Bio-physical coupling in the formation of zooplankton and fish aggregations over abrupt topographies

Amatzia Genin*

Department of Evolution, Systematics and Ecology, The Hebrew University of Jerusalem and The Interuniversity Institute for Marine Sciences, P.O. Box 469, Eilat 88103, Israel

Received 11 April 2003; accepted 10 October 2003
Available online 14 May 2004

Abstract

Aggregations of zooplankton, micronekton and fish are frequently observed above seamounts, canyons and shelf breaks. The aggregations are produced by five different mechanisms, all driven by ocean currents. Upwelling is frequently generated when ambient currents impinge on abrupt topographies. Nevertheless, upwelling enhances local production of zooplankton and fish only over large topographies such as shelf breaks, where the residence time of the upwelled water is sufficiently long to allow enrichment in primary production to propagate up the food web and augment the growth of resident animals. Daily accumulations occur over topographies at shallow and intermediate depths when the topography blocks the morning descent of migrating zooplankton. This mechanism is common over seamounts. Two other mechanisms are driven by behavioral response to vertical currents when zooplankton swims vertically in order to maintain depth: accumulations by depth retention against upwelling are common at depths to which migrating zooplankton descend during the day, while depth retention against downwelling seems to operate only in the upper water column (e.g., along topographically generated fronts). The fifth mechanism is driven by the amplification of currents over abrupt topographies. Strong currents enhance population growth of resident animals by augmenting fluxes of suspended food. A feed-rest hypothesis is proposed to explain how site-attached planktivorous fish can benefit from strong currents at sites with ample quiescence shelters in which the fish rest during non-feeding intervals. Four of the above mechanisms generate “trophic focusing”, a process by which prey from immense volumes of flowing water is accumulated (or trapped) in a relatively small confined area. The ensuing subsidy of prey propagates up the food web, supporting aggregations of higher predators, such as fish, marine mammals and fishermen. Abrupt topographies can have an important role in determining trophic interactions in the marine realm.

Keywords: Seamount; Canyon; Shelf break; Front; Upwelling; Downwelling; Depth-retention; Behavior

1. Introduction

The main objectives of this review are to examine the conditions under which aggregations of zooplankton, micronekton and their predators occur over marine abrupt topographies and to critically evaluate the bio-physical mechanisms involved. The topographies addressed include seamounts, canyons and shelf breaks, classified as “shallow”, within the photic layer; “intermediate”, below the photic layer but shallower than \( \sim 400 \) m, and “deep”. The latter
category extends to a depth of approx. 1500 m, as very little quantitative information is available for abrupt topographies at greater depths.

Following Simard et al. (1986), I use the term aggregation to refer to the grouping together of animals regardless of the mechanism of formation, which can be passive, active or due to population growth. An accumulation is an aggregation where the individual animals gradually concentrate due to a mechanism other than behavioral interactions between the aggregated individuals, e.g. accumulation of floating individuals at downwelling fronts (Owen, 1981). Local aggregations are classified as resident or transient. The former type indicates an aggregation of individuals that have lived for a long time (>weeks) at the same site, while the latter refers to ephemeral (<days) accumulations that disperse once the accumulation mechanism ceases to operate. A special case of transient accumulation is that of highly mobile animals (e.g., birds, marine mammals) that follow accumulations (resident or transient) of planktonic prey. Aggregations related to intra-specific behavioral interactions (e.g. mating, spawning) are not addressed.

Ample literature is available on the biology of seamounts, shelves and canyons. Since the objective of this review is to understand mechanisms, descriptive reports with little or no quantitative data as well as studies relating to systematics and taxonomy were, by and large, excluded. The review focuses on demersal and pelagic animals, not on benthos.

2. Aggregations

2.1. Seamounts

The term “seamounts” is used in reference to isolated submarine mountains, excluding very large topographies such as ridges, rises and great banks. The high variations in the topography, physiography, depth and location of seamounts render similarly diverse the prevailing ecological processes that determine the structure of local communities (reviewed by Boehlert and Genin, 1987; Rogers, 1994). Nevertheless, as discussed below, some unified patterns are apparent. The two most noteworthy trends are: (i) many seamounts harbor resident aggregations of demersal fish and micronekton; (ii) open-ocean, migrating plankton are usually depleted over shallow and intermediate seamounts.

Up until the start of intensive seamount fisheries several decades ago, extremely large stocks of commercial fishes inhabited numerous intermediate and a few deep seamounts (Uchida and Tagami, 1984; Rogers, 1994; Clark, 2001). Unfortunately, many seamount fisheries have since been over exploited. Key species included rockfishes (Sebastes spp.) and sablefish (Anoplopoma fimbria) on shallow and shallow-intermediate seamounts, pelagic armouredhead (Pseudopentaceros wheeleri) and alfonsin (Beryx splendens) on intermediate seamounts and orange roughy (Hoplostethus atlanticus) on deep seamounts (Isaacs and Schwartzlose, 1965; Brodeur and Pearya, 1983; Uchida and Tagami, 1984; Pearson et al., 1993; Rogers, 1994; Clark, 2001). Most of those fishes are much less common in open waters.

