A physical context for gelatinous zooplankton aggregations: a review

William M. Graham[1], Fransesc Pagès[2] & William M. Hamner[3]

[1]*Dauphin Island Sea Lab and Department of Marine Sciences, University of South Alabama,*
101 Bienville Boulevard, Dauphin Island, AL, 36528, U.S.A.
E-mail: mgraham@disl.org
[2]*Institut de Ciències del Mar (CSIC), Plaça del Mar s/n, 08039 Barcelona, Catalonia, Spain*
[3]*University of California, Los Angeles, Department of Organismal Biology, Ecology and Evolution, Box 951606,*
Los Angeles, CA, 90095-1606, U.S.A.

Abstract

The magnitude and extent of jellyfish blooms are influenced not only by the biology and behavior of the animal, but also by the geographic setting and physical environment. Hydrography alone is often thought to cause or favor gelatinous zooplankton aggregations, however, it is clear that interactions between biology of the animal and physics of the water are very important sources of population variations, especially at local scales. We summarize the role of physical processes and phenomena that promote aggregations of gelatinous zooplankton. We have identified and discussed a suite of physical gradients that can be perceived by gelatinous zooplankton. These include light, gravity, temperature, salinity, pressure and turbulence. A recurring theme is accumulation of jellyfish around physical discontinuities such as fronts (shelf-break, upwelling, tidal and estuarine) and pycnoclines (thermoclines and haloclines). Interestingly, there are few data to suggest that large-scale, quasi-stationary features, such as the largest oceanic fronts, serve to physically aggregate gelatinous animals at a similar scale. Rather, examples of local aggregations appear to dominate the literature. We also discuss various jellyfish behaviors that are theorized to promote aggregation, feeding and reproduction in relation to physical discontinuities.

Introduction

The sudden appearance and disappearance of jellyfish aggregations or swarms is a common yet enigmatic characteristic of jellyfish populations. Most gelatinous zooplankters have life-histories with asexual reproduction and extraordinary growth rates that allow them to undergo rapid population increases. Moreover, their gelatinous structure, absence of complex neural framework and apparent weak swimming suggest that they passively drift with the water current. To the naive observer, therefore, the sudden appearance of large numbers of jellyfish implies that a bloom has somehow occurred when no one was watching. Indeed, blooms, by definition, appear or occur unexpectedly or in surprising quantity, almost over night. We now know, however, that the apparently simple body plan of jellyfish often disguises sophisticated interactions with their biological, chemical and physical environ-

ment that contribute to patchy distribution of jellyfish throughout the marine environment. Advances in the use of *in situ* techniques over the past 30 years (Hamner, 1985) have enormously increased our knowledge about the behavioral complexity of gelatinous animals.

Rapid changes in jellyfish concentrations can be due either to rapid population growth (a true bloom) or to a re-distribution or re-dispersion of a stable population (an apparent bloom). Since population changes are addressed elsewhere in this volume, we will address only physical factors implicated in apparent blooms. We distinguish between advective and concentrating factors. Advection means that a patch or aggregation of animals is translocated to a previously uninhabited location, whereas concentration means that the density of a population has changed. Advection of planktonic populations occurs passively whenever a water mass moves, whereas concentration changes, in the absence of population growth or

mortality, require an element of active behavior or physiological alteration by the jellyfish that promotes changes in local density.

Animal aggregations constitute a fascinating and complex research topic that requires theory and modeling studies linked to empirical work (Parrish & Hamner, 1997; Parrish & Edelstein-Keshet, 1999). Nonetheless, *in situ* observations using SCUBA (Hamner et al., 1975), research submersibles and remotely operated vehicles (Larson et al., 1992; Mills et al., 1996; Brodeur, 1998; Raskoff, 2001) and profiling video (Paffenhöffer et al., 1991; Davis et al., 1992), have been crucial for investigating the relationship between biology, behavior and the physical environment of marine organisms (Hamner, 1985). In this paper, we review those physical factors that contribute to aggregation of gelatinous zooplankton. As the literature base is comparatively new and rarely pre-dates the 1970s, we cast a broad net to include mostly medusae, but also siphonophores, ctenophores and pelagic tunicates. The ultimate goal of the paper is to provide the underlying physical context of aggregations as they occur in conjunction with, or the absence of, biology and behavior of the animal, and when possible we discuss adaptive implications of these interactions. While we recognize the importance of physical transport of a bloom as an important source of apparent population variability (e.g., Nielsen et al., 1997), we emphasize here only physical attributes that lead to local aggregation of gelatinous animals.

This review is organized to provide the reader first with an understanding of how gelatinous animals perceive, and respond to, specific physical characteristics and physical gradients. Biological and chemical gradients may also mediate gelatinous zooplankton distribution (e.g. Arai, 1992; Purcell et al., 1994; Purcell et al., 2001), but we are limiting this discussion to physical-biological interactions. We then move to specific examples of aggregations that have been described in both the horizontal and vertical dimensions. And finally, we discuss future directions that scientists might follow to advance our understanding of gelatinous zooplankton aggregations.

Passive and active responses to environmental physical gradients

Changes in physical properties of the environment serve as important cues for initiating biological and ecological processes that result in gelatinous zo-

oplankton aggregation. Physical cues provide the primary, proximal information for movements of individuals within an aggregation, as well as for movement of the entire aggregation. Active responses to physical cues can also facilitate aggregation through the interplay between local circulation and the directed swimming movements of the animals. Another response, but not described in further detail, is seasonal changes of physical environmental variables that can herald the onset of ultimately favorable conditions for reproduction, resulting in population changes that also culminate in locally high densities of plankton, as in blooms of red tide. In the following section, we discuss the role of physical properties and gradients as cues mediating gelatinous zooplankton migrations and aggregations.

