

SHORT COMMUNICATION

Predictability of patches of neritic salps and doliolids (Tunicata, Thaliacea)

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The occurrence of large patches of gelatinous zooplankton has for decades been considered to be unpredictable. An evaluation of our own data and published results on abundances of doliolids and salps from ocean margins reveals that a considerable degree of prediction is possible, based upon meteorological and boundary current intrusion dynamics.

Thaliaceans are a class of planktonic tunicates made up of the orders Salpida, Doliolida and Pyrosomida. Although most thaliacean species occur in the open ocean, a few of the most abundant live in continental shelf waters (Deibel, 1998; Madin and Deibel, 1998). Thaliaceans are of ecological, evolutionary and biogeochemical importance. They collect a wide size range of food particles with fine mucous filters. They also contribute to a shunt of the microbial loop by consuming small microbes and packaging them into large faecal pellets which have sinking velocities approaching 1000 m day⁻¹ (Yoon *et al.*, 2001; Ramaswamy *et al.*, 2005).

Neritic thaliaceans occur aperiodically in dense swarms, or patches, which may contain several thousand animals per cubic metre (Heron, 1972; Deibel, 1998). It has been assumed that patches of thaliaceans are ephemeral, occurring only at unpredictable times and places. This viewpoint was summarized recently by Boero *et al.* (Boero *et al.*, 2008) for gelatinous zooplankton generally. However, there is limited understanding of the causes of patch formation by thaliacean tunicates. In

this paper, we summarize research conducted during the past 30 years on patches of neritic salps and doliolids from the South Atlantic Bight (SAB) off the coasts of Florida, Georgia and the Carolinas, USA. The 30-year length of this regional historical record provides the opportunity to explore hypotheses concerning causal mechanisms and predictability of thaliacean patches.

Both salps and doliolids have complex life cycles, with obligatory alternation of sexual and asexual generations (Bone, 1998). Asexual reproduction results in thaliaceans being able to respond to favourable conditions by producing offspring quickly (Paffenhöfer *et al.*, 1984; Paffenhöfer and Lee, 1987a). As a consequence, thaliacean patches are generally dominated by the progeny of asexual reproduction, i.e. the aggregate stages of salps and the phorozoid and gonozoid stages of doliolids (Deibel, 1985; Paffenhöfer and Lee, 1987a; Huskin *et al.*, 2003; Ramaswamy *et al.*, 2005). For example, the gonozoid proportion of doliolid patches increases as a function of the total abundance of all zooids, indicating that patches form primarily as a

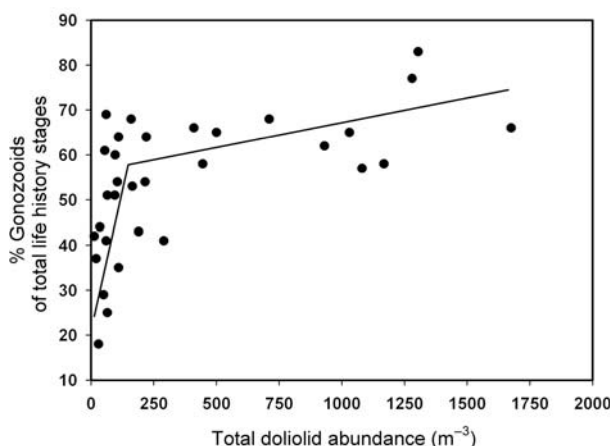


Fig. 1. The proportion of gonozooids, which result from asexual reproduction, within a population of the doliolid *D. gegenbauri*, vs. total doliolid abundance at a group of drogue stations in the SAB. The abundance data were estimated by eye from Fig. 1 of Deibel (Deibel, 1985), and the gonozooid proportion came from Table 1 of Deibel (Deibel, 1985). The two-segment line of best fit was estimated by eye to show the general shape of the relationship.

result of the asexual production of gonozooids by phorozoids (Fig. 1). During these periods of intense asexual reproduction, the population growth rates of neritic salps and doliolids approach those of the bacteria and phytoplankton on which they feed (Heron and Benham, 1984; LeBorgne and Moll, 1986; Tsuda and Nemoto, 1992; Paffenhöfer and Gibson, 1999). Thus, the life history stage composition of thaliacean patches suggests that they respond to favourable environmental conditions by high rates of asexual reproduction. But what are these environmental conditions and how do they come about?

