Journal of Plankton Research, 2024, **00**, 1–7
https://doi.org/10.1093/plankt/fbae044
Original Article

OXFORD

Unravelling Plankton Behaviour: A Tribute to Rudi Strickler's Legacy and Innovations

High prey capture efficiencies of oceanic epipelagic lobate and cestid ctenophores

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Corresponding editor: Marja Koski

ABSTRACT

Ctenophores are numerically dominant members of oceanic epipelagic communities around the world. The ctenophore community is often comprised of several common, co-occurring lobate and cestid genera. Previous quantifications of the amount of fluid that lobate ctenophores entrain in their feeding currents revealed that oceanic lobates have the potential for high feeding rates. In order to more directly examine the trophic role of oceanic lobate ctenophores, we quantified the encounter and retention efficiencies of several co-occurring species (*Bolinopsis vitrea, Ocyropsis crystallina, Eurhamphea vexilligera* and *Cestum veneris*) in their natural environments. Encounters and predator–prey interactions were video recorded in the field using specialized cameras and SCUBA techniques. The lobate species encountered, on average, 2.4 prey per minute and ingested 40% of these prey. This translated to an estimated ingestion rate of close to 1 prey per minute. *Cestum veneris* and most of the lobate species retained prey as efficiently as the voracious coastal lobate predator *Mnemiopsis leidyi*, suggesting that these oceanic species have a similar predation impact in their environments as *M. leidyi* does in coastal ecosystems. Hence, quantified *in situ* predatory-prey interactions indicate that epipelagic ctenophores have a significant impact on oceanic ecosystems worldwide.

KEYWORDS: ctenophores; suspension feeder; retention efficiency; zooplankton

INTRODUCTION

Lobate and cestid ctenophores are ubiquitous in epipelagic zones throughout world's oceans. Despite their global and often numerically dominant distributions, there have been few studies that have attempted to assess their trophic ecology. As a result, ctenophores are often lumped in with "jellyfish" in ecological and carbon flux models of the mixed layer. However, it has been shown that the coastal lobate ctenophore, *Mnemiopsis leidyi*, has a significantly greater trophic impact than medusae (Colin *et al.*, 2015) and recent studies on oceanic lobate species suggest that they may be capable of removing prey at similar rates to *M. leidyi* (Cordeiro *et al.*, 2022; Potter *et al.*, 2023). Therefore, understanding the feeding ecology of oceanic lobate and cestid ctenophores will affect our understanding of the trophic ecology of the epipelagic zone and predictions about the fate of carbon in the epipelagic mixed layer.

The feeding rates of feeding-current predators like lobate and cestid ctenophores are determined by the volume of fluid they process (termed F_{max}) and the efficiency of prey retention from that fluid. Lobate ctenophores produce a slow, laminar and continuous feeding current that transports fluid and entrained prey past sensory and capture surfaces (Colin *et al.*, 2010). The feeding current of *M. leidyi* is largely undetectable by even the most sensitive zooplankton prey such as copepods. However, the sensory auricles, and other unidentified sensory structures, are able to scan the feeding current for prey (Colin *et al.*, 2015). As a result, *M. leidyi* is able to capture prey with high efficiency (Colin *et al.*, 2015). This sensory-scanning strategy of *M. leidyi* elevates its trophic impact above the impact of medusae and enables it to have dramatic impacts on zooplankton communities in coastal ecosystems (Costello *et al.*, 2006; Daskalov *et al.*, 2007; Dinasquet *et al.*, 2012; Tiselius and Møller, 2017).

Oceanic ctenophores have been much less studied than *M. leidyi* because oceanic species are much less accessible (Jaspers *et al.*, 2023). However, a few recent studies of oceanic lobate ctenophores have suggested that oceanic species possess similar feeding mechanisms to *M. leidyi* and likely feed at rates comparable to *M. leidyi* (Cordeiro *et al.*, 2022; Potter *et al.*, 2023). The co-occurring and globally distributed species *Bolinopsis vitrea, Ocyropsis crystallina, Eurhamphea vexilligera and Leucothea multicornis* produce feeding currents with similar stealthy, continuous hydrodynamic traits as *M. leidyi* (Cordeiro *et al.*, 2022). In addition, all of the oceanic species process fluid at a similar rate to *M. leidyi* and some species, such as *O. crystallina* and *E. vexilligera*,

Received: February 2, 2024. **Editorial decision:** August 2, 2024. **Accepted:** August 11, 2024

process more fluid because of their more rapid swimming speeds. The behavior and hydrodynamics of these species suggests that they may feed at rates similar to *M. leidyi*. Indeed, a study on *Ocyropsis* spp. demonstrated that *Ocyropsis* captures prey with high efficiency and at rates comparable to *M. leidy* (Potter *et al.*, 2023).

