creasing cell buoyant density. This apparent gradient was not matched by the associative behavior of the cells as monitored by the size of the aggregates. The largest aggregates formed from cells of fraction 3; the aggregates of fraction 1 and 4 were considerably smaller. It appears then that IMP density is a characteristic that is not directly related to the size of aggregates of the cells. The size of the 24-hour aggregates, however, does appear to correlate with the number of flat cells that grow out in stationary cultures. Since the flat cells are able to adhere not only to artificial substrates but also to dissimilar cell types, they could form a bridge between cells in the aggregate. This would allow a large aggregate to form by alternately adding flat cells and other cells.

The appearance of the stationary cultures of fractions 2 and 3 suggests that the smaller cells adhere more readily to the flat cells than to each other. The cells of fraction 4, however, tended to adhere more closely to each other than to the flat cells, but not at all to the substrate. This led, in stationary cultures, to the formation of compact clusters on top of flat cells and a significant population of unattached aggregates.

The associative interactions between the cells in the different fractions are extremely complex, but it is now possible to use our separation procedure to isolate and analyze components of the mixture. This analysis is currently under way.

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18 December 1979; revised 22 May 1980

Influence of Siphonophore Behavior upon Their Natural Diets: Evidence for Aggressive Mimicry

Abstract. *Collection by divers permitted determination of the natural diets of siphonophore species within 11 genera. Siphonophores that swim rapidly to spread their tentacles capture small prey, whereas those that swim very weakly capture much larger prey. Nematocyst batteries of two species of weak swimmers closely resemble copepods and fish larvae. Morphology, behavior, and diet suggest that these two species attract large prey by mimicking other zooplankton.*

Siphonophores, pelagic cnidarians of the class Hydrozoa, have been likened to spiders in capturing prey that bump into a nearly invisible sticky network (*1*). The tentacles of siphonophores form a three-dimensional web, armed with millions of nematocysts that inject toxin into the prey on contact. The diets of these nonvisual predators depend in part on prey behavior, including avoidance of the predators and the ability to escape if contacted (*2*). The diets of siphonophores must also depend on predator behaviors that counteract prey avoidance and escape. The types and sizes of prey captured by various siphonophores differ according to the swimming activity and gastrozooid size of the siphonophore species. In addition, two of the siphonophore species examined may attract large prey by the movements of tentacular structures that resemble small zooplankton, an indication of aggressive mimicry among zooplankton.

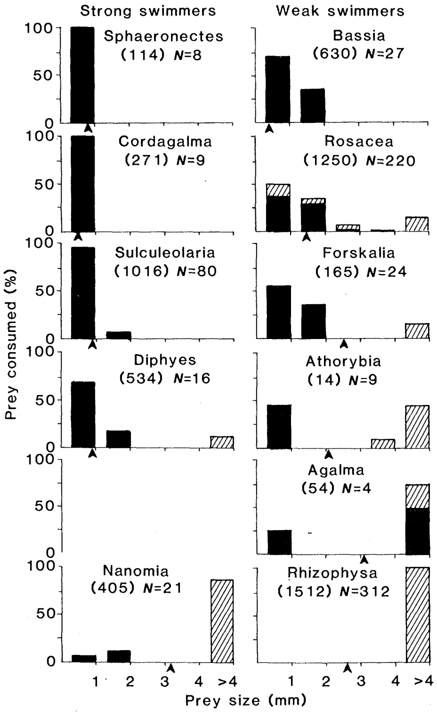

Fig. 1. Comparison of the sizes (measure of the greatest dimension, usually length) of natural prey captured by strongly and weakly swimming siphonophores. Gastrozooid length is indicated by an arrowhead under each horizontal axis. Copepod prey are indicated by black bars, noncopepod prey by diagonally shaded bars. Numbers of gastrozooids examined are in parentheses. Percentages are based on *N*, the number of measurable prey items.

