FEEDING PREFERENCES AND RATES OF THE SNAIL, *IANTHINA PROLONGATA*, THE BARNACLE, *LEPAS ANSERIFERA*, THE NUDIBRANCHS, *GLAUCUS ATLANTICUS* AND *FIONA PINNATA*, AND THE FOOD WEB IN THE MARINE NEUSTON[1)]

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With Plates III–IV and 1 Text-figure

On the afternoon of November 5, 1965 during strong north-northwest winds, *Porpita, Velella, Physalia, Glaucus, Lepas, Fiona,* and three species of *Ianthina* were blown onto the north beach of the Seto Marine Biological Laboratory. In the Laboratory with an ample supply of running sea water, many of these animals lived for several days and I was able to observe their feeding preferences and rates. On the basis of these obervations and the reports of other workers it is possible to construct a preliminary diagram of the neuston food web.

Ianthina prolongata

Of the three species of *Ianthina* washed ashore, *I. janthina* forma *balteata*, *I. umbilicata*, and *I. prolongata*, *I. prolongata* was most abundant. I was able to collect more than 160 of them in less than an hour. All were placed in jars of running sea water to observe their behavior. The next morning most were dead but twelve kept in small jars were still alive. In the large jars the flow of water was not fast enough to prevent a sharp drop in temperature during the night and in the morning the water was between 15 and 16 degrees C. Probably it was even lower during the night. In the small jars with more rapid water flow, the temperature in the morning was about 22 degrees C. Some of these specimens lived for two weeks and one individual lived for 16 days. This accidental experiment agrees with the field observatios of SAVILOV (1965), who found the northern limit of the Northwest Pacific neuston community at 15°C.

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Although SAVILOV (1956) reported that *Ianthina* floats expanded far in front of itself, *Ianthina prolongata* in the laboratory normally rested quietly on the surface with the head and snout drawn back against the shell. On November 5, using a face mask about 10 meters from shore, I watched a specimen of *Ianthina prolongata* for several minutes. The water was rough with waves about 70 cm high. Once the *Ianthina* was carried about 15 cm below the surface by a breaking white cap. It popped immediately to the surface. At no time did it extend its snout. In the two weeks they were kept in the laboratory, only rarely was the snout extended without the provocation of nearby food.

Ianthina prolongata when feeding did not emit purple fluid as observed by DAVID (in WILSON and WILSON, 1956) in the feeding of *I. janthina.* This could be due to species or size differences or differences in the laboratory environments. SAVILOV (1956) indicated that as in other gastropods the release of the purple dye may be related to defense, as reported by many other authors (LAURSEN, 1953). This seemed to be the case in the present study because the dye was released only when I disturbed the animals.

A. *Velella* as food:

When a *Velella* 20 mm long was placed near three ianthinas (shell widths of 20, 25, and 30 mm) they immediately began a very active, almost violent, searching process extending the snout as much as twe centimeters and waving it back and forth. By chance the *Velella* drifted close to one of the ianthinas and was grasped immediately at the rim in a firm grip. The mouth flaps, with a sucking appearance, spread over a large part of the *Velella.* It began to rasp off the rim, gonozooids and dactyls of the *Velella* and ate around the rim completely in 28 minutes. It then let go of the *Velella* even though the float was still covered with tissue and there were still a few gonozooids under the float. When this partially eaten *Velella* was pushed to the *Ianthina* several times, it refused to eat it although it explored it briefly with its snout. Immediately after this I offered the same *Ianthina* a fresh *Velella* of the same size and it grasped it and began feeding, repeating its first feat of eating the rim, dactyls, and some gonozooids in about 18 minutes. Again it released the partially eaten *Velella.* Because the supply of *Velella* was limited, this individual was not fed unil the next day. It then ate in the same manner a *Velella* 15 mm long. After this meal it did not feed again for two days although food was offered several times.