We have been studying patches of salps and doliolids from the outer continental shelf of Florida, Georgia and the Carolinas, USA (i.e. the SAB) since the middle 1970s (Atkinson *et al.*, 1978; Paffenhöfer *et al.*, 1984, 1987, 1995; Deibel, 1985). The predominant species that form these patches are the small salp *Thalia democratica* and the doliolid *Dolioletta gegenbauri*. Patches have been reported for both species at various times of year, but are most common between February and August. Seven of the eight patches of thaliaceans we studied in the SAB between 1976 and 1981 were closely associated in time and space with intrusions of cool, high nutrient water originating from aphotic depths of the Gulf Stream. For example, on 8–12 August 1981, doliolid abundances $>4000\text{ m}^{-3}$ occurred within the cold core of a stranded intrusion at temperatures $<19^{\circ}\text{C}$ (Fig. 2). Earlier, on 22–24 July 1981, maximum abundances of doliolids and salps were also associated with water temperatures $<19^{\circ}\text{C}$ in newly upwelled water close to the shelf break (Fig. 2).

Intrusions are shelf-break upwellings which contain high concentrations of nitrate, silicate and phosphate (Atkinson *et al.*, 1984). They can be advected across the shelf, resulting in increased rates of primary production (Yoder *et al.*, 1983), and of concentrations of chlorophyll and particulate matter in near-bottom waters (Figs 2 and 3) (Atkinson *et al.*, 1978). These intense phytoplankton blooms trigger rapid increases in asexual reproduction by salps and doliolids, resulting in mesoscale thaliacean patches containing several thousand animals per cubic metre (Tables I and II; Figs 2 and 3). Over time, the patches can approach the dimensions of the stranded intrusions themselves, i.e. $>100\text{ km}$ in the along-shelf direction and up to 60–80 km cross-shelf, covering an area of up to $10\,000\text{ km}^2$ (Fig. 2; Paffenhöfer *et al.*, 1987; Paffenhöfer and Lee, 1987a).

Intrusions are spun off from cyclonic meanders and eddies of the western wall of the Gulf Stream as it flows along the shelf break of the SAB (Fig. 4; Atkinson *et al.*, 1987; Lee and Pietrafesa, 1987). During spring and summer, southwesterly winds produce Ekman drift of surface shelf waters offshore and compensatory onshore flow of the upwelled water from the cold cores of the eddies (Atkinson *et al.*, 1987). If the upwelling favourable winds are fairly strong and the shelf water warm (i.e. primarily in summer), intruded water masses may be transported far onto the shelf, sometimes reaching the 20 m isobath (Atkinson *et al.*, 1987). Although the intrusions are generally confined to a near-bottom water mass, because the shelf is shallow, even these bottom intrusions are in the euphotic zone and foster high rates of phytoplankton production, resulting in high concentrations of particulate matter and chlorophyll (Figs 2 and 3, Paffenhöfer and Lee, 1987a).

Intrusions occur at predictable times and places. They are most common in the SAB north of Cape Canaveral, FL, where diverging isobaths reinforce upwelling from Gulf Stream meanders and eddies (Fig. 4) (Atkinson *et al.*, 1987). They are also common in the lee of a topographic high known as the Charleston Bump, where a quasi-permanent, cyclonic gyre causes the upwelling of Gulf Stream water onto the South Carolina shelf near Cape Romaine (Fig. 4; Blanton *et al.*, 1981; Lee and Pietrafesa, 1987). Finally, intrusions are common in Onslow Bay, NC, resulting from eddy-driven upwelling downstream from Cape Fear (Atkinson *et al.*, 1980; Blanton *et al.*, 1981). In our studies on intrusions, i.e. 1976 (Table II, Onslow Bay, NC), 1979 (Paffenhöfer *et al.*, 1984, several intrusions) and 1981 (Paffenhöfer *et al.*, 1987, several intrusions), each one contained doliolids, and in fewer cases also salps. Since Gulf Stream intrusions are predictable in time and space, and can be tracked in real time using satellite

