University of North Carolina Asheville
Journal of Undergraduate Research
Asheville, North Carolina
December 2020

Distribution and Environmental Characteristics of Neustonic Animals

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Abstract

The ocean's surface is a unique environment, characterized by a variety of environmental stressors and high concentrations of organic matter. This environment is home to floating marine organisms, including animals, bacteria, plankton, and algae. The free-living animals of this ecosystem, known as the neuston, are diverse, with a wide variety of adaptations to survive at the ocean's surface. They play important ecosystem roles and connect disparate marine food webs. The first goal of this project was to characterize the distributions of several important neustonic animal genera. To do this, nearly 4,000 observations from dozens of sources were collected, and then generated minimum bounding polygons were generated to outline the ranges in which they occur. After determining these minimum ranges, Bayesian additive regression trees, a new species distribution modeling algorithm, were used to identify the most important environmental correlates to the range of each species. For thirteen of fifteen taxa, temperature range or temperature mean were ranked as the most important variables, corresponding with the finding that the ranges of most neustonic species exhibited variation primarily in latitude, with strong latitudinal upper and lower bounds. These findings correspond with and expand upon the existing literature on the neuston, highlighting the importance of revisiting historical records using new strategies and tools.

1. Introduction

While the open ocean covers nearly half the surface area of our world, we know very little about the ecosystem at its surface. This ecosystem includes cnidarians, gastropods, and insects, and it connects diverse food webs. Free-living species at the surface are known as the neuston. These animals are adapted to near-constant wave action, freshwater inundation via rain, storms, hydrophobic chemicals[1-3], intense UV radiation[4], and ever-shifting locations as they are moved by surface currents and wind. Because animals at the ocean's surface are in near-constant motion, finding them presents major challenges, and we currently have no methods for predicting when and where they occur. The remote habitat of these organisms adds to the difficulty of studying them, as open-ocean vessels are required to access and research them.

Neustonic animals have a host of unusual adaptations, because the sea surface microlayer is an environment that poses unique challenges for the organisms that live there. This environment generally has much higher concentrations of organic matter than the underlying water, which results in the formation of a gelatinous microlayer in the upper 1 mm of the water[1-3,5,6]. This material comes largely from dead organic matter[4]. Large quantities of both biogenic and anthropogenic organic carbon, sometimes including living microorganisms, reach the ocean surface from the atmosphere via rainfall and dry deposition[1,7,8].

The animals that make up the neuston come from a variety of metazoan phyla. Hydrozoan cnidarian genera *Physalia*, *Porpita*, and *Velella* are important components of the neuston[4,9,10]. These three groups are a food source for other neustonic animals such as the nudibranch genus *Glaucus* (blue sea dragons)[9,10] and the gastropod mollusk genus *Janthina*[9-11], as well as for animals such as birds and sea turtles[9-12]. They also serve as a substrate for eggs of the insect genus *Halobates*[9.]

Neustonic animals have a wide variety of adaptations that allow them to remain at the ocean's surface. *Halobates* is the only pelagic ocean insect genus, and it remains at the ocean's surface by utilizing surface tension[9.] *Janthina* produce mucus bubbles that they adhere to, hanging upside down at the ocean's surface for their adult lives[9,11.] *Porpita* and *Velella* have chitinous floats, and *Velella* have chitinous sails which allow them to be propelled by wind[9,13]. *Physalia*, in contrast, have gas-filled pneumatophores, allowing them some control over the degree to which they are propelled by wind[9.]

While neustonic animals are widely distributed at the ocean's surface, they are also ephemeral, being present in some areas of the ocean but not others. Additionally, neustonic animals, particularly hydrozoans, can appear in large 'rafts', reaching extremely high biomass densities[4,9]. The spotty nature of neustonic distributions has made it difficult to determine the exact ranges of these animals. In addition, there is a high degree of variability in the organisms that make up the neuston ecosystem at different latitudes and longitudes[9.] Some neustonic organisms are found at more extreme latitudes, while others are more limited in latitudinal distribution, and others vary in longitudinal distribution as well.

A seminal publication on the neuston was published by A.I. Savilov in 1969 and translated to English in 1970, which details some of the biology and distribution of the neuston in the Pacific Ocean. Savilov found six neustonic eco-regions in the Pacific, each containing unique species combinations[9.] He describes the distribution of the hydrozoan genera *Physalia*, *Porpita*, and *Velella*, as well as those of several species of the marine snail *Janthina* and the insect genus *Halobates*. While these animals are all present in the Pacific Ocean, their ranges vary, and the factors affecting this variation are unclear. In addition, his work only describes the ranges of these animals in the Pacific Ocean.

One of the primary goals of the project is to review existing data on the global distribution of the neustonic animal genera *Glaucus, Halobates, Janthina, Porpita, Physalia,* and *Velella* to generate distribution profiles. We used these distribution profiles to determine the environmental factors affecting the ranges of these animals.

2. Materials and Methods

2.1 Data collection

Data for this project were collected from peer-reviewed literature and museum collection records. Sources were collected via searches of the electronic databases Biodiversity Heritage Library, Google Scholar, the library of the Marine Biological Laboratory, ScienceDirect, Springerlink, and Wiley Online Library. These sources were searched for coordinates, specific descriptive locations, or maps of neustonic animal sightings.

For sightings provided in text form, the genus, species, observer, sighting date, latitude, longitude, literature source, and page number were recorded. Dates were recorded to the greatest accuracy available from the source. For sightings without a date listed, a "before" date was provided corresponding with the publication date of the source. For sources that provided only a locality, the locality was found in Google Maps, and if the described location indicated accuracy to within three decimal places latitude and longitude, the coordinates were recorded. If a description did not provide sufficient specificity, the sighting was discarded.

Many sightings were recorded on maps, most of which were hand-drawn. These data were converted to coordinates using ArcMap 10.6.1. ArcMap was formatted to match the source map as closely as possible in two ways: the ocean basin centered in ArcMap was changed to match the source map, and the projection was chosen that most closely approximated the source map. Either Plate Carree or Robinson projections were used for all sources. Each map was then pasted into ArcMap as a .png file, and control points were used to match the source map to the ArcMap projection. A multipoint shapefile was created for each map, and a point was created for each recorded observation. The shapefile was converted from multipart to singlepart and XY coordinates were added. The coordinates were then converted from the ArcMap default coordinate system to a standard decimal geographic coordinate system. The shapefile data were exported to Microsoft Excel and the genus, species, observer, observation date, and page number of the map were added.

2.2 Minimum Bounding Polygons for Neustonic Species

Data for generation of Minimum Bounding Polygons (MBPs) were compiled into spreadsheets organized by genus or species. Sightings of beach-stranded animals were discarded. The remaining sightings were separated by ocean basin and by northern or southern hemisphere in the Pacific and Atlantic Oceans to resolve taxa with temperate distributions in the northern and southern hemisphere.

Each dataset was imported into ArcMap 10.6.1, and the XY coordinates were displayed to ensure that no stray data points were present outside of the intended ocean basin. For ocean basins with fewer than three observations, individual observations were displayed on the map. The data were then exported to a new shapefile. Then, the ArcMap Minimum Bounding Geometry tool was used to generate a convex polygon encompassing all relevant observations for each ocean basin or hemisphere.

In cases where species identification is well-established (within the genera *Janthina*, *Halobates*, and *Glaucus*) we mapped to species level. However, for *Velella*, *Physalia*, and *Porpita*, numerous synonyms exist in the literature. Currently each of these genera only has one recognized species, but this may not reflect the true phylogeny of these animals. Based on this uncertainty, we labelled the observations of these animals only to genus. For species where there were fewer than three sightings in a given ocean basin, the individual observations are displayed on the map. For several species, the distribution maps generated include areas of land. Though these are strictly marine species, the polygons were not modified to preserve map fidelity. For congeners with distributions coinciding in a given ocean basin, these ranges are displayed on the same maps.

2.3 Embarcadero Distributions Models for Neustonic Species

We gathered environmental data from BIO-ORACLE 2 via sdmpredictors call in the R Package Embarcadero[14.] Environmental factors used for modeling include mean cloud cover, mean phytoplankton concentration, mean current velocity, mean sea surface salinity, mean sea surface temperature, and sea surface temperature range at the location of each recorded observation. Embarcadero uses Bayesian additive regression trees to estimate species distributions and the factors affecting these distributions[14.] No model was generated for *Glaucus mcfarlanei*, because there were only two sightings of this animal and these sightings were geographically close.

Embarcadero operates on the assumption that the observed prevalence in samples is the true prevalence of the species, so for the program to work properly, the number of absences must be equal to the number of presences[14.] For several species, particularly the cnidarians, this would have meant removing a large number of presence observations from the data set. Given the mismatch between absence and presence observations for most species, pseudo-absences were used for all species distribution models.

Embarcadero was also used to generate variable importance plots for each species, which indicate the proportion of splits in the model each environmental trait accounted for[14.]

3. Results

3.1 Data collection

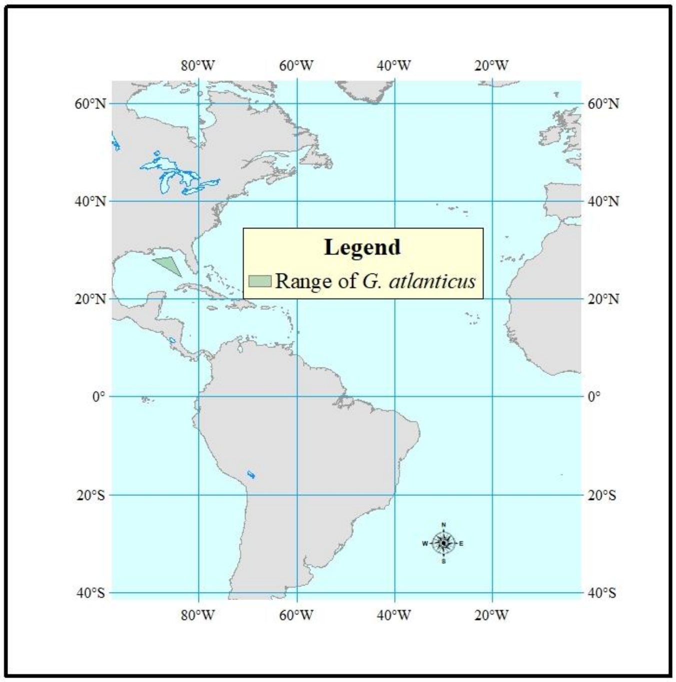
Table 1 displays the number of sightings, the date ranges, and the sources of sightings from scientific literature and the online database GBIF.

