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Ocean Internal Waves as Sources of Small-scale Patchiness in Seabird Distribution on the Blake Plateau

J. CHRISTOPHER HANEY[1]

Skidaway Institute of Oceanography, P.O. Box 13687, Savannah, Georgia 31416 USA

Seabirds inhabit marine environments that are highly structured by physical processes and features. This physical structure can affect the availability and locations of prey (Haury et al. 1978), in turn ultimately influencing seabird occurrence within marine habitats (Hunt and Schneider 1986). Distributional ecology of seabirds has been interpreted primarily on the basis of large-scale (100–1,000 km) physical variation arising from currents, water masses, and large density fronts (e.g. Brown et al. 1975, Pocklington 1979, Ainley and Jacobs 1981, Gould 1983). Physical structure or patchiness in seabird distribution may occur at much smaller scales, however. Schneider and Duffy (1985) found several seabird species aggregated at spatial scales ranging from 0.3 to 23 km in the Benguela Current region. They did not identify the cause of the aggregations, which could have arisen from species-specific responses to the physical-biological environment (Haney 1986a), variation in flocking or social interactions (Hoffman et al. 1981), or random differences in flock encounters caused by artifacts of sampling during ship-board censusing.

In this paper I describe small-scale (1–10 km) heterogeneity generated by internal waves and its effect on seabird distribution on the Blake Plateau off the coast of the southeastern United States. The Blake Plateau is a topographic anomaly that lies seaward of the continental shelf between Cape Hatteras, North Carolina, and the east coast of Florida. The gently sloping plateau interrupts the continental slope and widens considerably from north to south. As a consequence, waters deeper than 1,000–2,000 m are absent within 150–250 km of the coastline in this region. The Gulf Stream flows over the relatively shallow western third of the plateau, and the current's central axis or region of maximum velocity (6 km/h) occurs approximately 30–40 km east of the continental shelf edge (200-m isobath). The Gulf Stream is altered or deflected where irregular bathymetry on the plateau influences stream flow (Legeckis 1979). Internal waves were observed within the central axis of the stream at two locations with steep bathymetric gradients: the Stetson Mesa (30°20′N, 79°25′W; Fig. 1) and Hoyt Hills (32°00′N, 78°30′W). I censused seabirds at these sites on 1–3 October 1983 and 9–11 May 1984 during investigations of the biological effects of topographic mixing (McGillivary et al. 1986).

Surface turbulence, including that related to internal waves, was conspicuous at both the Hoyt Hills and Stetson Mesa. Internal waves are subsurface waves found between water layers of different density or within water layers with vertical density gradients (LaFond 1959). They can be caused by current flow through straits, around peninsulas, or over irregular bottom (see lower part of Fig. 1), as well as by atmospheric disturbances, tidal forces, and shear flow. Except at wind speeds exceeding 15 knots (Owens 1981), internal waves have visible surface mani-

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[1] Present address: Alaska Fish and Wildlife Research Center, U.S. Fish and Wildlife Service, 1011 E. Tudor Road, Anchorage, Alaska 99503 USA.
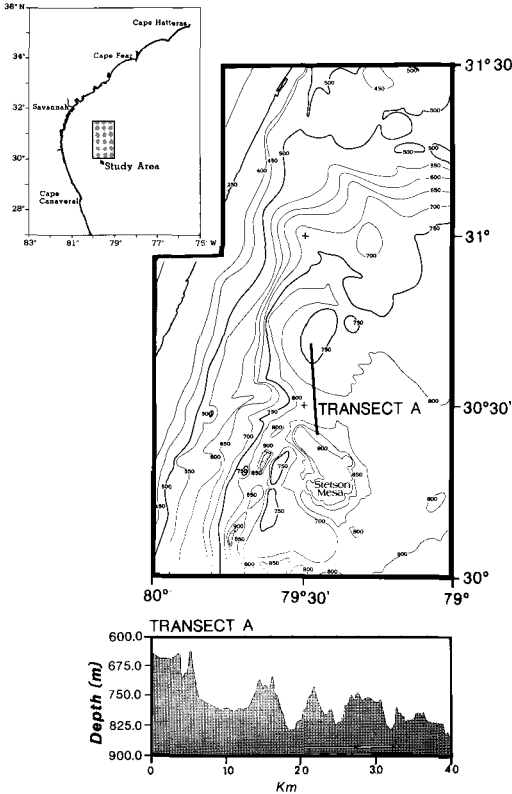
Fig. 1. Location of seabird counting transect (see Fig. 3) where topographic mixing and internal waves were studied off the coast of the southeastern United States, 11 May 1984. The irregular bathymetry along the 35.6-km cruise track is illustrated at the bottom of the figure. The left side of the bathymetric tracing corresponds to the northern part of the transect.
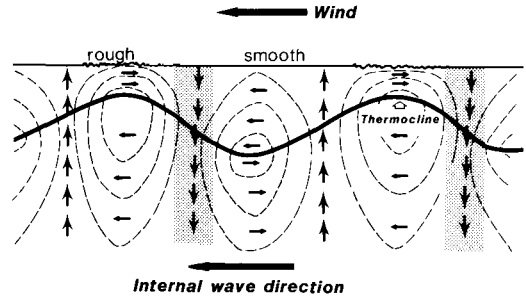
Fig. 2. Schematic representation of internal waves. Dashed lines indicate circulation of particles and their relationship to sea surface convergence slicks (shaded wave troughs). Zone of extension (divergence) at the surface (wave crest) is illustrated and marked as "rough."

