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Prey resource use by coexistent hydromedusae from Friday Harbor, Washington

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Abstract

Prey selection patterns were quantified for a sympatric group of hydromedusae from Friday Harbor, WA. Selection patterns varied between species, but were largely replicable between sample dates and resembled dietary patterns found in similar studies from neighboring regions. Ambush-foraging medusae (*Aglantha digitale, Sarsia tubulosa,* and *Proboscidactyla flavicirrata*) fed primarily on crustacean and ciliated prey but the dietary niches of these hydromedusan species centered on different fractions of the available plankton. Consequently, little dietary overlap occurred between the ambush foraging hydromedusae. In contrast, the dietary niches of cruising predators (*Aequorea victoria, Mitrocoma cellularia,* and *Phialidium gregarium*) overlapped substantially because those species all fed on similar soft-bodied prey such as eggs and appendicularians. These results have two important implications for trophic patterns involving medusae. First, different mechanisms of prey encounter and capture used by hydromedusae (ambush vs. cruising patterns) result in important interspecific dietary differences and, hence, trophic roles of the medusae. Second, whereas cruising medusae may consume similar prey and hence form a feeding guild, ambush-foraging medusae may experience substantially less prey overlap and, for the community examined here, do not experience potentially strong feeding competition from other medusan species.

Predation by hydromedusae can substantially affect prey populations of zooplankton (Larson 1987*a;* Matsakis and Conover 1991) and fish eggs or larvae (Purcell et al. 1987, Purcell and Grover 1990). Although hydromedusae prey on a wide spectrum of planktonic taxa, many hydromedusan species appear to selectively consume particular prey types (Larson 1987*a;* Purcell 1990; Mills 1995) via a variety of mechanisms (reviewed in Purcell 1997).

Full understanding of the predatory impacts of hydromedusan predation requires information on the synergistic impacts of multiple species of coexisting hydromedusae. This is important because hydromedusan species often coexist (Mills 1981*a*), and the trophic impacts of sympatric species do not occur in isolation from one another. The use of similar, potentially limiting prey (Purcell 1991*a*) suggests that these species may experience competition for planktonic prey resources. Differential prey selection patterns by hydromedusae (Larson 1987*a;* Purcell 1990; Mills 1995) could help relieve intraguild competition among medusae, but the trophic niches of species comprising hydromedusan guilds have received little attention. We asked whether, first, prey resource partitioning occurred between sympatric hydromedusae and, second, what patterns were identifiable that would affect the dietary interactions of species comprising hydromedusan feeding guilds.

We chose a group of sympatric hydromedusae (Fig. 1) from waters surrounding Friday Harbor Laboratories for our study. The members of this group (*Aglantha digitale, Sarsia tubulosa, Proboscidactyla flavicirrata, Aequorea victoria, Mitrocoma cellularia,* and *Phialidium gregarium*) commonly coexist in Pacific Northwest waters (Mills 1981*a*) and have been the subject of several studies (Larson 1987*b;* Purcell and Mills 1988) that provide comparative data and a larger framework within which to view our results.

Predator and prey collection—Medusae were collected by hand-dipping medusae from waters adjoining the floating docks at Friday Harbor Laboratories on 5 June and 9 July 1992 and 2 July 1993. Medusae were immediately preserved in a 5.0% formalin solution after collection. All species were collected during a 2–3 h interval on each sample date. Surface plankton tows at the dock were made immediately prior to the beginning of hydromedusan collection and at the termination of the collection. Tows were made with a 0.5-m diameter, 102-μm mesh net equipped with a flow meter. Prey species distributions found in replicate net tows collected at the outset, and termination of hydromedusan collections were similar (χ^2, $P > 0.6$ for all sample dates). Therefore, data from the two sets of net tows were combined to give an average available prey species distribution that could be compared with a consumed prey distribution on each sample date.

Prey quantification—Determination of dietary patterns of hydromedusae required the use of a dissecting microscope to quantify all prey within a medusa's guts. All prey were identified and subsequently grouped into the general taxa listed in the results section (e.g. Fig. 2 below). Preserved net tows were subsampled with a Stempel pipette (minimum 400 prey identified per subsample). Prey were identified to similar taxonomic categories in the gut contents.

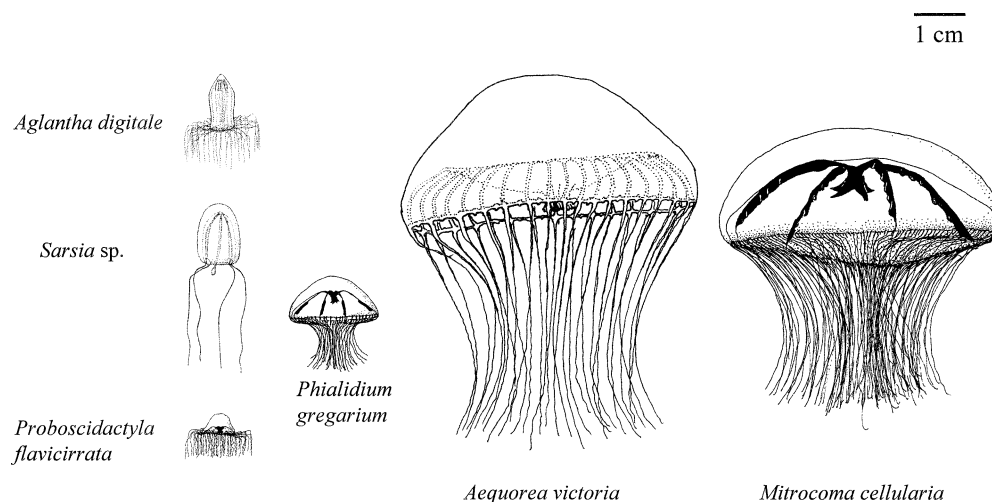Prey selection patterns were quantified by use of Pearre's

