Bangarang Backgrounder[1]

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TNT Trophic Explosions

(Tidal 'n' Topographic Trophic Events)

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Abstract

When strong tides rip through topographically complex coastal habitats, areas of particularly turbulent rips and jets can become hotspots for feeding frenzies. Fish and marine tetrapods gather in tidally dynamics passages in diverse and energetic assemblages to exploit the planktonic production that has been aggregated there. The trophic explosion that results is a thrill to witness firsthand and a challenge to document scientifically. This Backgrounder briefly outlines the seabird and marine mammal literature that addresses these tidal and topographic trophic events. More details on the processes and importance of such tidal processes has already been explored in the "Fjords!" and "Plankton Processes" backgrounders. This document merely caps them with some information on how higher trophic levels take advantage of those processes.

Contents

[1] Bangarang Backgrounders are imperfect but rigorous reviews – written in haste, not peer-reviewed – in an effort to organize and memorize the key information for every aspect of the project. They will be updated regularly as new learnin' is incorporated.

“Tidal Coupling Hypothesis”

Tidal channels, rips and jets are well-known foraging hotspots for marine predators (e.g. Lweis & Sharpe 1987, Simard et al. 2002). Tidally-driven phenomena have been relatively well-studied because they occur over short spatial and temporal scale, making efficient and effective sampling possible (Hunt et al. 1999). Rorquals feed on tidally aggregated krill along a shoreline in the St. Lawrence estuary (Cotte & Simard 2005) and caplin in the Glacier Bay area (Chenoweth et al. 2011), short-tailed shearwaters gather at tidal fronts in the Aleutians (Vlietstra et al. 2005), bottlenose dolphins feed at tidal intrusions in rivers (Hastie et al. 2003), harbor porpoises and rorquals feed at an island wake system in the Bay of Fundy (Johnston et al. 2005b, Johnston & Read 2007), and both seabirds and pinnipeds feed in tidal passes in the Gulf Islands (Vermeer et al. 1987, Zamon 2003) – among many other studies.

Several studies, including Uda & Ishino 1958, Brown 1980, Johannes 1981, Wolanski & Hammer 1988, review in Hunt et al. 1999, Zamon 2001, have suggested that in habitats were rips and jets are present, energy flow to piscivorous predators is strongly associated with tides. Zamon (2003) referred to this hypothesis as the “tidal-coupling hypothesis”. This remains an area of active research.

Foraging Seabirds

Tides induce physical and biological features in local oceanography that facilitate feeding for marine tetrapods. I will not dive into seabird foraging strategy here, but it should be established that seabirds (and cetaceans too, to some unknown degree cetaceans) associate strongly with physical oceanographic features. Foraging seabirds may be aggregating according to threshold levels of prey abundance, which vary seasonally and with reproductive status (Ballance et al. 2001), and to do so they are likely using oceanographic cues to target suitable prey conditions. The depth and temporal stability of the pycnocline, the relative geography of winds and thermohaline forcing and consequent rate of upwelling and current convergence, etc., all serve to determine the local and global distribution of seabirds.

“Physical gradients, including boundaries between currents, eddies, and water masses, in both the horizontal and vertical plane, are often sites of elevated seabird abundance. Seabirds respond to the strength of gradients more than the presence of them.” (Ballance et al. 2001). “Piatt (1990) found evidence for threshold foraging for common guillemots and Atlantic puffins foraging on capelin in the northwest Atlantic…Piatt (1990) found that at scales of 2 to 6 km, searbids showed sigmoidal response to prey density.” (Hunt et al. 1999). In the Bering Sea, breeding auklets ignore smaller but more readily available zooplankton in order to target more energy-dense (though more distant) prey species (Ballance et al. 2001). Obst et al.

In shelf-systems, depth is a strong determinant of seabird community composition, due to 1) the diversion of production into either benthic or pelagic food webs, 2) the interaction of flows with the seafloor changes prey predictability and governs which seabird species are most competitive in an area, and/or 3) the fact that some birds may be able to exploit bottom substrate and others may not (Ballance et al. 2001). The relationship between seabird predators and their marine prey is also scale-dependent (reviewed in Hunt et al. 1999 and Ballance et al. 2001); the relationships seems to break down at small spatial scales, suggesting that seabirds sample prey randomly at close-range (Schreiber 2006).

