from: Reproduction and Development of Marine Invertebrates (1994) pp. 313–319
edited by W. H. Wilson Jr., S. A. Stricker, and G. L. Shinn
The Johns Hopkins University Press, Baltimore

24 Seasonal Swimming of Sexually Mature Benthic Opisthobranch Molluscs (*Melibe leonina* and *Gastropteron pacificum*) May Augment Population Dispersal

Claudia E. Mills

ABSTRACT Although adults of the opisthobranch gastropods *Melibe leonina* and *Gastropteron pacificum* are primarily benthic crawlers, they are also capable swimmers. Long-term observations (13–15 years) of plankton in surface waters at Friday Harbor, Washington, reveal that swimming of adult animals in these species is highly seasonal. For *M. leonina*, which appears to have no permanent populations within at least 2 km of the study site, nearly all swimming adults were observed in surface waters between September and March. Most swimming *G. pacificum*, with a resident population on the sloping mud-sand bottom 5–18 m immediately below the observation site, were also seen near the surface between September and February. Swimming individuals from both species were sexually mature, or nearly so, as shown by their ability to reproduce in the laboratory after collection. Although both species have planktonic veliger larvae, commonly considered to be their chief agents for dispersal, these observations suggest the additional importance of seasonally swimming adults in achieving population movements.

Introduction

Dispersal of benthic marine invertebrates can be accomplished by at least three common routes: planktonic larvae or egg capsules, rafting of either egg capsules or juveniles or adults attached to movable substrata, and benthic migration of juveniles or adults. In this chapter, I will discuss a fourth, less common route for population dispersal—intermittent seasonal swimming by reproductively capable adult animals.

Although movement through the water column is a seemingly unlikely mechanism for transport of benthic species, the literature reveals an increasing number of reports that such movement may be an important source of dispersal for postsettlement benthic animals in many phyla (see also ch. 23 of this volume, by W. H. Wilson, Jr.). The list of waterborne benthic adults includes many representatives living in quite different habitats, from infaunal leptosynaptid sea cucumbers (Costello, 1946), bivalves (Highsmith, 1985; Sörlin, 1988), crustaceans (Highsmith, 1985), and polychaetes (Wilson, this volume), to small shelled gastropods and bivalves in the rocky intertidal (Martel and Chia, 1991), to ascidians living attached to eelgrass blades (Worcester, 1992).

In this chapter, I present new data on seasonal swimming by two opisthobranch molluscs

Claudia E. Mills, Friday Harbor Laboratories, University of Washington, 620 University Road, Friday Harbor, WA 98250.

already known to be good periodic swimmers. From many years of observation of the surface plankton, it has become apparent that both *Melibe leonina* (Gould, 1852) and *Gastropteron pacificum* Bergh, 1893, are frequently seen swimming near the surface in the colder months, while only sometimes appearing in the plankton at other times of the year. I have not explored the reason for such seasonality in prolonged swimming, but want to emphasize the strong likelihood that these swimming events are important for dispersing reproductively capable adult animals, which can then spawn after arrival in new locations.

Melibe leonina (Nudibranchia, Dendronotacea) occurs on the west coast of North America from Kodiak Island, Alaska, to the Gulf of California (MacFarland, 1966). In Washington State, *M. leonina* lives primarily on *Zostera marina* eelgrass growing in shallow, protected embayments, where it feeds on small zooplankton closely associated with the eelgrass (Hurst, 1968). Although usually attached to eelgrass blades by its long slender foot, *M. leonina* swims well by side-to-side flexure of the entire body. Animals may swim between grass blades, but swimming in this species is generally considered to be an escape response. *M. leonina* can be easily stimulated to swim by various kinds of physical disturbance (Hurst, 1968) and also swims in response to pinching of the cerata by predatory crabs (Bickell-Page, 1989).

Gastropteron pacificum (Cephalaspidea) has been found from the Aleutian Islands, Alaska, to the Gulf of California (MacFarland, 1966). It is a small infaunal snail with bilateral extensions of its foot (parapodia) that are folded up and over the visceral mass while it creeps in the mud using cilia on the foot. The diet of *G. pacificum* is benthic, especially diatoms and foraminiferans (Reinhart, 1967). *G. pacificum* is also known to be a periodic and active swimmer; the broad, rounded parapodia can be flapped like two large wings for very effective swimming. Swimming by *G. pacificum* is not easily elicited by physical disturbance in the laboratory, but can be predictably stimulated by contact with the predatory cephalaspidean mollusc, *Chelidonura phocae* (Reinhart, 1967).