While scuba diving at depths of 0 to 25 m, I collected siphonophores in jars and immediately killed them in situ with formaldehyde solution. I examined ingested prey in the following numbers of colonies of these species: 60 *Bassia bassensis*, 53 *Nanomia bijuga*, 47 *Rosacea cymbiformis*, 14 *Agalma okeni*, 6 *Sulculeolaria quadrivalvis*, 3 *S. turgida*, and 11 *Diphyes dispar* from the Gulf of California (*3*); 6 *Athorybia rosacea*, 10 *S. chuni*, 3 *S. monoica*, 15 *Forskalia edwardsii*, and *F. tholoides* from both the Sargasso Sea (*4*) and the Gulf of California; 11 *Cordagalma cordiformis* and 2 *S. biloba* from the Sargasso Sea; and 13 *Sphaeronectes gracilis*, 7 *Diphyes dispar*, 5 *S. quadrivalvis*, and 2 *S. chuni* from the California current (*5*). Since species of *Sulculeolaria* and of *Forskalia* consumed similar prey, data are presented by genus. All gastrozooids ("stomachs") were dissected or mounted whole on microscope slides with cover slips for prey identification and measurement at magnifications of ×25 to ×100.

Differences in the diets of several siphonophore species corresponded to differences in their swimming patterns. Some species swim rapidly (strong swimmers), often in an arc or in spirals (*1*, *6*). These siphonophores drift be-

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tween brief bouts of swimming that last 2 to 12 seconds and may be repeated up to 100 times per hour (*1*). Other species (weak swimmers), exhibit only subtle contractions or rotations to supplement water turbulence in spreading their tentacles.

The diets of strongly swimming siphonophores that have small gastrozooids consisted chiefly of small copepods (Fig. 1). In contrast, weakly swimming species that have larger gastrozooids captured a variety of relatively large prey. Regardless of swimming patterns, siphonophores that have large gastrozooids consumed large prey and, generally, a wide range of prey sizes. For example, *Nanomia*, a strong swimmer with large gastrozooids, consumed many large prey in addition to small prey. The distribution of prey sizes available in the environment, determined by plankton net tows (*7*), showed that 89 percent of available prey measured 1 mm or less, and 7 percent measured more than 4 mm (*8*). Thus the distributions of sizes of the ingested prey (Fig. 1) differed significantly (*9*) from that in the environment.

Rosacea cymbiformis, a weak swimmer, captured the widest variety of prey. Commonly consumed noncopepod prey measuring less than 4 mm included mollusk veliger larvae, crab zoea larvae, atlantid heteropods, and thecosome pteropods. Noncopepod prey larger than 4 mm included chaetognaths, fish larvae, crab megalopae, stomatopods, and juvenile shrimps. *Rhizophysa eysenhardti* is of special interest since it captured only fish larvae (*10*).

Siphonophores may affect the probability of encounters with different prey types by their swimming behavior. Strongly swimming siphonophores having numerous small gastrozooids captured small, common prey. These predators change locations, thus increasing their chances of encountering high-density patches of copepod prey. Weakly swimming siphonophores having fewer and larger gastrozooids captured relatively large, less common prey. Their inactivity could reduce avoidance by the more active noncopepods. Swimming to increase chance encounter with active uncommon prey would be energetically costly.

Two of the weakly swimming species may further enhance the capture of large prey by mimicking small zooplankton foods. Each siphonophore gastrozooid bears a tentacle with several branches (tentilla). In two of the three siphonophore suborders, each tentillum bears a complex, highly ordered battery of nematocysts (*11*), which fires explosively upon stretching of an elastic ligament that joins one or two terminal filaments to the battery. The coiled nematocyst batteries of *Agalma okeni* are red, with two terminal filaments projecting from one end. These structures resemble copepods with two long antennae (Fig. 2A). Laboratory observations of six specimens, which spread their tentacles in containers of seawater, showed that each tentillum contracts independently at variable intervals between 5 and 30 seconds. This motion resembles the darting swimming of a calanoid copepod. A specimen of *A. okeni* with two gastrozooids had 18 such "lures." *Agalma okeni* gastrozooids contained crab megalopa larvae (*1*), large copepods, and euphausiids, all of which eat copepods (*12*). This suggests that predators of copepods may be attracted by either visual or vibrational stimuli (*13*) to feed upon the nematocyst-packed lures, thus becoming prey for the siphonophore instead.