Table 1. Numbers of sightings, date ranges, and sources of neustonic animal sightings from scientific literature and GBIF

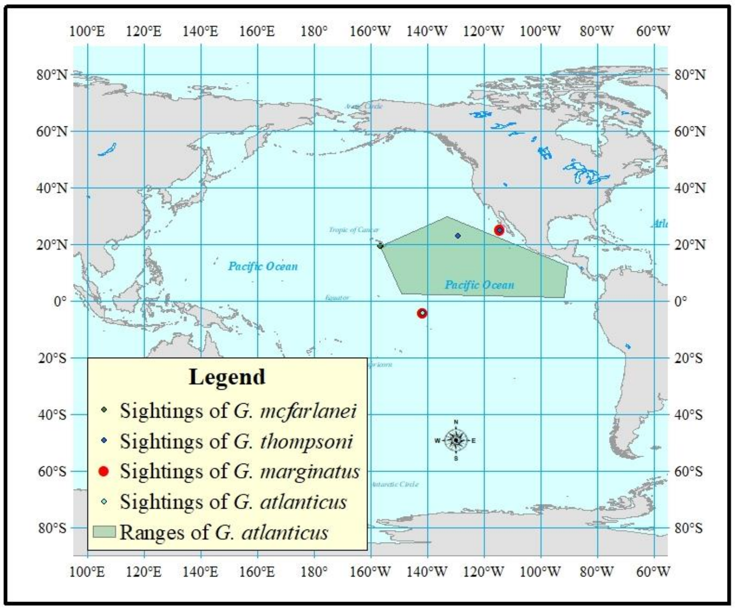
Genus	Species	Number of Sightings	Date Range	Sources
Glaucus	*atlanticus*	19	1976–2014	15-17
	marginatus	4	2014–2017	16,18,19
	thompsoni	2	before 2014	16,20
Halobates	*germanus*	214	1981–2004	21,22
	micans	947	1955–2004	9,21-24
	sericeus	572	1955–2004	9,21,22,25
	sobrinus	132	1979–2004	21,22,26
	splendens	78	1982–2004	21,22,27

Janthina	*exigua*	68	1955–1961	9,11,28
	janthina	399	1955–1988	9,11,29,30
	pallida	72	1953–2017	9,11,31-33,39
	umbilicata	116	before 1975	9,11,34
Porpita		499	1955–2017	9,19,35-42
Physalia		83	1955–2015	9,37,43-47
Velella		734	1886–2017	9,12,29,37,39,48-58

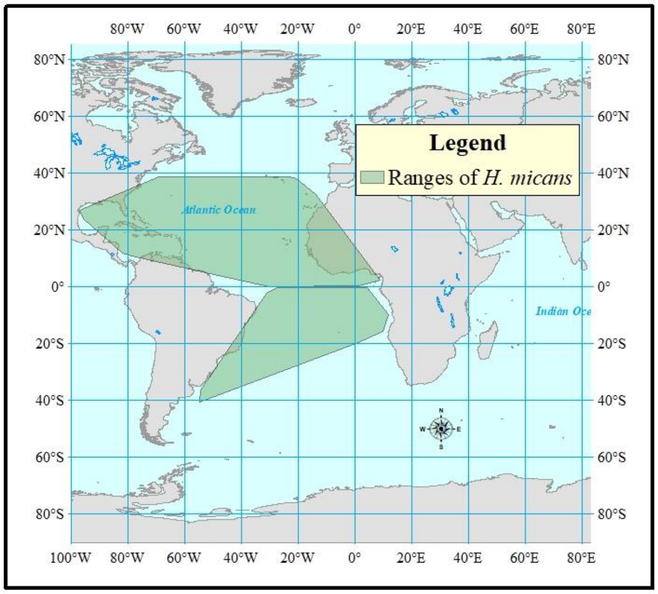
3.2 Minimum Bounding Polygons for Neustonic Species



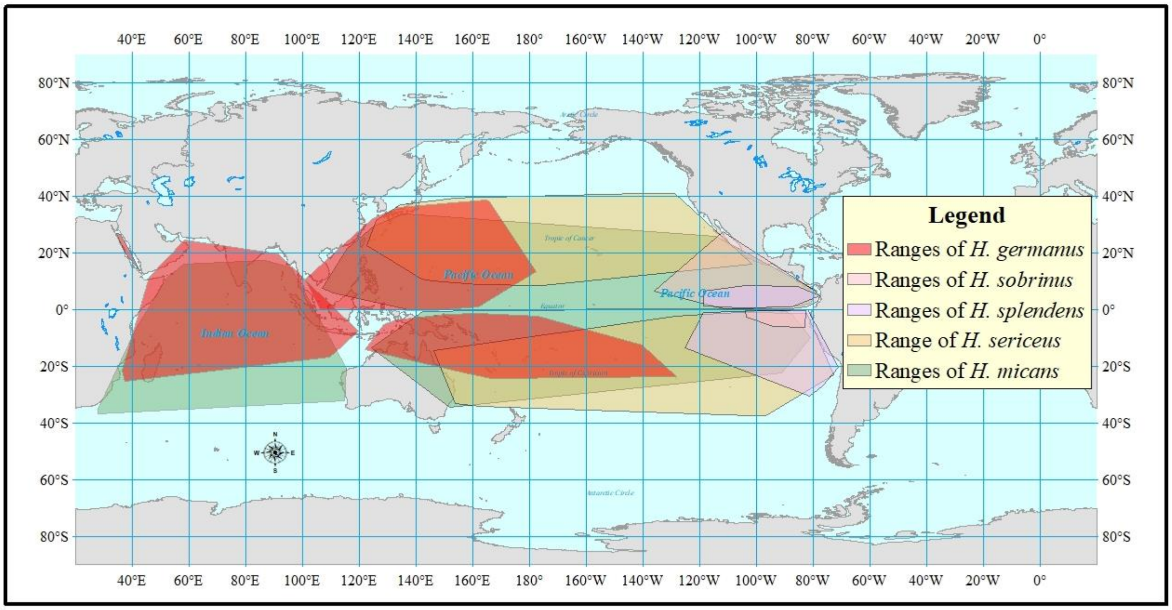
a)


100°E
120°E
140°E
160°E
180°
160°W
140°W
120°W
100°W
80°W
60°W
80°N
60°N
40°N
20°N
0°
20°S
40°S
60°S
80°S
Tropic of Cancer
Pacific Ocean
Pacific Ocean
Equator
Antarctic Circle
N
S
W
E
Legend
Sightings of G. mcfarlanei
Sightings of G. thompsoni
Sightings of G. marginatus
Sightings of G. atlanticus
Ranges of G. atlanticus

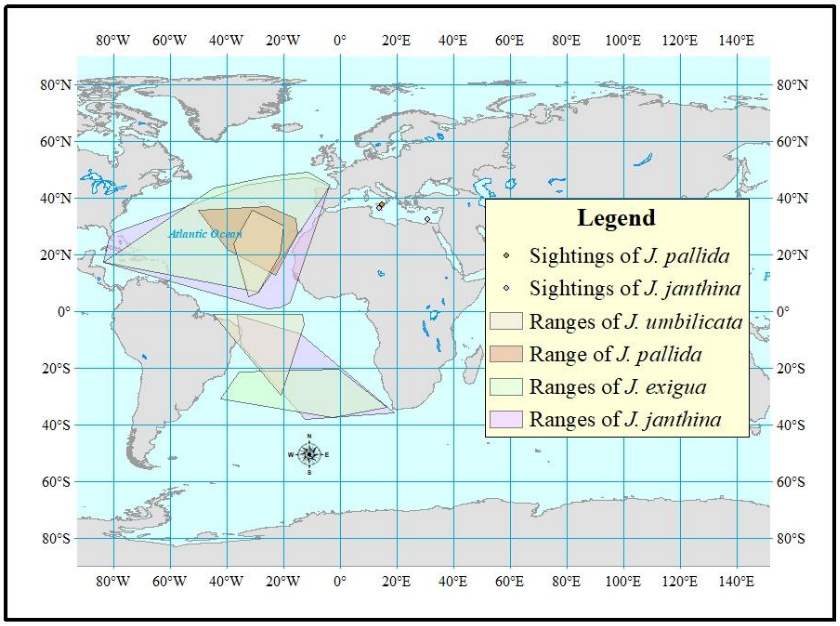
b)


100°W
80°W
60°W
40°W
20°W
0°
20°E
40°E
60°E
80°E
80°N
60°N
40°N
20°N
0°
20°S
40°S
60°S
80°S
Atlantic Ocean
Indian Oce
N
S
W
E
Legend
Ranges of H. micans

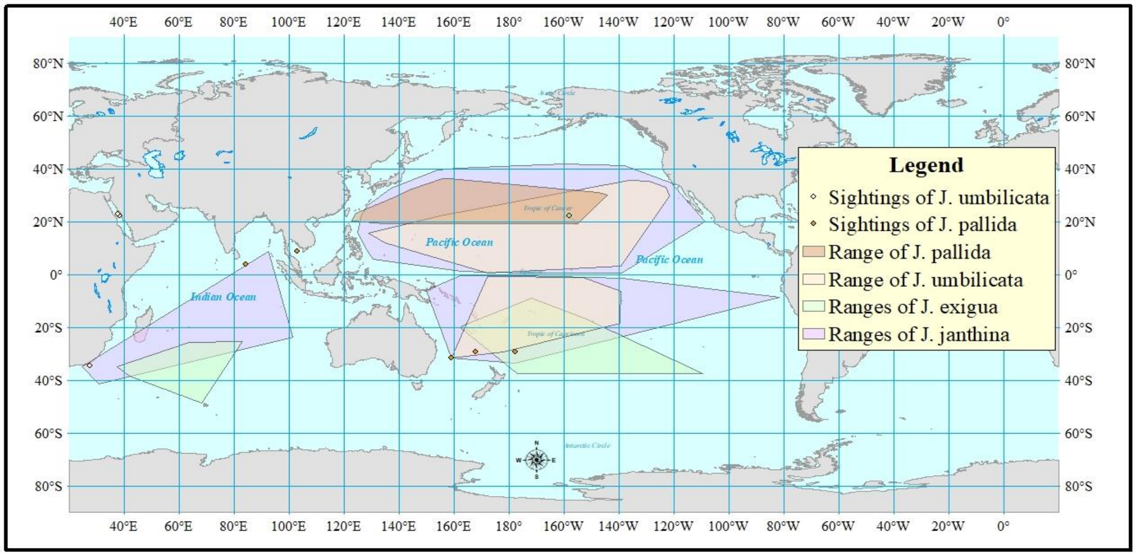
c)


40°E 60°E 80°E 100°E 120°E 140°E 160°E 180° 160°W 140°W 120°W 100°W 80°W 60°W 40°W 20°W 0°
80°N 60°N 40°N 20°N 0° 20°S 40°S 60°S 80°S
Indian Ocean
Pacific Ocean
Pacific Ocean
Tropic of Cancer
Equator
Tropic of Capricorn
Arctic Circle
Antarctic Circle
N
W
E
S
Legend
Ranges of *H. germanus*
Ranges of *H. sobrinus*
Ranges of *H. splendens*
Range of *H. sericeus*
Ranges of *H. micans*

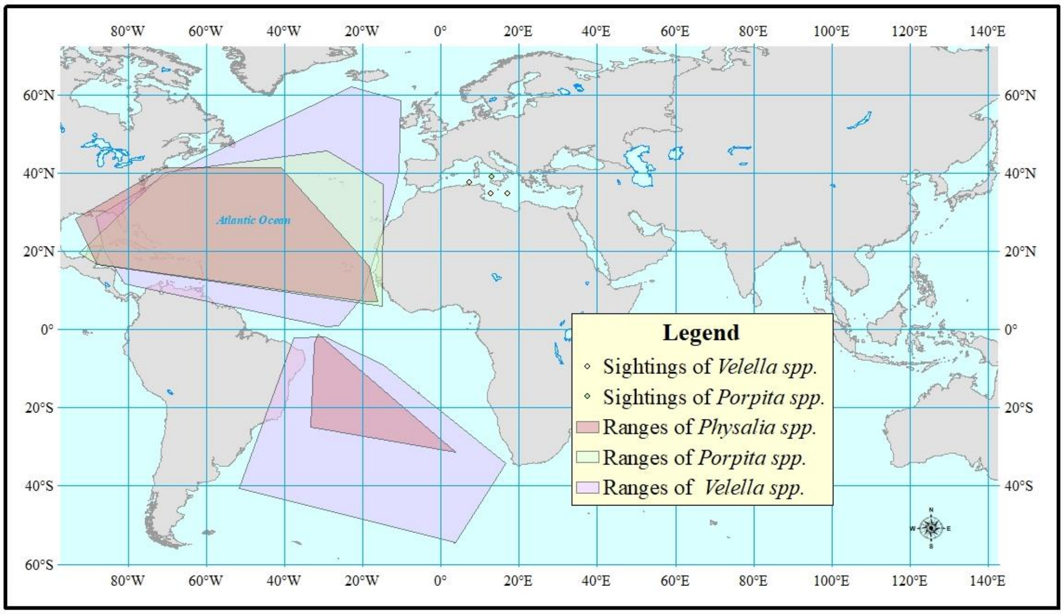
d)