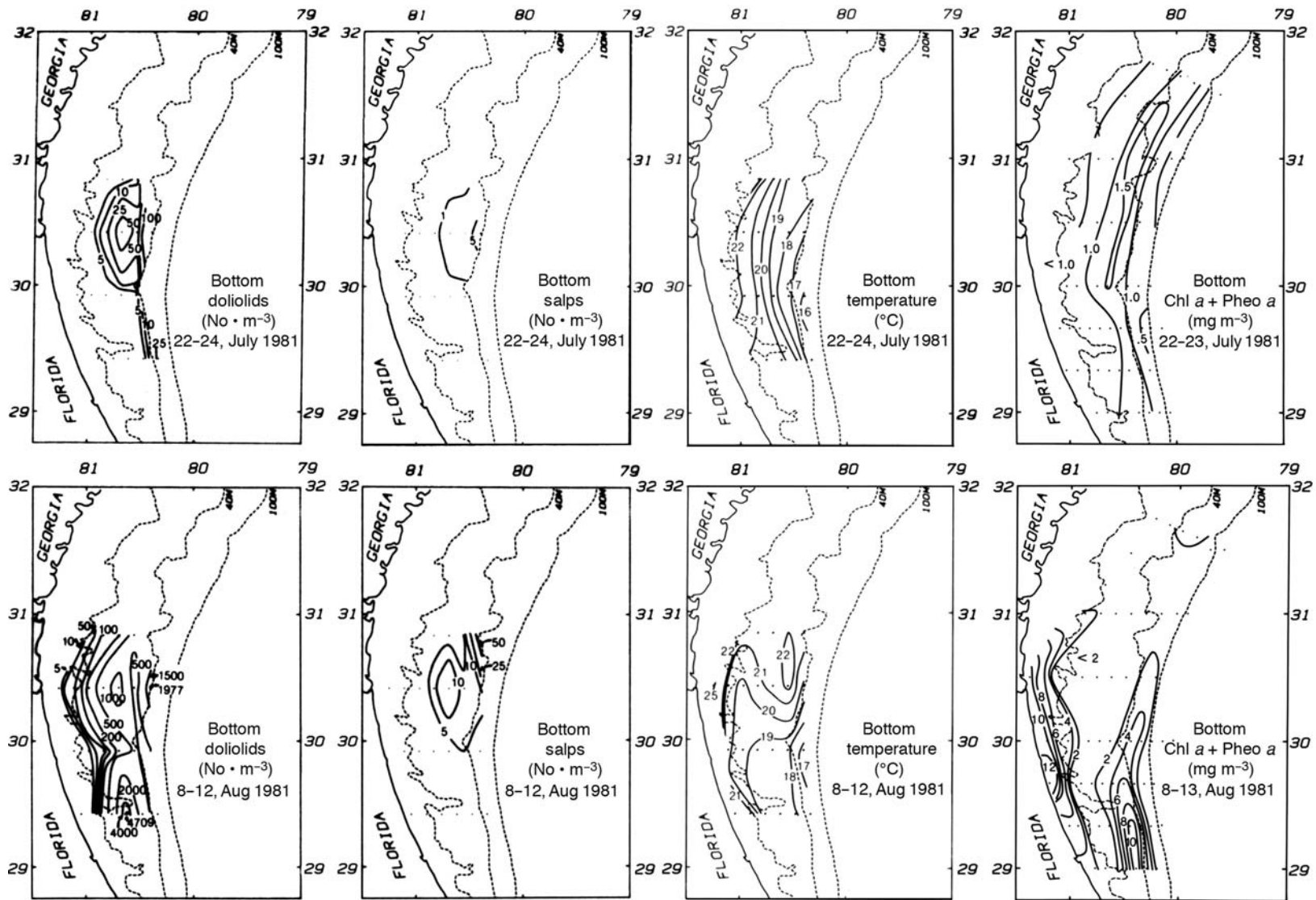


Fig. 2. Horizontal maps of near-bottom water temperature, chlorophyll *a* + total phaeopigments (Yoder *et al.*, 1985) and doliolid (adapted from Paffenhöfer *et al.*, 1987) and salp (Paffenhöfer unpublished) patches off St Augustine, FL, USA. Dotted lines depict the 20, 40 and 100 m isobaths. On 22–24 July 1981 (upper), doliolid and salp patches had been displaced onto the middle and outer shelf, inshore of the 40 m isobath, in association with near-bottom chloropigment maxima on the outer shelf $>1.5 \text{ mg m}^{-3}$. By 8–12 August (lower), the salps remained mainly on the middle and outer shelf whereas the doliolids now covered most of the shelf, and also revealed the influx of a new patch near $29^{\circ} 30' \text{ N}$ in association with a cold core eddy with temperatures $<18^{\circ}\text{C}$ and chloropigment concentrations from 8 to 10 mg m^{-3} .