In order to determine whether the high fluid processing rates of oceanic ctenophores result in high ingestion rates, we quantified the retention efficiencies of several co-occurring oceanic lobates feeding in their natural field environment. The species included were the lobates, *B. vitrea, O. crystallina, E. vexilligera,* and the cestid, *Cestum veneris.* We did this by measuring feeding interactions of oceanic ctenophores in their oceanic environments using SCUBA combined with *in situ* high-speed imaging. Based on these interactions, we were able to evaluate the success rate of ctenophores at each stage of the feeding process from encounter through ingestion.

METHODS

Ctenophore-prey interactions were obtained from video collected by SCUBA diving in the epipelagic zone (upper 20 m) in oceanic waters off of West Palm Beach, FL (26^0 43′ 93" N, 79^0 59′ 15" W) and Kona, HI (19° 40′ 10.5" N, 156° 02' 46.4" W). The interactions were quantified from video recordings of undisturbed individuals in the water column using high-resolution 4 K video cameras (Sony AX100 and Z-cam E2-M4) with brightfield collimated light optical systems (Townsend *et al.*, 2020; Colin *et al.*, 2022) with a field of view of ~12 cm × 7 cm. The collimated light systems allowed resolution of small zooplankton prey and details of ctenophore anatomy (Colin *et al.*, 2022). The brightfield system used a white light source which likely attracted prey to the field of view at night. This has the potential to artificially increase the number of prey encounters for sequences taken at night and resulted in overestimation of ingestion rates. However, a comparison between daytime and nighttime encounter rates for *C. veneris* and *E. vexilligera* (the only species were we used nighttime sequences) showed that encounter rates during the day were not significantly different from nighttime rates (T-test, $P > 0.2$). Individual ctenophores were followed in the field and recorded for different durations ranging from 1 to 10 min. A total of 29.6 hrs of interactions were examined for four lobate species, *E. vexilligera* ($n = 26$ individuals; Fig. 1A), *O. crystallina* ($n = 33$ individuals; Fig. 1B), *B. vitrea* ($n = 12$ individuals; Fig. 1C) and *C. veneris* ($n = 28$ individuals; Fig. 1D). The sizes of the analyzed lobate ctenophores were relatively small, ranging from 2 to 4 cm, to ensure that we could visualize the whole animal and the surrounding fluid. This size limitation precluded quantification of size effects on ctenophore encounter rates or retention efficiencies. Additionally, we analyzed relatively small *C. veneris* (<20 cm long) because the camera often created hydrodynamic disturbance with larger individuals. Only portions of the bodies of even small *C. veneris* were included in the field of view, therefore, we likely missed encounter events and our estimates of encounter rates for *C. veneris* can be regarded as conservative. While focusing on smaller individual would lead to our encounter rate estimates being conservative because larger individuals would encounter more fluid (Cordeiro *et al.*, 2022), it should not impact our estimates of retention efficiency because it has been shown for the lobate *M. leidyi* that prey selection and prey retention patterns do not change for lobates once they have reached 3 cm (Rapoza *et al.*, 2005). So retention rates we estimate should apply to the full size range of adult ctenophores.

Predator–prey interactions were broken into a series of steps—encounter, contact, capture and ingestion (Fig. 2A)—to determine variations in the predation process among ctenophore species. An encounter occurred when a prey individual was either transported between the lobes, contacted the ctenophore or reacted with an escape jump from a region within the path of the ctenophore. Any prey that touched the surface of the ctenophore was identified as a contact. If the prey stuck to the surface (even for a short duration) then it was considered a capture. Captured prey were followed over time to identify if they were transported to the mouth for ingestion.