Fig. 1. Representative examples of the hydromedusae from Friday Harbor, WA, selected for comparative study (after Colin and Costello 2002). Medusae are shown with their bells relaxed. Medusae are drawn to relative size scale among species. *A. victoria* and *M. cellularia* can grow to be twice as large as depicted.

(1982) electivity index, C. This index relies on χ^2 analysis (Statistica, Statsoft, Inc.) of the numbers of individual prey taxa in predator diets compared with those present in the plankton on a specific sample data. Index values were calculated as

$$C = \pm(\chi^2/z)^{0.5}$$

where z was the total number of all prey counted in the diet and in the net tows. χ^2 and C values were calculated for each prey taxa of interest. Values of C range from 1.0 to -1.0, with values of 0.0 indicating no selection. Positive C values represent disproportionately high occurrence of a prey type in a predator's diet, whereas negative values indicate disproportionately low occurrence of a specific prey type in a medusa's gut.

Analyses of medusan gut contents were adjusted for differential prey digestion rates (following Matsakis and Conover 1991; Sullivan et al. 1994; Suchman and Sullivan 2000) because prey selection patterns based on gut-content analyses can be strongly influenced by differential digestion rates of prey within a predator's guts. Longer gut residence times increase the probability of overestimating ingestion of a prey type. Likewise, low gut residence time can bias ingestion rates toward underestimation of prey ingestion (Martinussen and Båmstedt 1999). As noted by Purcell (1997), accurate determination of digestion times is a laborious effort, although typically most digestion times do not exceed 4 h. Generally, digestion times increase with prey size (Suchman and Sullivan 2000) and the number of prey in the gut (Martinussen and Båmstedt 1999). Additionally, digestion rates of the same prey types can vary substantially between different species of medusan predators (Martinussen and Båmstedt 1999; Suchman and Sullivan 2000). Consequently, estimates of digestion times require cautious consideration. The digestion time estimates that we used to correct gut content data for differential digestion rates were based on literature values (Matsakis and Conover 1991; Sullivan et al.

1994; Suchman and Sullivan 2000) and digestion rates were scaled such that small prey (e.g., copepod nauplii or rotifers) had shorter digestion times (1.5 h) and larger prey were characterized by longer times (copepods, 3.5 h and fish larvae, 3.7 h). Potential effects of digestive rate variability were evaluated by altering digestive rates estimates by 10-fold for prey that were either positively or negatively selected. For comparison, eightfold variations were the most extreme found by Martinussen and Båmstedt (1999). Therefore, electivity results that remained significant (χ^2, $P < 0.05$) after these 10-fold digestive rate variations represent highly conservative estimates of prey selection by hydromedusae.

Although the index C is termed an electivity index, we did not interpret the index data to infer active choice by the medusae. Consequently, we used a term with a less volitional connotation, selection, to describe patterns of prey ingestion by medusae.

The taxonomic diversity within the diet of hydromedusan species was measured by use of the Shannon diversity index H' (Brower and Zar 1984),

$$H' = -\Sigma p_i \log p_i$$

where p_i is the proportion of the total number of prey in the gut composed of prey species i and prey species range from $i \ldots n$. The index H' reflects both dominance and evenness of prey composition within hydromedusan guts and is relatively insensitive to variations in sample size because the inclusion of rare species associated with increased samples sizes has little effect on the index value. H' has been used elsewhere to examine gut content diversity of a scyphomedusa (Graham and Kroutil 2001). H' values range from 0 to 1.0.