Materials and Methods

During the course of regular observations and collections of medusae and ctenophores from the floating docks at the Friday Harbor Laboratories (FHL) in the San Juan Archipelago of Washington State, I have observed numerous individuals of *Melibe leonina* and *Gastropteron pacificum* in the surface plankton. These observations have been logged and tabulated from 1979 to 1993 for *M. leonina* and from 1977 to 1993 for *G. pacificum* (Fig. 24.1).

Dock observations of plankton were usually made several hundred times per year during the nearly 15 years reported here; a typical observation period consisted of slowly strolling along the approximately 100 m of the floating docks for 10–30 min at a time. Figure 24.2 represents a rough approximation of the total number of hours spent searching; estimates for the summer months are probably too low by at least one-half, but represent time actually recorded in my notebooks. Observations were fairly evenly spaced throughout each year, except for occasional lapses of 1–5 weeks and from October 1981 to February 1982, January to June 1986 and March to September 1988, all due to my absence. Observations were made in the day as well as night, although night observations were most numerous during the first 5 years of the study.

Animals collected in the surface waters during late autumn and winter were sometimes brought into the laboratory for observations of general healthiness and spawning. These animals were kept, often for months, in a running sea water table at ambient field temperatures (about 9–12°C).

A small number of *Gastropteron pacificum* were also either collected by plankton net in

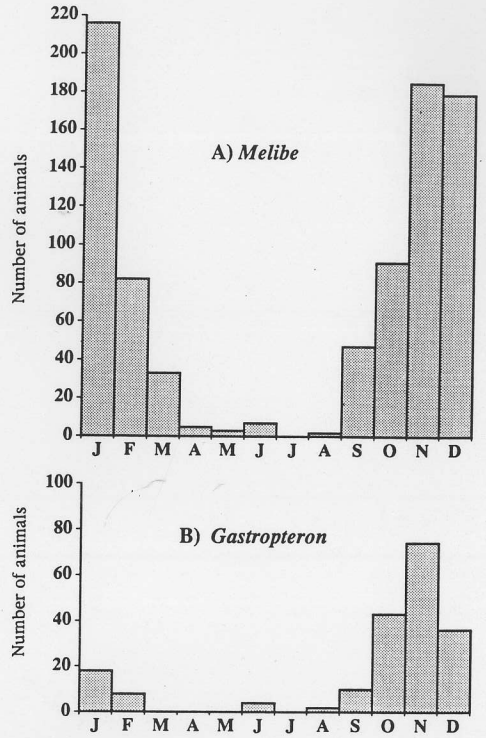

FIGURE 24.1. Total number of individuals seen in the surface plankton in Friday Harbor, Washington, plotted by month of the year. *A. Melibe leonina*, 1979–1993; *B. Gastropteron pacificum*, 1977–1993.

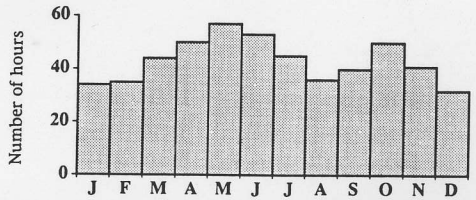

FIGURE 24.2. Approximate total number of hours spent 1977–1993 observing plankton from the floating docks at the Friday Harbor Laboratories to arrive at the numbers presented in Figure 24.1.

nearby Saanich Inlet, British Columbia (1979–80) or seen from the windows of the manned submersible *Pisces IV* in Saanich Inlet or the Strait of Georgia, British Columbia (1980, 1982). A single *Melibe leonina* was seen at the surface in the center of Saanich Inlet, at least 3 km from shore, in November 1980 while I was preparing to make a submersible dive.

Having spoken to numerous marine biologists who work in the vicinity, and made a number of cursory searches myself over the years, I am not aware of any resident populations of *Melibe leonina* existing within Friday Harbor during the course of this study. In late August 1992 I made a

thorough 3-day search throughout Friday Harbor for *M. leonina*, using a kayak during a low-tide series. No *M. leonina* were seen, nor were any of its egg masses in evidence on eelgrass. In a bay having resident *M. leonina*, such a search from the surface at low tide should have revealed its presence. It is noteworthy that swimming *M. leonina* began appearing in the plankton in Friday Harbor within 3 weeks of this 1992 search, before any autumn storms had strongly disrupted the region.