In 1950 off California I caught a *Velella* 54 mm long that was being eaten by a 6 mm wide *Ianthina* of undetermined species. The *Ianthina* was attached to the ventral surface of the *Velella* and had eaten a circular patch of tissue from the *Velella.* However, in this case the rate of feeding must have been much slower, a matter of days, because the hole was partially healed over with a thick tissue growth and a *Lepas* cyprid had settled on the exposed skeleton of *Velella.*

DAVID (in WILSON and WILSON, 1956) reported two different methods of feeding. *Ianthina janthina* may abandon its float and attach itself to the *Velella* or it may keep its float and merely hold onto the prey. The first method of feeding was described by SAVILOV (1956) and is the same as I observed off California. In the present study *I. prolongata* fed in the second way and did not abandon its float. Although the method of feeding may be different in different species, it is probably a matter of size relationship. If the *Velella* is large and the *Ianthina* small, the *Ianthina* abandons its float and climbs aboard to feed for several hours or longer. In this case all of the tissue may be stripped from the skeleton. If the *Ianthina* is large and the *Velella* small, then the float is not abandoned and after the quick meal the partially cleaned skeleton is cast adrift. This does mean, however, that small species of *Ianthina* such as *Ianthina umbilicata* would more often feed in the first way.

B. *Porpita* as food:

Another starved *Ianthina prolongata* (shell width 20 mm) was placed in a jar with two porpitas (float diameter 10 mm). As in the case with *Velella*, the *Ianthina* immediately began frantic search activity but after several minutes could not reach the porpitas. The porpitas apparently could not sense the *Ianthina* because they continued their normal pulsating contractions of the dactyls (Pl. III A). When pushed close to one *Porpita*, the *Ianthina* struck at it viciously and took a large chunk out of the ring of blue dactyls spread on the surface. The *Porpita* immediately stopped its pulsations and the force of the encounter pushed the two animals apart so that the *Ianthina* could no longer reach the *Porpita*. The widespread, blue tentacles of *Porpita* act as a fender, sometimes keeping *Ianthina* from reaching the float. The blue dactyls do not contract in the pulsations of the lower parts, but do hide the white underparts from above. On November 5, several specimens of *Porpita* with sections of the blue dactyls missing were collected, so it appears that this happens in nature.

On the other hand, if the *Ianthina* is pushed strongly against the *Porpita* as might occur in rough weather, it can grasp the float (Pl. III B). Then, as it does with *Velella*, it eats around the edge of the float, removing all dactyls and almost all gonozooids but casting out the float skeleton still covered with epidermis (Pl. III C). If the *Ianthina* is left isolated for several days with only this stripped float for food, it will eat all of the tissue from the float, but apparently the dactyls and gonozooids are preferred and the partially stripped animal is cast adrift. Most of the specimens of *Porpita* collected on November 5 were in this stripped condition. The 20 mm wide *Ianthina* completed the circuit around a *Porpita* (skeleton diameter 10 mm) in fifteen minutes, while another *Ianthina* about the same size completed its feeding on a *Porpita* 10 mm in diameter in eighteen minutes.

GANAPATI and RAO (1959) reported that off Waltair *Ianthina janthina* attaches to the underside of *Porpita* in feeding. As in feeding on *Velella* this is probably related to size difference between predator and prey.

C. *Physalia* as food:

Two starved individuals of *Ianthina prolongata* were offered a *Physalia* (float length 25 mm). Although they explored the tentacles and dactyls, they refused to eat it and withdrew to the normal resting position. T. TOKIOKA (personal communication) reports that he has seen captive *Ianthina* eat *Physalia*. It may be that the *Physalia* I provided was damaged and had lost some of the parts that *Ianthina* eats, but it appeared to be in good condition, and was the best of the several specimens I had available for experimentation.

D. *Glaucus* as food:

Several times I placed active individuals of *Glaucus* close to *Ianthina prolongata* but they were never attacked and never elicited the feeding response in *Ianthina*.

E. *Ianthina* as food:

When *Velella* was first offered as food, the *Ianthina* struck out wildly and one attacked another, taking hold of it. The one being grasped withdrew into its shell at which point they were pulled apart. Near the end of these laboratory studies, when the *Ianthina* were again starving, I twice saw them attack one another. This agrees with the report of LAURSEN (1953) on stomach contents, that *Ianthina* is cannibalistic.