Aggregations of gelatinous zooplankton are three-dimensional entities, and therefore both vertical and horizontal physical gradients facilitating aggregation will be considered. Gradients and variations of physical properties are far more pronounced in the vertical dimension than in the horizontal, therefore physical–biological interactions tend to be more easily observed and documented in the vertical axis. Jellyfish aggregations in the vertical dimension can be envisioned as 'layers' in three dimensions. The vertical extent of these layers may be from a few centimeters to hundreds of meters thick. By contrast, horizontal dimensions of aggregations can be on the order of tens of meters to hundreds of kilometers. Physical gradients and discontinuities implicated in gelatinous zooplankton aggregations include light, pressure, turbulence, currents, temperature and salinity (thus density). While active responses to both horizontal and vertical gradients or discontinuities are often mediated by behavior, we also discuss evidence for passive accumulation along physical discontinuities.

Light-mediated migrations

Jellyfish are generally considered to be planktonic, i.e., not capable of extensive movements against currents. Consequently, their vertical migration patterns have been documented more thoroughly than have their horizontal migrations. Vertical migrations for zooplankton have been described repeatedly in the literature, with induction of migration implicitly linked to the diel cycle of light. 'Diurnal Vertical Migration', or DVM, usually refers to a pattern of diel behavior in the water column wherein individuals swim upward toward the surface during the night, and swim down-

ward toward the bottom during the day. The behavioral swimming response seen during DVM can result in either the entire population moving *en masse* as a migrating layer, or a vertically dispersed population may become locally concentrated at the sea surface during a specific time of day (usually at night). In fact, daily nocturnal ascent and diurnal descent is by far the dominant type of vertical migratory behavior in nature (Bayly, 1986). Perhaps the most studied migrating layer of gelatinous zooplankton is the 'Deep Scattering Layer' (DSL) discovered in the late 1940s from the acoustic properties of physonect siphonophores - primarily *Nanomia bijuga* delle Chiaje (Barham, 1963; see Pugh, 1977 for review).

Light-mediated DVMs range from a few to hundreds of meters, and they are widespread among hydromedusae (Russell, 1927; Arai, 1973, 1992; Mills, 1981; Arkett, 1985; Mills & Goy, 1988), siphonophores (Barham, 1963; Pagès & Gili, 1991) and scyphomedusae (Yasuda, 1973; Mackie et al., 1981; Hamner, 1995; Schuyler & Sullivan, 1997). There is little evidence that ctenophores exhibit DVMs mediated by light (Frank & Widder, 1997). This is perhaps due to the lack of light sensing machinery within the phylum. Vertically migrating animals must have biological equipment that is sensitive to directional environmental information. Many gelatinous zooplankton have sensory apparati that can detect gravity or light, and these two types of sense organs clearly are sufficient to provide the information needed to discriminate 'up' from 'down'. While ocelli are typically present in light-mediated migrators, ocelli are not specifically required for perception of light by medusae, although medusae seem to require illumination to stimulate migrations (Mackie et al., 1981). Direct photo-stimulation of neurons has been described for jellyfish (Anderson & Mackie, 1977), and a number of cases of DVM have been described in species believed to lack ocelli: *Solmissus albescens* Gegenbaur (in Mills & Goy, 1988), *Chrysaora quinquecirrha* (Desor) (in Schuyler & Sullivan, 1997) and *Pelagia noctiluca* (WMG, unpublished observations). Moreover, direction and magnitude of illumination or the rate of change of illumination driving migrations seems to be species dependent (e.g. Mackie et al., 1981; Arkett, 1985; Schuyler & Sullivan, 1997).

Almost all experiments and observations regarding DVM, for all oceanic animals, have involved only light and gravity (Bayly, 1986). DVMs invariably correspond with diel changes in ambient illumination within the water column. It is tempting, therefore, to conclude that animals migrate up or down in simple, direct response to changes in the intensity of light during a 24-h day, by maintaining a species-specific, constant level of illumination as long as possible during twilight, the so-called 'constant isolume hypothesis' (Bayly, 1986). Nonetheless, there is surprisingly little evidence in the literature to suggest that the coincidence of swimming depth and penetration depth of light during twilight is anything more than a necessary consequence of the irrevocable rise and set of the sun [but see Backus et al. (1965) and Enright & Hamner (1967)].

Various alternative hypotheses regarding the cues that trigger DVM are also tenable. For example, changes in light intensity at dawn may provide the cue to initiate downward swimming, whereas the depth to which the population descends during the day might be determined by a secondary cue such as pressure, temperature, salinity or light intensity. At dusk, alternatively, upward swimming might well be triggered by decreasing light intensity but the upward or downward extent of the migration may be constrained simply by the physical presence of the sea surface, by pressure, or by temperature or salinity discontinuities (e.g. Purcell & Madin, 1991). Another hypothesis invokes the presence of an internal circadian rhythm with which the animals tell time of day and thereby anticipate dawn and dusk (Enright & Hamner, 1967). An internal clock could trigger directed swimming behavior, with final position in the water column adjusted according to information provided by pressure, temperature, salinity, light intensity or the presence of the sea surface (Enright & Hamner, 1967). Unfortunately, there is no evidence in the literature, to our knowledge, about how any gelatinous zooplankter determines when to migrate vertically or about what cues are used to determine a suitable depth to terminate vertical migrations.