Results

Melibe leonina

Although there are no known *Melibe leonina* populations within at least 2 km of the FHL floating docks, 850 animals were observed from the docks either floating or swimming freely in surface waters, or in a few cases attached to drift algae or eelgrass (Fig. 24.1). These "swimmers" were highly seasonal, with 833 (98 percent) of the individuals collected between September and March. Over half of the total number of animals were collected in the autumn-winter 1992–93, which appears to have been an unusually good year for *M. leonina* in this area. Pelagic specimens ranged from approximately 3 to 12 cm in length from expanded hood to tip of the tail; the full range of sizes occurred throughout the swimming season.

Typically, only a few *Melibe leonina* (usually less than 5) were seen swimming or floating near the surface at any given time. Large numbers of *M. leonina* were seen near the docks on ten dates: 17 and 31 December 1987; 30 September 1992; 9, 12, and 24 November 1992; 6 December 1992; and 2, 4, and 5 January 1993. A "large" number of *M. leonina* adrift near the docks would be on the order of fifty to a few hundred (not thousands of) individuals visible over 1–2 hours. To normalize collection times, since invariably I spent more time looking if many were present, only twenty *M. leonina* were recorded on each of these dates.

Most of the pelagic *Melibe leonina* were seen on autumn and winter days when the semidiurnal tide resulted in two high tides in a row, with very little drop between them. On such days, the tide flows in from the south nearly all day, sometimes bringing in oceanic water, as evidenced by the exotic ctenophore fauna it may also carry. When *M. leonina* appeared on such occasions, it was often accompanied by broken pieces of eelgrass or (only during the autumn) the hydromedusa *Polyorchis penicillatus*, which is restricted in habitat to shallow protected bays. It appears that at least some shallow bays may be flushed by such tides.

Melibe leonina is reproductive all year; egg masses have been reported in the field in every month (Hurst, 1967). Swimming and floating animals collected in Friday Harbor surface waters and brought into the laboratory lived for several months and regularly produced viable egg masses in a running sea water table.

Gastropteron pacificum

A resident population of *Gastropteron pacificum* exists 5–18 m below the FHL floats on a sloping mud-sand bottom (Reinhart, 1967). Individuals seen in surface waters at the FHL floats seem likely to have swum up from this population. It is interesting to note, however, that swimming by *G. pacificum* appears to be as seasonal as swimming by *Melibe leonina* in this region and that most swimming *G. pacificum* were also collected on days with double high tides. Of 195 *G. pacificum* seen swimming in surface waters during the collection period, 189 (97 percent) were seen between September and February (Fig. 24.1). On only four dates were more than 4 *G. pacificum* recorded; 6 were seen on 8 October 1991; 5 on 27 November 1991; 6 on 11 November 1992; and 9 on 24 November 1992. On most observation dates, only one swimming individual was recorded.

Autumn–winter 1992–93 was a good year for observations of swimming *G. pacificum*, producing approximately one-fourth of all sightings. Although I report only a few swimmers during the summer (these were juveniles), more juvenile *G. pacificum* can be found swimming in the summer months if the observer devotes hours rather than minutes per day to the collection effort (Reinhart, 1967; R. A. Satterlie, pers. comm.). Autumn and winter swimming *G. pacificum* were usually 9–15 mm long.

About twenty *Gastropteron pacificum* individuals were brought into the laboratory and placed in a silt-covered running sea water table during October–December 1990 and 1991. Two fertilized egg masses were seen in this laboratory water table in February and March 1991; none was seen in spring 1992. In the field, *G. pacificum* lays eggs throughout the year, but they may be most numerous from January through June (Hurst, 1967; Reinhart, 1967).

Gastropteron pacificum was also found high in the water column above a frequently anoxic 180–200 m bottom about 2 km from shore during the winter in Saanich Inlet, indicating that its swimming capabilities are adequate for significant vertical or, more likely, horizontal transport. Single specimens were taken in vertical plankton tows from 25 to 50 m on 13 November 1979, and from 0 to 25 m on 4 November 1980 (replicated in two tows) above a 200-m bottom. *G. pacificum* was not taken in the upper water layers in any other of nearly 600 stratified plankton tows taken bimonthly over a 2-year period in Saanich Inlet. Ten *G. pacificum* were seen from the *Pisces IV* submersible from 16 to 28 m over a 180-m bottom in Saanich Inlet on 6 November 1980, and one was seen at 84 m above a 384-m bottom in the Strait of Georgia, south of Texada Island, British Columbia, again about 2 km from shore.

Discussion

Tidal currents are relatively strong in the San Juan Archipelago. In the area near the study site, current speeds are frequently in the 1–5-km/h range, with occasional currents approaching 8 km/h (U.S. National Ocean Service, 1991). Such currents could well transport swimming opisthobranchs significant distances.