Processes of Production

Tidal currents are inherently dynamic. They wax and wane on the scales of hours, days, months and seasons (Chenoweth et al. 2011). The effect of tides on biota in complex coastal habitats therefore cycles at similar temporal scales.

Topography
Shallow or coastal topographic features can induce fronts, internal waves and wake that influence the vertical and horizontal distribution of biota in an area. “Within water masses, locations where tidal currents impinge on bathymetric features provide opportunities for seabird foraging” (Hunt et al. 1999). When tidal currents interact with the sea floor, friction with the bottom can induce mixing. With sufficiently vigorous mixing in sufficiently shallow water, “structural” or “tidal” fronts result (Pingree et al. 1974; Simpson & Pingree 1978; Schumacher et al. 1979). “These fronts can have both zones of convergence, at which buoyant materials may concentrate at the surface (Pingree et al. 1974), and enhanced vertical transport of nutrients (Sambroto et al. 1986; Whitledge et al. 1986; Whitledge & Walsh 1986), which support primary production in the vicinity of the front (Pingree et al. 1975; Richardson & christoffersen 1991; Franks 1992a). Structural fronts are usually associated with gradually shoaling depths and do not require the strong tidal currents associated with violent mixing and upwelling commonly seen in narrow passes between islands or over shallow reefs. At structural fronts, seabirds make use of both convergences and production-related increases in prey biomass” (Hunt et al. 1999).

Bathymeric sills, islands, and headlands all divert or constrict water flow so as to create wake features both downstream and upstream of their topography. See the “Fjords!” Backgrounder for more on features created by tidal flows of fjord sills. Headlands, islands and reefs create 3-dimensional ‘island wake’ ecosystems that aggregate biota at multiple trophic levels (Wolanski & Hamner 1988). Theoretically, when a headland interacts with tidal currents, a leeward and tide-ward microhabitat is created. The leeward side experiences complex downstream current patterns including eddies (Chenoweth et al. 2011).

In Situ vs Auxiliary Production
Fronts and other physical gradients are important determinants of prey capture, either because 1) they enhance primary production which in turn enhances prey supply or 2) fronts concentrate prey into exploitable patches (Ballance et al. 2001). That is, abundance of prey in a tidally active area may result from in situ production passed through a local food web or the advection of prey organisms produced elsewhere and produced elsewhere (Hunt et al. 1999, Zamon 2002, Schneider 1990). This means that both overall prey biomass and their dispersion in the water column is likely to be influenced by tidal events (Zamon 2003).

Regarding the advection option, “tidal currents provide a mechanism to supply what oceanographers call ‘auxiliary energy’ (Mann & Lazier 1996) and terrestrial ecologists call ‘allocthonous energy’ (Polis et al. 1997) to local food webs (Zamon 2002). Tidal currents in constrictions can force prey to the surface (Hunt et al. 1999). They can also induce upwelling on the upstream side of a bathymetric feature and downwelling on the leeward side. Species can distribution themselves throughout this vertical advection space according to their target prey (Hunt et al. 1998). When currents slacken, prey are able to descend out of reach and foraging flocks disperse (Hunt et al. 1999). Tidally forced variation in prey availability have been observed in the type and amount of food brought to chicks at colonies (Frank 1992, Frank & Becker 1992).

For ephemeral tidal events, auxiliary and aggregated production is likely the driver of mixed-taxon foraging aggregations. The prey made available in the area is typically advected in rather than local in origin (Hunt et al. 1999). Zamon (2003) found that during flood tides fishes are more dispersed in the water column (i.e., higher encounter probability) but not necessarily more abundant.

These mechanisms are particularly important in shelf systems, where aggregations can be so predictable that “seabirds learn where and when to be in order to eat.” (Ballance et al. 2001)

Event Dynamics

Prey Availability

In addition to aggregation by physical processes (Begg & Reid 1997), prey can be trapped and herded by their predators. Subsurface predators (such as large predator fish, marine mammals and diving seabirds) increase prey availability for seabirds by 1) driving prey to the surface, 2) injuring or disorienting prey who drift up within range of surface predators, and 3) leaving scraps on which seabirds forage (Ballance et al. 2001). Diving auklets are particularly effective at making subsurface prey available to surface foragers (e.g. gulls) by chasing prey to the surface and trapping them there (e.g. Hoffman et al. 1981, Grover & Olla 1983).