Overlap in diet composition between species was analyzed by determining the percentage of similarity index (Brower and Zar 1984). The percentage of similarity between the diets of two hydromedusae (e.g., species x and y) was calculated by summing the lowest percentage of each prey taxa
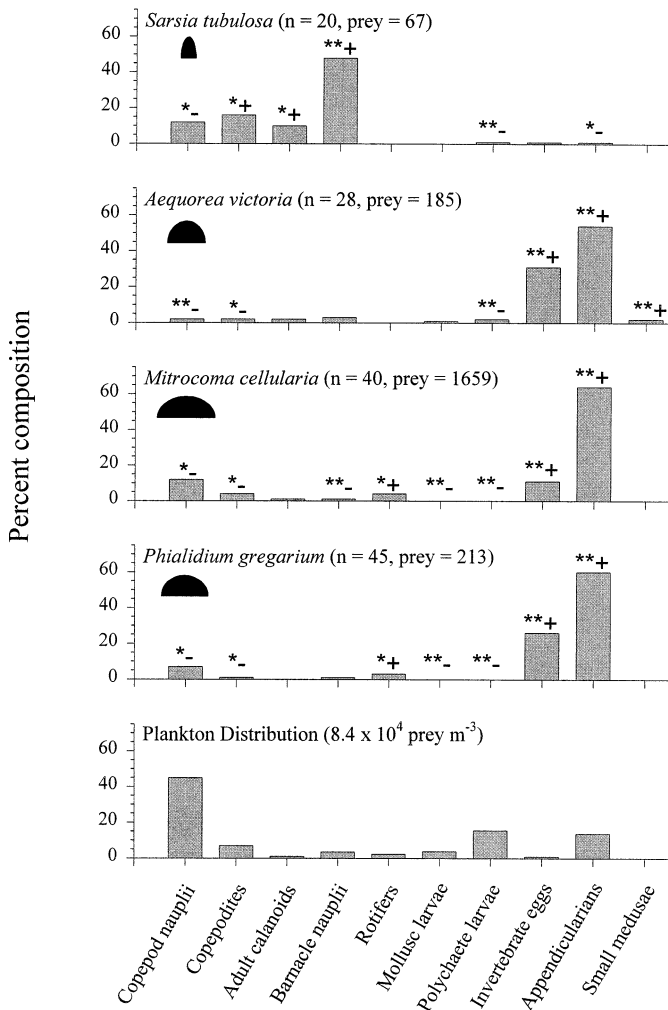
Fig. 2. The percentage taxonomic composition of plankton and diets of hydromedusae collected on 5 June 1992. Average bell shape is outlined below the name of each medusan species. The number of medusae examined (n) and total prey found in their guts are listed for each species of hydromedusa. Single asterisks (*) indicate significant positive (+) or negative (−) selection. Double asterisks (**) indicate selection patterns that remained significant after a 10-fold alteration in digestion time estimates.

Fig. 3. The percentage taxonomic composition of plankton and diets of hydromedusae collected on 9 July 1992. Symbols as in Fig. 2.

($i \ldots n$) that was shared by both hydromedusan species such that percentage similarity was $\Sigma(x_i$ or y_i, whichever was lower). The percentage similarity between species ranges from 0 to 100% and has been used elsewhere to compare dietary overlap between scyphomedusan species (Purcell and Sturdevant 2001).

Prey selection patterns—Prey selection patterns, as indicated by electivity indices, varied among medusae but were generally consistent within one species across multiple sample dates. Invertebrate eggs dominated the diet of *P. gregarium* on two of three sample dates and were significantly selected on all three dates (Figs. 2–5). Appendicularians were also a frequent prey item and strongly selected relative to their abundance in the plankton.

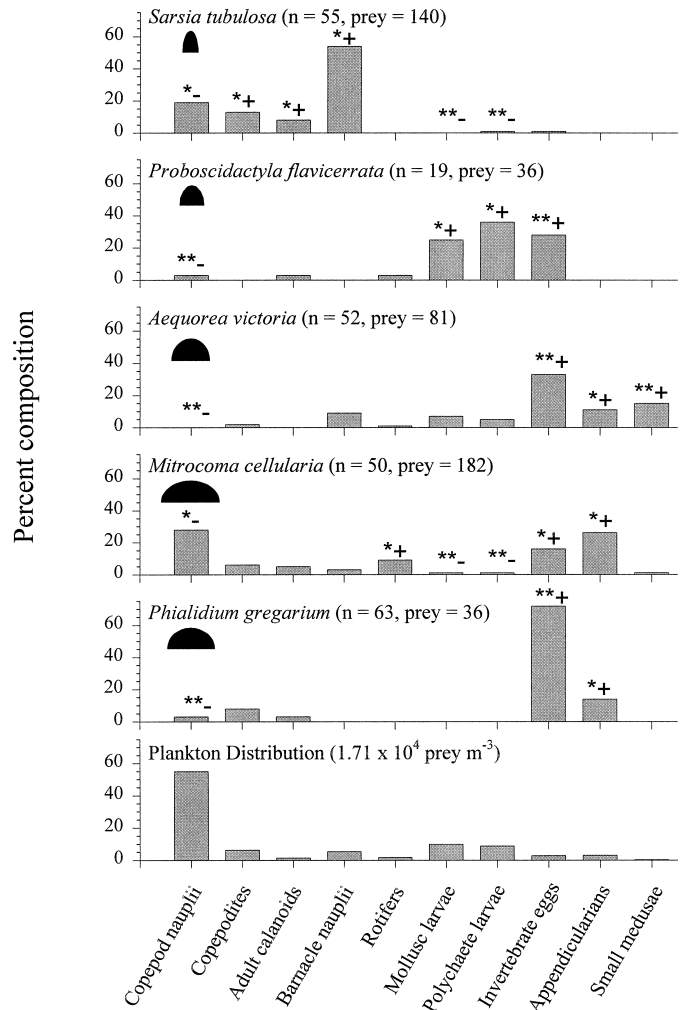Three prey items dominated the diet of *A. victoria:* in-

vertebrate eggs, appendicularians and small medusae (Figs. 2–4). These three prey were consistently significantly positively selected on all sample dates and were the only prey types with net positive electivities (Fig. 5). Other prey types, particularly copepod nauplii, were generally negatively selected (Figs. 2–5).