These observations indicate that *Ianthina prolongata*:

1. prefers *Velella* and *Porpita* to *Physalia* and is occasionally cannibalistic.
2. can detect, probably by taste, *Velella* and *Porpita* when within six to eight cm of them, but cannot swim to the prey. They can only strike out randomly with the snout. *Ianthina* depends on chance contact due to wind, waves or currents to reach its prey.
3. probably changes its method of feeding depending on its size and the size of its prey. If the prey is large, it may abandon its float and climb on board to eat all the tissue, but if the prey is small, it keeps its float and casts the partially eaten prey adrift.
4. when wider than 15 mm it prefers the float margin, dactyls and gonozooids to the epidermis covering the float of *Velella* and *Porpita*, and generally casts out the partially eaten animal.
5. can eat the dactyls, gonozooids and float margin from a 20 mm long *Velella* in 20 minutes and a 10 mm diameter *Porpita* in 18 minutes. They probably can eat at least two a day.
6. is sometimes prevented from grasping the float of *Porpita* by the widespread, easily detached blue dactyls of *Porpita*.

Lepas anserifera

Several *Velella* were stored overnight in a shallow plastic dish with two pieces of pumice and a plastic zôri or sandal that had the barnacle, *Lepas anserifera* attached. The next day I found one of the velellas attached to a *Lepas* (capitulum length 6 mm). Close examination showed that the *Lepas* had hold of the *Velella* which had to be forcibly removed. I then pushed a *Velella* so that it drifted against several *Lepas* and it was quickly caught by two of them (Pl. IV A). The legs of this barnacle are able to act independently of one another and can manipulate *Velella* into the orifice to be eaten. This species of *Lepas* often remains motionless for long periods with the legs fully extended, an excellent position to catch a large object that drifts against it.

The captured *Velella* was not completely eaten by the two barnacles but was "passed" along the group until it was completely stripped of all epidermis. Only the transparent plastic float remained. SAVILOV (1956) shows a specimen of *Lepas fascicularis* eating a completely intact *Velella.* I fed *Lepas* several of the velellas only partially eaten by *Ianthina* and they finished cleaning the float. Specimens only 4 mm in capitulum length were able to hold onto a *Velella* 10 mm long. The feeding rate is quite variable. It took 12 hours for the group on the pumice to clean one 15 mm long *Velella,* while another group cleaned a 10 mm diameter *Porpita* partially stripped by *Ianthina* in about 3 hours. In both these groups the barnacles averaged 5 mm capitulum length. *Lepas anserifera* also caught and held the tentacles of a *Physalia* (float length 30 mm). I removed the *Physalia* from the *Lepas* but parts of the siphonophore were well down inside the barnacle. When the supply of *Velella* was gone, I fed *Lepas* for several weeks on 5 mm square pieces of raw fish and squid. They seemed to prefer the fish to the squid.

Glaucus atlanticus

Twenty-one live *Glaucus* ranging in length from 5 to 32 mm were tested for food preferences. They would not eat *Ianthina* and seemed only mildly interested in *Velella* and *Porpita,* but they actively attacked *Physalia.* One *Glaucus* fed on *Vellella* from underneath for 20 minutes as shown by SAVILOV (1956), but when it stopped, there were still many dactyls and gonozooids left. It ate only a small amount of the total animal. Feeding on *Physalia* was much more active. *Glaucus* pushes under the float and feeds on the gastrozooids (Pl. IV B). They were slow feeders, a 32 mm long *Glaucus* took several hours to eat all the gastrozooids and gonozooids of a *Physalia* with a 30 mm long float. All of the *Glaucus* died two days after these experiments so these results may not be representative. *Glaucus* frequently attacked one another and bit off pieces of the tail and "arms". One 20 mm long individual ate all but the head and trunk of a 15 mm long individual in 30 minutes.

Savilov (1956) indicated that *Glaucus lineatus* (possibly a synonym for *G. atlanticus*) swims to its prey, but the *Glaucus* at Shirahama could not swim. Furthermore specimens 5 to 30 mm long are extremely buoyant and pop immediately to the surface if pushed below. They do not depend on surface tension for support.