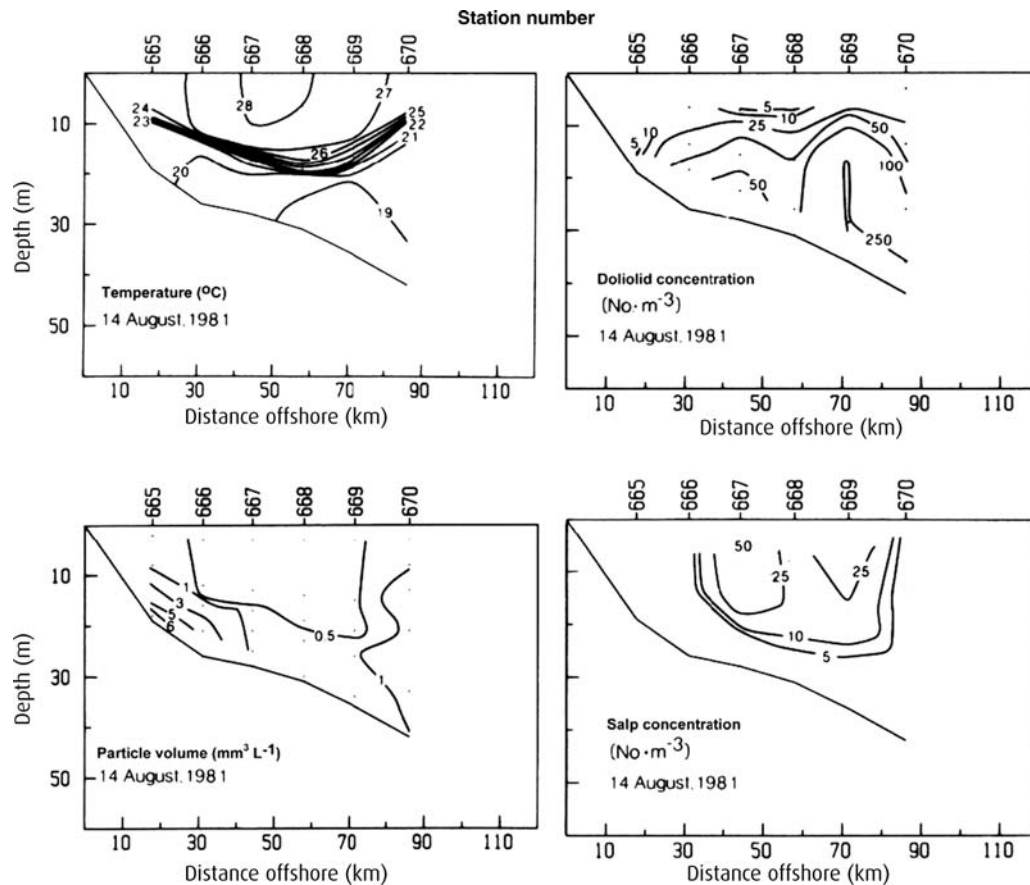


Fig. 3. Vertical sections of the relationship between the abundance of salps, doliolids, temperature and particle concentration (adapted from Paffenhöfer and Lee, 1987a). Particulate matter concentration includes particles from 2 to 100 μm equivalent spherical diameter.