Although the physical cues required to trigger DVM are poorly understood, there is no question that many species of medusae regularly engage in diurnal vertical migratory behavior. For example, in several of the marine lakes in Palau, two species of scyphomedusae exhibit quite different DVM patterns. Hamner et al. (1982) found that the moon jelly, *Aurelia aurita* (L.), engaged in typical DVM, swimming to the surface at night and down during the day. However, unlike many diurnal vertical migrators that descend during the day presumably to avoid visual predators, *A. aurita* has no pelagic predators in these lakes. *Aurelia aurita* may simply be tracking their copepod prey, which mi-

grate down to darker waters in daytime, probably to avoid visual predators such as silverside fishes. Thus, the vertical diurnal migration patterns of *A. aurita* in Jellyfish Lake may be the result of optimal foraging behavior rather than a response to daily changes in ambient illumination. *Aurelia aurita* does engage in active foraging behavior in the laboratory. Bailey & Batty (1983) demonstrated that starved *A. aurita* remained quiescent at the top of a laboratory aquarium, but immediately after the introduction and capture of one fish larva the jellyfish began vigorously swimming throughout the tank, clearly engaged in active foraging behavior.

Variations in migratory behavior within the genus *Aurelia* (and quite possibly within the species *A. aurita*) are pronounced. During the summer in Saanich Inlet, Vancouver Island, Canada, a large population of presumably *A. aurita* (possibly *A. labiata* Chamisso & Eysenhardt) does not engage in DVM but remains at the surface both day and night (Hamner et al., 1994). By contrast, *A. aurita* in Eil Malk Jellyfish Lake (now called Tourist Lake), Palau, engaged in normal vertical diurnal migration behavior until 1998. At that time an extreme 'La Niña' occurred in the western Pacific and the marine lakes in Palau became exceptionally warm. The high lake temperature did not affect the size of the *A. aurita* medusa population, but all 1.6 million of the *Mastigias* sp. medusae disappeared (Dawson et al., 2001). For unknown reasons, the remaining population of *A. aurita* ceased its daily vertical diurnal migration and these medusae now remain at the surface both day and night. While other environmental changes cannot be discounted, this behavioral shift suggests that *A. aurita* can exhibit considerable behavioral plasticity. Prior to their disappearance, the *Mastigias* sp. exhibited an unusual example of reverse vertical migrations, wherein the animals remained at the surface throughout the day and migrated to depth during the night. The *Mastigias* sp. made individual, repeated vertical excursions at night to the permanent chemocline of this meromictic marine lake, presumably to bathe the symbiotic zooxanthellae in nutrients, but the medusae remained at the sunlit surface waters during the day presumably to provide the zooxanthellae with light for photosynthesis (Hamner et al., 1982).

DVM is also reported in several salp species, including *Salpa aspera* Chamisso (Wiebe et al., 1979), *Salpa fusiformis* Cuvier (Franqueville, 1971), and *Cyclosalpa bakeri* (in Purcell & Madin, 1991). Wiebe et al. (1979) described long-distance vertical migra-

tions of at least 800 m for the large salp, *S. aspera*, in northwestern Atlantic slope water. These long-distance vertical migrations were attributed to nighttime feeding in surface waters. The similar, but shallower (<30 m), migration pattern of *Cyclosalpa bakeri* in the subarctic Pacific was attributed instead to near-surface spawning (Purcell & Madin, 1991). In fact, as discussed by Purcell & Madin (1991), diel periodicity of light seems to be inherently linked to both swimming activity and gamete release in many gelatinous zooplankton.

Horizontal movements of jellyfish were overlooked for the most part until the 1980's when *in situ* ethological descriptions of planktonic organisms began to appear in the literature (reviewed in Hamner, 1995). Published accounts of horizontal migrations are still somewhat rare, yet in existing examples some generalizations have emerged about the physical cues used during horizontal migration and, in at least one instance, the adaptive advantages of horizontal migration seem clear. Horizontal migrations, like vertical migrations, are possible only if the animals can perceive, and respond to, horizontal environmental cues. Furthermore, horizontal cues must be scaled to jellyfish swimming to elicit an effective response. As such, only small-scale horizontal movements have been documented for gelatinous zooplankton. Light appears to be the dominant cue used by gelatinous zooplankton for directed horizontal migrations that lead to aggregation.

The first documented case of horizontal migration in a jellyfish was for *Mastigias* sp. in the marine lakes of Palau (Hamner & Hauri, 1981). *Mastigias* has symbiotic zooxanthellae in its tissues and obtains much of its daily nutrition from these algae (Muscatine & Marian, 1982; Muscatine et al., 1986; McCloskey et al., 1994). Sunlight governs the life of *Mastigias* and 70% of the population is concentrated in the top 2.5 m of the water column during daytime. In Eil Malk Jellyfish Lake the entire population of *Mastigias* migrates horizontally each morning towards the east end, a maximum distance of about 0.5 km. The jellyfish stop swimming eastward when they reach the shadow line beneath the mangroves at the end of the lake. When the population exceeded one million medusae, they were compressed into an intense, milling aggregation at the eastern end by mid-day, with densities often exceeding 1000 medusae m^{-3}. In the present smaller population, the accumulation at the eastern shadow line is less dense, but still the medusae all reorient to the west by the early afternoon. By late afternoon all of

the medusae have migrated back to the western basin, where they remain until dawn and engage in nocturnal vertical migration, as described above.

Since *Mastigias* sp. are nutritionally dependent on photosynthesis by their symbiotic algae, it is tempting to postulate that their migrations are simple eastward phototactic responses toward the sun in the morning and westward toward the sun in the afternoon. But on partially overcast days *Mastigias* sp. often begins its westward migration as early as 10:00 h two hours before the sun has passed its zenith, before there is clear phototactic directional information from the sun (L. Colin, pers. com.). Moreover, in two other jellyfish lakes in Palau, *Mastigias* sp. migrates in quite different compass directions during the day, west to east in one lake and north to south in the second (Hamner & Hauri, 1981). Consequently, we do not yet fully understand the environmental cues used by *Mastigias* sp. for horizontal migration.