Fiona pinnata

Several specimens of *Fiona pinnata* were found among the collection of *Lepas anserifera*. Two individuals, each about 15 mm long were isolated on a single piece of pumice with 41 *Lepas* two to ten mm long attached to it. In twelve hours the two ate 18 of the barnacles. Kropp (1931) reported that the blue-colored *Fiona marina* (possibly a synonym of *F. pinnata*) in the Mediterranean is an active predator on *Velella*. Savilov (1956) showed *Aeolis* (*Fiona marina* ?) together with *Lepas* on a cleaned float of *Velella* and reported that this specimen ate all the polyps off the lower surface and bored into the bell itself.

Discussion

These observations and earlier reports indicate that in the neuston community there is considerable niche differentiation in type of food eaten. For example, *Ianthina* eats *Velella* and *Porpita* in preference to *Physalia*, while *Glaucus* prefers *Physalia*. *Lepas* will eat all three but is especially effective at eating the tissue left on *Velella* and *Porpita* by larger ianthinas which prefer the dactyls and gonozooids. *Fiona pinnata* feeds largely on *Lepas*. On the other hand, when food is in short supply or after periods of prolonged starvation, this niche differentiation probably breaks down and then even cannibalism is practiced by *Ianthina* and *Glaucus*. These relationships are shown schematically in Fig. 1. The heavy arrows indicate major routes of energy transfer, light arrows less important sources of energy, dashed arrows conjectural energy routes. The diagram is a simplified picture of the local population observed at Shirahama over a period of several weeks. It does not include many animals that probably play a minor role in the distribution of energy, for example, the crab *Planes cyaneus* (=*minutus*), the polychaete *Amphinome*, a flatworm commensal on *Porpita*, the trematode parasites of *Physalia*, the parasitic nematodes of *Porpita* and many other animals.

However, several points seem clear. *Velella*, the central food source of many neuston animals is three to four steps from the phytoplankton and even when *Porpita* is available as food, *Ianthina* is far removed from the primary energy source. Similarly, *Glaucus* is four steps from the phytoplankton. *Fiona* *pinnata* is at least four steps from the energy base of phytoplankton. These three top carnivores have no known predators in the juvenile and adult stages, but their protective coloration, countershading in *Glaucus* and *Ianthina* and mimicry in *Fiona*, indicates that they are preyed upon by animals with good vision, either fishes or birds or both. This is indicated in Fig. 1 by the arrows with question marks. The fish *Nomeus* is known to feed on *Physalia* (KATO, 1933) and larger fish such as *Coryphaena* or *Mola* may feed on *Ianthina*, *Glaucus* and *Fiona*. Among the oceanic birds petrels might be a possible predator on the larger individuals and phalaropes on the smaller individuals.