Like *P. gregarium* and *A. victoria,* the diet of *M. cellularia* included large proportions of invertebrate eggs and appendicularians. Additionally, rotifers were positively selected on one date (Fig. 3). Although typically significantly negatively selected, copepod nauplii nonetheless comprised an important portion of *M. cellullaria*'s diet.

S. tubulosa consumed primarily crustacean prey and positively selected barnacle nauplii on both dates for which gut contents were collected (Figs. 2, 3). Electivities were typically negative for invertebrate eggs and larvae, rotifers, and copepod nauplii (Fig. 5).

P. flavicirrata medusae consumed primarily invertebrate eggs and larvae of polychaetes and molluscs (Figs. 3–5). Weakly positive selection of rotifers was evident on one date
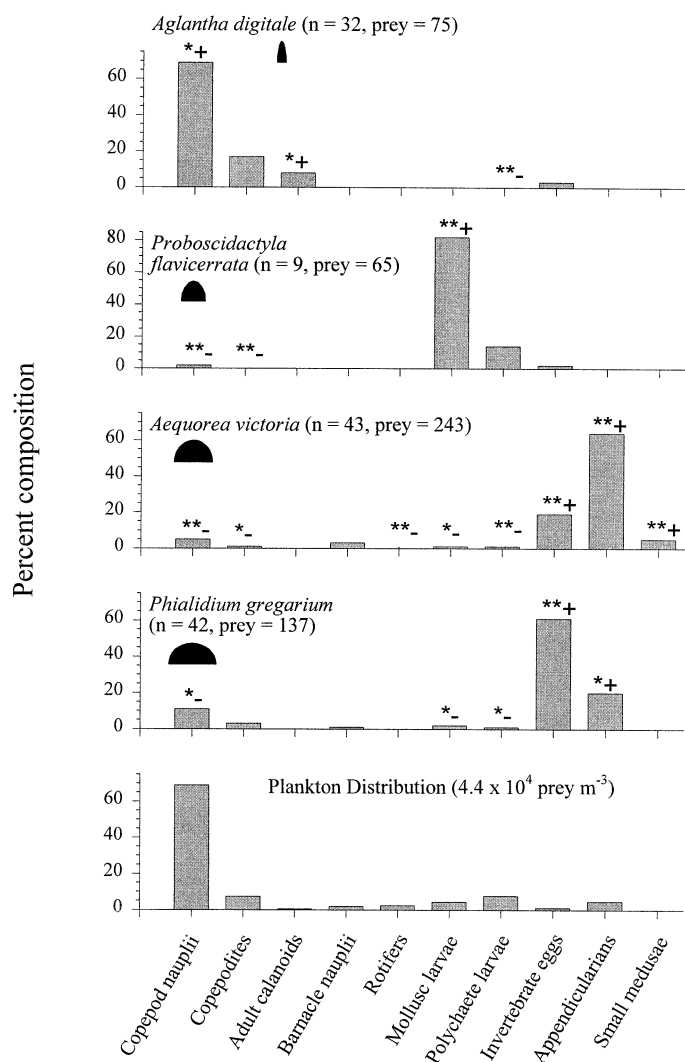
Fig. 4. The percentage taxonomic composition of plankton and diets of hydromedusae collected on 2 July 1993. Symbols as in Fig. 2.

(Fig. 3), but the pattern was not significant. Other prey types, particularly copepod nauplii, were uncommon in the diet and were characterized by negative electivity values (Fig. 5).

Selection data for *A. digitale* was more limited than for other hydromedusan species because of its absence from all but one of the sample dates. On that date (2 July 1993), *A. digitale* consumed primarily copepod nauplii but also smaller numbers of copepodites, adult copepods, and some invertebrate eggs (Fig. 4). Electivities were positive for these prey types but negative for all others (Fig. 5).

Dietary diversity and overlap—Although the types of prey consumed were not the same for all medusan genera, dietary diversity (Fig. 6) was not significantly different between any of the medusae studied (analysis of variance, $P > 0.38$). Thus, diet composition, but not diversity, varied significantly among medusan species.

The diversity of hydromedusan diets entailed dietary overlap between some hydromedusan species. Diets of the oblate (bells flattened or disc-shaped) species, *A. victoria, M. cellularia,* and *P. gregarium,* overlapped (Fig. 7) because all three species fed simultaneously on appendicularians and invertebrate eggs. Dietary overlap between the oblate species was reflected in their high proportional similarity indices (Table 1). In contrast, the prolate (bells streamlined) species (*A. digitale, S. tubulosa,* and *P. flavicirrata*) overlapped little in diet composition either between themselves or with oblate species (Table 1). Instead, the prolate species utilized distinctly different components of the available prey spectrum (Fig. 7).

