\pm$ 1.8
	No euphausiid eggs present		0.5 $\pm$ 0.3

<sup>a</sup>Stations where euphausiid eggs were present. Differences between medusae from stations with or without euphausiid eggs were not significant (Mann-Whitney test,  $p > 0.05$ )

Table 4. *Chrysaora fuscescens*. Simple linear regression of feeding rate as a function of prey density for specific zooplankton groups, with  $y$  = feeding rate by a single medusa ( $d^{-1}$ ) and  $x$  = density of zooplankton prey ( $m^{-3}$ ). Medusa diameter was not a significant covariate. ns = not significant ( $p > 0.05$ ). Sample sizes are available in Table 1 and prey proportions in Figs. 4 & 5

Zooplankton group	p-value	Model	$r^2$ adjusted
Euphausiid eggs	<0.001	$y = (-1.6) + 30.2(x)$	0.428
Euphausiid nauplii-calyptopes	0.008	$y = 120.2 + 1.2(x)$	0.189
Calanoid and cyclopid copepods	ns	average = 377 $\pm$ 330	
Gelatinous zooplankton	<0.001	$y = 45.4 + 2.7(x)$	0.7

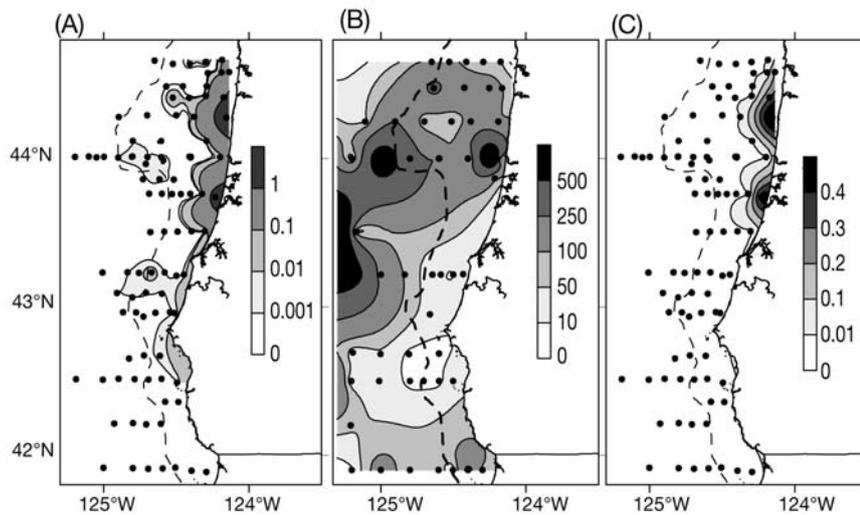


Fig. 7. *Chrysaora fuscescens* and Euphausiidae. (A) Abundance (no.  $100\text{ m}^{-3}$ ) and distribution of *C. fuscescens* collected in surface trawls during August 2002. *C. fuscescens* medusae were present in 55% of trawls in the region (Suchman & Brodeur 2005), with highest abundances near the coast and north of Cape Blanco. (B) Abundance (no.  $\text{m}^{-3}$ ) and distribution of euphausiid eggs collected in vertical tows during August 2002. (C) Predation potential of *C. fuscescens* on standing stock of euphausiid eggs during August 2002 (fractional removal of standing stock  $\text{d}^{-1}$ ). Maximum predation pressure coincided with highest abundances of *C. fuscescens*, reaching  $60\% \text{ d}^{-1}$  and averaging  $32.5\% \text{ d}^{-1}$  nearshore and north of  $43.5^\circ\text{N}$ . ---: shelf break (200 m isobath). •: locations of surface trawls (A & C) or plankton tows (B)

significant covariate, although it may have been had we used a larger sample size encompassing a wider range of bell diameters (e.g. Purcell 2003).