80°W 60°W 40°W 20°W 0° 20°E 40°E 60°E 80°E 100°E 120°E 140°E
80°N 60°N 40°N 20°N 0° 20°S 40°S 60°S 80°S
Atlantic Ocean
N
W
E
S
Legend
Sightings of *J. pallida*
Sightings of *J. janthina*
Ranges of *J. umbilicata*
Range of *J. pallida*
Ranges of *J. exigua*
Ranges of *J. janthina*

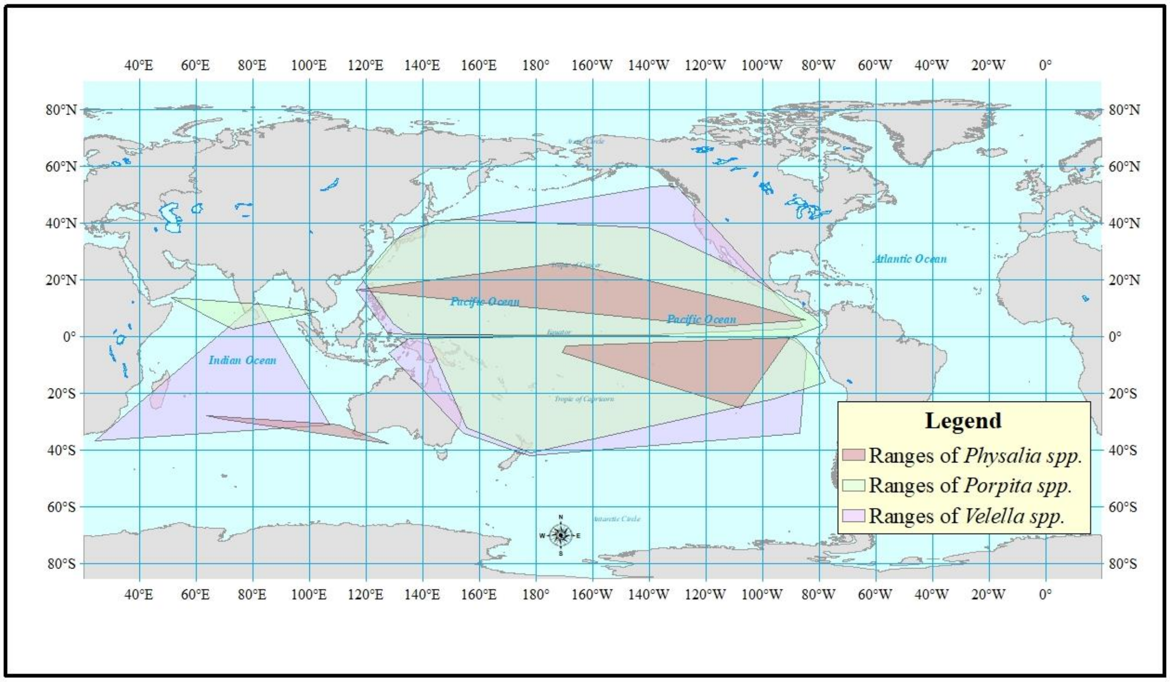
e)


Legend
Sightings of J. umbilicata
Sightings of J. pallida
Range of J. pallida
Range of J. umbilicata
Ranges of J. exigua
Ranges of J. janthina
Pacific Ocean
Pacific Ocean
Indian Ocean
Tropic of Cancer
Tropic of Capricorn
Arctic Circle
Antarctic Circle
40°E
60°E
80°E
100°E
120°E
140°E
160°E
180°
160°W
140°W
120°W
100°W
80°W
60°W
40°W
20°W
0°
80°N
60°N
40°N
20°N
0°
20°S
40°S
60°S
80°S
N
E
S
W

f)


Legend
Sightings of *Velella spp.*
Sightings of *Porpita spp.*
Ranges of *Physalia spp.*
Ranges of *Porpita spp.*
Ranges of *Velella spp.*
Atlantic Ocean
80°W
60°W
40°W
20°W
0°
20°E
40°E
60°E
80°E
100°E
120°E
140°E
60°N
40°N
20°N
0°
20°S
40°S
60°S
N
E
S
W

g)



h)

Figure 1. Minimum bounding polygons and individual observations of neustonic species generated in ArcMap and separated by ocean basin. **(a)** Glaucus atlanticus in the Atlantic Ocean. **(b)** Glaucus atlanticus, G. marginatus, G. mcfarlanei, and G. thompsoni in the Pacific Ocean. **(c)** Halobates micans in the Atlantic Ocean. **(d)** Halobates germanus, H. micans, H. sericeus, H. sobrinus, and H. splendens in the Pacific Ocean, Indian Ocean, and Red Sea. **(e)** Janthina exigua, J. janthina, J. pallida, and J. umbilicata in the Atlantic Ocean. **(f)** Janthina exigua, J. janthina, J. pallida, and J. umbilicata in the Pacific Ocean. **(g)** Physalia spp., Porpita spp., and Velella spp. in the Atlantic Ocean and Mediterranean Sea. **(h)** Porpita spp., Physalia spp., and Velella spp. in the Pacific and Indian Oceans.

Figure 1 displays the MBPs generated in ArcMap for each neustonic species or genus studied.

Only one species of *Glaucus*, *G. atlanticus*, is present in the Atlantic Ocean (Fig. 1(a)). It is present only in a small portion of the Gulf of Mexico. *Glaucus atlanticus*, *G. marginatus*, and *G. thompsoni* are all present in the Pacific Ocean (Fig. 1(b)). There are two sightings each for *G. marginatus* and *G. thompsoni*, one for each species located just off the coast of the Baja California Peninsula. The other sighting of *G. marginatus* is slightly south of the equator near 140° W, co-located with the only southern sighting of *G. atlanticus*. The range of *G. atlanticus* reaches from approximately 160° W to 90° W and from the equator to approximately 30° N in the northern hemisphere. There are only two sightings of *G. mcfarlanei*, both just off the southern coast of Hawai'i.

Of the species in the insect genus *Halobates*, only *H. micans* is present in the Atlantic Ocean, ranging across the ocean longitudinally and to 40° N (Fig. 1(c)). The range of *H. micans* reaches to 40° S in the western Atlantic and to around 20° S in the eastern Atlantic (Fig. 1(c)). Only two *Halobates* species, *H. germanus* and *H. micans*, are present in the Indian Ocean or Red Sea (Fig. 1(d)). *Halobates germanus* is the only species of *Halobates* present in the Red Sea, and it is present throughout most of that sea. *H. germanus* and *H. micans* are present across most of the longitudinal area of the Indian Ocean, with *H. germanus* reaching from around 25° S to 25° N and *H. micans* exhibiting a more southern range from around 35° S to 15° N (Fig. 1(d)). *Halobates germanus* extends slightly further east to 120° E. All five *Halobates* species are present in the Pacific Ocean (Fig. 1(d)). In the Pacific Ocean, *H. germanus* is found in the western region, reaching to 180° longitude in the northern hemisphere and 130° W in the southern hemisphere, and extending into Oceania and Indonesia. This species reaches 40° N and 25° S. *Halobates micans* is longitudinally widespread in the Pacific, reaching 35° N and 35° S and extending into Oceania and the Philippines. *Halobates sericeus* is also longitudinally widespread in the Pacific, but it exhibits an equatorial gap. In the northern hemisphere, this species reaches from 10° N to 40° N, and in the southern hemisphere it reaches from the equator in the east and 10° S in the west to 40° S. *Halobates sobrinus* and *H. splendens* are only present in the eastern Pacific, with both species bordering the coast of the Americas. *Halobates sobrinus* reaches to 135° W in the northern hemisphere and 105° W in the southern hemisphere, reaching from 30° N to 5° S. *Halobates splendens* reaches to around 100° W and ranges from 30° S to 5° N.

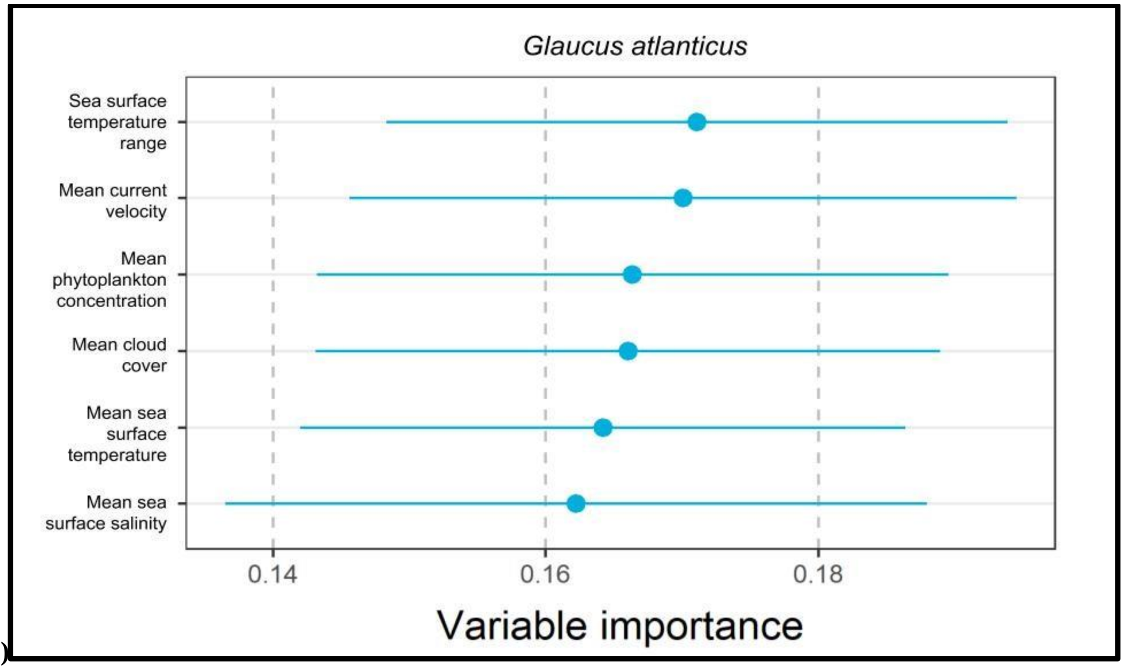
The genus *Janthina* is widely distributed throughout the Atlantic Ocean, with latitudinal separation of some species, and it is present in the Mediterranean Sea (Fig. 1(e)). *Janthina janthina* and *J. pallida* are both present in the Mediterranean Sea. *Janthina exigua* exhibits an equatorial gap from 20° S to 10° N in the Atlantic Ocean. It is longitudinally widespread from 20° S to 40° S and from 10° N to 50° N, although it is absent near the eastern coast of North America. *Janthina janthina* is also longitudinally widespread, reaching from 40° S to 50° N and also being absent near the eastern coast of North America, but lacking a significant equatorial gap. *Janthina pallida* is only present in the northwestern Atlantic, reaching from the African coast to 50° W and ranging from 10° N to 35° N. *Janthina umbilicata* is present between 20° W and 40° W and from 5° N to 35° N in the northern Atlantic; it is present between 10° W to 45° W and from the equator to 30° S in the southern hemisphere.