Identification of dietary niche patterns—Each hydromedusan species was characterized by distinctive selection patterns which were generally replicable between sample dates. The exception to this was *A. digitale,* for which there was no replication because we had data for only a single sample date. The sum of both positive and negative selection patterns of each hydromedusan species form the outline of its dietary niche (Fig. 7). A comparison of dietary patterns found in this study with data from other studies (Table 2, Fig. 7) indicates that the dietary patterns of each species are remarkably consistent over time (multiple years) and space (a variety of North American northwest Pacific locations). This suggests that although the proportional contribution of specific prey types to the diet may vary for hydromedusae between locations, the general patterns of prey selection found in the current study represent reasonable estimates of dietary niches for these species in this region. Additionally, the general similarities of dietary niche patterns among studies indicates that several methods of medusan collection (via hand collection in this study, Purcell 1990 and Mills 1995 but via nets in Larson 1987*a*) yield similar results.

Bases of hydromedusan dietary niche patterns—Diets of individual hydromedusan species are governed by the mechanical traits governing a medusa's predatory process (Purcell 1997). These mechanical traits paralleled taxonomic grouping of the hydromedusae we considered. *A. victoria, M. cellularia,* and *P. gregarium* are all members of the subclass Leptomedusae (Bouillon and Boero 2000). Prey encounter with these medusae is functionally dependent on entrainment of slowly moving prey (e.g., eggs or appendicularians in their houses) in feeding currents created while the medusae "row" through the water (Colin and Costello 2002). Additionally, the nematocyst arrays of these medusae favor successful capture of soft-bodied prey. The leptomedusae possess nematocysts termed "mastigophores" and "isorhizas" that effectively penetrate soft-bodied prey (Purcell and Mills 1988). The pronounced selection of eggs and appendicularians by these medusae reflects their bias toward encounter and capture of soft-bodied prey. Similarities in dietary selection of the leptomedusan species resulted in substantial overlap of their dietary niches (Fig. 7). Dietary overlap of ≥70% has been viewed as resulting in direct competition for food resources when the latter are limited (Stiling 1996).

Dietary niche patterns of the more prolate medusae contrasted sharply with the oblate leptomedusae. *A. digitale* (subclass Trachymedusae), *S. tubulosa* (subclass Anthome-
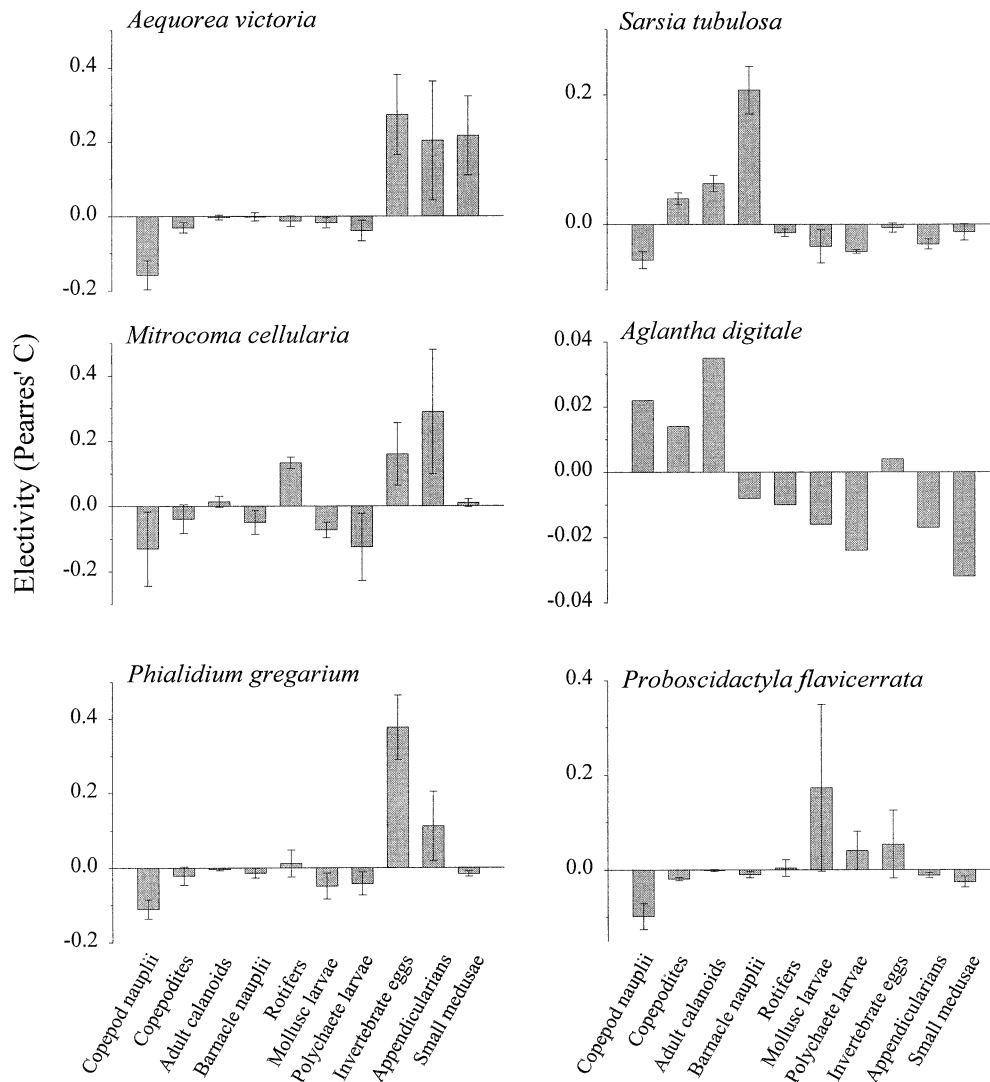
Fig. 5. Average electivity indices (Pearre's *C*) for hydromedusae over the dates for which the individual species were present during sampling. Error bars represent standard deviation of the mean value of Pearre's C.