The 'sun-compass' hypothesis for oriented swimming is supported by a large population of *Aurelia aurita* (or *A. labiata*) in Saanich Inlet, British Columbia (Hamner et al., 1994). When the sun is shining, *Aurelia* sp. exhibits southeasterly migration during the morning, however, when the sun is obscured either by clouds or by shadows cast by the eastern ridge of the fjord, the population becomes randomly oriented. Likewise, the population is also randomly oriented at night. In the absence of solar cues, the population is dispersed by both randomly oriented swimming and tidal currents, but in the presence of direct sun, concentrated aggregations of medusae form along the southeastern shore of the fjord. This type of navigation also requires time-compensated celestial navigation ability because the medusae swim toward the southeast all day long, irrespective of the position of the sun in the sky. Directed swimming of the population toward the southeast during the day increases population retention in the fjord and locally also greatly increases the population density along the south east side of the fjord. This results in a high density of sexually mature medusae, facilitating fertilization by minimizing gamete dilution. Two of us (WMG and WMH) have observed similar patterns for *A. aurita* along the eastern Monterey Bay during a recent investigation. While medusae can clearly navigate, the neurological mechanisms mediating the behavior are unknown. More specifically, no one yet understands how a rotating, radially symmetrical medusa can orient to a point source of light.

Vertical layers associated with temperature, salinity and density discontinuities

Zooplankton aggregations are quite often most concentrated around sharp density discontinuities (Owen, 1989). Earliest evidence of this distributional pattern are from SCUBA observations. Gradients of temperature and salinity (and hence density) are especially pronounced in fjords, estuaries, and the coastal transition zone. Therefore it is not surprising that gelatinous zooplankton layers are most pronounced in these physical regimes as well. Layering of jellies along gradients and discontinuities can be attributed to both active behavioral responses and passive accumulation.

Most of the experimental work to date has been on the interaction of gelatinous zooplankton with haloclines since, logistically at least, artificially constructed layers of temperature are far more difficult to construct than salinity layers (Harder, 1968). However, Arai (1976) did make a direct comparison between temperature and salinity stratification. With few exceptions, for instance some upwelling centers, vertical structure of coastal water columns is often established by salt content rather than temperature. While temperature contributes to water column stabilization during periods of surface warming, rapid cooling during the night-time or during cold front passage also leads to water column destabilization.

As jellyfish approach sharp haloclines, two situations develop that can independently lead to localized accumulation along the discontinuity. The first is passive accumulation. Since jellies are mostly water of the same ionic concentration of the surrounding seawater, they tend to remain along isohalines. The medusae also may exhibit active behavioral or physiological responses to the sudden osmotic stresses encountered at sharp haloclines, which may cause jellyfish to either slow their swimming while salts are being adjusted in tissues, or perhaps the animals simply turn around to remain in a specific range of physiological tolerance.

Much of our understanding of jellyfish around haloclines derives from a series of simple artificial water column experiments conducted in the 1960s and 1970s. The first experiments by Harder (1968) tested the general tendency of zooplankton to accumulate at discontinuities using artificially created haloclines and thermoclines in 2 l graduated cylinders. The breadth of taxa used by Harder (1968) included non-gelatinous zooplankton (e.g. copepods, mysids, barnacle larvae, veliger larvae and fish eggs), as well as the ctenophore, *Pleurobrachia pileus* O. F. Müller. Most test anim-

als, including *P. pileus,* accumulated at an artificial halocline that was only a few millimeters thick and represented a <3 ppt gradient. Harder concluded that accumulation of zooplankton at the artificial halocline was entirely passive.

Arai (1973) expanded on Harder's (1968) single observation of *P. pileus* by stepping the 2–3 ppt salinity gradient over a broader range of absolute salinities. She found that swimming behaviors accounted for changes in position within the cylinders with respect to salinity discontinuity. In higher salinity layers (>25 ppt), animals tended to accumulate higher in the column, while in lower salinity layers (~20 ppt), animals accumulated at the bottom. A similar reaction was observed for the hydromedusa *Sarsia tubulosa* M. Sars but was less clear for the hydromedusa *Phialidium gregarium* L. Agassiz (= *Clytia gregaria*).

Jellyfish are osmoconformers, and they maintain an ionic concentration of tissue and mesoglea that reflects the surrounding seawater medium (reviewed by Arai, 1997). Gelatinous zooplankton may actively pump sulfate ions to modify density as a form of buoyancy regulation in stratified water columns (Bidigare & Biggs, 1980). However, a simple experiment by Mills & Vogt (1984) showed sulfate ion regulation was not responsible for short-term density changes and that vertical migration in medusae and ctenophores was most likely accomplished by swimming. As such, small jellyfish such as hydromedusae and ctenophores attempting to cross a sharp halocline will be constrained within the halocline until the relatively slow process of osmosis across cell membranes has occurred (Mills, 1984). Recent experimental work by Wright & Purcell (1997) indicates that regulation of specific cations such as potassium, magnesium and sulfate is important in the estuarine jellyfish *Chrysaora quinquecirrha*, but that sulfate equilibration time for *C. quinquecirrha* was on the order of 40 h, too long to be of value for osmotic adjustments when medusae cross sharp haloclines.