We used abundances of *Chrysaora fuscescens* and zooplankton to estimate trophic impact of the *C. fuscescens* population throughout the study region during August 2002. *C. fuscescens* medusae were present in 55% of trawls (Suchman & Brodeur 2005), with maximum abundance of 2 individuals  $100\text{ m}^{-3}$  along the inner continental shelf north of Cape Blanco (Fig. 7A). Because medusae analyzed for gut contents had highest feeding rates on euphausiid eggs (up to  $20\,920\text{ eggs d}^{-1}$ ), we expected to see the largest impact on this zooplankton group. Except for one nearshore area at  $44^\circ\text{N}$ , the highest densities of eggs (up to  $1092\text{ m}^{-3}$ , from counts of net tows) were found offshore from the shelf break in areas spatially separated from *C. fuscescens* (Figs. 7B & 8). Where medusae were most abundant, they removed an average of  $32.5\%$  and up to  $60\% \text{ d}^{-1}$  of the standing stock of euphausiid eggs (Tables 5 & 6, Fig. 7C). In contrast, the calculated maximum removal rates of the standing stocks of copepods (using average feeding rate across copepod densities, Table 4), gelatinous taxa and euphausiid nauplii, metanauplii, and calyptopes were  $<1$ ,  $10.5$  and  $12.2\% \text{ d}^{-1}$ , respectively (Table 5). As with euphausiid eggs,

predation impact was highest in nearshore areas where *C. fuscescens* were most abundant (Fig. 9). Copepods, the prey category least vulnerable to predation by *C. fuscescens*, had highest densities along the inner shelf, coinciding with the predator's population maximum (Figs. 7 & 9).

## DISCUSSION

Our results suggest (1) differential vulnerability of zooplankton prey to scyphomedusae of the Northern California Current, with early stages of euphausiids and gelatinous taxa particularly vulnerable to predation (Fig. 6), and (2) a potential for depletion of the standing stock of euphausiid eggs in the nearshore zone at times and locations when medusae are most abundant (Table 6, Fig. 7). *Chrysaora fuscescens* in August 2002 was restricted to more northern, nearshore areas of the study region (Suchman & Brodeur 2005), so predation on populations of *Euphausia pacifica* and *Thysanoessa spinifera* over seasonal and interannual time periods is likely to be focused in these shallow areas close to shore. Other medusae in the region may also ingest euphausiid eggs, so we have likely underestimated the impact of gelatinous predators on euphausiid popula-

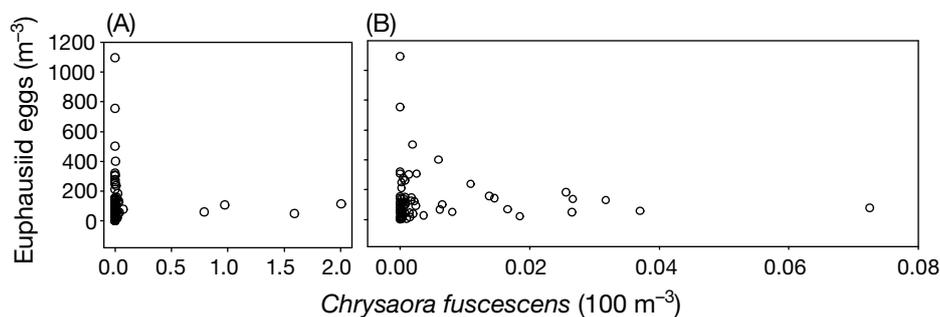


Fig. 8. *Chrysaora fuscescens*. Relationship between abundance of *C. fuscescens* and euphausiid eggs at mesoscale sampling stations (Fig. 1). (A) Includes all stations; (B) shows same data without 4 stations having highest abundance of *C. fuscescens*

Table 5. *Chrysaora fuscescens*. Summary of predation impact at 44.45° N, 124.19° W, a mesoscale sampling station with highest abundance of *C. fuscescens* (2 medusae 100 m<sup>-3</sup>)

Prey taxa	Prey ingested (no. m <sup>-3</sup> d <sup>-1</sup> )	% standing stock d <sup>-1</sup>
Euphausiid eggs	69	60.6
Euphausiid nauplii, metanauplii, calyptopes	3	12.2
Gelatinous zooplankton	2	9.7 <sup>a</sup>
Copepods	7 <sup>b</sup>	0.5

<sup>a</sup>Maximum of 10.5 % d<sup>-1</sup> at 44.41° N, 124.17° W  
<sup>b</sup>Using 377 copepods medusa<sup>-1</sup> d<sup>-1</sup> (Table 4)

tions. In addition, distribution and abundance of predators and prey can shift with climatic (Peterson et al. 2002, Lynam et al. 2004), hydrographic (Keister et al. 2000), or anthropogenic factors (Mills 2001, Purcell et al. 1999), and these shifts have the potential to intensify trophic interactions.

Diets of *Chrysaora fuscescens*, *Aurelia labiata*, and *Phacellophora camtschatica* were similar (Fig. 6).