Melibe leonina and *Gastropteron pacificum* exhibit most of their sustained swimming in the upper water column at the same time of the year, but the dispersive consequences of swimming may be different for the two species. *M. leonina* seen from the FHL floating docks have already moved on the scale of kilometers, because there are no known populations nearby. A few of the traveling *M. leonina* were attached to drift algae or eelgrass, but the resulting transport should be about the same as for those swimming solo. It may be speculated that many of the swimming *M. leonina* have been torn from their senescing eelgrass beds in winter storms, but animals are also frequently seen swimming in the plankton during long periods of quiescent autumn and winter weather. Nothing in the literature suggests any seasonal behavior for *M. leonina* merely letting go of their eelgrass in the winter, yet the large number of free individuals suggests that such could be the case (see also the report of Ajeska and Nybakken [1976] below).

Gastropteron pacificum seen swimming off the FHL floating docks are likely to have come from the population immediately below. *G. pacificum* swimming appears to consist mostly of bouts of vertical swimming up from the bottom. Although *G. pacificum* individuals are not very buoyant, and therefore may fall rapidly out of the water column when they stop swimming, they are still likely to be transported at least as far in a single swimming bout in the presence of tidal currents as they might crawl in a day. Reinhart (1967) reports *G. pacificum* swimming continuously in the laboratory for up to 5½ h after collection, so prolonged presence in the plankton with significant transport is certainly possible and perhaps quite common for this species. The correla-

tion of swimming *G. pacificum* with double high tides in the autumn and winter is intriguing, but, so far, unexplained.

Dispersal of both species of opisthobranchs reported here is usually considered to be accomplished by their planktonic larvae. *Melibe leonina* has planktotrophic veliger larvae that are capable of settlement and metamorphosis 30–48 days after hatching (Bickell and Kempf, 1983). *Gastropteron pacificum* also has planktotrophic veliger larvae (Hurst, 1967), and preliminary studies imply that they probably also spend about 4–6 weeks in the plankton (G. D. Gibson, pers. comm.). Displacement of larvae during several weeks in the plankton seems likely to be an important means of dispersal for these species, but one must now recognize the further ability of reproductive adults to be moved during extended swimming bouts in the water column.

Dispersal by swimming or floating adults is thought to be an important source of general population transport for another species of *Melibe*. Large numbers of *Melibe fimbriata*, an Indian Ocean species, were recently reported for the first time in the Mediterranean Sea near Greece, where many swimming and floating adult animals were aggregated in Astakos Inlet of the Ionian Sea (Thompson and Crampton, 1984). It is assumed that *M. fimbriata* entered the Mediterranean Sea through the Suez Canal, but it is noteworthy that the first sighting was of large numbers of adult animals many hundreds of kilometers west of this presumed point of entrance.

Further evidence of mass movement of adults is provided by Ajeska and Nybakken (1976), who studied a large *Melibe leonina* population (an estimated 20,000 individuals) in a kelp bed in California for several months in 1970–71. The entire population, apparently healthy from August onward, disappeared suddenly within 8 days of the last observation in November. Two months later, a smaller population (2000 individuals) was reestablished at this site. According to the authors, *M. leonina* populations in California are typified by periodic rapid appearances and disappearances at given locations.

Populations of *Melibe leonina* in northwest Washington State and southwest British Columbia have also been observed to come and go, although on a less abrupt schedule (G. D. Gibson and L. R. Page, pers, comm.). Agersborg (1923) cites Trevor Kincaid's 1917 observation in Hood Canal, Washington, of a bay filled with "millions" of *M. leonina*. These animals even covered pilings under a dock, an unlikely habitat for this species, further emphasizing, in my view, their recent influx into the area. Near-shore plankton tows taken in late winter in the Strait of Georgia, Washington, included numerous planktonic *M. leonina* whose stomachs were filled with herring larvae (C. M. Eaton, pers. comm.). One might extrapolate that swimming of adults is an important dispersal mechanism of this species in both Washington and California.

As a final note, only one other species of benthic gastropod was seen in the plankton off the FHL floating docks during this study. Eight times between 1990 and 1993, (seven between October and January), *Dendronotus* spp. (probably all *D. iris* Cooper, 1863) nudibranchs were seen swimming at the sea surface (one was rafting on a plastic bag [W. H. Watson, pers. comm.]). On five of these occasions, *Dendronotus* was collected together with *M. leonina*. *D. iris* feeds on cerianthid anemones on muddy bottoms, but it is also known to be a strong and capable swimmer (Agersborg, 1922; Robilliard, 1970). No pattern should be deduced from the small number of *Dendronotus* observed, although individuals were sometimes seen at the surface for more than 30 min., again offering the opportunity for reproductive adults to travel substantial distances by means of tidal currents.