Feeding retention efficiency has been defined differently by previous authors, so for this study we defined different retention efficiencies based on the sequential steps (Fig. 2A). Retention efficiencies for individual ctenophores were calculated as ratios of prey proceeding through different stages of the feeding process:

$$\textit{Contact efficiency} = \frac{\textit{number of contacted}}{\textit{number of encountered}}$$

$$\textit{Capture efficiency} = \frac{\textit{number of captured}}{\textit{number of encountered}}$$

$$\textit{Ingestion efficiency} = \frac{\textit{number of ingested}}{\textit{number of encountered}}$$

Only individual ctenophores that were recorded for more than one minute were included in the analysis.

RESULTS

Encounter process and efficiencies

Using SCUBA to observe interactions between planktonic organisms in their natural environment is difficult and time consuming. In order to collect sufficient observations to quantify the interactions, *in situ* encounter events were observed over many days and multiple years. The variability in the composition of the prey field resulted in high variability of the encounter and interaction data. As a result, we did not find statistical differences in any of the rates and efficiencies among the ctenophore species examined (ANOVA, $P > 0.05$ for all comparisons, Fig. S1). However, the data are useful for revealing important capture mechanisms, consistent patterns among species and overall predation process patterns.

Lobate ctenophores beat their ctene rows to swim while also entraining fluid that passes between their outstretched lobes. The three lobate species we examined (*O. crystallina*, *B. vitrea* and *E. vexilligera*) encountered prey by drawing them into the volume between the lobes. In contrast, the cestid *C. veneris* is highly modified so that its streamlined, wing-like body encountered prey while swimming through the water. In the vicinity of the ctenophores (i.e. between the lobes or near the wing for *C. veneris*), many active prey, such as copepods, sensed and reacted to the presence of the ctenophore with an escape jump