Table 6. *Chrysaora fuscescens* and Euphausiidae. Summary of average predation rates (% d<sup>-1</sup>) on euphausiid eggs by *C. fuscescens* according to geographic location, with n = number of stations. Highest impact was in shallow, nearshore areas in the northern part of the study region. Predation impact in other areas was negligible

Station depth (m)	% euphausiid eggs ingested d <sup>-1</sup> (± SD)	
	North of 43.5° N	South of 43.5° N
<50	32.5 ± 23.2 (n = 5)	0.02 ± 0.02 (n = 4)
50–100	0.5 ± 0.6 (n = 18)	0.01 ± 0.02 (n = 8)
>100	0.03 ± 0.08 (n = 38)	0.03 ± 0.1 (n = 27)

These results are not surprising, given feeding mechanics of medusae. Gut contents integrate across fine and intermediate-scale prey patchiness as these large animals swim through their feeding environment, accumulating prey during the several hours it takes to digest them (Hansson & Kiørboe 2006). Moreover, the term 'prey selection' should be understood as the effect of differential vulnerability of prey to encounters rather than the outcome of active pursuit by the predator. Previous studies of interactions between scypho-

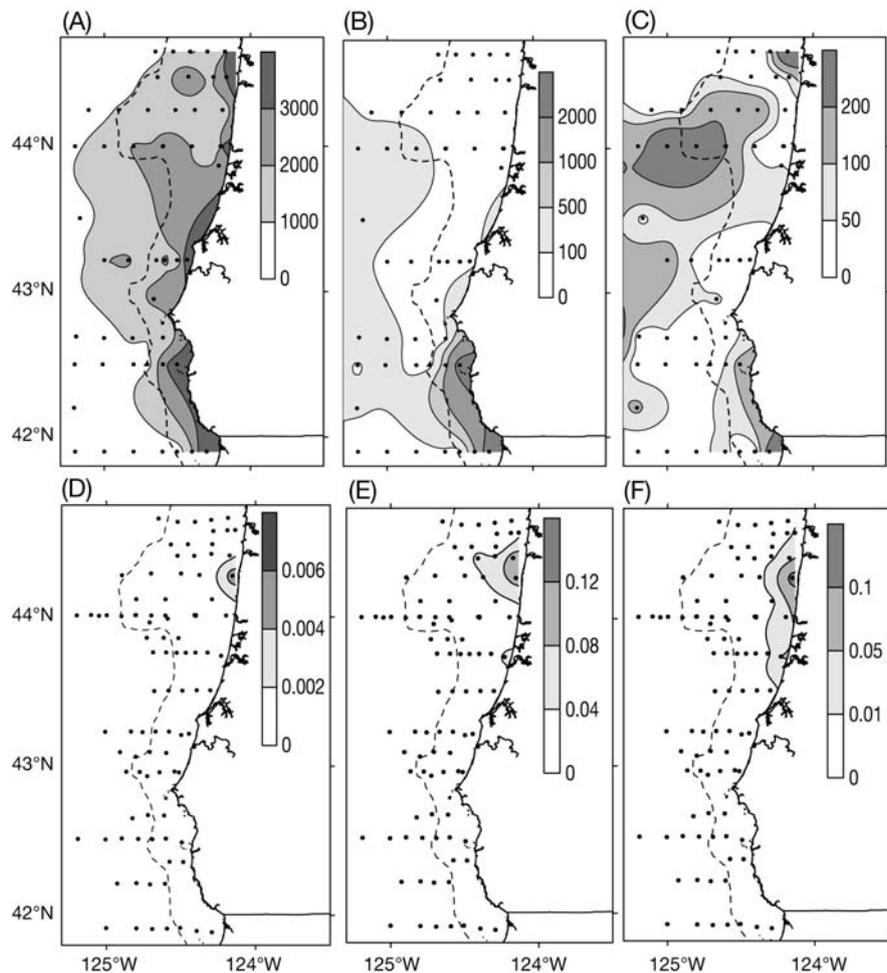


Fig. 9. *Chrysaora fuscescens* and zooplankton prey. Abundance (no. m<sup>-3</sup>) and distribution of (A) copepods, (B) gelatinous zooplankton, and (C) euphausiid nauplii and calyptopes, collected by vertical net tows (•) during August 2002. Predation potential of *C. fuscescens* on standing stock of (D) copepods, (E) gelatinous zooplankton, and (F) euphausiid nauplii and calyptopes during August 2002 (fractional removal of standing stock d<sup>-1</sup>; •: locations of trawls used to determine abundance of medusae). Maximum predation pressure coincided with highest abundances of *C. fuscescens* (see Fig. 7A). ---: shelf break (200 m isobath)