Janthina species exhibit similar variation in range in the Pacific Ocean (Fig. 1(f)). *Janthina janthina* has the largest Pacific range of all species in the genus, extending from 30° S in the eastern Pacific to just north of 40° N, and it is longitudinally widespread. *Janthina umbilicata* is similarly widely distributed in the northern Pacific with a narrower distribution in the southern Pacific, but its range does not extend to the edges of that of *J. janthina*. The range of *J. pallida* in the northern Pacific reaches from 20-35° N and 120° E to 140° W. There are three sightings of this species in the southern hemisphere, in a line just north of New Zealand. The range of *J. exigua* overlaps with the southern ranges of *J. janthina and J. umbilicata*, extending further south to 40° S and east to 110° E. There is one northern sighting of *J. umbilicata*, at around 20° N, 160° W. In the Indian Ocean, *J. janthina* is present from 50° E to 100° E and from 40° S to 10° N. *J. exigua* is present from 40° E to 80° E and from 50° S to 30° S. There is one sighting of *J. umbilicata* on the southern coast of Africa, and there are two sightings of *J. pallida* in the northeastern Indian Ocean.

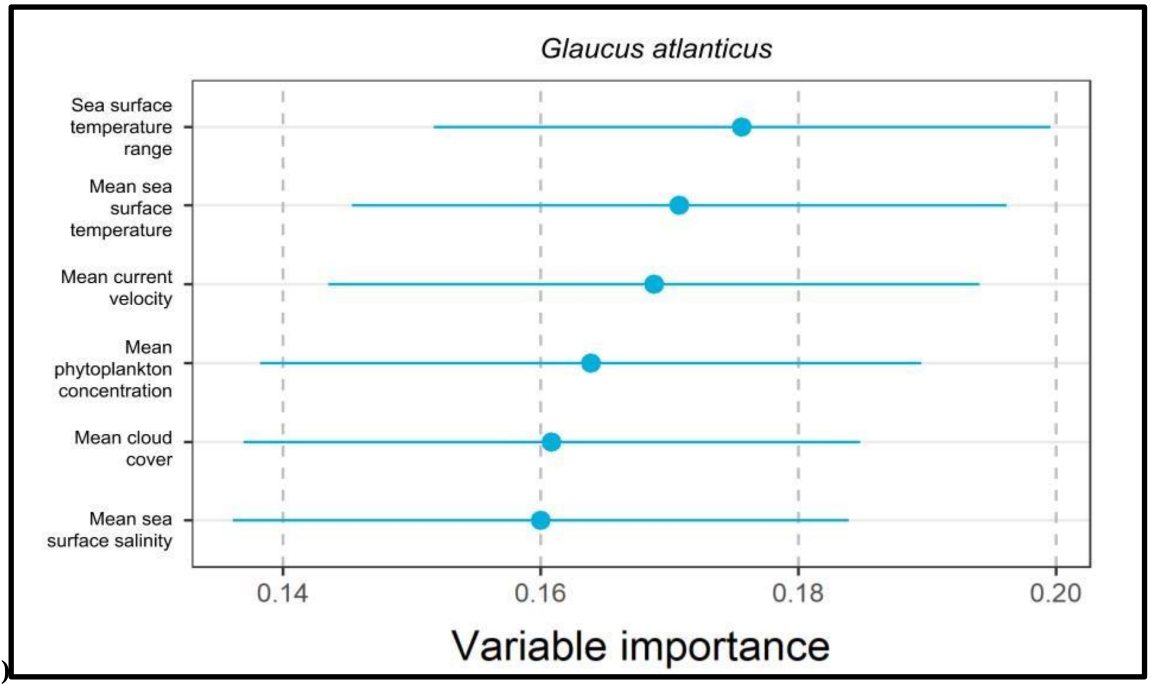
Hydrozoan genera *Porpita*, *Physalia*, and *Velella* are all present at varying latitudes in the Atlantic Ocean, with sightings of *Porpita* and *Velella* in the Mediterranean Sea (Fig. 1(g)). The genus *Physalia* is present across most longitudes in the northern Atlantic Ocean, extending into the Gulf of Mexico and reaching from 10° N to 40° N. Its range in the southern Atlantic is more limited, reaching from 30° W to 0° longitude and from the equator to 30° S. *Porpita* exhibits a similar northern Atlantic range to *Physalia*, but its range does not extend as far into the Gulf of Mexico, and it reaches to 45° N and 25° W in the northeastern Pacific, while *Physalia*'s range does not extend as far in this direction. There are two sightings of *Porpita* in the southern Pacific, one near the equator at 20° W and one at approximately 30° S and 5° W. There is one sighting of this genus in the Mediterranean, off of the southwestern coast of Italy. *Velella* extends even further north and south than the other two species, reaching from 55° S to 60° N and being present in most of the Atlantic, except near the southwestern coast of Africa.

The three hydrozoan genera described above are also present in the Pacific and Indian Oceans (Fig. 1 (h)). *Velella* is widespread in the Indian Ocean, reaching from the southern tip of India to 40° S and from 35° E to 105° E. *Physalia* and *Porpita* have more limited ranges in the Indian Ocean. *Porpita* is present in a narrow band from 50° E to 100° E and from the equator to 10° N, while *Physalia* is present in a narrow band from 50° E to 130° E and from 25° S to 40° S. *Physalia* is present in the Pacific predominantly near the equator, reaching from 25° S to 25° N. The genus is present across most longitudes in the northern Pacific, but reaches only from 90° W to 170° W. *Porpita* is longitudinally widespread in the Pacific and its range reaches from 40° S to 40° N, although its range extends only to 20° S in the eastern Pacific. *Velella* reaches from 40° S to 50° N, but its range reaches to 35° S in the eastern Pacific, while only reaching to 40° N in the western Pacific.

3.3 Embarcadero Distribution Models for Neustonic Species



a)



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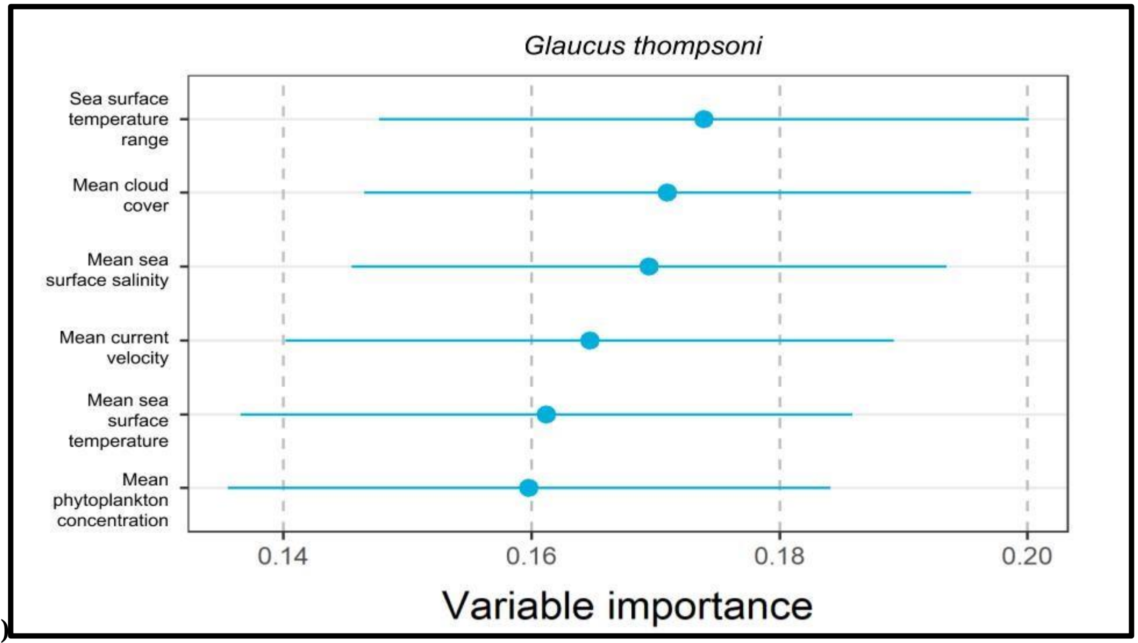
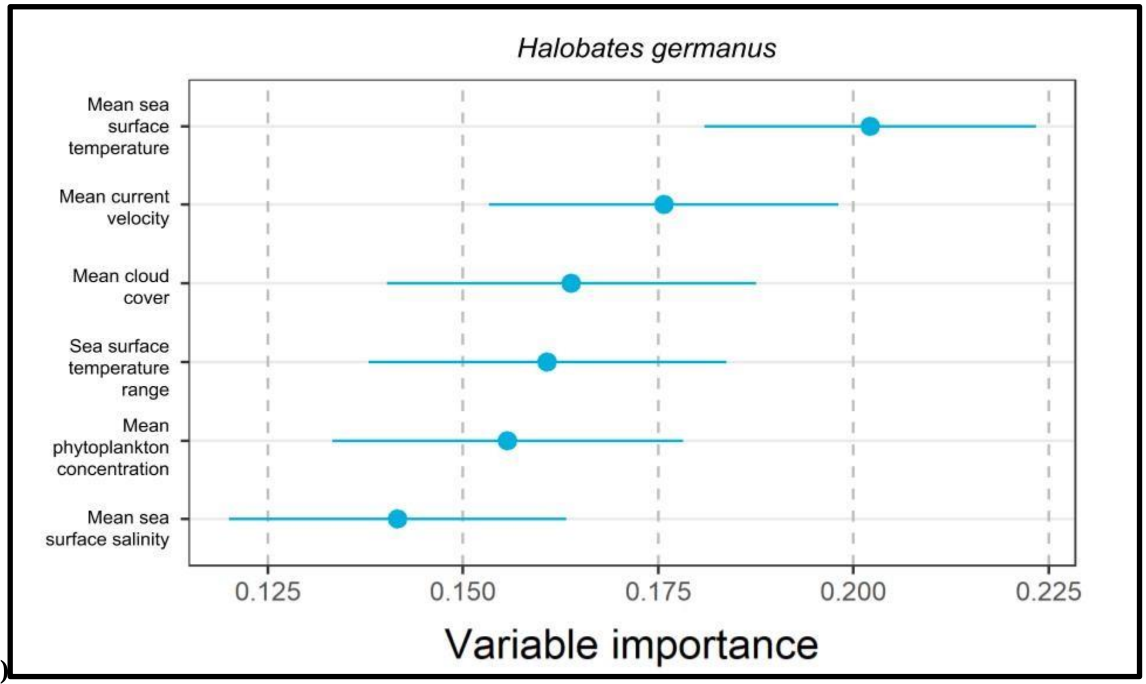
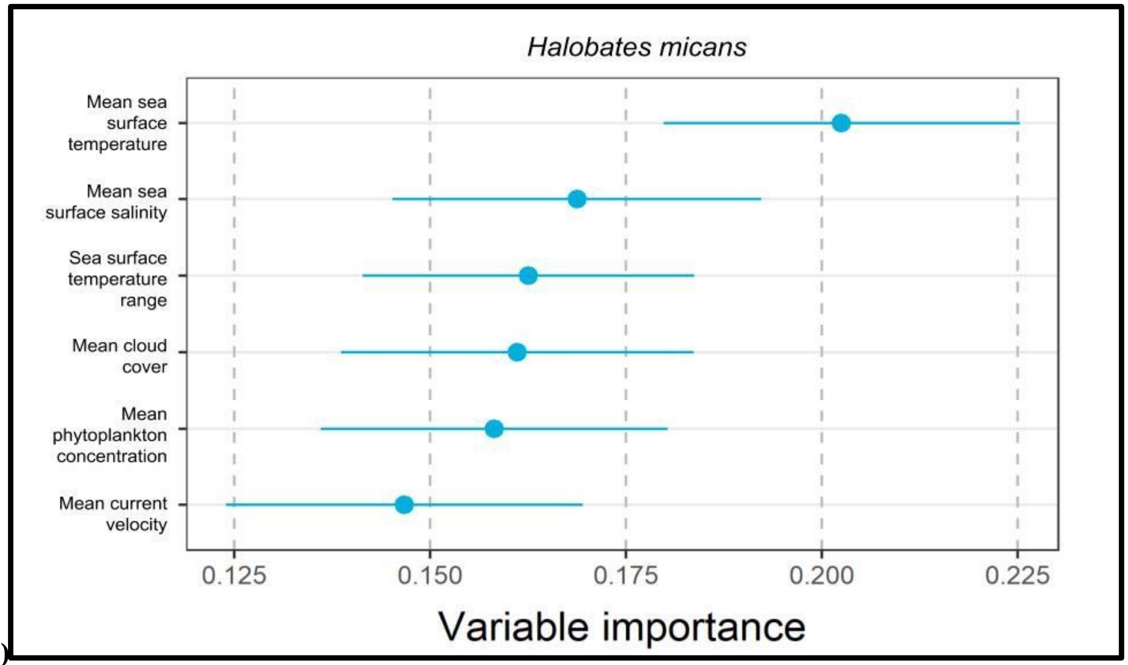