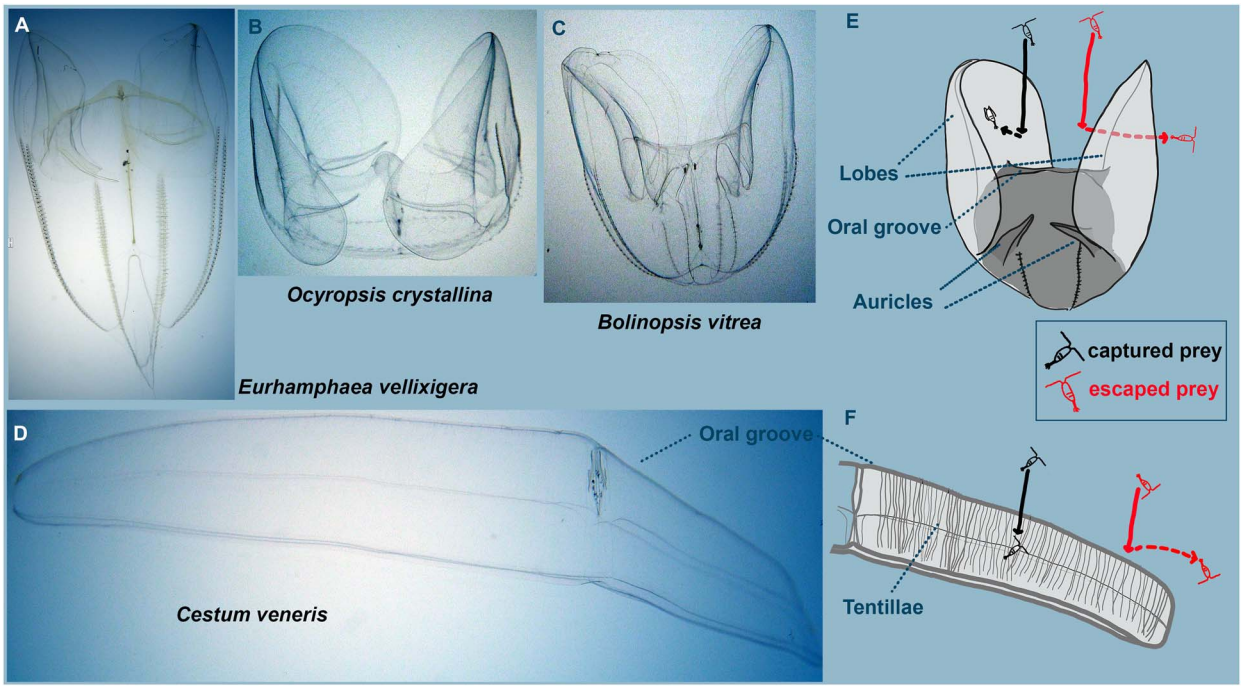

Fig. 1. Oceanic lobate and cestid ctenophores. The lobates studied are (**A**) *E. vexilligera*, (**B**) *O. crystallina*, (**C**) *B. vitrea* and the cestid studied is (**D**) *C. veneris*. (**E** and **F**) is a schematic of the morphology of the lobates (E) and the cestid (F) and examples showing how prey are encountered and captured vs. escape. Note: (F) is only showing half of *C. veneris*.

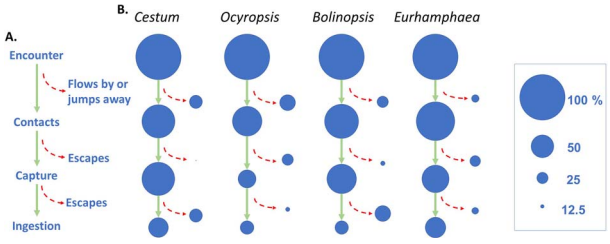

Fig. 2. Overall retention efficiencies of the different ctenophores. (**A**) Events quantified during *in situ* predatory-prey interactions. (**B**) Percent of prey experiencing each event. The diameters of the circles are proportional to the percent. *Cestum veneris* ($n = 28$ individuals), *O. crystallina* ($n = 33$), *B. vitrea* ($n = 12$), *E. vexilligera* ($n = 26$).

(Fig. 1E and F). This jump either resulted in an escape (red copepod, Fig. 1E and F) or in a contact with a capture surface of the ctenophore (black copepod, Fig. 1E and F). In contrast, non-active prey continued to flow past capture surfaces which often (but not always) resulted in contact. Of the prey encountered, between 65 and 83% contacted the ctenophores (Fig. 2, Fig. S1). If contacted, greater than 80% were captured (i.e. stuck to the ctenophore), except *O. crystallina* where only 60% were captured. If captured, greater than 55% were ingested. Overall, the lobate species studied ingested 30–44% of the prey they encountered *in situ* (Fig. 2, Fig. S1).

A closer examination of encounter events for *C. veneris*, *O. crystallina* and *E. vexilligera* demonstrated that at least half of the prey encountered were not ingested because they never came into physical contact with the ctenophore (Fig. 3C). These prey were either able to detect the ctenophore before contact and escape or flowed past all the capture surfaces and were transported safely away without contact (red vs. black copepods, respectively, Fig. 3A). However, for *B. vitrea* most of the prey not captured did make contact but were not able to be retained after contact. Most of prey that were ingested were captured on the lobes (Fig. 3D) of *O. crystallina* (92%), *B. vitrea* (83%) and *E. vexilligera* (95%). A much smaller proportion were captured directly by the tentillae or oral groove. *Bolinopsis vitrea* captured more prey on the tentillae (17%) than *E. vexilligera*. *Ocyropsis crystallina* do not have tentillae so the prey not captured on the lobes were captured directly along the oral groove (8%). Most of the prey ingested by the cestid, *C. veneris,* were captured either directly by the oral groove along the leading edge of the wing or on the tentillae covering the wing surface (Fig. 3B and D). For all species, a majority of the prey captured were ultimately ingested. For example, the proportion of captured prey ingested was greater than 70 and 80% for *C. veneris* and *E. vexilligera* (Fig. 3E).

Encounter and ingestion rates

On average, all four lobate species encountered at least 2 prey min^{-1} and *O. crystallina*, *B. vitrea* and *E. vexilligera* at times were observed encountering > 6 prey min^{-1} (Fig. 4A). If we consider the ingestion efficiencies (ingested/encountered), where the four lobate species ingested 30–44% of the prey they encountered (Fig. 4B), we can estimate the ingestion rates of the different species. We found that lobate and cestid ctenophores ingested 0.82 ± 0.99 ($n = 96$) prey min^{-1} (Fig. 4C). Under some circumstances, *C. veneris*, *O. crystallina* and *E. vexilligera* ingested > 2 prey min^{-1}. However, despite relatively high encounter rates, low ingestion efficiencies limited the maximum ingestion rates observed for *B. vitrea*.