100–200-m pinnacles near the Stetson Mesa (Fig. 1). Wavelengths (shortest distances between wave crests) were approximately 2–4 km. Because these physical patches were smaller than the 5-km transect that resulted from the 15-min, 300-m count method I used during censusing (Haney and McGillivary 1985), the relative abundances of seabirds in wave crests and troughs could not be expressed per unit area or distance traveled.

Between 9 and 11 May 1984, I used the same transect methodology at the mesa and Hoyt Hills, but divided each transect into wave crest and trough categories by measuring the time to the nearest minute spent crossing each zone. Because ship speed was constant, I could estimate the distance traveled and surface area censused in both wave crests and troughs. Seabird abundances within the 300-m count zone were then quantitatively compared between the zones of divergence and convergence (Table 1).

I tested the hypothesis that seabirds were as likely to occur in wave troughs as in wave crests with Pearson's test for homogeneity. For combined species, seabirds were significantly more likely to occur in the wave crest ($\chi^2 = 22.2$, df = 1, $P < 0.005$). Except for a single bird observed during one of the four transects conducted at the topographic features (e.g. Fig. 3), all seabirds were flying over or sitting on internal wave crests. Of the three species observed in the count zone along the cruise tracks (Table 1), Black-capped Petrels ($\chi^2 = 14.0$, df = 1, $P < 0.005$) and Audubon's Shearwaters ($\chi^2 = 6.4$, df = 1, $P < 0.025$) were significantly more likely to occur in wave crests than in wave troughs.

Observations of seabirds made outside the 300-m count zone and while the ship was on-station indicated that additional species and individuals were affected by internal waves. Sooty Tern (*Sterna fuscata*) flocks ($n = 8$, $\bar{x} = 6.3$, range = 2–12 individuals) were located only over internal wave crests. Single White-tailed Tropicbirds (*Phaethon lepturus*), Leach's (*Oceanodroma leucorhoa*) and Band-rumped (*Oceanodroma*

festations in the form of wide slicks alternating with and separated by rippled or rough water arranged in parallel bands. Small-scale currents generated by vertical undulations of the thermocline cause a convergence (= smooth water) over the wave trough and a divergence (= rough water) over the wave crest (Fig. 2; Ewing 1950). The higher velocity of water moving over the wave crest, and variations in wind stress caused by small differences in dynamic topography between wave crests and troughs, create the rippled effect.

On 2 October 1983 I observed Black-capped Petrels (*Pterodroma hasitata*) foraging and feeding over the crests of internal waves at the Stetson Mesa. Along a 75-km cruise track, petrels and a few Audubon's Shearwaters (*Puffinus lherminieri*) and Pomarine Jaegers (*Stercorarius pomarinus*) aggregated at some but not all wave crests. No seabirds were observed over wave troughs. Internal waves were oriented perpendicular to the Gulf Stream current downstream of

castro) storm-petrels were seen with mixed-species flocks of Black-capped Petrels, Audubon's Shearwaters, and Wilson's Storm-Petrels (*Oceanites oceanicus*) at wave crests. The majority of seabirds were actively foraging or feeding at these sites, with the remaining individuals confining their flight over the wave crests.