Altogether, these data appear to support the hypothesis that transport of reproductive adults by swimming up into the water column provides a second mechanism for population dispersal of some opisthobranchs, in addition to the more familiar migrations by planktonic veliger larvae. I

have not attempted to evaluate the contribution to recruitment afforded by this mechanism. A forthcoming study by S. E. Worcester (pers. comm.) makes a much more thorough attempt to quantify the importance of such adult transport in an ascidian population in California, and in fact, preliminary results (Worcester, 1992) indicate that in this case the seemingly unlikely rafting by adult tunicates may be more important than larval dispersal in colonizing new habitats.

Acknowledgments

I am grateful to the staff and scientists at the Friday Harbor Laboratories for use of the facilities and intellectual companionship over many years. Thanks to Tom Schroeder, Louise Page, Glenys Gibson, Alan Kohn, Richard Strathmann, Jon Havenhand, Richard Palmer, and Herb Wilson for comments on this manuscript and discussions about the animals involved.

Literature Cited

Agersborg, H. P. 1922. Notes on the locomotion of the nudibranchiate mollusk *Dendronotus giganteus* O'Donoghue. Biol. Bull. 47: 257–266.

———. 1923. A critique on Professor Harold Heath's *Chioraera dalli*, with special reference to the use of the foot in the nudibranchiate mollusk, *Melibe leonina* Gould. Nautilus 36: 86–96.

Ajeska, R. A., and J. Nybakken. 1976. Contributions to the biology of *Melibe leonina* (Gould, 1852) (Mollusca: Opisthobranchia). Veliger 19: 19–26.

Bickell, L. R., and S. C. Kempf. 1983. Larval and metamorphic morphogenesis in the nudibranch *Melibe leonina* (Mollusca: Opisthobranchia). Biol. Bull. 165: 119–138.

Bickell-Page, L. R. 1989. Autotomy of cerata by the nudibranch *Melibe leonina* (Mollusca): ultrastructure of the autotomy plane and neural correlate of the behaviour. Philos. Trans. Roy. Soc. Lond. B. 324: 149–172.

Costello, D. P. 1946. The swimming of *Leptosynapta*. Biol. Bull. 90: 93–96.

Highsmith, R. C. 1985. Floating and algal rafting as potential dispersal mechanisms in brooding invertebrates. Mar. Ecol. Prog. Ser. 25: 169–179.

Hurst, A. 1967. The egg masses and veligers of thirty Northeast Pacific opisthobranchs. Veliger 9: 255–288.

———. 1968. The feeding mechanism and behaviour of the opisthobranch *Melibe leonina*. Symp. Zool. Soc. Lond. 22: 151–166.

MacFarland, F. M. 1966. Studies of opisthobranchiate mollusks of the Pacific coast of North America. Mem. Cal. Acad. Sci. 6: 1–546.

Martel, A., and F.-S. Chia. 1991. Drifting and dispersal of small bivalves and gastropods with direct development. J. Exp. Mar. Biol. Ecol. 150: 131–147.

Reinhart, J. M. 1967. The swimming behavior of *Gastropteron pacificum*. Master's thesis. University of Washington, Seattle.

Robilliard, G. A. 1970. The systematics and some aspects of the ecology of the genus *Dendronotus*. Veliger 12: 433–479.

Sörlin, T. 1988. Floating behavior in the tellinid bivalve *Macoma balthica* (L.). Oecologia 77: 273–277.

Thompson, T. E., and D. M. Crampton. 1984. Biology of *Melibe fimbriata*, a conspicuous opisthobranch mollusc of the Indian Ocean, which has now invaded the Mediterranean Sea. J. Moll. Stud. 50: 113–121.

U.S. National Ocean Service. 1991. Tidal Current Tables 1992: Pacific Coast of North America and Asia North. U. S. Department of Commerce, Coast and Geodetic Survey, Washington, D. C.

Wilson, W. H. This volume. Dispersal of soft-bottom benthos: Migration through the water column or through the sediment? Ch. 23.

Worcester, S. E. 1992. Adult rafting and larval swimming: Does dispersal mode affect the recruitment of a colonial ascidian into new habitats? Am. Zool. 32: 122A.