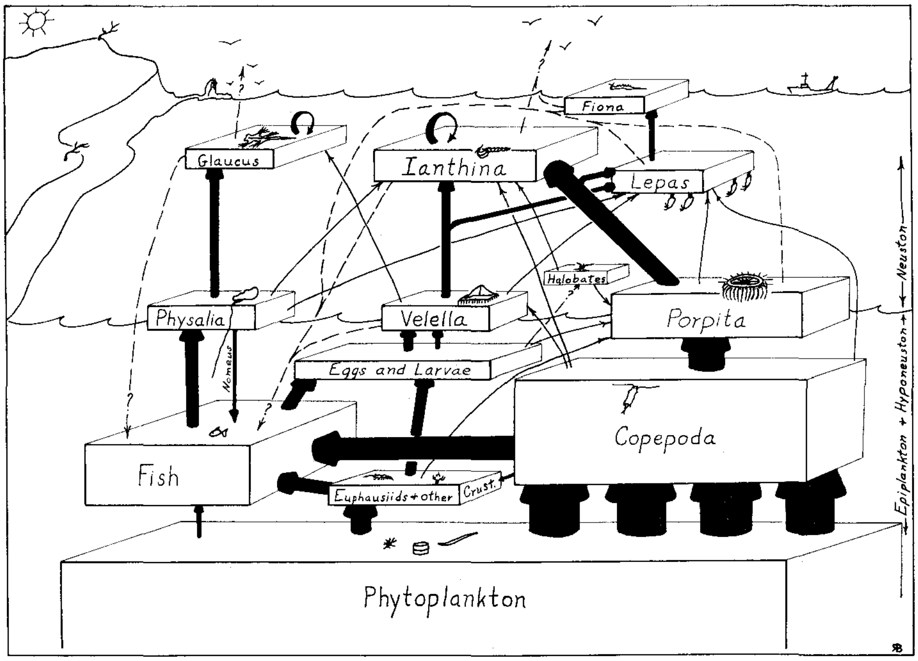

Fig. 1. The neuston food web at Shirahama in the fall of 1965 simplified by the omission of parasites and some minor commensals. Solid arrows indicate the major routes of energy flow. Dashed arrows are hypothetical routes. The food of *Porpita* is based on unpublished data of the author.

SAVILOV (1956) reported that albatrosses do not feed on *Velella* or *Janthina*. *Lepas* holds a singular position in having more sources of food to draw upon than any other organisms in the neuston. The problem of niche separation between the different species of *Ianthina* and *Lepas* needs further study. At present there does not seem to be any degree of niche separation based on the food of these species.

Summary

1. Large *Ianthina prolongata* (20–30 mm shell width) eat *Velella* and *Porpita*

in preference to *Physalia* and will not eat *Glaucus*. The float margin, dactyls and gonozooids are preferred to the epidermis. The larger ianthinas retain their float while feeding and cast adrift the partially eaten animal. A 20 mm wide *Ianthina* can eat a *Porpita* 10 mm in diameter in 15 minutes, and a *Velella* 20 mm long in 25 minutes. They probably can eat two animals of this size every three or four days.

2. Small *Ianthina prolongata* (10 mm or smaller shell width) abandon their floats and climb onto *Velella* and *Porpita* to feed. They feed slowly, taking days to strip the chondrophoran. Apparently they eat all the tissue from the animal.

3. Although *Ianthina* appears to detect its prey by taste over distances of 5 to 10 cm, it is unable to swim to the prey and depends on chance contact for capture. The widespread dactyls of *Porpita* sometimes prevent *Ianthina* from reaching the float margin and the *Porpita* escapes with only slight tissue loss.

4. *Lepas anserifera* as small as 4 mm capitulum length can catch and eat large objects such as *Velella*, *Physalia*, and *Porpita*, and is particularly effective at cleaning all epidermis from carcasses discarded by *Ianthina*. Several barnacles feed on the animal at the same time. The rate of feeding is quite slow. Barnacles averaging 5 mm capitulum length took 3 hours to consume a 10 mm diameter *Porpita* and 12 hours to consume a 15 mm long *Velella*. The food is passed along the edge of the colony.

5. *Glaucus* will eat *Velella* and *Porpita* but feeds most actively on *Physalia*. Apparently it requires several hours to eat the gastrozooids from a 30 mm long *Physalia*.

6. *Fiona pinnata* attacks *Lepas anserifera*. A 15 mm long individual can eat 9 of the barnacles each about 5 mm long in about 12 hours.

7. When food is scarce *Ianthina* and *Glaucus* become cannibalistic.

8. The food web in the neuston is based on the three floating coelenterates, *Physalia*, *Velella*, and *Porpita*, each of which eats a different component of the life below the surface. There is also considerable niche separation in the feeding of *Ianthina*, *Glaucus*, and *Lepas*. *Ianthina*, *Lepas*, *Glaucus*, and *Fiona* are three to five steps from the primary energy source, phytoplankton.

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EXPLANATION OF PLATES III–IV

PLATE III

A. *Ianthina prolongata* with snout partially extended towards *Porpita*. The lower, white gastrozooids are contracted about one-half their maximum length. The blue dactlys at the surface are not contracted.