dusae), and *P. flavicirrata* (subclass Limnomedusae), swim primarily via jet propulsion (Colin and Costello 2002) and prey encounter occurs via ambush of active prey that swim into the outstretched tentacles of non-swimming, drifting medusae (Mills 1981*b*). The nematocyst arrays of these hydromedusae complement their ambush foraging modes. These species possess nematocysts termed "stenoteles" and "euryteles," which penetrate tough exterior surfaces, or "desmonemes," which adhere to surfaces too difficult to penetrate (Purcell and Mills 1988). As a consequence of their ambush predatory modes and the retention characteristics of their nematocyst arrays, these medusae are more likely to retain the mobile crustaceans and spined or shelled larvae that swim into the tentacles. The closely spaced tentacles of *A. digitale* (Fig. 1) favor retention of small, motile prey, whereas the fewer, more widely spaced tentacles of *S. tubulosa* are more suitable for capture of larger crustacean prey. The mechanisms favoring retention of ciliated prey by *P.*

flavicirrata have not been determined, but the possession of numerous, closely spaced tentacles (Fig. 1) covered with desmonemes (Purcell and Mills 1988) probably contribute to capture success of those prey.

Implications of hydromedusan dietary niche patterns for the planktonic community—Conceptual illustration of hydromedusan dietary niches emphasizes that not all components of the planktonic community are used equally by hydromedusae (Fig. 7). In fact, important disparities in resource use characterized predation by this group of hydromedusae. We can use the feeding guild concept to illustrate these disparities. The term "guild" was initially intended to describe a group of species that fed on the same resources in a similar way (Root 1967). Although the hydromedusan species examined here all consume planktonic prey, feeding mechanisms and prey composition are not uniform among all the medusae. Perhaps because of mechanical constraints on prey
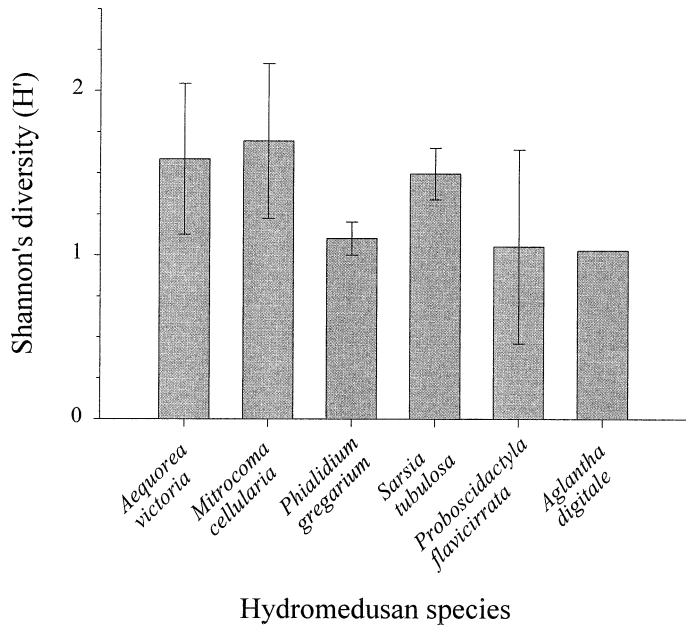
Fig. 6. Taxonomic diversity of hydromedusan diets as based on Shannon's H' index. Error bars represent standard deviation of the mean value of Shannon's H'.

capture, diets of the oblate medusan predators were similar (PS $\geq$ 67% for comparisons of *A. victoria, M. cellularia,* and *P. gregarium;* Table 1), and these species can be considered to make up a flow-based medusan guild preying on soft-bodied zooplankton. However, the prolate, ambush-foraging medusae partition the prey spectrum such that their diets overlap minimally (PS $\leq$ 37% for comparisons between these species and any hydromedusae examined; Table 1). A minimum dietary overlap of 50% has been suggested for association of species as a guild (Jaksic and Delibes 1987). Consequently, the prolate species do not constitute a feeding guild among themselves or with the oblate, cruising medusae. Their low dietary overlap values imply a low probability that the prolate genera experience competition for prey resources from each other or the oblate medusae.