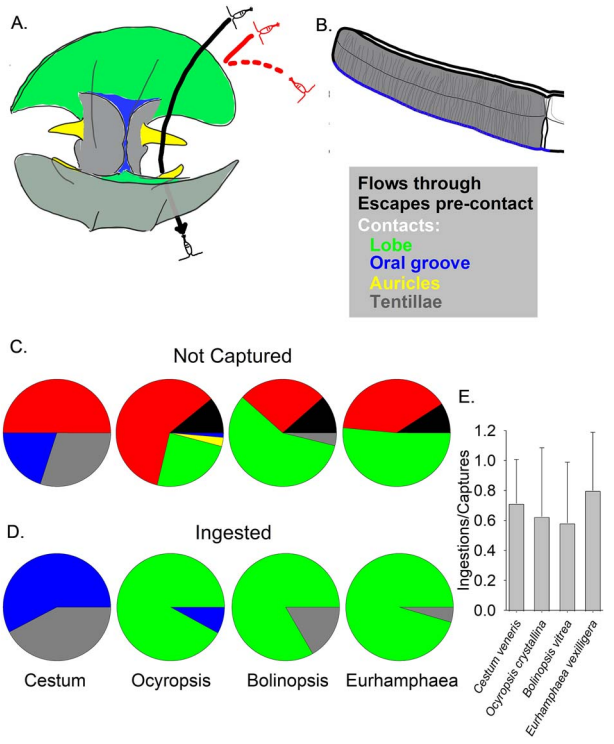

Fig. 3. Encounter and capture locations. (**A** and **B**) Schematic showing what event and capture locations correspond to the different color piece of the pie charts in (**C** and **D**) for the lobates (A) and cestid (B). (C) Events and location of encounters where prey were not captured. (D) Locations where ingested prey were initially captured. (**E**) Proportion of captured prey that were ingested for each species. Note: (B) is only showing half of cestid. N-values are the same as Fig. 2.

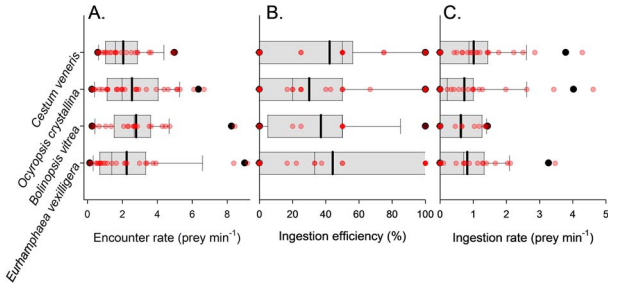

Fig. 4. Encounter (**A**) and ingestion rates (**C**) of different lobate and cestid species. Ingestion rates were calculated by multiplying encounter rates (A) by ingestion efficiencies (**B**) *C. veneris* ($n = 28$ individuals), *O. crystallina* ($n = 33$), *B. vitrea* ($n = 12$), *E. vexilligera* ($n = 26$). Heavy black lines in box plot are means, light lines are medians, error bars are standard deviations. Circles are individual data points.

Comparison among species

The prior results (Figs 2–4) are based on aggregated data from multiple dives with potentially different predator and prey distributions. To more directly compare different species experiencing similar conditions, we compared efficiencies determined for different species sampled during the same dive (Fig. 5). This ensured that the prey fields were the same and differences could be attributed to the ctenophore predatory process. On 15 September 2019, we found for *C. veneris* and