All of the experimental evidence for passive accumulation of jellyfish along haloclines has been for small hydromedusae and ctenophores. Similar experimental studies have not been performed on the larger, faster swimming scyphomedusae. However, *in situ* observations from profiling video of large scyphomedusae and from SCUBA shows that larger medusae exhibit little difficulty in transiting sharp haloclines or thermoclines (WMG unpublished observations). Observations made on large (35–50 cm bell diameter) *Phyllorhiza punctata* von Lendenfeld in the north-

ern Gulf of Mexico showed that these scyphomedusae made extensive vertical excursions across steep haloclines (gradients of >10 ppt) without slowing as they approached the salinity discontinuity. Therefore, larger medusae that accumulate along a salinity discontinuity may be behaviorally motivated.

Interactions of jellyfish with thermoclines are less clear because an experimental approach with artificial water columns is difficult (e.g. Harder, 1968) and because the *in situ* effect of thermocline and halocline cannot be easily separated because the density effects of thermoclines and haloclines invariably interact. Arai (1976) showed that *Pleurobrachia pileus* and *Sarsia tubulosa* had a modest affinity to the thermal discontinuity that was similar to the effect to salinity. Her results indicated that a combined effect of thermal and salinity stratification led to greater concentration than experienced by either factor alone.

A drawback of the experimental studies described here is that they were all performed under artificial laboratory circumstances of reduced scale and an absence of natural halocline-related turbulence. While salt gradients are often very steep in estuaries and fjords, natural settings will always have a higher degree of shear creating turbulent mixing at discontinuities. Thus unmixed laboratory water columns tend to create gradients over millimeters to a few centimeters, whereas in nature these gradients tend to exist from centimeters to meters. Scaling is very important since the animals in question range from millimeters to almost meters in length. Future experiments in the laboratory will need to recreate realistic scales of salinity and temperature stratification.

Field evidence of thermocline effects is difficult to evaluate since there are few places where thermoclines exist in the absence of haloclines. Graham (1994) showed layering of a large scyphomedusa, *Chrysaora fuscescens* Brandt, along the thermocline in the Monterey Bay upwelling system. Solar heating controls structure of the water column in this and other upwelling regions, and the absence of a sharp halocline suggests that the thermocline is important in determining layering of this species. By contrast, *Chrysaora hysoscella* (L.) swims unimpeded through steep thermal gradients (Pagès & Gili, 1992). Pagès & Gili (1991) reported that upward migrations of some siphonophore species were restricted by a thermocline that created a density barrier. They also showed evidence that *Chelophyes appendiculata* Eschscholtz can pass easily through steep thermal gradients. In the subarctic Pacific, the 30 m thermocline (and halo-

cline) serves as a lower boundary to the daytime depth distribution of the salp, *Cyclosalpa bakeri* (Purcell & Madin, 1991). However, long-distance migrations of *Salpa aspera* are unaffected by the presence of a thermocline (Wiebe et al., 1979).

One physical characteristic that is difficult to evaluate experimentally is current shear. Current shear occurs at the air–sea interface, the benthic-boundary layer and within strong density discontinuities. Though there are a number of examples where gelatinous animals populate boundary-layers, mechanisms that function to perceive shear are very limited. In the western Mediterranean, the population of the mesopelagic appendicularian, *Oikopleura villafrancae* Fenaux, is associated with a persistent convergent flow that produces localized concentrations of food particles along the strongly stratified isopycnals (Gorsky et al., 1991). The ctenophore *Pleurobrachia pileus* also has been observed to vertically migrate in the Seine estuary in response to currents (Wang et al., 1995). A time-series of *P. pileus* in relation to the semi-diurnal tidal cycle showed that ctenophores generally had a hyperbenthic distribution, but the distribution extended to the surface in phase with tidal cycle during flood tides. This migration pattern is believed to contribute to estuarine retention of the *P. pileus* population (Wang et al., 1995). Strong horizontal shear within a surface front (Graham & Largier, 1997) may be important in maintaining aggregations of *Chrysaora fuscescens* in Monterey Bay (Graham, 1994).

Other cues: hydrostatic pressure and turbulence

Hydrostatic pressure, more than any other physical characteristic of the sea including light attenuation, potentially provides the best indication of depth to planktonic organisms. In a survey of hydrostatic pressure effects on swimming orientation, Rice (1964) illustrates that gelatinous zooplankton tend to respond to pressure variations using gravity as the proximal directional cue (with the exception of anthomedusae which lack a statocyst). A variety of threshold behavioral responses to pressure (termed barokinesis) for gelatinous zooplankton are discussed by Knight-Jones & Morgan (1966). Some of these response thresholds are remarkably small. For instance, the hydromedusae, *Gossea corynetes* Gosse and *Clytia hemispherica,* increase pulse rates following pressure increases of only 3–5 decibars. The physonect siphonophre, *Nanomia bijuga*, a major component of the

DVM community, is similarly responsive to pressure change (Jacobs, 1937). Among the Ctenophora, *Pleurobrachia pileus* and *Mnemiopsis* sp. are responsive over this same range of pressure change. Knight-Jones & Morgan (1966) argue that this consistent range of response threshold may play an important role in the feeding process as many gelatinous animals rely on activity (swimming) followed by inactivity while performing tentaculate fishing. Sensitivity in this manner to pressure changes would allow for maintenance of a layered aggregation of animals that still require a degree of vertical movement to feed. Unfortunately, pressure receptors for most of these taxa have not been identified.