What are the consequences of uneven predatory pressure due to guild and nonguild feeding by sympatric hydromedusan predators on the planktonic community? We would expect that planktonic prey that are not the primary target of a hydromedusan feeding guild, such as crustacean prey, would experience less predation pressure than prey that are. Peak selection patterns of the medusae indicated that most of the crustacean prey were positively selected by relatively few of the hydromedusae. Copepods, despite their numerical and biomass dominance, were primary targets of predation by only two (*A. digitale,* and *S. tubulosa*) out of six of the hydromedusae examined. Copepod nauplii were significantly negatively selected by all hydromedusae with the exception of *A. digitale.* Larson (1987*a*) believed that copepod nauplii were absent from the diets of gelatinous predators in Saanich Inlet, British Columbia, because the nauplii were too small to cause sufficient stimuli for cnidarian nematocyst discharge. In that study, copepods formed a dominant part of the diet of only one hydromedusa—*Sarsia princips.* As a
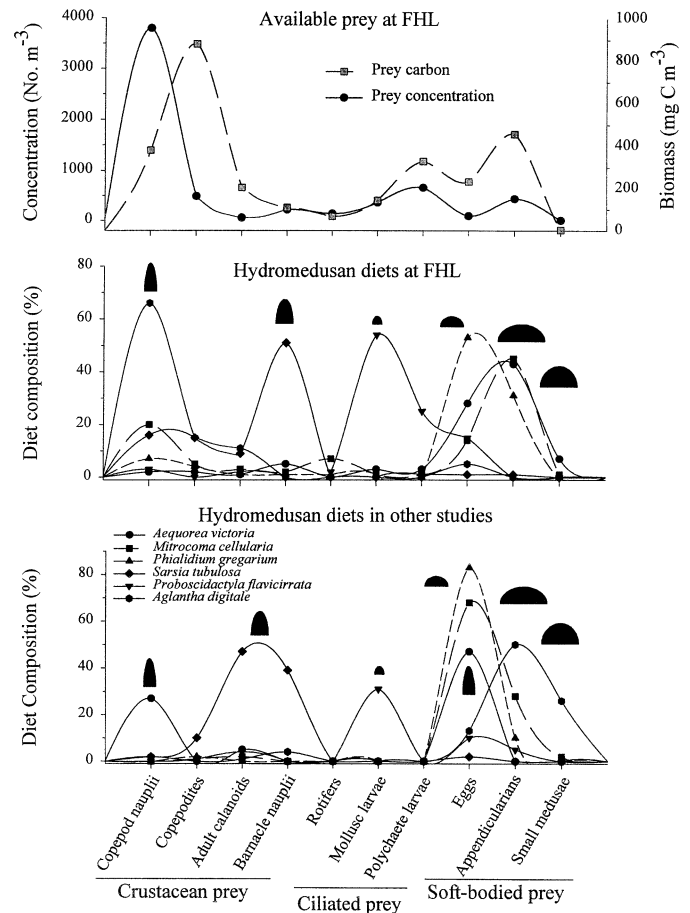

Fig. 7. Conceptual comparison of prey availability and medusan dietary niches. Prey categories are class variables of discrete levels, and magnitudes of prey types are connected by a smoothed curve to emphasize the comparative dimensions of the dietary niches. Friday Harbor Laboratories (FHL) prey concentrations (top panel) were based on net tow data taken in association with diet data of FHL hydromedusae. Biomass estimates combined prey concentrations with literature values (Ikeda 1974; Larson 1987*a*) for carbon content of individual taxa. Dietary data for FHL hydromedusae (middle panel) represent averages of all sample dates presented individually in Figs. 2–4. Bell shapes indicate species as in Figs. 2–4. Dietary niche patterns found in other studies (lower panel) represent average diet compositions of hydromedusae based on other studies (Table 2) of the same species in northwest Pacific waters of North America. FHL prey concentration and biomass do not apply to hydromedusan dietary niche patterns of other studies.

Table 1. Percentage similarity in the diets of hydromedusae from Friday harbor, WA.

Species	M. cellularia	P. gregarium	S. tubulosa	P. flavicirrata	A. digitale
A. victoria	72	75	13	17	8
M. cellularia		67	23	15	22
P. gregarium			15	16	14
S. tubulosa				5	37
P. flavicirrata					7

Table 2. Percentage of ingested prey composition from comparative studies from the northwest Pacific, North America containing relevant hydromedusan dietary data. Source locations for the data were Saanich Inlet, Canada (Larson 1987*a*), variable locations ranging from Friday Harbor, WA, to southern British Columbia (Purcell and Mills 1988), Vancouver Island, Canada (Purcell 1990), Friday Harbor, WA, region (Mills 1995; this study).

Medusa	Copepod nauplii	Copepodites	Adult calanoid	Barnacle nauplii	Rotifers	Mollusc larvae	Polychaete larvae	Eggs	Appendicularian	Small medusae	Reference
A. victoria	—	—	2	12	—	—	—	49	35	—	Purcell (1990)
	—	—	—	—	—	—	—	—	—	90	Mills (1995)
	—	—	—	—	—	—	—	—	94	—	Larson (1987*a*)
	7	—	—	2	—	—	—	5	71	12	Purcell and Mills (1988)
	2	2	1	5	—	3	3	28	43	7	This study
M. cellularia	—	2	—	—	—	—	—	98	—	—	Larson (1987*a*)
	—	—	3	—	—	—	—	39	55	3	Purcell and Mills (1988)
	20	5	3	2	7	1	1	14	45	1	This study
P. gregarium	—	3	—	—	—	—	—	94	2	—	Larson (1987*a*)
	—	3	—	—	—	—	—	95	1	—	Larson (1987*a*)
	—	3	—	—	—	—	—	94	2	—	Larson (1987*a*)
	—	—	2	—	—	—	—	60	36	—	Purcell (1990)
	—	—	—	—	—	—	—	71	11	—	Mills (1995)
	7	4	1	1	1	1	—	53	31	—	This study
S. tubulosa	—	29	67	—	—	—	—	3	—	—	Larson (1987*a*)
	3	—	13	84	—	—	—	0	—	—	Purcell (1990)
	3	—	61	32	—	—	—	3	—	—	Purcell and Mills (1988)
	16	15	9	51	—	—	1	1	1	—	This study
P. flavicirrata	—	3	11	—	—	39	—	30	14	—	Larson (1987*a*)
	1	—	—	1	—	28	—	—	—	—	Purcell (1990)
	—	—	—	—	—	25	—	—	—	—	Purcell (1990)
	3	—	2	—	2	54	25	15	—	—	This study
A. digitale	—	1	5	—	—	—	—	94	—	—	Larson (1987*a*)
	10	—	10	—	—	—	—	20	—	—	Purcell (1990)
	71	—	—	—	—	—	—	27	—	—	Mills (1995)
	66	15	11	—	—	—	—	5	—	—	This study