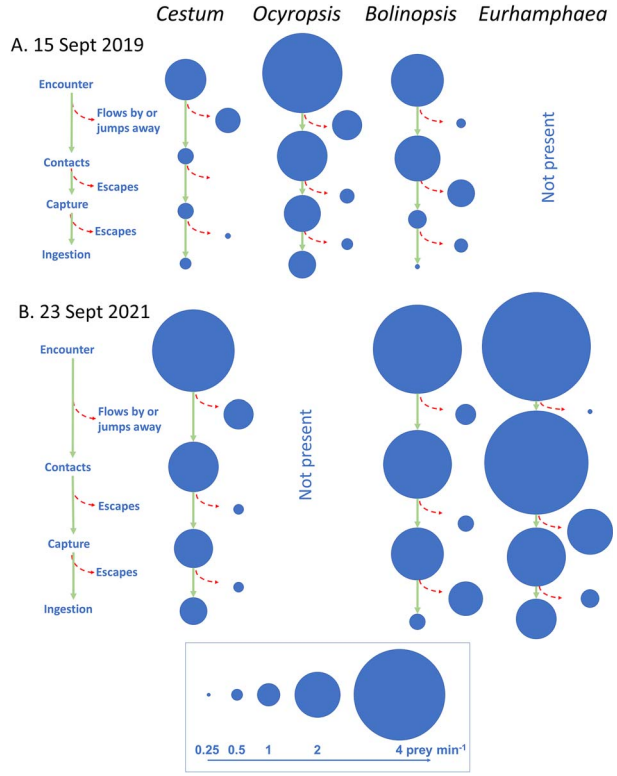

Fig. 5. Outcome of predator prey interactions that occurred on two separate days. The diameters of the circles are proportional to the rates that prey were encountered, contacted, captured, lost and ingested. *E. vellixigera* and *O. crystallina* were not present on (**A**) 15 September and (**B**) 23 September, respectively.

O. crystallina that most prey losses occurred pre-contact and that both species retained most contacted prey (Fig. 5A). This was particularly evident for *C. veneris* (which ingested 71% of the prey it contacted). In contrast, *B. vitrea* contacted most prey but was not as efficient at retaining contacted prey. Consequently, low post-contact retention efficiencies resulted in *B. vitrea* ingesting the least prey on this day and ingesting only 10% of the encountered prey. The high post-contact losses observed for *B. vitrea* on this day were consistent with the averaged observations from Figs 2 and 3.

On 23 September 2021, encounter rates were high for all ctenophores (likely the result of an abundant prey field that day). Again, most prey not ingested by *C. veneris* were lost because they were able to sense and jump away prior to contact. In contrast, losses for both *B. vitrea* and *E. vexilligera* occurred post-contact. *Eurhamphea vexilligera* had the highest ingestion rate on that day due to its high encounter rate (3.9 prey min^{-1}) and relatively high ingestion efficiency (38%). In contrast, *B. vitrea* has the lowest ingestion rate as a result of a low ingestion efficiency of 18%.

DISCUSSION

The inherent difficulty of quantifying the feeding process of delicate oceanic ctenophores has limited estimates of ctenophore feeding rates in the literature. Therefore, little is known about the predatory impact of this guild of epipelagic predators. By observing *in situ* encounter and capture events, we found overall

that oceanic lobate and cestid ctenophores encounter 2.4 ± 1.8 ($n = 96$) prey min^{-1} and are capable of ingesting ~30–44% of the prey they encounter (overall average 40%). Based on this, we estimate that they ingested ~0.8 prey min^{-1}. The only previous study to estimate *in situ* predation rate of an oceanic ctenophore (*O. crystallina)* used gut contents and digestion times and found an ingestion rate of ~0.5 prey min^{-1} (Potter *et al.*, 2023). This is consistent with our estimate for *O. crystallina* of 0.7 prey min^{-1}. At this rate, each ctenophore in the feeding guild consumes ~1200 prey day^{-1}. This predation rate represents the average of our field observations under natural prey conditions occurring in epipelagic waters over 22 days of sampling (spread over 4 years). These data suggest that oceanic ctenophore populations consume much more prey than necessary to meet their metabolic demands (estimated by Kremer *et al.*, 1986), allowing sufficient energy for reproduction and, subsequently, population growth.