Glaucus thompsoni
Sea surface temperature range
Mean cloud cover
Mean sea surface salinity
Mean current velocity
Mean sea surface temperature
Mean phytoplankton concentration
0.14
0.16
0.18
0.20
Variable importance

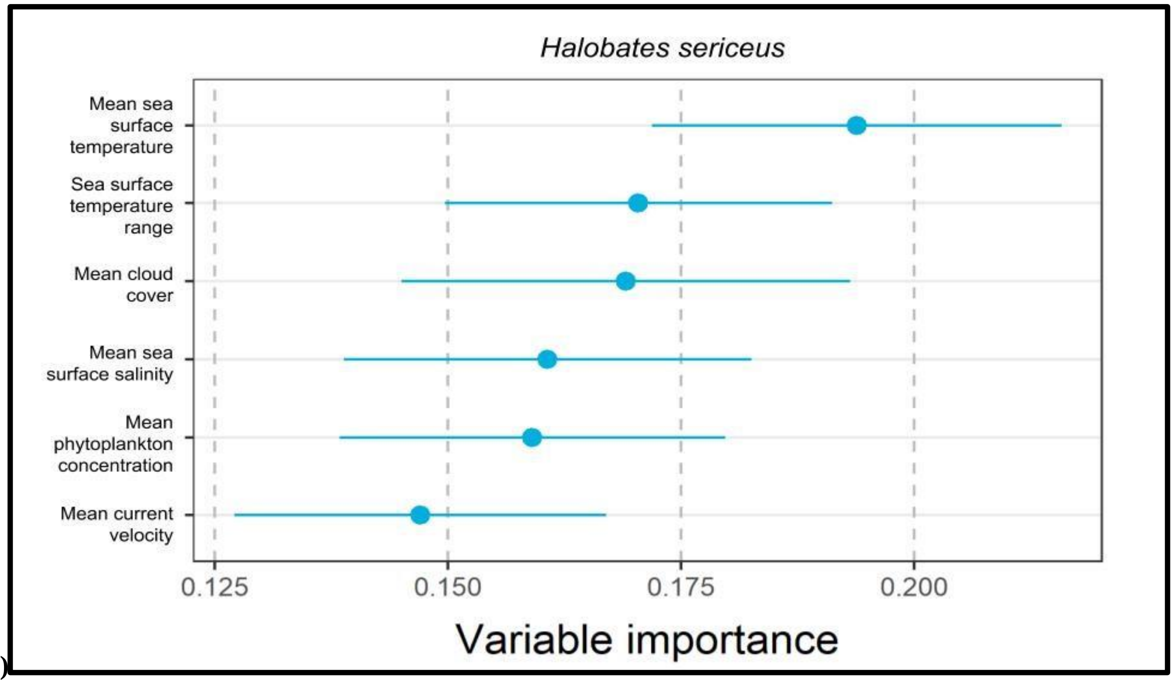
c)


Halobates germanus
Mean sea surface temperature
Mean current velocity
Mean cloud cover
Sea surface temperature range
Mean phytoplankton concentration
Mean sea surface salinity
0.125
0.150
0.175
0.200
0.225
Variable importance

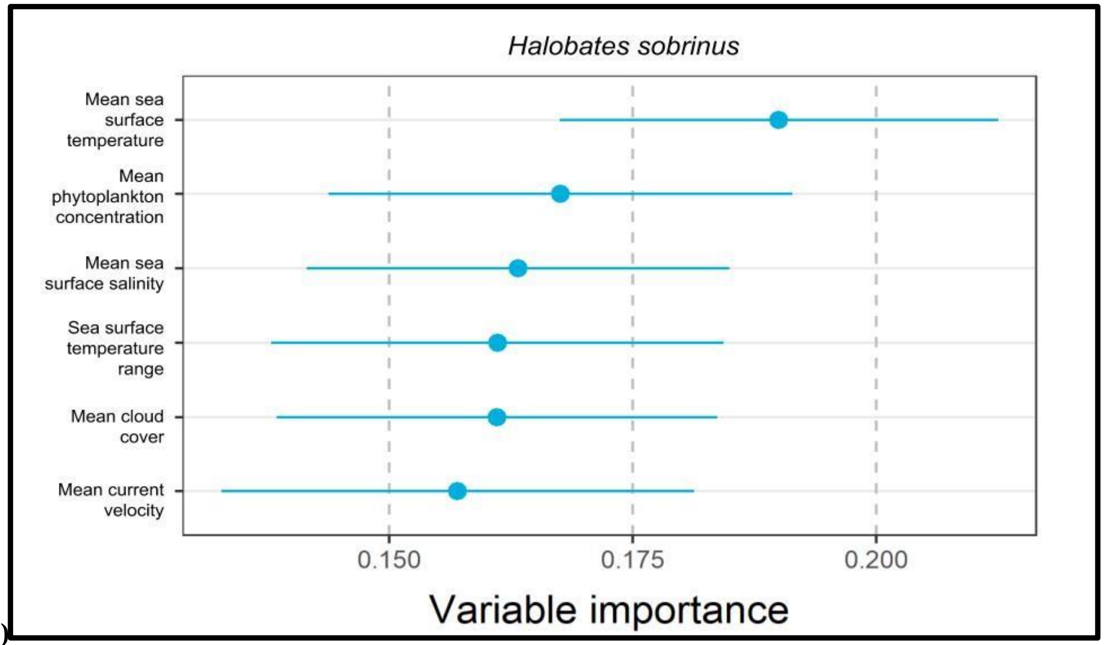
d)


Halobates micans
Mean sea surface temperature
Mean sea surface salinity
Sea surface temperature range
Mean cloud cover
Mean phytoplankton concentration
Mean current velocity
0.125
0.150
0.175
0.200
0.225
Variable importance

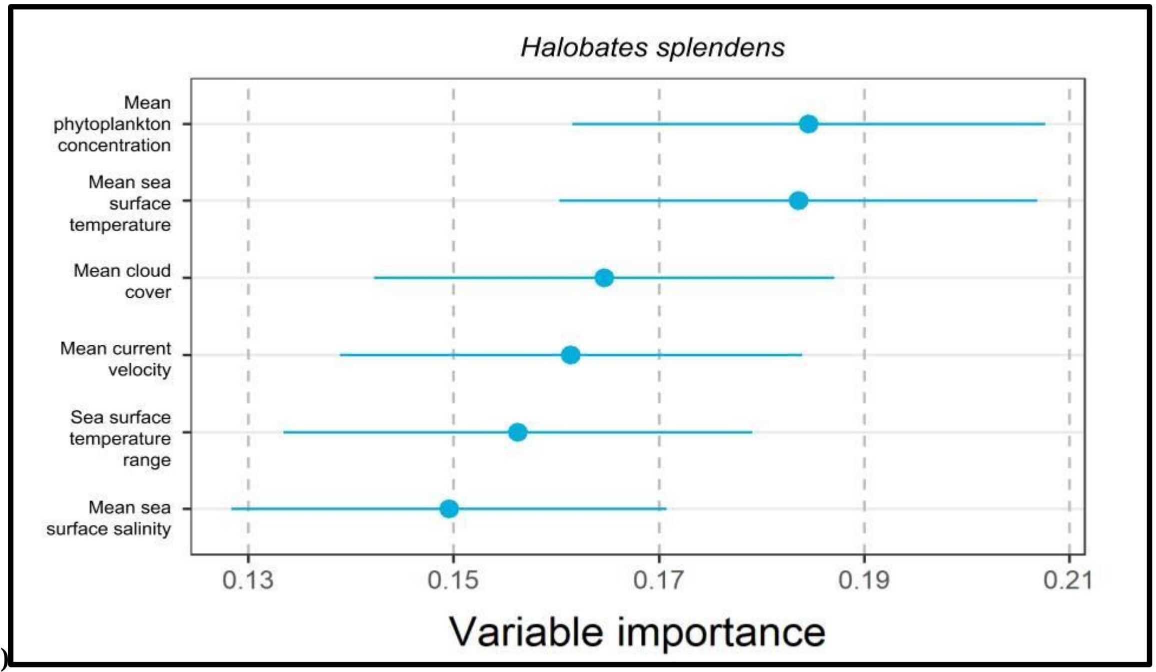
e)


Halobates sericeus
Mean sea surface temperature
Sea surface temperature range
Mean cloud cover
Mean sea surface salinity
Mean phytoplankton concentration
Mean current velocity
0.125
0.150
0.175
0.200
Variable importance