Turbulence might be sensed as pressure waves detected across the body of an animal (Knight-Jones & Morgan, 1966). Many gelatinous animals are susceptible to tissue damage from excessive turbulence near the sea surface or close to shore where waves and bottom currents create intense shear stresses that could easily damage them. The abilities of gelatinous animals to sense and, accordingly, move away from these areas can contribute to observed layering and migrations of gelatinous zooplankton (e.g. Kopacz, 1994). In the Pamlico River estuary, wind and turbulence strongly affected the distribution of the ctenophore *Mnemiopsis leidyi* A. Agassiz (in Miller, 1974). Ctenophores remained at the surface until encountering turbulence that caused them to sound. They were then transported toward the shore in a bottom counter-current until turbulence diminished and they returned to the surface. This behavior tended to keep the ctenophores off the beach and out of rough water, unfavorable conditions for weakly swimming, soft bodied organisms. Shanks & Graham (1987) described a similar turbulence avoidance behavior for the rhizostome medusa, *Stomolophus meleagris* L. Agassiz, in coastal waters of North Carolina.

Accumulation at the shoreline

The formation and maintenance of gelatinous zooplankton aggregations often depends on impedance of swimming by physical barriers. In the next two sections, we review the literature that invokes physical barriers as mechanisms of gelatinous zooplankton aggregation. For this purpose, physical barriers include both geological (i.e. shoreline and seafloor) and hydrographic (i.e. horizontal fronts and vertical discontinuities) and therefore do not imply that the barrier

is impermeable to exchange across the barrier. In the following discussion, it is important for the reader to draw upon the earlier examples of behaviorally mediated swimming because it is the inherent interaction of behavior with physical barriers that creates aggregation of gelatinous zooplankton.

Dense aggregations of jellyfish frequently occur in the surface waters along coastal margins. Accumulations appear to be strongly influenced by the direction and energy of prevailing winds and surface currents such that populations of jellyfish are compressed along the shoreline (e.g. Shenker, 1984; Larson, 1990). Pleustonic species, such as *Physalia physalis* (L.) and *Velella velella* (L.), are routinely blown onto shore by sustained onshore winds as 'mass strandings'(Kennedy, 1972; Evans, 1986). Mass strandings of pleustonic jellies are typically seasonal and dependent on wind direction and duration. Interestingly, the origin of these populations is often unknown (Bieri, 1977; Shannon & Chapman, 1983).

Wind alone often does not explain formation and maintenance of jellyfish aggregations along shorelines. In many cases, local hydrology interacts with topography or coastal prominences to produce retentive features that support entrainment of aggregations. It is often the specialized circulation along the coastline that interacts with swimming behavior to create or maintain aggregations. One such example is the entrainment of upwelled water by a coastal prominences in northern Monterey Bay, California. This feature, described by Graham et al. (1992) as 'upwelling shadows' is a site of a semi-persistent aggregation of *Chrysaora fuscescens* (Graham, 1994; Lenarz et al., 1995).

Another example of shoreline interaction on jellyfish blooms is in the Mediterranean Sea where blooms of the scyphomedusa *Pelagia noctiluca* (Forskål) occur over approximately decadal cycles (Goy et al., 1989). These blooms have been particularly problematic during the past twenty years (Malej, 1989). Dense subsurface swarms of *P. noctiluca* up to 20 m thick and extending for several kilometers along the shore (Malej, 1989) show marked behavioral patterns that facilitate aggregation under varying wind and current regimes. In calm waters, individuals within a subsurface aggregation swim actively but are oriented randomly (Zavodnik, 1987). However, when a coastal geostrophic current exists, the swimming direction of individuals within the aggregation becomes uniform and directed with current. As we have already indicated, we know little about the mechanistic nature of how medusae can 'sense' a current. Perhaps medusae sense current shear and not the current itself. After several days of sustained wind, large aggregations of jellyfish form along the mainland and island shores. Tidal currents are also important in concentrating *P. noctiluca* along the shore. During the flood tide, hundreds of medusae m^{-2} accumulate near the sea surface along the coast. On the ebb tide, these medusae leave the surface layer, and they are then driven into deeper layers away from shore (Zavodnik, 1987).

Accumulations at surface convergences

Fronts

Ocean fronts are a class of circulation that develops along the interface between water bodies of different origin. As such, fronts are ubiquitous in the World Ocean and exist across a number of scales from the Antarctic Polar Frontal Zone at tens of thousands of kilometers to Langmuir circulation at tens of meters. Because of the breadth in scale, fronts are considered one of the principle mechanisms for the re-distribution of biological patterns and processes in the sea (Owen, 1981; Mackas et al., 1985). Fronts are also quasi-ordered phenomena and tend to follow a set relationship between spatial and temporal scale (Mackas et al., 1985), i.e. larger features tend to be temporally persistent (but see Graham, 1993). Characteristic circulation of ocean fronts, in both the horizontal and vertical dimensions, manifest as convergence, divergence and shear. While divergent flow tends to disperse gelatinous zooplankton, convergent flow at fronts is often implicated in the formation and maintenance of gelatinous zooplankton aggregations. Current shear is a potential mechanism for orientation and thus may be an important, albeit poorly understood, mechanism for gelatinous zooplankton aggregation as well. Since the research on current shear perception by jellies is still in its infancy, our overview of surface fronts emphasizes convergent features.

Accumulation of gelatinous zooplankton within surface fronts is probably the most commonly reported type of jellyfish 'patchiness' in the sea. Yet, there are surprisingly few published examples describing the fine-scale mechanistic relationships between gelatinous zooplankton and fronts. Moreover, there is the common misperception that accumulation of gelatinous animals, especially large medusae, is entirely passive. This misperception is almost certainly based

on the high water content of gelatinous animals, which would appear to make them either weak swimmers or passive tracers. In fact, many large medusae are quite capable of swimming speeds that approach or exceed vertical (plunging) flow velocities within convergent fronts.