Table I: Abundance maxima of salps from various studies around the world

Species	Location	Maximum conc. (no m^{-3})	Reference
<i>Thalia sibogae</i>	Ambon Bay, Indonesia	530	Troost <i>et al.</i> (1976)
No species given	Ivory Coast	ca. 80	Binet (1976)
<i>Thalia democratica</i>	Bay of Bengal	150	Madhupratap <i>et al.</i> (1980)
<i>T. democratica</i>	Queensland	26	Greenwood (1980)
<i>T. democratica</i>	SE Australia	44	Heron and Benham (1984)
<i>Salpa fusiformis</i>	North Atlantic	>700	Bathmann (1988)
<i>Salpa thompsoni</i>	Antarctica	25	Siegel and Harm (1996)
<i>T. democratica</i>	Agulhas Bank	300	Gibbons (1997)
<i>S. thompsoni</i>	Antarctica	4	Perissinotto and Pakhomov (1998)
<i>S. fusiformis</i>	Humboldt Current	2	Gonzalez <i>et al.</i> (2000)
<i>S. fusiformis</i>	NW Spain	225	Huskin <i>et al.</i> (2003)
<i>T. democratica</i>	coastal Taiwan	53	Tew and Lo (2005)
<i>Thalia orientalis</i>		51	
<i>S. fusiformis</i>		1.6	
Various species	Baja California	>1	Hereu <i>et al.</i> (2006)
No species given	Aegean Sea	275	Isari <i>et al.</i> (2006)
<i>T. democratica</i>	S. Atlantic Bight	200	Atkinson <i>et al.</i> (1978)
<i>T. democratica</i>	Onslow Bay, NC		Paffenhöfer (unpublished)
	18 July 1976	40	
	23 July 1976	45	
	5 August 1976	5	
<i>T. democratica</i>	S. Atlantic Bight	100	Paffenhöfer and Lee (1987a)

Table II: Abundance maxima of doliolids from various studies around the world

Species	Location	Maximum conc. (no m ⁻³)	Reference
<i>Doliolletta gegenbauri</i>	Block Island Sound	1500	Deevey (1952)
<i>Doliolum nationalis</i>	Mediterranean Sea	500	Braconnot (1967)
<i>D. nationalis</i>	Cabo Frio (Brazil)	1280	Monteiro <i>et al.</i> (1975)
Doliolids	Ivory Coast	90	Binet (1976)
<i>D. gegenbauri</i>	Bay of Bengal	600	Madhupratap <i>et al.</i> (1980)
Doliolids	S. California coast	1700	Pieper and Holliday (1984)
<i>Doliolum denticulatum</i>	Inland Sea, Japan	7200	Koga (1986)
<i>D. gegenbauri</i>	E. China shelf	450	He <i>et al.</i> (1988)
<i>D. gegenbauri</i>	Inland Sea, Japan	48 000	Nakamura (1998)
<i>D. gegenbauri</i>	S. Atlantic Bight	2100	Deibel (1985, winter)
<i>D. gegenbauri</i>	S. Atlantic Bight	1500	Atkinson <i>et al.</i> (1978, spring)
Doliolids	Onslow Bay, NC		Paffenhöfer (unpublished)
	18 July 1976	424	
	23 July 1976	308	
	5 August 1976	80	
	15 August 1976	8	
<i>D. gegenbauri</i>	S. Atlantic Bight	1100	Paffenhöfer <i>et al.</i> (1984)
<i>D. gegenbauri</i>	S. Atlantic Bight	4000	Paffenhöfer and Lee (1987a)

thermal images of spin-off eddies, it follows that patches of thaliaceans are predictable as well.

Although Gulf Stream intrusions and phytoplankton blooms seem to be necessary for the formation of thaliacean patches, also required is a seed population of animals. In the absence of knowledge of the source of seed populations in the SAB, we can hypothesize that patches develop either from low abundances of locally occurring animals or from animals residing in the Gulf Stream and thus originating from outside of the SAB.

There is circumstantial evidence in support of both of the above possibilities. It is known that thaliaceans are abundant in the Gulf of Mexico, upstream of the SAB (Esnal, 1978; Esnal and Simone, 1982). Upwelling occurs during most of the year offshore of the Yucatan peninsula (Bogdanov *et al.*, 1968; Paffenhöfer *et al.*, 1995, Merino, 1997) and along the outer shelf off western Florida (Atkinson *et al.*, 1978). These large areas of high phytoplankton productivity along the western wall of the Gulf Stream could provide food for the thaliaceans as they advect northward. Given mean current velocities of the Gulf Stream, it would take thaliaceans from the Gulf of Mexico <1 week to pass through the Straits of Florida and reach the SAB. This time period is near the generation time of *Thalia* (Braconnot, 1963), and less than that of doliolids at ambient water temperatures (Paffenhöfer and Gibson, 1999). Thus, seed populations from the Gulf of Mexico could reach the SAB within about one generation. Using time-series observations of patch formation, we have found that thaliaceans initially occur only at the shelf break and outer shelf (Fig. 2), suggesting that seed populations originate from upstream. Presently, unavailable genetic evidence from animals collected in the

Gulf of Mexico and the SAB would help to test this hypothesis.