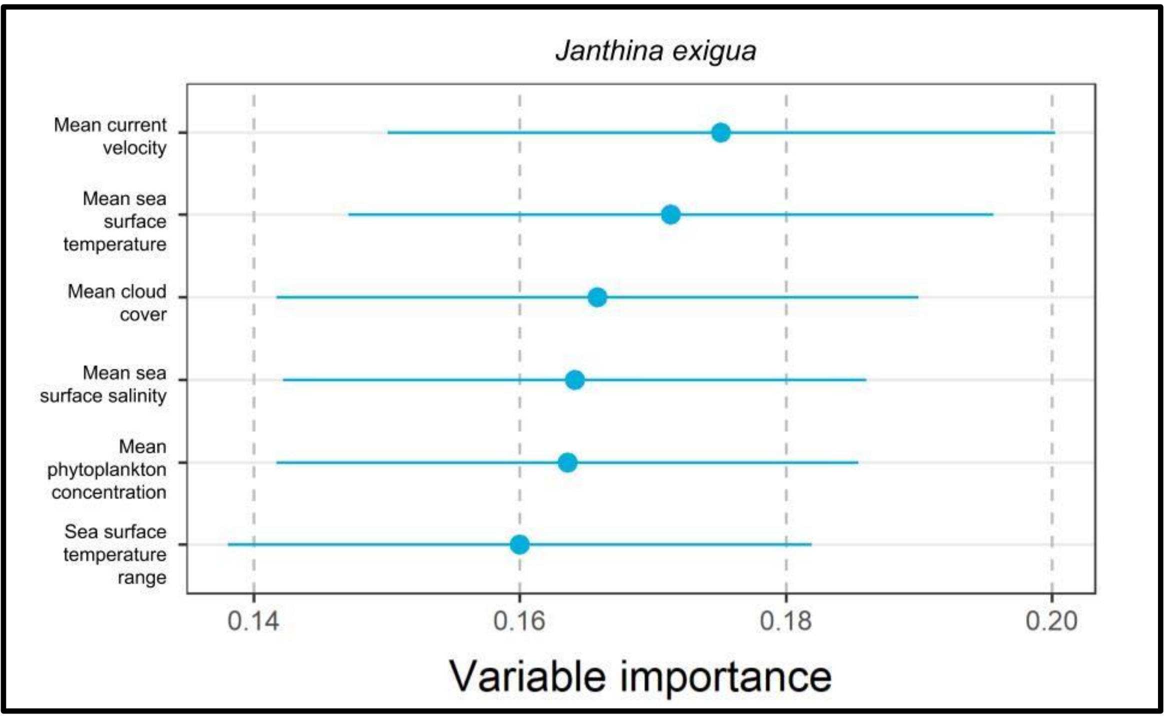
f)


Halobates sobrinus
Mean sea surface temperature
Mean phytoplankton concentration
Mean sea surface salinity
Sea surface temperature range
Mean cloud cover
Mean current velocity
0.150
0.175
0.200
Variable importance

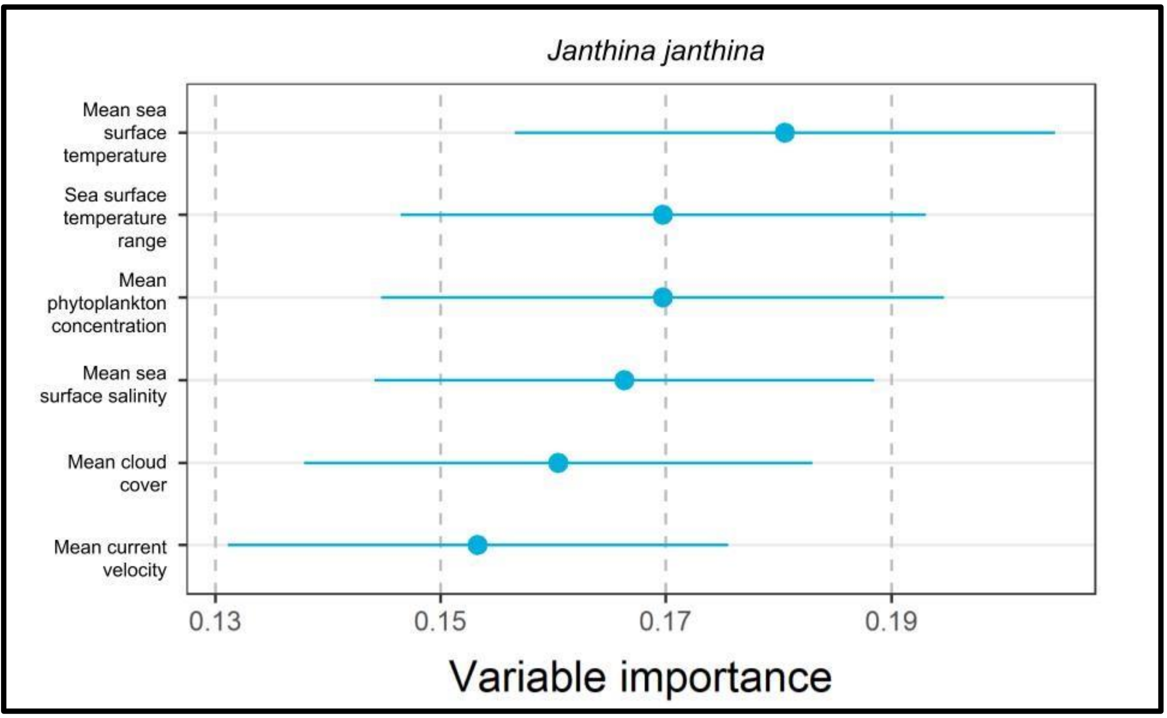
g)


Halobates splendens
Mean phytoplankton concentration
Mean sea surface temperature
Mean cloud cover
Mean current velocity
Sea surface temperature range
Mean sea surface salinity
0.13
0.15
0.17
0.19
0.21
Variable importance

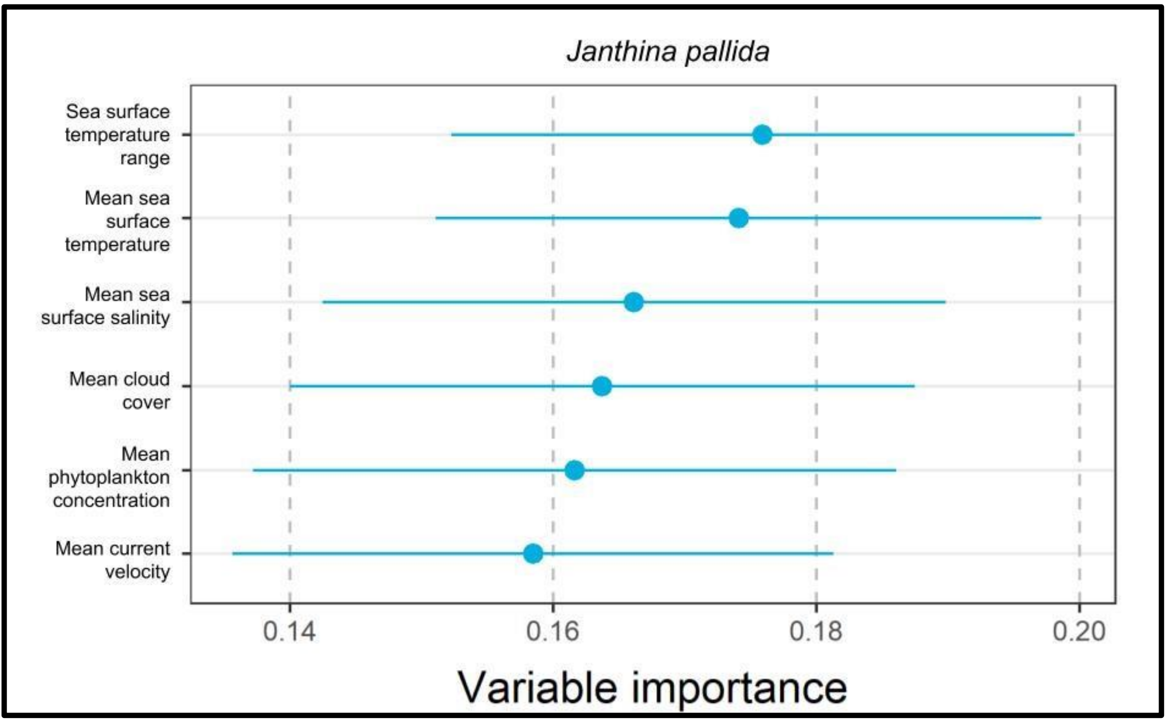
h)


Janthina exigua
Mean current velocity
Mean sea surface temperature
Mean cloud cover
Mean sea surface salinity
Mean phytoplankton concentration
Sea surface temperature range
0.14
0.16
0.18
0.20
Variable importance

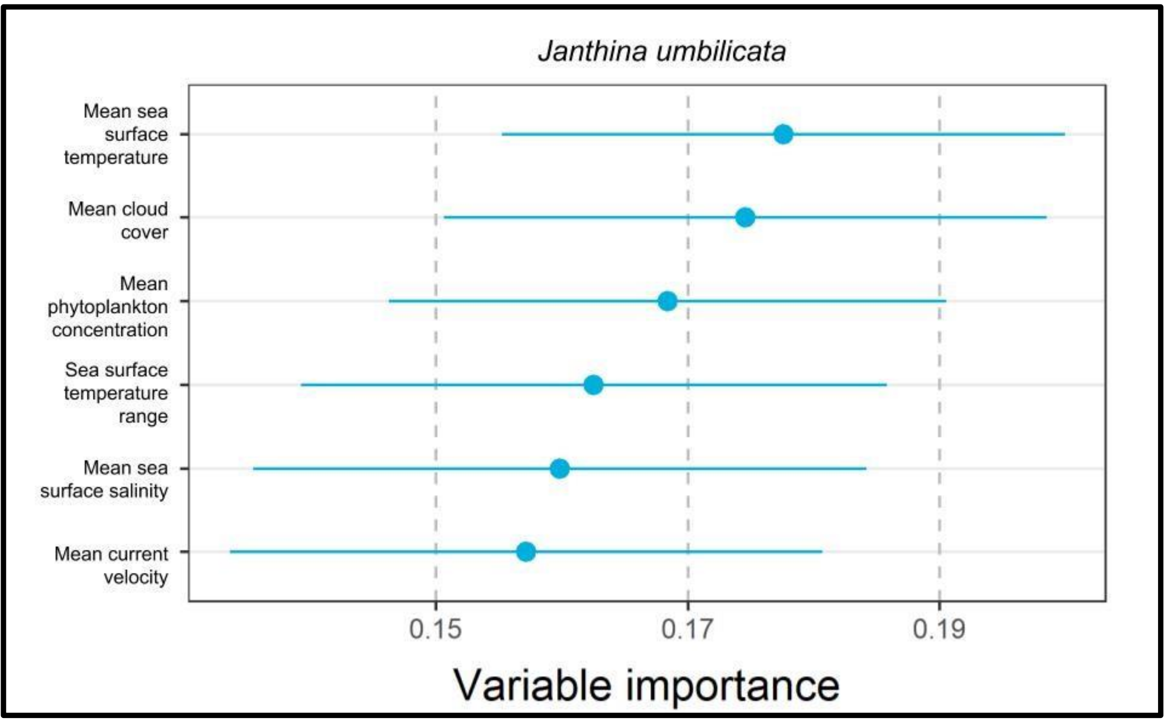
i)


Janthina janthina
Mean sea surface temperature
Sea surface temperature range
Mean phytoplankton concentration
Mean sea surface salinity
Mean cloud cover
Mean current velocity
0.13
0.15
0.17
0.19
Variable importance