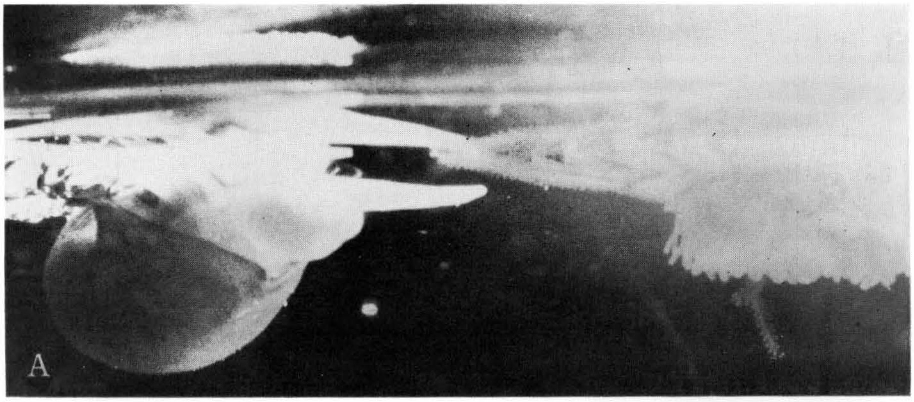
B. *I. prolongata* has just grasped *Porpita* at the float rim. The dactyls of *Porpita* just above the snout of *Ianthina* are missing, possibly from an earlier encounter with *Ianthina*.

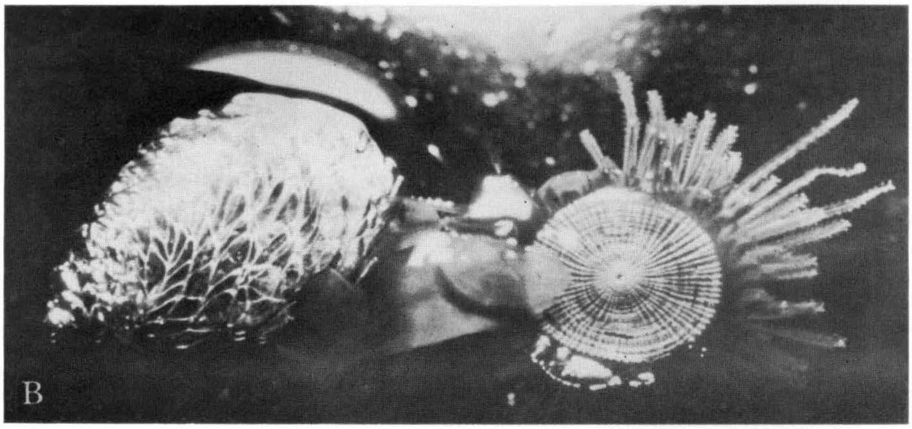
C. *I. prolongata* has finished eating the rim, all dactyls and is finishing the last of the gastrozooids below before casting off the *Porpita* with some tissue still attached to the float skeleton.

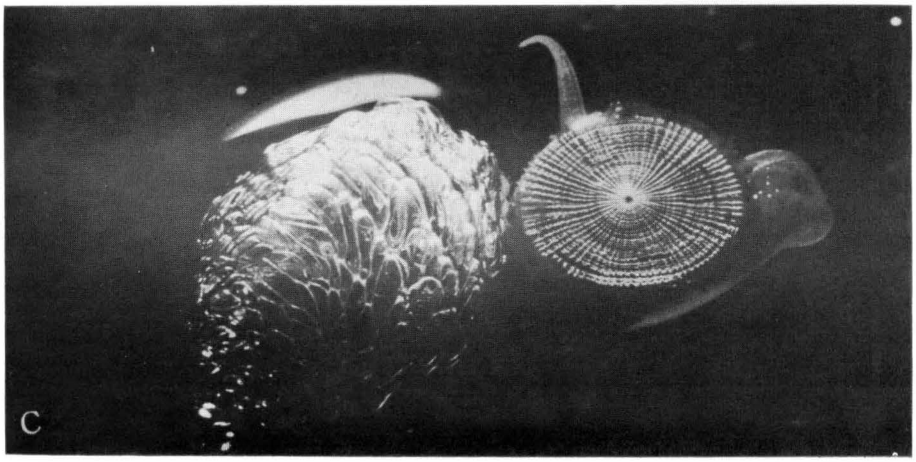
PLATE IV

A. *Lepas anserifera* eating *Velella* (skeleton length 23 mm). Part of the rim has been eaten at the side and right end. At the left end two barnacles are feeding. The skeleton will be completely free of tissue when released by the group of barnacles.