There is also evidence supporting the seeding of patches from more local sources. Mazzocchi and Paffenhöfer (unpublished) have frequently found nurse stages of doliolids at ~75 m depth south of Bermuda, and Paffenhöfer *et al.* (Paffenhöfer *et al.*, 1995) found nurses to make up 75% of doliolid populations near the shelf break in the vicinity of the Charleston Bump intrusion. The nurse stage is critical for patch formation, as each can produce thousands of progeny asexually in <1 week (Paffenhöfer and Gibson, 1999). For example, doliolids increased in abundance from 5 m⁻³ to more than 500 m⁻³ in <10 days off Jacksonville, FL, in August 1981 (Table II; Fig. 2, bottom; Paffenhöfer *et al.*, 1987). This is a population doubling time of 3–4 days, with maximum abundances at a few of the stations reaching >4000 m⁻³ (Paffenhöfer and Lee, 1987a). This hypothesis is further supported by the laboratory studies of Gibson and Paffenhöfer (Gibson and Paffenhöfer, 2002), which show that *D. gegenbauri*, phorozoids can reproduce at food levels of only 7 µg C L⁻¹, typical of deep, shelf break waters. Licandro *et al.* (Licandro *et al.*, 2006) concluded that high abundances (i.e. several hundred × m⁻³) of *T. democratica* in the Mediterranean Sea were the result of reproduction by local seed populations rather than advection. This hypothesis could also be tested in the SAB and elsewhere using the genetic marker studies referred to above.

Thaliacean patches covering thousands of square kilometre contain large quantities of organic material (Deibel, 1985). Thus, the fate of thaliacean patches is of great biogeochemical significance. Possible fates are