While the term 'front' is often applied generically to describe the interface between water bodies, this is a gross over-simplification for contemporary research on the dynamics of frontal systems (Federov, 1983). Conceptually, fronts have two characteristics relevant to biological systems. These are maximal horizontal gradients (Federov, 1983) and laterally convergent flow at the surface with induced vertical flow below (Owen, 1981). In this sense, we discuss the role of fronts in forming and maintaining gelatinous zooplankton aggregations without describing the abundance and complexities of the various types of fronts (e.g. upwelling, estuarine, tidal, shelf-break, etc.) since all of these fronts share characteristics of horizontal gradients and three-dimensional flow. However, we do differentiate fronts by scale as suggested by Federov (1983) into (i) large-scale, quasi-stationary, (ii) meso-scale, and (iii) small-scale, local origin. We will also discuss a fourth category of surface feature that includes even smaller convergent structures such as Langmuir cells and internal waves.

Ocean fronts serve as regions of intense trophic activity. Phytoplankton and small zooplankton grazers usually have generation times appropriately scaled to express increased production in many stable frontal regions (e.g. Pingree et al., 1977; Yamamoto & Nishizawa, 1986; Wolanksi & Hamner, 1988; Franks, 1992). Within the gelatinous zooplankton, perhaps only pelagic tunicates (Alldredge, 1982; Deibel, 1985; Purcell & Madin, 1991), ctenophores (Kremer, 1994; Sullivan et al., 2001) and siphonophores (Pagès et al., 2001) also have reproductive life-history characteristics that allow population responses to increased production within fronts. However, both hydromedusae and scyphomedusae have relatively long generation times when accounting for the benthic polyp stages. It is unlikely that aggregation of large medusae within fronts reflects locally increased reproduction, but rather an accumulation of animals by an interaction between the front's circulation and the animal's swimming behavior (or relative density).

There are relatively few data suggesting that the large, quasi- stationary oceanic frontal regions physically aggregate gelatinous zooplankton. Perhaps this is due to a paucity of large-scale cross-frontal surveys, or

perhaps it indicates that smaller scale, local circulation is more coherent with jellyfish aggregations. Mackas et al. (1985) suggested that ecological processes like behavioral aggregation are matched to physical processes that occur at scales of a few kilometers and less. Therefore, we would expect the largest scale fronts to reflect population and community level increases in abundance due to increased reproduction and population growth. Pagès et al. (1996) and Pagès & Schnack-Schiel (1996) have conducted large-scale frontal surveys in the vicinity of the Antarctic Polar Frontal Zone and Antarctic Slope Front, respectively. They indicate that these zones serve as boundaries for entire communities of gelatinous animals, but the evidence for physical aggregation in this large front is weak. Young et al. (1996) found no increase in biomass of gelatinous zooplankton in the sub-tropical convergence between East Australian Current water and sub-Antarctic water.

Meso-scale frontal regions such as shelf/slope fronts and meso-scale eddies are associated more with population-level changes of organisms than with physical-behavioral aggregation (Mackas et al., 1985). However, secondary circulation that develops along the boundaries of these systems may be quite important in creating local conditions that facilitate aggregation of gelatinous animals. A divergent shelf/slope front along the Catalan coast is a region of increased secondary production (Sabatés et al., 1989), however, only salps appear to be concentrated in this particular front. This indicates that salps are accumulating through population increases (i.e. blooms) rather than physical accumulation, which is unexpected in a divergent flow. Pagès & Gili (1992) reported substantially increased abundance of siphonophores and medusae in an upwelling front within the Agulhas Current system.

The literature is replete with examples of small fronts with local origin that serve as aggregation centers for gelatinous zooplankton. Coyle & Cooney (1993) conducted an acoustical study of zooplankton abundances around hydrographic fronts in the vicinity of the Pribilof Islands, Bering Sea. Fronts in this region exhibit both strong salinity and temperature gradients and contribute greatly to the overall variability of biological production in the southeast Bering Sea (Coachman, 1986). In the study by Coyle & Cooney (1993), sound-scattering around surface frontal features was dominated by cnidarian assemblages. However, the authors attributed this increased abundance to the elevated chlorophyll, trophic transfer in the region and numerical increase due to

reproduction. We suggest that medusae were probably physically accumulated in fronts, but other gelatinous (and non-crustacean) animal populations, such as chaetognaths and larvaceans, may have experienced population growth. Brodeur et al. (1997) also found that populations of large medusae are delineated by numerous tidal fronts in the eastern Bering Sea.

Local circulation patterns found within sounds, bays and estuaries also contribute to physical aggregation of gelatinous animals. In Prince William Sound, Alaska, Purcell et al. (2000) observed aggregations of up to millions of *Aurelia labiata*. Vertical swimming behaviors, up and down, likely promoted concentration within numerous convergences in this dynamic coastal region. Small swarms (20 m long, 5 m deep) of *Liriope tetraphylla* Chamisso & Eysenhardt in concentrations up to 3000 m^{-2} were reported in Hiroshima Bay within an estuarine front (Ueno & Mitsutani, 1994). Although the front's role could not be ascertained, they concluded that individuals within the swarm were reproducing. A similar swarm was described in the Río de la Plata estuary, Argentina, by Mianzan et al. (In press). In Tokyo Bay, *Aurelia aurita* aggregate at the innermost part near the estuarine frontal region, especially at the edge of the low salinity water mass (Toyokawa et al., 1997). Aggregations of gelatinous predators have been described from river-plume fronts in the Chesapeake Bay (MacGregor & Houde, 1996). In Monterey Bay, California, a frontal region between warm nearshore water and colder offshore water is a consistent location for large aggregations of *Chrysaora fuscescens* (Graham, 1994). Oriented swimming in Monterey Bay populations of *C. fuscescens* is described by Graham (1994), and this behavior likely contributes to their nearshore concentration. However, the cues for *C. fuscescens* swimming are not completely understood.