B. *Glaucus* 25 mm long feeding on *Physalia*. Note the small *Glaucus* to the right. All photographs are copies from Fujicolor positives.







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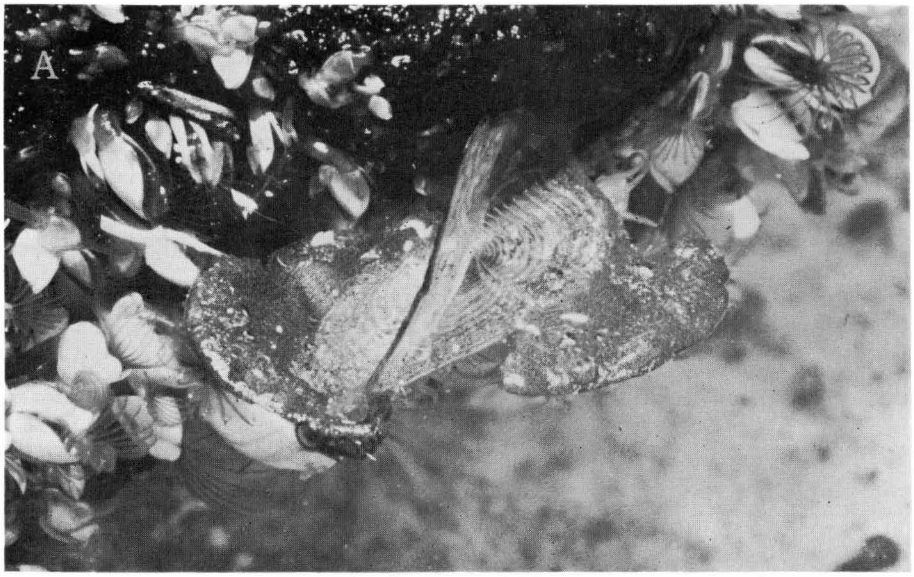

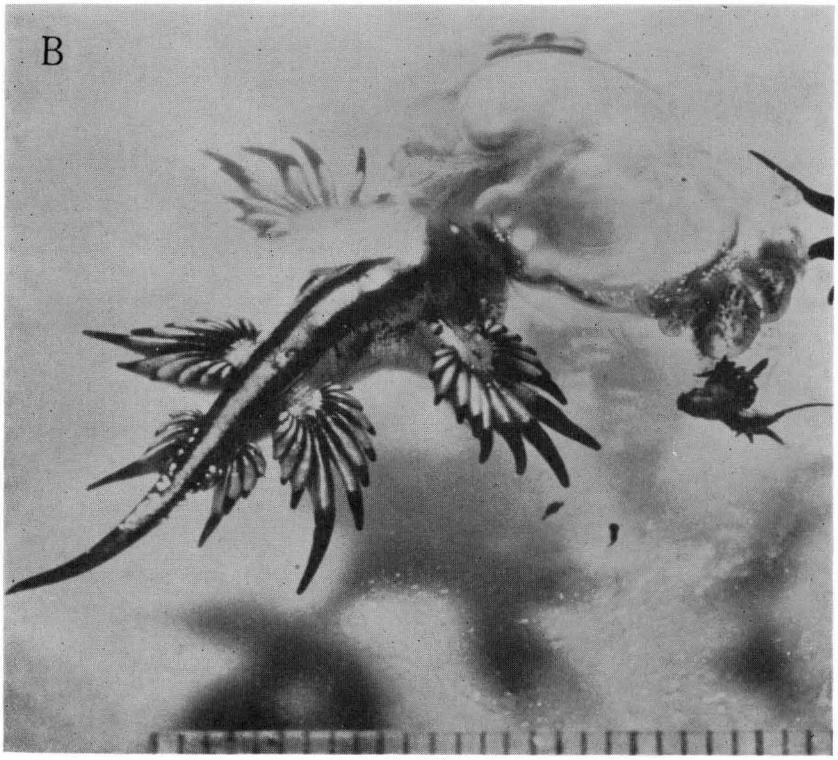

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