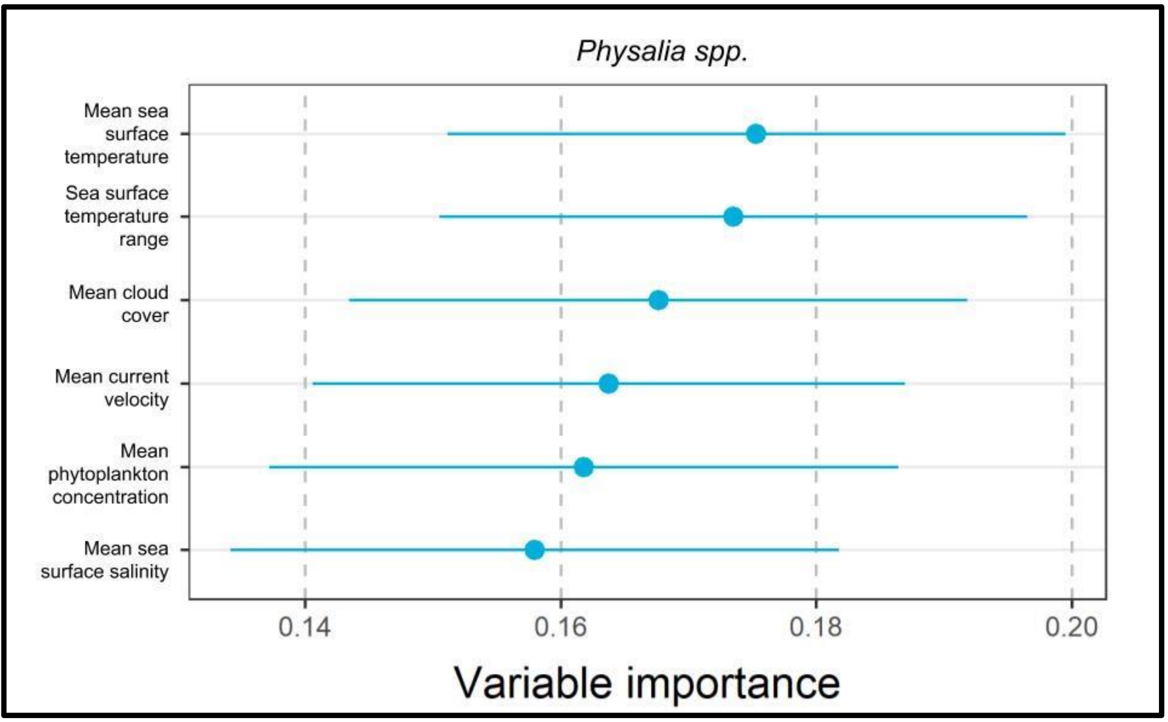
j)


Janthina pallida
Sea surface temperature range
Mean sea surface temperature
Mean sea surface salinity
Mean cloud cover
Mean phytoplankton concentration
Mean current velocity
0.14
0.16
0.18
0.20
Variable importance

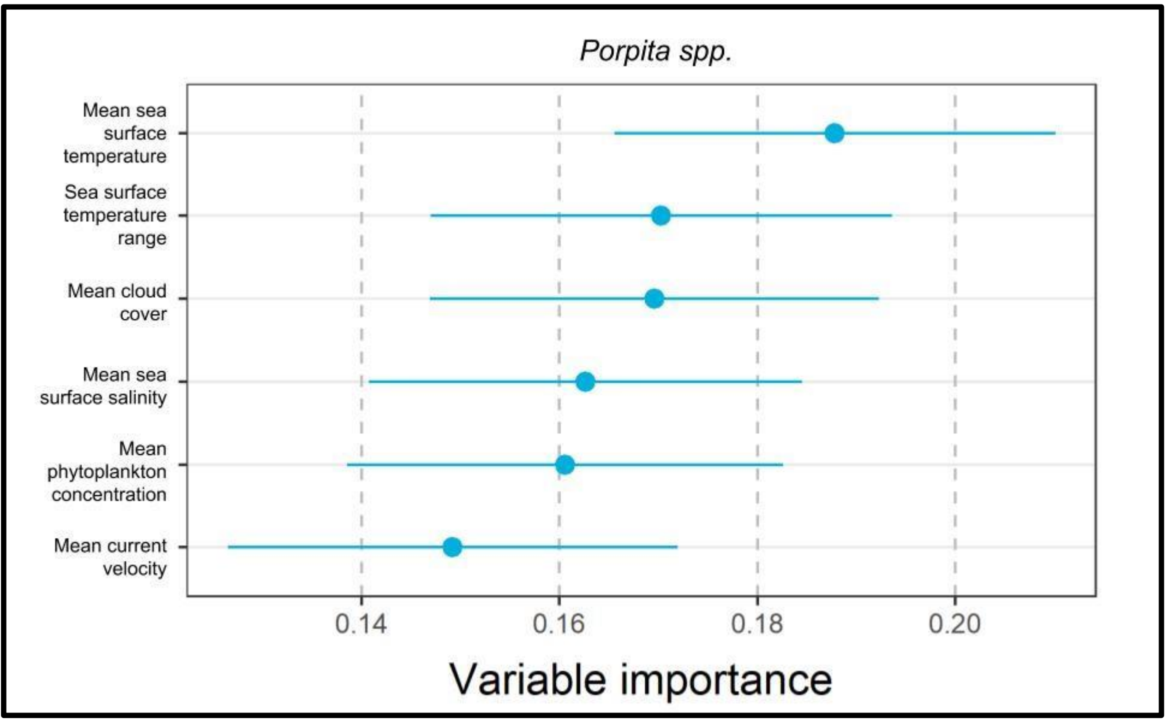
k)


Janthina umbilicata
Mean sea surface temperature
Mean cloud cover
Mean phytoplankton concentration
Sea surface temperature range
Mean sea surface salinity
Mean current velocity
0.15
0.17
0.19
Variable importance

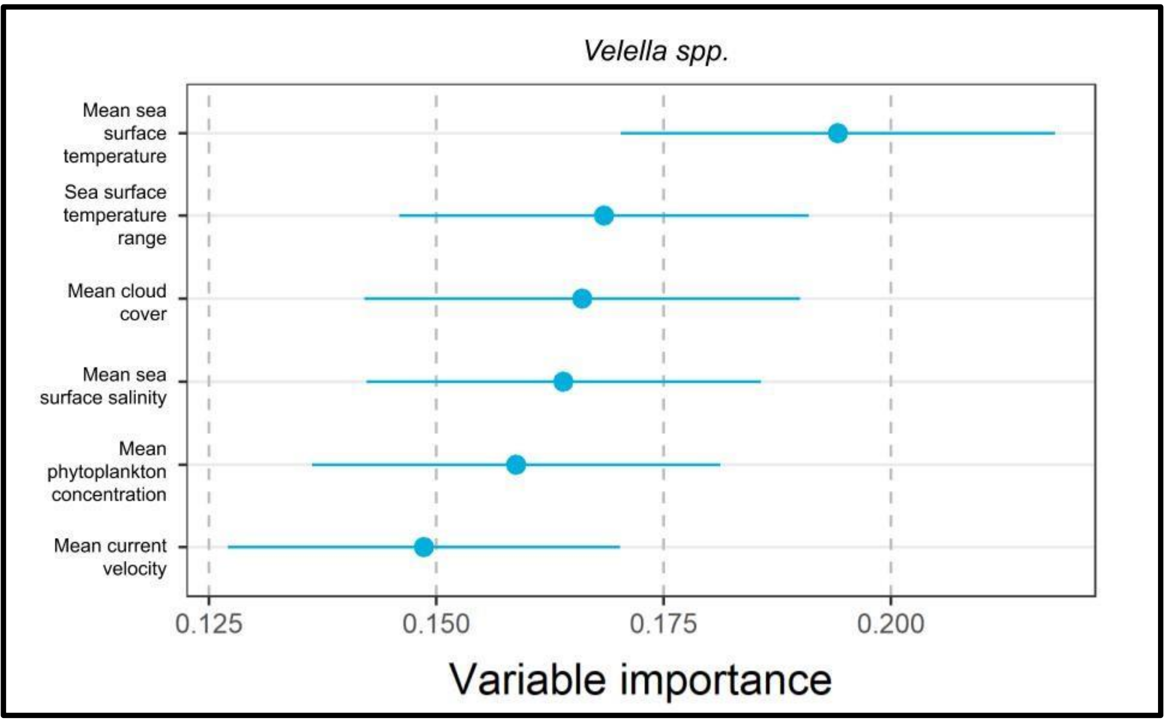
l)


Physalia spp.
Mean sea surface temperature
Sea surface temperature range
Mean cloud cover
Mean current velocity
Mean phytoplankton concentration
Mean sea surface salinity
0.14
0.16
0.18
0.20
Variable importance

m)


Porpita spp.
Mean sea surface temperature
Sea surface temperature range
Mean cloud cover
Mean sea surface salinity
Mean phytoplankton concentration
Mean current velocity
0.14
0.16
0.18
0.20
Variable importance

n)



o)

Figure 2. Variable importance plots of distribution models for neustonic species generated by Embarcadero using pseudo-absences the variable importance displayed as the proportion of splits in the model occurring due to sea surface temperature, sea surface temperature range, mean sea surface salinity, mean cloud cover, mean current velocity, and mean phytoplankton concentration. ***(a)*** *Glaucus atlanticus.* ***(b)*** *Glaucus marginatus.* ***(c)*** *Glaucus mcfarlanei.* ***(d)*** *Halobates germanus.* ***(e)*** *Halobates micans.* ***(f)*** *Halobates sericeus.* ***(g)*** *Halobates sobrinus.* ***(h)*** *Halobates splendens.* ***(i)*** *Janthina exigua.* ***(j)*** *Janthina janthina.* ***(k)*** *Janthina pallida.* ***(l)*** *Janthina umbilicata.* ***(m)*** *Physalia physalis.* ***(n)*** *Porpita porpita.* ***(o)*** *Velella velella.*

Figure 2 displays variable importance plots for the species distribution model of each neustonic species.

Sea surface temperature range is the most highly ranked variable for all three *Glaucus* species (Fig. 2 (a-c)). Current velocity is the second-ranked variable for *G. atlanticus* and the third-ranked for *G. marginatus*. Other than these similarities, there is a high degree of variation in the importance of variables for *Glaucus* species. Mean phytoplankton concentration is the third-ranked variable for *G. atlanticus*, and mean temperature is the second-ranked for *G. marginatus*. The second and third most highly ranked variables for *G. thompsoni* are mean cloud cover and mean sea surface salinity.

Mean sea surface temperature is the most highly ranked variable for all *Halobates* species except for *H. splendens*, for which it is the second-ranked variable by a small margin, following mean phytoplankton concentration (Fig. 2 (d-h)). Mean current velocity and mean cloud cover are the second- and third-ranked variables for *H. germanus* (Fig. 2 (d)). Mean sea surface salinity and sea surface temperature range are the second- and third-ranked variables for *H. micans* (Fig. 2 (e)). Sea surface temperature range and mean cloud cover are the second- and third-ranked variables for *H. sericeus* (Fig. 2 (f)). Mean phytoplankton concentration and mean sea surface salinity are the second- and third-ranked variables for *H. sobrinus* (Fig. 2 (g)). Mean cloud cover is the third-ranked variable for *H. splendens* (Fig. 2 (h)).

Mean sea surface temperature is the most highly ranked variable for *Janthina janthina* and *J. umbilicata*, and it is the second-ranked variable for *J. exigua* and *J. pallida* (Fig. 2 (i-l)). Sea surface temperature range is the most highly ranked variable for *J. janthina* and the second-ranked for *J. pallida* (Fig. 2 (j) and (k)). Mean sea surface current velocity and mean cloud cover are the second- and third-ranked variables for *J. exigua* (Fig. 2 (i)). Mean phytoplankton concentration is the third-ranked variable for *J. janthina* (Fig. 2 (j)). Mean sea surface salinity is the third-ranked variable for *J. pallida* (Fig. 2 (k)). Mean cloud cover and mean phytoplankton concentration are the second- and third-ranked variables for *J. umbilicata* (Fig. 2 (l)).