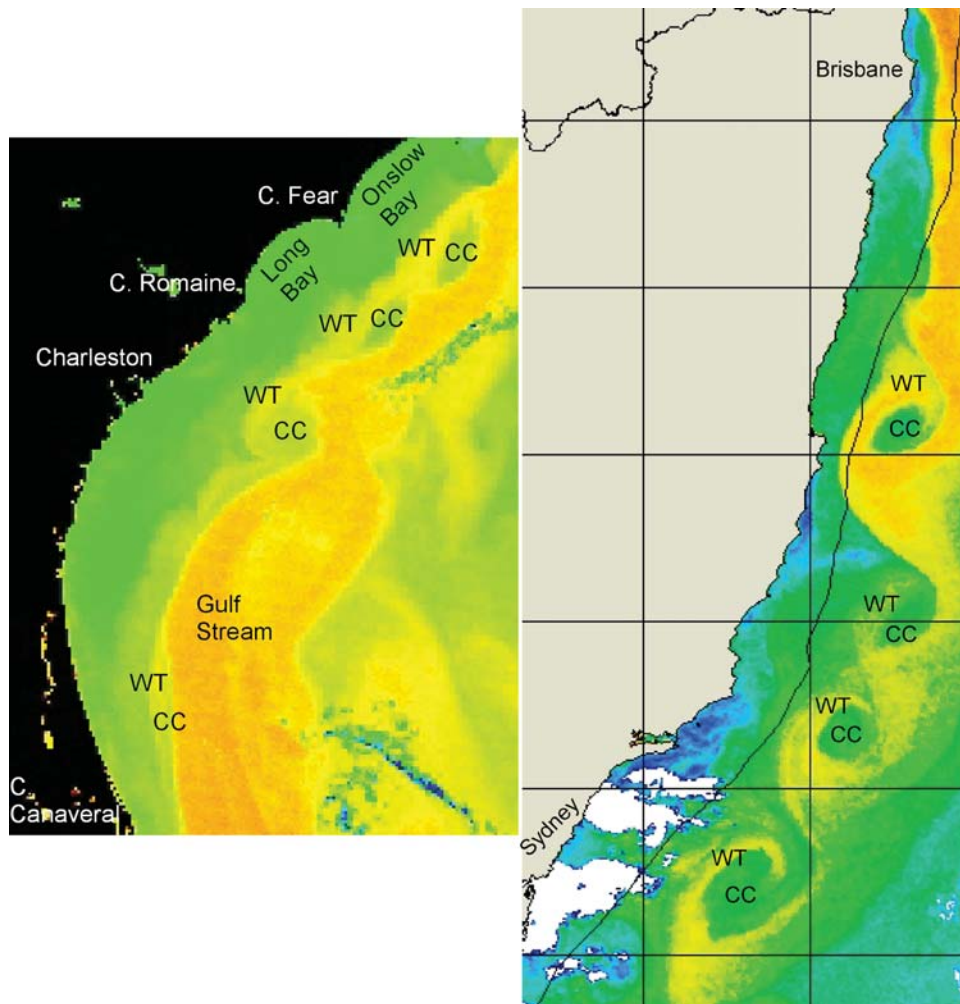


Fig. 4. Boundary current spin-off eddies from the Gulf Stream off the coast of the SAB, USA (left), and from the East Australian Current, off southeastern Australia (right). Shown are satellite images of sea surface temperature, where yellow is warmer and green is colder. WT, warm tongue of a given eddy; CC, cold core of a given eddy. The South Atlantic Bight image (left) is an enlargement of an image in the public domain at: http://upload.wikimedia.org/wikipedia/commons/6/63/Gulf_Stream_water_temperature.jpg. The Australian image (right) is an enlargement of an image in the public domain, from NOAA 12 SST on 13 December 2002 (courtesy of CSIRO Marine Research, Hobart, <http://www.marine.csiro.au/~lband/021213a.gif>).

advection offshore, predation, and food limitation followed by starvation. Each of these fates has different biogeochemical consequences. Advection would benefit Gulf Stream plankton and benthic food webs of the continental slope. Predation would benefit higher trophic levels on the shelf, and starvation would benefit shelf microbial and benthic communities.

The formation and persistence of Gulf Stream intrusions in the SAB depend in large part on wind speed and direction. Prevailing winds from the southwest in spring and summer are favourable for the formation and persistence of intrusions. When the winds shift to the northeast, there are often current reversals on the SAB continental shelf, transporting surface water towards shore and bottom intrusions back off the shelf

(Atkinson *et al.*, 1987). These atmospheric events become more common in September and October (Weber and Blanton, 1980), when there is a seasonal shift in the prevailing wind regime (Lee and Pietrafesa, 1987). We have found that these northeasterly wind events and subsequent current reversals on the SAB generally disrupt and disperse both intrusions and their associated thaliacean patches. For example, average residence times of stranded intrusions on the SAB during summer are ~1 month (Atkinson *et al.*, 1984), essentially the same as the observed lifetimes of thaliacean patches at that time (Paffenhöfer *et al.*, 1987). When wind events and current reversals are more frequent during spring and fall, patches commonly persist for only a few days to a week (Paffenhöfer and Lee, 1987a).

While there is sometimes evidence of moderate levels of sexual reproduction in thaliacean patches (Deibel, 1985), the ca. 1 week to 1 month duration of patches is essentially equivalent to the generation time of *T. democratica*, and *D. gegenbauri* (Deibel, 1982, Paffenhöfer and Gibson, 1999), rendering sexual reproduction of minimal significance in patch growth. An average-sized doliolid patch that is advected offshore during north-easterly winds could transport several thousand metric tons of nitrogen off the shelf. A dedicated drogue study is required to further determine the fate of thaliacean patches due to advection.

Predators may also be attracted to thaliacean patches. Although many predators of salps have been reported (Harbison, 1998; Pakhomov *et al.*, 2002), there is less information available on potential predators of doliolids. Whereas doliolids pump water by a combination of ciliary and muscular mechanisms, salps rely on muscular pumping alone, meaning that they pulse continuously throughout their lives. Muscular contraction likely produces a much larger hydrodynamic disturbance in the immediate vicinity of salps than does ciliary pumping in doliolids. Thus, salps should be more vulnerable to predators than are doliolids. There is much opportunity for future research into predators of thaliaceans.

The above difference in feeding mechanism between salps and doliolids also has ecological consequences. The mucous filter of large, oceanic salps clogs at chlorophyll concentrations $>1 \mu\text{g L}^{-1}$ (Harbison *et al.*, 1986). However, it seems that doliolids are much less susceptible to clogging (Deibel and Paffenhöfer, 1988), and cells up to ca. $60 \mu\text{m}$ are removed from suspension within doliolid patches (Deibel, 1985; Paffenhöfer and Lee, 1987b). Thus, we hypothesize that doliolid patches could decline due to overgrazing of preferred particle size classes. For example, Paffenhöfer and Lee (Paffenhöfer and Lee, 1987b) documented high rates of particle removal by a doliolid patch off St Augustine, FL. In addition, Paffenhöfer *et al.* (Paffenhöfer *et al.*, 1995) showed evidence of overgrazing of nano- and picoplankton at high abundances of doliolids. This doliolid overgrazing hypothesis is presently being explored by G.-A.P. (G.-A.P., unpublished).