medusae and zooplankton have suggested that in general, larger, slow-escaping prey will be most vulnerable (Suchman & Sullivan 2000) because they are more readily entrained in the flow created by a swimming medusa (Costello & Colin 1994). This study supports this hypothesis, with selection for relatively slow taxa (early stages of euphausiids, gelatinous zooplankton, cladocerans) and selection against organisms that detect and respond to fluid disturbance quickly (copepods) (e.g. Fields & Yen 1997). Euphausiid eggs are relatively large and have no ability to escape, making them particularly vulnerable to ingestion following encounters with medusae.

Based upon feeding patterns and ingestion rates reported here, copepod populations in the Northern California Current were not subject to heavy predation by *Chrysaora fuscescens* during August 2002. Predation on standing stock was always  $<1\% \text{ d}^{-1}$  (Fig. 9). Similarly, in the central Baltic Sea, predatory impact of medusae on copepods was 0.06 to  $1.15\% \text{ d}^{-1}$  (Barz & Hirche 2005). In Prince William Sound, Alaska, medusae ingested at most  $0.3\% \text{ d}^{-1}$  of the copepod standing stock (Purcell 2003). In each case, medusae removed other zooplankton prey items (early stages of euphausiids, cladocerans, larvaceans) at higher rates than copepods.

When euphausiid eggs were present, they constituted most of the prey items found in guts of both *Chrysaora fuscescens* and *Aurelia labiata* (Figs. 4 & 5). At stations close to shore and north of Cape Blanco, where *Chrysaora fuscescens* were most abundant, medusae ingested an average of 32.5% and up to 61% of the standing stock of euphausiid eggs each day (Tables 5 & 6, Fig. 7). At the same stations, ingestion of other vulnerable prey (naupliar and calyptopis stages of euphausiids, and gelatinous taxa) reached 10 to  $12\% \text{ d}^{-1}$ . The estimate of  $61\% \text{ d}^{-1}$  is not an artifact of pairing relatively high densities of medusae with low densities of euphausiid eggs. The highest densities of medusae (2 individuals  $100 \text{ m}^{-3}$ ) would be capable of ingesting  $660 \text{ eggs m}^{-3} \text{ d}^{-1}$  or  $60\% \text{ d}^{-1}$  at the station with highest density of eggs ( $1092 \text{ m}^{-3}$ ) (Table 5).

Fig. 8 suggests an inverse relationship between density of euphausiid eggs and *Chrysaora fuscescens*, at least where medusae or eggs were most abundant. Even though factors such as predation by other taxa, advection or retention, and spawning frequency and location will also contribute to distribution of euphausiid eggs, in August 2002, densities of eggs were highest at stations with relatively few *C. fuscescens* medusae. In particular, the one nearshore station north of Cape Blanco with high euphausiid egg densities (at  $44^\circ \text{N}$ , Fig. 7B) coincided with a local minimum of *C. fuscescens* (Fig. 7A).

Because we were unable to measure digestion time of euphausiid eggs, we need to be confident that our estimate is reasonable, particularly as relatively few data are available for such large medusae or from field studies where euphausiid eggs would be abundant. Clearance rates for *Chrysaora fuscescens* feeding on euphausiid eggs were  $30 \text{ m}^3 \text{ d}^{-1}$  (Tables 4 & 5), and we can check whether this rate is reasonable in several ways. First, it is comparable to clearance rates of  $15.5 \text{ m}^3 \text{ d}^{-1}$  reported by Purcell (2003) for smaller *Cyanea capillata* ingesting larvaceans in certain subregions of Prince William Sound, Alaska. Second, for stationary prey, encounter rates will depend upon encounter area (square of medusa's bell diameter) and the swimming speed of the predator (Gerritsen & Strickler 1977). For example, a medusa of 20 cm diameter swimming  $1 \text{ cm s}^{-1}$  can sweep more than  $100 \text{ m}^3 \text{ d}^{-1}$ . Capture efficiencies will be highest for stationary prey such as euphausiid eggs, and high capture to encounter ratios are likely (66% for slow-escaping prey in the laboratory, Sullivan et al. 1997). Finally, even with such high clearance rates, carbon analysis reveals relatively low daily rations for those *C. fuscescens* individuals collected during 2002 and 2003. For all stations, *C. fuscescens* ingested an average of  $1.3\% \text{ body C d}^{-1}$ ; when euphausiid eggs were present, the average was  $1.9\% \text{ d}^{-1}$  (Table 3). These are not particularly high feeding rates from a carbon perspective and in fact, suggest that this population may be food-limited. Other studies have estimated a  $2\% \text{ d}^{-1}$  metabolic requirement (Sotje et al. 2007), or calculated  $>3\% \text{ d}^{-1}$  body weight consumed (Brodeur et al. 2002).