Because of internal wave structure, it is possible to conclude that all seabirds were associated with small-scale zones of divergence (cf. Figs. 2 and 3). Continuous ship-board measurements revealed that sea surface temperatures within the internal wave crests were 0.2–0.3°C cooler than in the troughs. Expendable bathythermograph (XBT) casts indicated that the Gulf Stream thermocline at the Stetson Mesa and Hoyt Hills was deflected 50–100 m upwards, consistent with topographic induction of the waves (LaFond and Cox 1962). The irregular spacing of wave crests and troughs (Fig. 3) may have been due to the orientation of the cruise track, but irregular spacing (deformation) of internal waves is not uncommon downstream of topographic features (Melville 1986). Small-scale (2–6 km) patchiness in seabird distribution corresponded exactly to the irregular patchiness of these internal waves.

Internal waves apparently have influenced small-scale patchiness in seabird distribution elsewhere (cf. Brown et al. 1979, Brown 1980). Tidal currents interrupted by irregular bathymetry are one of the primary sources of internal waves (Rattray 1960). Brown (1980) found Red Phalaropes (*Phalaropus fulicaria*) associated with an area of divergence caused by tidal flow over ledges off Brier Island, Nova Scotia. Phalaropes were feeding on zooplankton entrained from deeper waters at the wave crest, but most individuals were in the convergence or wave trough (Brown pers. comm.). Internal waves may have been the source of the very slight bimodal distribution of Cory's Shearwaters (*Calonectris diomedea*) normal to the Gulf Stream front observed by Haney and McGillivary (1985). Internal waves often occur within ocean frontal systems, particularly when these fronts are situated near a continental shelf break (LaFond and Cox 1962, Melville 1986).

Seabird associations with internal waves carry several significant implications. The role of divergence in structuring the marine habitats of seabirds has been largely overlooked or ignored. Most seabird studies (e.g. Brown 1980, Briggs et al. 1984, Haney 1986b) emphasized lateral advection and convergence as
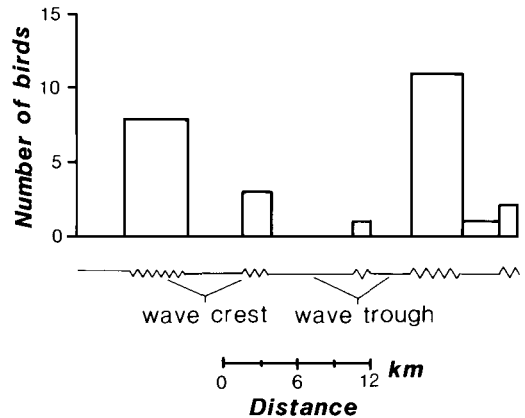

Fig. 3. Small-scale variation in seabird distribution along one of four horizontal transects (see Fig. 1) at the Stetson Mesa. Bar heights indicate number of birds and bar width indicates width of alternating internal wave crests and troughs along the ship's cruise track.

mechanisms that localize seabird prey and in turn attract seabirds. Although ocean fronts (water mass boundaries) and convergences have often been considered synonymous by marine ornithologists, fronts may contain zones of both convergence and divergence (Bowman and Esaias 1978, Pietrafesa and Janowitz 1980), and other physical features may be predominately or partially characterized by convergence (e.g. Langmuir windrows, internal waves, and eddies). Many of the seabird aggregations attributed to ocean fronts (for a review see Hunt and Schneider 1986) are difficult to evaluate for lack of physical evidence, and may have been due to the process of divergence or to other physical features such as internal waves.

It is not clear why seabirds avoided the convergence zones (wave troughs). Seabirds might be expected to be more abundant in wave troughs, where the horizontal and vertical flow aggregates surface animals that swim upward to compensate for downward displacement. Previous studies have indicated that concentrations of epipelagic zooplankton and fish can be 100–200× higher in internal wave troughs than in wave crests (Zeldis and Jillet 1982; Shanks 1983, 1985; Kingsford and Choat 1986). Although the rippled, rough water provided visual cues similar in

TABLE 1. Relative abundances of seabirds in internal wave crests and troughs at the Stetson Mesa region of the Blake Plateau. Total transect length was 35.6 km, 21.2 km in wave troughs and 14.4 km in wave crests.