The occurrence of thaliacean patches may be predictable from boundary current dynamics elsewhere in the world. We present only a small subset of cases here. Humphrey (Humphrey, 1963) and Hallegraeff (Hallegraeff, 1981) reported that salp patches (primarily *T. democratica*) occur intermittently from late winter and spring to early and mid-summer (austral) off Sydney, Australia. This is similar to the seasonal timing of thaliacean patches in the SAB. These patches had up to three orders of magnitude more wet weight biomass than did

zooplankton samples from non-patch stations nearby (Tranter, 1962). More recently, McClean-Padman and Padman (McClean-Padman and Padman, 1991) have described mesoscale eddies of the East Australian Current which appear to be of similar scale and dynamics to those of the Gulf Stream in the SAB (Fig. 4). During periods of upwelling favourable winds (from the northeast in the southern hemisphere), upwelled water masses from these eddies result in phytoplankton blooms which are displaced across the shelf (Hallegraeff, 1981; McClean-Padman and Padman, 1991). The phytoplankton blooms off Sydney are dominated by large diatoms at concentrations of up to $15 \mu\text{g L}^{-1}$ of chlorophyll *a* (Hallegraeff, 1981). However, within patches of *T. democratica*, the phytoplankton concentrations are much lower, sometimes $<1 \mu\text{g L}^{-1}$ chlorophyll *a*, and inorganic nutrients are often not exhausted (Humphrey, 1963). About 2 weeks after reaching their maximum abundance, *T. democratica* decreased to very low levels while the phytoplankton reached 2–5 μg chlorophyll *a*, L^{-1} , and higher. Thus, there appears to be an inverse correlation between phytoplankton and salp abundance off eastern Australia. The decline of patches in this case could be due to a combination of loss to predators and to clogging of the salp mucous filters (Harbison *et al.*, 1986). Similar to our hypothesis for the SAB, upstream waters to the north are likely source areas of thaliacean patches off Sydney, as salp patches occur frequently in Moreton Bay, near Brisbane, in the fall (Fig. 4; Greenwood, 1980).

Similar wind-driven dynamics occur off northwestern Spain in winter. In this case, winds from the northeast drive surface water offshore, resulting in upwelling and salp patches near the shelf break (Huskin *et al.*, 2003). Maximum abundances of *Salpa fusiformis* reach ca. 22 m^{-3} . These salp patches occur along the offshore edge of shelfbreak salinity fronts over a narrow temperature range of $15.4\text{--}16.6^\circ\text{C}$ (Huskin *et al.*, 2003). This is similar to the narrow temperature range of waters containing doliolid patches in the SAB (Deibel, 1985) and to the temperature minima required for thaliacean patches in the Mediterranean Sea (Licandro *et al.*, 2006).

A 3-year time-series of monthly sampling off the Ivory Coast revealed a regular, high seasonal abundance of doliolids and fewer salps (Binet, 1976; his Fig. 2). The doliolid maxima occurred during the so-called Cold Season, when upwelling lead to phytoplankton increases during summer to early autumn. Thus, it appears that enhanced phytoplankton abundance from regular, seasonal upwelling and cooler temperatures resulted in enhanced doliolid production.

We have shown that high rates of phytoplankton production in response to upwelling are a primary

condition necessary for regularly occurring thaliacean patches on continental shelves. The SAB case study illustrates that thaliacean patches require a broad, shallow continental shelf, a strong boundary current with eddies and meanders, and along-shelf, upwelling favourable winds. This set of conditions occurs at various places in the world, many of which have been documented to have mesoscale thaliacean patches. To the degree that these boundary current and meteorological factors are known and predictable for a specific region, we believe that the presence of thaliacean patches should be predictable as well. Additional research would contribute to document linkages between thaliacean patches and their source populations, and causes for the decline of patches. To increase our understanding of patch dynamics will require long-term, mesoscale studies having a full suite of variables including hydrography and physical oceanography.

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