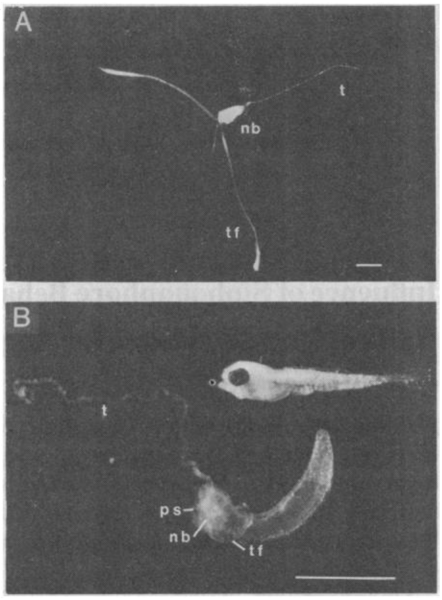

Fig. 2. (A) *Agalma okeni* nematocyst battery resembling a copepod. The terminal filaments (*tf*) appear similar to the antennae of a copepod. (B) Comparison of a fish larva (top) with a nematocyst battery from *Athorybia rosacea*. Two pigmented spots (*ps*) at the enlarged "head" resemble eyes, and two terminal filaments (*tf*) curl back in the position of pectoral fins; *t*, tentillum; *nb*, nematocyst battery. Scale bars, 1.0 mm.

Some of the nematocyst batteries in *Athorybia rosacea* are elongated structures resembling small fish larvae (Fig. 2B). The tentilla of five specimens observed in the laboratory contracted rapidly two or three times, with a pause of a few seconds separating each bout. The resultant motions of the nematocyst battery are similar to the swimming or feeding movements of a larval fish. In a specimen of *A. rosacea* having two gastrozooids, nine of the nematocyst batteries resembled fish larvae. These were interspersed among 76 small oval batteries that resembled small copepods or nauplii. The *A. rosacea* gastrozooids contained fish larvae, chaetognaths, and a shrimp larva. Chaetognaths are known to consume fish larvae (*14*). This suggests that predators of fish larvae may be attracted to the fishlike nematocyst batteries. In addition, fish larvae may be attracted to school with the batteries that resemble other fish larvae.

The significance of the above results is threefold. (i) The methods enabled the determination of the natural diets of siphonophores. The few previous studies on other gelatinous planktonic carnivores have been limited to species that could be collected relatively undamaged in nets or at the surface (*2, 15, 16*). Ingestion of prey concentrated in nets can introduce artifacts in feeding studies (*17*). (ii) Differences in the diets of several siphonophore species showed a correlation with differences in their structure and behavior. (iii) This appears to be the first report of aggressive mimicry in zooplankton. Other animals which use lures to entice prey include angler fish (*18, 19*), bolus spiders (*18*), and fireflies (*20*).

Studies of the natural feeding of zooplankton species are necessary for understanding the ecology of pelagic communities.

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8. These percentages probably underestimate small zooplankton that passed through the net. Chaetognaths comprised 33 percent of prey measuring more than 4 mm.
9. Small sample size prevented statistical testing for *Diphyes*, *Athorybia*, and *Agalma*. The percentage of available prey measuring less than 2 mm was compared to that consumed by each genus. All genera tested showed significant dif-

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23 January 1980; revised 20 March 1980

Oil and Gas in Offshore Tracts: Inexactness of Resource Estimates Prior to Drilling

The report of Uman *et al.* *(1)* illustrates that the estimation of oil and gas resources prior to drilling is a very inexact process. Uman *et al.* compare the resource estimates made by the U.S. Geological Survey (USGS) for a series of tracts on the federal outer continental shelf (OCS) prior to leasing and drilling with the estimated reserves discovered after drilling. They also compare the current estimation procedures with those that have been used in the past. The most important conclusion that can be drawn from their report is not that the present procedures are significantly better than earlier procedures (they are not) but that both procedures are ineffective. As Uman *et al.* point out, there is a significant positive correlation between prelease sale estimates and postdrilling estimates, but the correlation for the current Monte Carlo estimation procedure *(2)* is only $r = .45$. This means that only 20 percent of the variation in postdrilling estimates can be associated with the predrilling estimates; 80 percent of the variance is independent of the prior estimates. The standard error of the estimate is very large, and there is thus a wide confidence interval about the regression (Fig. 1). Figure 1 also shows the confidence bands of the forecast, which exceed two orders of magnitude at the means. These results suggest that current estimation procedures are very imprecise at best. Figure 1 of Uman *et al.* *(1)* shows a line having a slope of $y = x$, or perfect agreement between presale and postdrilling estimates; however, the slope of the regression between presale estimates and postdrilling estimates is significantly less than 1.0, and the intercept is significantly greater than 0.0. Therefore, there is a tendency to overestimate resources in advance of drilling when the presale estimates are less than about 10 million barrels of oil equivalent (MMBOE) and to underestimate resources when the presale estimate is greater than 10 MMBOE.