Temporary aggregations of gelatinous zooplankton often develop in small linear surface convergences during Langmuir circulation. Langmuir circulation cells typically develop under sustained winds that exceed about 2 m s^{-1} (but break down at wind speeds exceeding about 10 m s^{-1}). Under these conditions, surface convection cells form along the axis of the wind, creating alternating patterns of convergence and divergence. Within convergences, trapping of buoyant material is nearly 100% (Owen, 1981). Pleustonic animals like the Portuguese Man-O'-War, (*Physalia physalis*) are effectively entrained by Langmuir circulation cells (Woodcock, 1944). Upward-swimming epiplanktonic animals are also entrained within Lang-

muir cells. Alldredge (1982) observed long, parallel rows of appendicularians, *Oikopleura longicauda* Vogt, that were created by Langmuir circulation. High concentrations of appendicularians (up to 3565 ind l^{-1}) in these aggregations were believed to be spawning. A separate mechanism was proposed to explain the formation of rows of *O. longicauda* in surface waters by Owen (1966) who observed dense reddish concentrations of this appendicularian in calm weather. He suggested that under calm wind, small thermohaline circulation cells called Bénard cells (Owen, 1981) develop surface slicks that can also effectively trap organisms. Owen (1981) suggests that under a freshening wind, Langmuir circulation cells may develop from Bénard circulation cells.

There are also a number of examples of medusae being concentrated within Langmuir cells. In the Bering Sea, both hydromedusae and scyphomedusae form dense aggregations at the surface in summer (Hamner & Schneider, 1986). On windy nights, medusae reached concentrations of 1000 ind m^{-3} in regularly spaced, linear rows that ran parallel to the wind. In the Caribbean Sea, the small scyphomedusan, *Linuche unguiculata* Schwartz, formed dense, elongated patches with the elongated axis being parallel to the wind (Larson, 1992). These medusae were apparently maintained in these convergences by upward swimming. Patch-maintenance behavior of *L. unguiculata* appears to be a form of reproductive swarming (Larson, 1992). Shanks & Graham (1987) also observed dense aggregations of the scyphomedusa, *Stomolophus meleagris*, in Langmuir circulation cells. Development of *S. meleagris* aggregations was apparently facilitated by oriented swimming of medusae into or against wind and /or wave direction. Kingsford et al. (1991) reported concentrations of *Aurelia aurita* up to 29 ind m^{-3} in Langmuir slicks in an Australian coral reef lagoon.

In addition to the often-cited benefit of spawning within locally concentrated aggregations, there are a number of other additional advantages for gelatinous zooplankton. Purcell et al. (2000) suggest that, in addition to increased fertilization, accumulation of medusae within nearshore fronts may aid in the retention of aggregations close to shore and near hard substrate required by benthic polyps. In addition to retention, locally increased zooplankton prey populations are also distributed within these features (e.g. Graham, 1994; Purcell et al., 2000). Purcell et al. (2000) also noted that large aggregations of jellies might be an effective defense against predation, especially other gelatinous predators. We offer a final

advantage that highly concentrated aggregations of jellyfish may serve to exclude other potential competitors such as zooplanktivorous fishes and possibly other gelatinous species. Such exclusion of competitors might be facilitated by exudation of chemical 'scents' or unfired nematocysts (Shanks & Graham, 1988).

Conclusions and future directions for research

In this review, we have suggested that the highly aggregated dispersion of gelatinous zooplankton populations may, in part, be attributed to the distribution of physical processes and gradients in the sea. In many instances, local perception of large numbers of jellyfish may be misinterpreted as a real population increase, when in fact it is the local re-distribution of a population by some physical and/or behavioral mechanism. Moreover, long-term population changes may be important on an ecosystem scale, but local aggregations mediated by physical processes may be vastly more important on short-term ecological scales.

In many instances, locally enhanced concentrations of ctenophores, siphonophores and pelagic tunicates within fronts may be due to a rapid population increase. However, the presence of large medusae at physical discontinuities such as fronts and thermo- and haloclines indicates that physical accumulation has occurred because population increases of these large animals is almost always decoupled from water column processes. The physical accumulation of medusae may be linked to a variety of behavioral swimming responses to environmental cues, many of which are physical cues such as light, gravity, temperature, salinity (and density), current shear, pressure and turbulence. In some cases, weaker swimming hydromedusae and ctenophores may be passively accumulated in haloclines due to lagged adjustment of tissue salts.

Oceanographers have understood the distribution and dynamics of physical gradients and discontinuities for at least a hundred years longer than they have understood how these gradients influence marine organisms. Yet, most of the research we have reviewed here is largely descriptive and qualitative, and the few experimental studies that have been conducted were performed at unrealistically small scales (i.e., in small cylinders and aquaria). We suspect that inherent difficulties of working with gelatinous animals contribute to the paucity of information. With the continued de-velopment of novel *in situ* optical and acoustical techniques (e.g., Davis et al., 1992; Monger et al., 1998), we will gain a much more thorough understanding of the relationship between individuals, their behaviors and their physical environment. These developing systems are directly applicable to fragile gelatinous zooplankton distributions and can be integrated with a suite of sensors to characterize fully the physical environment. However, these tools will continue to provide mostly qualitative descriptions unless biological oceanographers work more closely with physical oceanographers and hydrodynamicists. The future of research in this area depends on cross-disciplinary cooperation in order to apply proper theoretical aspects of the physical environment to the biology of these important animals.

Acknowledgements

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