Species	No. km traveled		No. km censused		No. min observation	
	Crest	Trough	Crest	Trough	Crest	Trough
Pterodroma hasitata	0.21	0.00	0.70	0.00	0.28	0.00
Puffinus lherminieri	0.13	0.01	0.45	0.04	0.18	0.01
Oceanites oceanicus	0.03	0.00	0.10	0.00	0.04	0.00

appearance to schooling fish or invertebrates, it is unlikely that seabirds would have so consistently oriented their foraging within well-defined physical patches in the absence of prey (cf. Briggs et al. 1984). Seabirds may have aggregated at wave crests on the Blake Plateau because of qualitative differences in prey composition. Shanks (1983) found that although zooplankton were less abundant in wave crests, species occurring there were entrained from deeper water near the thermocline. In the Gulf Stream thermocline, euphausiids, amphipods, and small lanternfishes were the most abundant zooplankters caught during the cruises. The spatial resolution of zooplankton sampling on the cruises was not fine enough to detect differences in prey availability between wave crests and troughs, and little information exists on how internal waves affect the large numbers of plankters found below the surface (see Kingsford and Choat 1986).

Aggregations of seabirds at internal waves illustrate the importance of understanding the small-scale physical structure of marine environments when interpreting seabird distributions. One reason so little variation in seabird abundance has been explained statistically (Abrams 1985) may be that small-scale patterns obscure seabird ecological patterns at larger scales (Hunt and Schneider 1986). Internal waves lie somewhere between Langmuir windrows (Brown 1980, Haney 1986b) and ocean fronts (Ainley and Jacobs 1981) on the spatial scale of physical features known to influence seabird distribution, but they may be nested within larger physical features (LaFond and Cox 1962) and their influence additive with other processes. The relative importance of internal waves in structuring the marine environments of seabirds will be difficult to assess. In a large proportion of the world's oceans, wind speeds rarely fall below 15 knots, the upper threshold for detecting the surface presence and effects of internal waves (Kingsford and Choat 1986). Seabird associations with internal waves on the Blake Plateau suggest, however, that to adequately evaluate the environmental determinants of seabird distribution, the correct identification, small spatial scales, and irregular spacing of physical features must be considered during ship-board or aerial surveys.

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Do Male Hooded Warblers Exclude Females from Nonbreeding Territories in Tropical Forest?

Eugene S. Morton,[1] James F. Lynch,[2] Kimberley Young,[1] and Patricia Mehlhop[2]
[1]*Department of Zoological Research, National Zoological Park, Smithsonian Institution, Washington, D.C. 20008 USA, and*
[2]*Smithsonian Environmental Research Center, P.O. Box 28, Edgewater, Maryland 21037 USA*

Male and female Hooded Warblers (*Wilsonia citrina*) defend exclusive feeding territories in the nonbreeding season (Rappole and Warner 1980). Rappole and Warner (1980) showed that individuals remain on their territories for the duration of the overwintering period, and return to the same winter territory each year. These authors presented data suggesting that females are rare or absent in mature forest, but also demonstrated that females are fully capable of defending their territories from intrusions by males. Lynch et al. (1985) documented clear-cut habitat segregation between the sexes of Hooded Warblers during the nonbreeding season. Surveying hundreds of Hooded Warbler territories in the Mexican states of Quintana Roo and Yucatan, they found males in canopied mature and second-growth forests and females in shrubby, low-stature woodlands and brushy old fields. The nonbreeding habitat of males appears more similar to the breeding habitat (*sensu* James 1971) than does the female nonbreeding habitat. Despite the large physiognomic differences between habitats used by males and females, the sexes do not differ sub-

stantially in foraging maneuvers or foraging heights (Table 1).

One hypothesis to explain the intersexual habitat segregation is that the larger males are behaviorally dominant over females and tend to exclude them from the preferred forest habitat in the nonbreeding period (Lynch et al. 1985). Any such behavioral dominance might be expressed most strongly when the birds first arrive on their tropical nonbreeding grounds. From 9 to 23 October 1984, we tested the "male dominance" hypothesis by mapping territories of color-banded Hooded Warblers and then removing males from territories adjacent to female territories. We then observed the females for any increase in their use of forest habitat in the absence of defending males.

Our study area straddled a gravel road ca. 3.5 km west of Puerto Morelos, Quintana Roo, Mexico. Hooded Warblers begin to arrive in the area by mid-August, and are abundant there by late September (pers. obs.). Most of the study area is covered by mature semi-evergreen forest dominated by *Manilkara*