Were conditions during this study typical of the region's upwelling season? Basin-scale forcing strongly influences both the biodiversity and biomass of copepod populations off the coast of Oregon (Hooff & Peterson 2006). The year 2002 concluded a 4-yr cool period in the California Current, associated with relatively low copepod biodiversity and high biomass. From the end of 2002 through 2006, however, the California Current warmed, and copepod biodiversity was high and biomass low. It is reasonable to expect that basin-scale conditions related to El Niño or the Pacific Decadal Oscillation will affect not only copepods, but also influence local populations of gelatinous taxa. Thus, in a region subject to interannual and interdecadal variability in climatic conditions, and with ecosystem productivity so dependent upon physical forcing, data collected over several years are needed to confirm this study's predictions about the role of gelatinous predators.

Nevertheless, given spatial and temporal patterns of predators and prey, the population of *Chrysaora fuscescens* may routinely ingest euphausiid eggs at rates similar to those in August 2002. Medusae are typ-

ically present in high densities along the inner shelf throughout summer months (Shenker 1984, Suchman & Brodeur 2005), overlapping in space and time with peaks in egg densities following spawning events (100s to ~1000 eggs m<sup>-3</sup> at a nearshore station off Newport, Oregon, Feinberg & Peterson 2003). Larvae of both *Euphausia pacifica* and *Thysanoessa spinifera* are found nearshore during summer months relative to cross-shelf or offshore distribution of adults, and spawning may be concentrated close to shore to minimize advection of less mobile early stages (Gómez-Gutiérrez et al. 2005). In fact, we probably underestimated the magnitude of predation on euphausiid eggs by other gelatinous predators that commonly occur in the region. These taxa, including ctenophores, hydro-medusae (*Mitrocoma cellularia*, *Aequorea* spp.) and the scyphomedusa *Aurelia labiata*, also ingest euphausiid eggs (Larson 1987, this study, and C. Suchman unpubl. data).

What we cannot determine from this study is the proportion of euphausiid production removed by *Chrysaora fuscescens* in the Northern California Current. It is challenging to resolve euphausiid population dynamics because egg production is highly variable and not well understood (Feinberg et al. 2007). Cross-shelf distributions of adult euphausiids, as well as their eggs and larvae, depend upon complex circulation patterns related to the coastal upwelling process (Gómez-Gutiérrez et al. 2005). Given high spatial and temporal overlap between medusae and euphausiid egg production on the Oregon shelf, however, we suggest that gelatinous predators may play a more important role in euphausiid population dynamics than previously recognized.

Our results should have broad implications for understanding upwelling ecosystems. This snapshot shows that where medusae are most abundant, they have the ability to deplete the standing stock of vulnerable prey. More focused research would be needed to link predation by gelatinous zooplankton to euphausiid population dynamics over seasonal or interannual time scales. In addition, gelatinous taxa such as *Chrysaora fuscescens* compete with fish and other nekton in the Northern California Current. Euphausiid eggs can be a large component of the diet of sardines and other forage fish (Emmett et al. 2005, Brodeur et al. 2008). Other nekton, such as salmonids, ingest later-stage euphausiids (Peterson et al. 1982, Brodeur & Pearcy 1992). Analysis of multi-year, mesoscale sampling in the Northern California Current, in combination with diet studies of fish and medusae, should yield interesting results. Given the importance of euphausiids to fish and other top predators, and the potential for changes in abundance and distribution of both predator and prey taxa with changes in climate, we hope

that other fisheries scientists and managers begin to monitor gelatinous zooplankton abundance and incorporate predation impacts within long-term studies and ecosystem models.

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