Perhaps it is most critical to note that Uman *et al.* are dealing with a censored data set, because they consider only those tracts that were leased and from which hydrocarbons were subsequently produced. They did not include tracts for which presale estimates were made although no commercial quantities of oil or gas were found. Since approximately 38 percent of Gulf Coast lease tracts that have been drilled have failed to produce *(3)*, there must be about 18 additional points that should have been plotted in figure 1 of *(1)* for sales 33 to 44. Since these additional points would all lie below any values shown, it is quite possible that these additional tracts would cause the correlation between prelease estimates and postdrilling estimates to become zero or even negative.

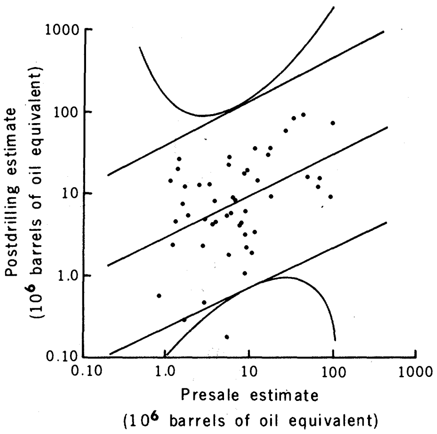

Fig. 1. Presale and postdrilling estimates of recoverable hydrocarbons for 49 tracts of lease sales 33 to 44 on the federal outer continental shelf. The central straight line is the regression of postdrilling estimates on the presale estimates; the outer straight lines are the upper and lower 95 percent confidence limits for the regression. The curved lines are the upper and lower 95 percent confidence limits for the estimates made prior to leasing.

The USGS prelease evaluation procedure is an extension of widely used reservoir analysis methods for economic appraisal *(4)*, but this procedure is applied under conditions of extreme uncertainty when used in advance of drilling. By using this method, one can calculate the volume of recoverable oil or gas in place in lease tracts on the basis of a consideration of 17 diverse geologic parameters such as reservoir thicknesses, volumes of closure, porosities, water saturations, and ratios of oil to gas *(5)*. Since these reservoir characteristics are not known prior to drilling, they must be estimated from seismic data and from logs and production histories of wells drilled elsewhere in the region. In an attempt to account for uncertainty, the parameters are given as distributions and the volumetric calculations are performed by Monte Carlo methods. The results are distributions of possible resources, which then are tempered by the analyst's assessment of the probability that no recoverable hydrocarbons exist at all in the tracts. The presale estimates given by Uman *et al.* *(1)* are the expected values of these distributions. In tract evaluation, further analysis is performed to yield expected monetary values, which can be used to establish fair market values and minimum acceptable bids set by the Bureau of Land Management.

The effort required to obtain the input distributions of geologic and reservoir properties required by the Monte Carlo analysis is substantial. The imprecise results reported by Uman *et al.* suggest that alternative estimation procedures should be investigated to determine if improved forecasts can be made or if estimates of equivalent precision can be obtained with substantially less effort. We have suggested *(6)* that it may be possible to make effective resource forecasts for tracts in the Louisiana OCS by regressing the oil and gas volumes of known reservoirs onto seismically perceivable variables, such as the apparent areas, heights, and volumes of closure of the structures which contain these reservoirs. A wealth of data are available in the Louisiana and Texas OCS that would permit these seismic properties, which are established in advance of drilling, to be statistically compared with the results of drilling. The regression could then be used to estimate the resources that may

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