Most previous studies examining feeding by oceanic ctenophores have been qualitative and provided descriptions of observed prey capture mechanisms used by lobate and cestid ctenophores. These studies detailed the mechanisms used by each species to capture prey (Hamner *et al.*, 1987; Matsumoto and Hamner, 1988; Matsumoto and Harbison, 1993; Haddock, 2007). They found that lobate ctenophores swim through the water column and prey are encountered when the ctenophore either approach prey or use their feeding current to draw them into the volume between the oral lobes. At this point, reactive prey generally sense the ctenophore and jump into the surrounding lobes or non-reactive prey are transported past the sensory auricles and into the tentillae. Our quantitative observations confirmed that the vast majority of captures (>80%) by lobate ctenophores occurred on the lobes. These capture mechanisms are very similar to patterns of *M. leidyi* feeding on reactive and passive prey (Costello *et al.*, 1999; Waggett and Costello, 1999; Colin *et al.*, 2015). Furthermore, we also found that *E. vexilligera* and *O. crystallina* relied primarily on the motions of their auricular ctenes to startle prey into their lobes while *B. vitrea* captured more prey on their tentillae. *Bolinopsis vitrea* also had consistently lower retention efficiencies which likely explains why it generally consumes smaller prey (Kremer *et al.*, 1986). Despite the absence of tentillae or colloblasts, *O. crystallina* was able to retain 63% of the prey that were initially captured. Our retention efficiencies from the field were similar to previous laboratory estimates (Potter *et al.*, 2023).

Less has been described for how cestid ctenophores capture prey (Harbison *et al.*, 1978; Stretch, 1982). Lacking lobes, cestids are essentially stealthy hydrofoils encountering prey transported along their streamlined surfaces as the ctenophore swims through the water. *Cestum veneris* encountered prey at rates similar to lobate species, however, their post contact retention efficiencies were higher than the lobates and this enabled *C. veneris* to maintain comparatively high ingestion rates. *Cestum veneris* captured > 70% of the prey that contacted its oral groove or tentillae and appeared to capture prey equally on both upper and lower wing surfaces. We only quantified the encounter events for relatively small *C. veneris* (<20 cm) because of the difficultly in video recording large individuals without disturbing them. Therefore, our estimates are likely highly conservative because *C. veneris* individuals are commonly > 40 cm and can grow to lengths > 1 m. More work is necessary to improve estimates of their trophic impact on epipelagic ecosystems.

The coastal lobate predator, *M. leidyi,* has been shown to be a voracious predator capable of significantly altering coastal pelagic ecosystems (Costello *et al.*, 2006; Daskalov *et al.*, 2007; Dinasquet *et al.*, 2012; Tiselius and Møller, 2017). Its predatory success has been attributed to its ability to stealthily and continuously process large volumes of fluid (Colin *et al.*, 2010), sensory scanning the fluid for prey (Colin *et al.*, 2015) and efficient retention of prey it contacts (Costello *et al.*, 1999; Waggett and Costello, 1999; Colin *et al.*, 2015). The oceanic lobate ctenophores have also been shown to process fluids stealthily and continuously at rates equal to and potentially greater than *M. leidyi* (Cordeiro *et al.*, 2022). In addition, we find that oceanic lobates and cestids were able to ingest 60–80% of captured prey. These rates are similar to capture success rates of *M. leidyi* which retained between 60 and 70% of captured prey in laboratory studies (Costello *et al.*, 1999; Waggett and Costello, 1999; Colin *et al.*, 2015). While little is known about the sensory capabilities of oceanic ctenophores, their demonstrated similarities to *M. leidyi* suggest they also likely sensory scan for prey to increase overall retention efficiencies. Similarities to *M. leidyi* imply that oceanic species may be as effective predators in oceanic waters as *M. leidyi* is in coastal ecosystems.