Prey can also place themselves at risk in these tidal events by feeding themselves. Actively feeding fishes are more vulnerable to visual predators than non-feeding fishes, because fish often exhibit C-start postures before feeding strikes that induce a “silvery flash” easily seen by above-surface predators (Denton & Rowe 1994).

Prey combat these vulnerabilities with behavioral responses to tidal state. For example, capelin herd against channel head slopes in the Gulf of St. Lawrence at the start of flooding currents then return to the central channel using the surface outflow during the ebb (Simard et al. 2002). Euphausiids aggregated near the seafloor at the sill of Knight Inlet during strong tides, perhaps to escape the strongest midwater currents (Ianson et al. 2011).

Birds

In complex nearshore habitats, tidally active sites are likely readily relocated by foraging birds (Hunt et al. 1999). Some seabird species are known to aggregate at a typically productive phase of the tidal cycle even when the expected prey don’t show up (Braune and Gaskin 1982). Individual black-legged kittiwakes exhibit foraging area fidelity to tidally active areas, and time their twice-daily foraging trips during the breeding season to coincide with daily tidal cycles (Irons 1998). Individuals possessing local knowledge of tidally induced wake systems may have an advantage over individuals without local knowledge (Irons 1998). Gull numbers in the Gulf Islands correlate with times of maximum upwelling and abundance of zooplankton prey in surface waters, and their diet differs within (planktonic crustaceans) and without (other foods, mainly benthic and intertidal) the upwelling zone at the pass (Vermeer et al. 1987).

During a tidal cycle in a confined passage, seabirds have been observed aggregating only when currents were sufficiently strong to facilitate foraging (Braune & Gaskin 1982, Vermeer et al. 1987, Cairns and Schneider 1990, Hunt et al. 1998).

Foraging flocks can result from uncoordinated aggregation at a common resource but often are exacerbated by the fact that feeding seabirds can benefit from each other. Certain “catalyst” species can trap prey at the surface while others are visual signals of underlying prey for other birds (Ballance et al. 2001).

Conversely, interference competition also occurs in foraging flocks (Ballance et al. 2001). Similar to how offshore species with high diet overlap use physiographic gradients to structure resource partitioning and distribution differences in the open ocean (Begg & Reid 1997), species in foraging flocks sort out along prey density gradients, regardless of prey identity. “Such segregation has been recorded even within the same prey patch, with certain species exploiting the center and others the periphery.” (Ballance et al. 2001). Inter-taxon competition can also occur. Foraging flocks are often disrupted by feeding whales in the Kitimat Fjord System (this author, pers. observation).

Different species are able to access different portions of a tidally aggregated prey field. Most seabird species take prey within a half meter of the sea surface (Ballance et al. 2001). Gulls are not likely to reach fishes deeper than 1 to 2m during surface feeding or plunging (Zamon 2003). Another group takes prey within about 20m of the surface by flying or plunging into the waters. Another group dives using their wings and feet for propulsion (usually confined to the upper 100m) (Ballance et al. 2001).

Marine Mammals

During her dissertation on tidal foraging ecology in the San Juan Islands, Zamon (2001) observed more seals and more captures of large fish on the northward-flowing, incoming tide, especially at the peak of flood tide. Fin whales in the Gulf of St. Lawrence are known to move up and down the channel with the tides (Simard et al. 2002)

Chenoweth et al. (2011) demonstrated that tidal amplitude significantly affects whale abundance in headland wake systems. Whales tended to select habitat that moderated rather than amplified fluctuations in tidal amplitude, “suggesting that headlands also have the potential to be important features in areas with less extreme tidal exchange.” (Chenoweth et al. 2011). They also found more whales in “faster” current locations and more whales in leeward conditions (Chenoweth et al. 2011), which coincides with other obervations of preference for leeward feeding (Wolanski & Hamner 1988, Alldredge & Hamner 1980, Johnston et al. 2005a,b; Johnston & Rad 2007). Chenoweth et al. suggested that humpback whales optimize current speed by selecting slowing current habitat during large amplitude tides and fast current habitat during low amplitude tides (Chenoweth et al. 2011). At strong tides foraging may become too energetically demanding for either whales or their prey to be profitable (Johnston et al. 2005a), and during slack/small tides fish may be widely dispersed or have greater ability to avoid predation (Chenoweth et al. 2011).

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