result, studies that have carefully quantified the predatory impact of hydromedusae on copepods have concluded that, under most field conditions, hydromedusae do not exert significant predatory impact on copepod populations (Daan 1986).

The predatory impact of the flow-based medusan guild focused on the soft-bodied fraction of the zooplankton. The leptomedusae all showed highly significant selection for invertebrate eggs and appendicularians and selection peaks of those medusae centered on these soft-bodied prey. Additionally, *A. digitale* and *P. flavicirrata* consumed invertebrate eggs in this and other studies from the same geographical region (Fig. 7). No hydromedusan species in our study significantly negatively selected invertebrate eggs. The consequences of these prey selection patterns are profound when considered in light of prey availability.

The soft-bodied fraction of the plankton is a substantially more limited food resource, both in terms of prey concentration and total carbon availability, than the crustacean component of the zooplankton (Fig. 7). Consequently, strong predatory selection by a guild of hydromedusae may substantially affect field populations of soft-bodied prey. For example, herring (*Clupea harangus pallasi*) eggs and early-stage larvae are vulnerable to predation by *A. victoria* (Purcell et al. 1987), and hydromedusan predation can be a major source of mortality for field populations of these larvae (Purcell and Grover 1990).

Strong predation pressure on a prey fraction of limited availability can also result in competition among predators for the finite prey resource. These are the essential conditions—use of similar prey resources when they are limiting (Polis et al. 1989)—that would be expected to foster intraguild predation among medusae (Purcell 1991*a*). In fact, *A. victoria* frequently consumes other hydromedusae including *P. gregarium* (Purcell 1991*b*). *P. gregarium* were also found in *M. cellularia* guts (Costello and Colin unpubl. data). Additionally, we witnessed *A. victoria* consuming *M. cellularia* in situ. The highest contribution of medusae to the diet of *A. victoria* in this study occurred on the 9 July 1992 sampling date (Fig. 3), when other soft-bodied prey were at the lowest concentrations in this study.

Interspecific interactions among hydromedusae reflect feeding guild associations. Whereas intraguild predation is very pronounced among the flow based hydromedusan predators, it is not characteristic of ambush hydromedusan species that are not members of a feeding guild. None of the prolate, jetting species (*A. digitale, S. tubulosa,* and *P. flavicirrata*) have been noted as predators on other hydromedusae (Purcell 1991*a*). From this perspective, intraguild predation may be viewed as an adaptive response by the

flow-based hydromedusan guild to resource competition for soft-bodied prey.

The similarities in flow-based feeding of leptomedusae (Costello and Colin unpubl. data) and several scyphomedusae (Costello and Colin 1995), particularly semaeostome scyphomedusae (Costello and Colin 1994), indicate that patterns found in this study may apply to other types of medusae. For example, the semaeostome scyphomedusae *C. quinquecirrha* is known as a copepod predator (Purcell et al. 1994), but it can also be an important predator of fish eggs and larvae (Cowan and Houde 1993; Purcell et al. 1994; Suchman and Sullivan 1997) as well as other soft-bodied prey such as ctenophores (Purcell and Cowan 1995) and appendicularians (Suchman and Sullivan 1997). In fact, clearance rates by *C. quinquecirrha* of eggs and ctenophores are substantially higher than those of crustacean plankton such as copepods (Purcell 1997). Consumption of soft-bodied prey yielded high growth rates by ephyral *C. quinquecirrha* and may be of critical importance for growth of ephyrae in natural field conditions (Olesen et al. 1996). Consumption of soft-bodied prey may be similarly important in the life cycles of other semaeostome medusae such as *Aurelia aurita* (Matsakis and Conover 1991; Sullivan et al. 1994) and *Cyanea capillata* (Båmstedt et al. 1997). Intraguild predation also occurs frequently among semaeostome scyphomedusae (Purcell 1991*a*) and is evident within in situ feeding results of these medusae (Hansson 1997).

These relationships among functional morphology, dietary niches, and guild associations of medusae indicate that fundamental ordering principles underlie trophic patterns involving medusae. More detailed empirical investigations into the integration of medusan functional morphology and trophic ecology will be necessary to bring these ordering principles into clearer focus.

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