Mean sea surface temperature, sea surface temperature range, and mean cloud cover, in order, are the three most highly ranked variables for *Porpita*, *Physalia*, and *Velella* (Fig. 2 (m-o)).

4. Discussion

The distributions of neustonic animals and the factors that affect them vary, but temperature is consistently important, and the distributions of some neustonic animals seem to affect the limits of the neuston as a whole. Temperature limitations, in the form of either mean temperature or temperature range, are highly-ranked variables for all of the genera and species studied.

Data on the distribution of the genus *Glaucus* are limited. However, the latitudinally limited range of *G. atlanticus* aligns with the results of the variable importance plots generated by Embarcadero (Fig. 2 (a-c)). These results indicate that temperature ranges may restrict the distributions of *Glaucus* species. This suggests that these animals are unable to survive in the lower temperatures of more extreme northern and southern areas.

The distributions of *Halobates* species found in our study are similar to those found by previous studies[9,59]. Savilov (1970) described *H. micans* as the only species present in the Atlantic Ocean[9,] and this was our finding as well. However, he found that *H. sericeus* and *H. micans* were observed predominantly in the open ocean[9.] Our findings did not suggest the absence of these species in coastal areas, although they were both present in the open ocean in the Pacific. Savilov's (1970) description of the range of *H. sericeus* is similar to our findings: it is present in the northern and southern Pacific Ocean, but it is largely absent near the equator (Fig. 1 (d))[9.] There is evidence that the populations of *H. sericeus* in the northern and southern Pacific Ocean are evolutionarily distinct from one another, indicating that these populations have remained largely separate since the late Pleistocene era[59].

The results of the variable importance plots for the genus *Halobates* indicate that mean temperatures are the most highly ranked factor determining the ranges of these animals (Fig. 2 (d-h)). This fits with the MBPs for this genus, in which all *Halobates* species are limited to the area between 40° S and 40° N (Fig. 1 (c) and (d)). This is likely due to a limited tolerance to low temperatures, preventing the insects from reaching beyond these ranges. The equatorial gap in the range of *H. sericeus* also aligns with this result, as it is likely caused by an intolerance of the species to higher temperatures near the equator. Other *Halobates* species, however, are present at the equator, indicating potential differences in the temperature tolerance of each species. *H. micans* also follows a pattern fitting of an animal limited in temperature tolerance, being longitudinally widespread in the Indian, Pacific, and Atlantic Oceans, but having fairly consistent latitudinal boundaries associated with temperature limitations. Based on the results of the variable importance plots, mean sea surface temperature accounts for more of the splits in the model than any other trait (Fig. 2 (e)). This higher ranking of mean temperature may explain why these two species are not longitudinally limited but exhibit consistent latitudinal limits in the Pacific. While the other three *Halobates* species have similar latitudinal limitations, they are inconsistently distributed longitudinally (Fig. 1 (d)). *Halobates germanus* is the only species present in the Red Sea, and its range only includes the western portion of the Pacific Ocean. This is also the only *Halobates* species for which current velocity is a highly-ranked factor (Fig. 2 (d)), which may help to explain why it is the only species whose range is limited to the western Pacific. *Halobates sobrinus* and *H. splendens* are only present in the eastern portion of this ocean, although the two species exhibit differing latitudinal ranges consistent with variation in temperature tolerance. These two are the only *Halobates* species for which mean phytoplankton concentration is among the three most highly-ranked variables (Fig. 2 (g-h)), and for *H. splendens* it is more highly-ranked even than mean temperature (Fig. 2 (h)), which may explain why these species exhibit longitudinal range limits not observed for other *Halobates* species.

Mean temperature is a highly-ranked variable in the ranges of all *Janthina* species (Fig. 2 (i-l)), indicating that these animals, too, are limited in latitudinal distribution by temperature tolerances. *Janthina janthina* is longitudinally and latitudinally widespread in the Atlantic, Indian, and Pacific Oceans (Fig. 1 (e) and (f)), corresponding with the high ranking of temperature traits found for this species and indicating a greater temperature tolerance than that of other *Janthina* species. Laursen (1953) notes that this species has never been observed in areas with temperatures below 10° C, and seems to prefer temperatures at or above 15° C[11.] *Janthina exigua* is similarly widely distributed in the Atlantic Ocean, but it exhibits an equatorial gap, and it is present only further south in the Pacific and Indian Oceans, with the exception of one northern Pacific observation (Fig. 1 (e) and (f). This indicates that it has a similar cold tolerance to *J. janthina*, but may not be as tolerant to hot temperatures close to the equator. Laursen (1953) described the range of *J. janthina* as reaching further south than that of *J. exigua*, which he stated prefers temperatures between 15° C and 25° C, near the southernmost coast of Africa[11], while our findings indicate that *J. exigua*'s range extends further south in the Indian Ocean as well as in the Pacific. *Janthina exigua* is one of only two species for which mean phytoplankton distribution is among the most highly-ranked variables (Fig. 2 (j) and (l)), which may explain its unique southern range in the Indian and Pacific Ocean. *J. pallida* is only present in the northern portion of the Atlantic and Pacific Oceans, with the exception of three observations in the southern Pacific (Fig. 1 (e) and (f)). This matches the observations of Laursen (1953), who observed *J. pallida* only in the northern hemisphere of the Atlantic, Indian, and Pacific Oceans and suggested that it prefers temperatures greater than 15° C[11.] It occupies similar extremes in the northern Pacific that *J. exigua* does in the southern Pacific, indicating a similar temperature tolerance but different actual niche space (Fig. 1 (f)). *J. umbilicata* is more limited in range, both latitudinally and longitudinally, than all other *Janthina* species in the Atlantic Ocean (Fig. 1 (e)). Laursen (1953) proposed, based on the limited data of the time, that this species had a range restricted to areas with temperatures greater than 18° C[11.] The limited range of this species in our results supports the conclusion that *J. umbilicata* has a lesser temperature tolerance than other *Janthina* species. This is the only species for which cloud cover is among the most highly-ranked variables (Fig. 2 (l)), and the importance of weather may explain the variations in its range compared to other *Janthina* species.

The three hydrozoan species studied also exhibit a pattern consistent with limitations of temperature tolerance (Fig. 2 (m-o)). All three genera are longitudinally widespread in Atlantic, Indian, and Pacific Oceans. *Velella* is most latitudinally widespread, indicating the greatest temperature tolerance, followed by *Porpita*, and then by *Physalia*, which is present primarily in the tropics, although it exhibits a small equatorial gap in the Atlantic Ocean (Fig. 1 (g) and (h)). This result of our study is supported by the findings of Savilov (1970), who suggested that the more limited range of *Physalia* compared to *Velella* is due to its more thermophilic nature[9.]

It is intriguing that the two hydrozoans with sails exhibit drastically different ranges, because they are both propelled by the wind. *Porpita*, however, has no sail, but exhibits an intermediate range between the two (Fig. 1 (g) and (h)). Savilov (1970) observed variation in the distribution patterns of sailing hydrozoans compared to non-sailors, with non-sailors congregating around the equator and sailors primarily to the north and south[9.] This description is similar to our own findings, except that we did not see an equatorial gap in the distribution of *Velella*. It is possible this is due to seasonal variation: Savilov (1970) acknowledged that there is known seasonal and local variation in where these animals occur[9.] Mean cloud cover is the third-ranked variable for all three hydrozoans (Fig. 2 (m-o)), indicating that variation in weather across the oceans and seasons may be a determining factor in the ranges of these animals. For this reason, these three cnidarians may be good candidates for future research on the seasonality of neustonic animals. Given the importance of these animals in the neustonic food chain, patterns in cloud cover may be determinants of the overall range of the neuston ecosystem.The mechanisms of range limitations in these animals are worthy of further study, and an analysis of distributional seasonality could be informative if sufficient data were available.

The ranges of *Porpita*, *Physalia*, and *Velella* may significantly affect the ranges of other neustonic animals. According to Savilov (1970), many animals, including other members of the neuston, feed on these three hydrozoans[9.] *Porpita* and *Velella* are key food sources for *Janthina* and *Glaucus*[9,] so it is unsurprising that *Janthina* and *Glaucus* occur only within the ranges of their primary food sources (Fig. 1 (a), (b), and (e-h)). The three hydrozoans themselves consume large amounts of small fish, animal eggs, and other materials[9,] and this opportunistic feeding behavior may help to explain why their ranges are very broad compared to some other neustonic organisms. Neustonic chondrophores (*Porpita* and *Velella*) are also a substrate for the deposition of eggs by other neuston species, including *Halobates*[9,] which may also help to explain why these two genera exist largely within the ranges of *Porpita* and *Velella* (Fig. 1 (a-d), (g), and (h)). Savilov (1970) describes the overall range of the neuston as being between 40° N and 40° S[9.] Our observed range of these animals is larger, with observations of *Velella* reaching as far as 60° N in the Pacific. However, this may be due to individual animals being blown outside of their more typical range, a phenomenon that Savilov (1970) acknowledges[9.]

As a whole, the most highly-ranked factor affecting the distributions of most neustonic animals is temperature (Fig. 2), however, many other factors play an important role in determining when and where these animals occur. In particular, the seasonality of neustonic organisms requires further study. In our study, we were unable to assess seasonality from the available data, but the high ranking of temperature in our models of neustonic animal ranges suggests that seasonal variation is likely, and there is some evidence of this in existing records[9.]

Environmental factors such as temperature have important effects on neustonic organisms, but anthropogenic effects such as climate change and floating plastic are a growing component of oceanic systems. Floating plastic at the ocean's surface has increased dramatically over the last 40 years, and much of this plastic occurs at the ocean's surface in areas we know many neustonic organisms are present (Fig. 1)[60-,62]. While it is unclear if this floating debris affects the free-living organisms studied here, Goldstein et al. (2012) found that concentrations of *Halobates* adults and eggs were higher in areas with greater densities of floating microplastics[62], indicating that floating plastic can affect these ocean-surface ecosystems. Given the degree to which neustonic animals are connected with each other and with other ecosystems, further study of the effects of plastic will be essential to understanding how anthropogenic change impacts these ecosystems. Given the importance of temperature in determining the ranges of many neustonic animals, it seems probable that climate change will affect these organisms, and this form of anthropogenic change at the ocean's surface will also require further study.

5. Conclusion

The ocean's surface is a unique ecosystem, affected by wind, sunlight, wave action, hydrophobic chemicals, and rainfall[1-4]. It is home to a wide variety of unusual animals, from cnidarians with sails to floating snails, and these animals have patchy populations, forming dense rafts in some areas and being entirely absent in others[4,9]. While we have identified the ranges numerous neustonic taxa, and that environmental factors, particularly temperature, play an important role in determining their ranges, there is much still to be learned about this ecosystem, particularly about the seasonality of the neuston and the effects that anthropogenic change may have on them.

6. Acknowledgements

The authors would like to thank Colin J. Carlson, who will be an author on the primary manuscript for this paper, for his assistance with the use of Embarcadero, a program which he created; and Jackie Langille, for her help with the use of ArcMap.

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