The predatory capabilities of oceanic ctenophores can influence our understanding of broader material flows in oceanic systems. As a result of their pre- and post-contact retention strategies, oceanic ctenophores ingest 40% of the prey they encounter. Not only do these efficiencies compare to *M. leidyi*, they also compare to the retention efficiencies observed for many fish species (Gemmell and Buskey, 2011; Sommerfeld and Holzman, 2019) and are much greater than those of cnidarian medusae (Colin *et al.*, 2006; Lucas *et al.*, 2013; Nagata *et al.*, 2016; Wagner *et al.*, 2020). Our ingestion efficiency estimates can be used to arrive at a first-order estimate the clearance rate of the different lobate species. The volume of fluid that ctenophores encounter over time (F_{max}) can be estimated by multiplying their swimming speed by the area of the opening between their lobes (Cordeiro *et al.*, 2022). By multiplying size dependent F_{max} values estimated in Cordeiro *et al.* (2022) by our observed ingestion efficiencies (ingested prey/encountered prey), we can estimate feeding clearance rates (Fig. 6). The range of ctenophore sizes in Fig. 6 are derived from the sizes used to estimate F_{max} in Cordeiro *et al.* (2022) but are beyond the limited size range used to estimate ingestion efficiency in the current study. However, this is reasonable for the purposes of this exercise because it has been shown that feeding patterns do not change in lobate ctenophores once they are at least 3 cm long (Rapoza *et al.*, 2005). Comparing the size dependent estimates of lobate clearance rates to the size dependent clearance rates of fish, medusae and crustaceans (based on body carbon) from Acuña *et al.* (2011) we estimate that the high ingestion efficiencies of lobate ctenophores enables them to forage at rates equal to or perhaps greater than most other zooplanktivorous predators (Fig. 6). While we recognize that this "back of the envelope" estimate of the clearance rates of oceanic ctenophores needs

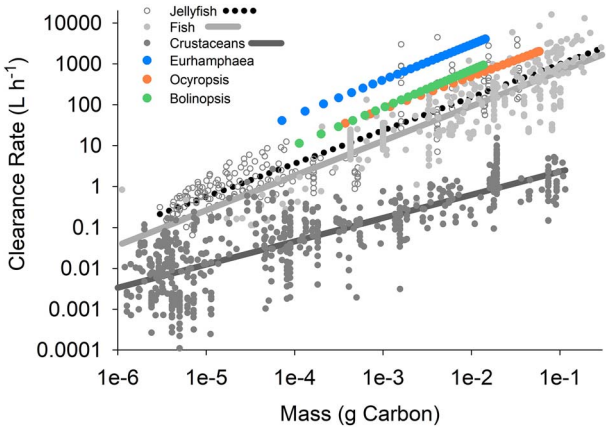

Fig. 6. Clearance rates vs. mass (in g Carbon) for different types of zooplanktivorous predators. Clearance rates of fish, jellyfish and crustaceans are from Acuña *et al.* (2011). Clearance rates of *E. vexilligera*, *O. crystallina*, *B. vitrea* were calculated by multiplying filter rate maxima (F_{max}) taken from Cordeiro *et al.* (2022) by their ingestion efficiency (ingestions/encounters). Lines represent least squares of data.

more extensive confirmation, it demonstrates that the predatory impact of the lobate-cestid feeding guild in epipelagic ecosystems may be much greater than previously considered.

CONCLUSIONS

Quantitative analysis of the interactions of lobate and cestid ctenophores with prey in their natural environment suggest that epipelagic ctenophores encounter and potentially ingest prey at high rates. Therefore, this guild of predators may have a profound impact on oceanic ecosystems worldwide. The species studied here are ubiquitous members of epipelagic oceanic ecosystems globally. Mounting evidence suggests that the oceanic lobate and cestid ctenophores encounter prey at similar rates and retain prey at similar efficiencies as the voracious coastal lobate predator *M. leidyi*. Consequently, it is likely that lobate and cestid ctenophores are highly effective epipelagic predators, comparable in the oceanic realm to the role played by *M. leidyi* in coastal systems. However, in contrast to coastal systems that are typically dominated by one ctenophore species, oceanic systems are often characterized by a guild of ctenophore predators. Therefore, oceanic predation impacts by ctenophores should quantify not only the impact of one species, but the synergistic impact of the entire ctenophore guild. Evaluation of these impacts depends strongly on abundances of oceanic ctenophores. However, distribution data of oceanic ctenophores remain a bottleneck in our understanding because the delicate gelatinous bodies and their resistance to formalin preservation have resulted in a virtual absence of oceanic ctenophore abundance data. This data hole remains a challenge for accurate evaluation of trophic impacts by this widespread planktonic group.

FUNDING

National Science Foundation (OCE-1829913 to S.P.C., OCE-1829945 to B.J.G., OCE-1829932 to K.R.S. and OCE-1830015 to J.H.C.).

DATA AVAILABILITY

The data underlying this article are available in the article, in its online supplementary material and are archived at https://www.bco-dmo.org/project/776095.

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