Southeast Hancock Seamount (summit depth 265 m, northern end of the Hawaiian Ridge) has been intensively studied by Boehlert and Seki (1984), Boehlert (1988), Wilson (1992), Wilson and Boehlert (1993) and Boehlert et al. (1994). This and other intermediate seamounts along the Hawaiian-Emperor ridge harbored extremely rich fisheries of pelagic armorhead and alfonsin (Uchida and Tagami, 1984). Bio-acoustic surveys of SE Hancock Seamount indicated a significantly higher biomass of smaller scatterers over the seamount than at a reference station in the open waters some 10 km away. Midwater trawls revealed that these scatterers consisted of micronektonic species, including a sternopythcid fish (Maurolicus muelleri), a mysid (Gnathophausia longispina) and a squid (Nectoteuthis iris) (Boehlert, 1988). “Typical” open-water species were less common above the seamount than away from it (Wilson and Boehlert, 1993). The trend of reduced abundances of typical pelagic species was also reported for migrating zooplankton from the Great Meteor Seamount (275 m depth; northeast Atlantic) by Nellen (1973) and from two seamounts at intermediate depth off California (Genin et al., 1988, 1994). The abundance of non-migrating zooplankters, however, was apparently unaffected by the seamounts (Genin et al., 1994).

The scatterers over SE Hancock seamount exhibited a repeated diel migration, consisting of an ascent from the seamount flanks around dusk,
foraging high above the summit during the night, and a rapid descent to the seamount flanks in the morning (Boehlert, 1988). The above trend was more conspicuous during summer than winter. A time series of acoustic transects showed that the scatterers were able to maintain their position above the seamount in spite of strong currents that should have displaced the animals (had they been passive particles) to the surrounding deep waters within several hours (Wilson, 1992). This ability to maintain location on the seamount, together with a local presence of all life stages of the *G. longispina* (Wilson and Boehlert, 1993) and the documented year-long increase in body size of an apparent cohort of *M. muelleri* (Boehlert et al., 1994), indicated that the aggregations of micronekton and fish of over SE Hancock were resident.

Other noteworthy resident aggregations are those of orange roughy (*H. atlanticus*) and orees (*Oreosomatidae*) on deep (400–1500 m) seamounts and other abrupt topographies around New Zealand and southeast Australia (Koslow, 1997; Clark, 2001). Orange roughy grows slowly and lives very long (>100 years) (Koslow, 1997). However, unlike “typical” deep-sea fishes, it swims fast, has a high metabolic rate and high protein and lipid content and requires a daily ration (of pelagic and benthopelagic prey, particularly small fish and squids) of about 1% of body weight (reviewed by Koslow, 1997). However, the metabolic maintenance of orange roughy aggregations is not fully understood, as local fluxes of organic matter sinking from the photic layer fall far short of the aggregations’ metabolic needs (Koslow, 1997; Clark, 2001). The common occurrence of considerable aggregations of resident fish and micronekton on intermediate and deep seamounts therefore indicates the occurrence of localized trophic subsidy.

2.2. Shelf breaks

Animal aggregations are common over many shelf breaks. Examples include aggregations of: Antarctic krill, *Euphausia superba*, over shelf breaks in the southern ocean (Macaulay et al., 1984; Pauly et al., 2000), copepods and other zooplankton at the shelf break off South Africa (Barange, 1994), euphausiids near the shelf breaks off Baja California, off British Columbia, and in the St. Lawrence estuary (Robinson and Gomez-Gutierrez, 1998; Simard and Mackas, 1989; Mackas et al., 1997; Simard et al., 1986), larval and juvenile cod in the northeastern North Sea and along a shelf-break front in the northwestern Mediterranean (Munk et al., 1995, 1999; Sabatés, 1990) and aggregations of tuna on the shelf break off New South Wales, Australia (Young et al., 2001).

Acoustic surveys and net tows carried out by Simard et al. (1986) across a narrow coastal shelf in the lower St. Lawrence estuary showed the presence of long (>100 km) narrow (1–7 km) aggregations of two euphausiid species, *Thysanoessa raschi* and *M. norvegica*. Earlier observations by Simard et al. (1986) and Sameoto (1976) indicated that the aggregations had a certain degree of permanence above the shelf break, which also attracted planktivorous fish.

A common feature reported for some shelf break aggregations was a correspondence between the aggregations and vertical currents. Barange (1994) found nocturnal aggregations of zooplankton in the upper 100 m along a thermal front above the shelf break off the south-east coast of South Africa. The strongest aggregations, dominated by copepods, were found where the horizontal thermal gradient was sharpest, likely a location of vertical currents. A trophic cascade from aggregated zooplankton to salmon was suggested by Healey et al. (1990) to explain the dense aggregations of fishing vessels along the upwelling front over the Vancouver Island shelf break during two consecutive seasons (April–September in 1982 and 1983). Healey et al. (1990) assumed that the fishing vessels followed an “ideal free distribution” that was directly affected by the salmon distribution. Aggregations of salmon, in turn, reflected accumulations of their zooplankton prey. Co-occurrence of upwelling at the aggregation sites was inferred from hydrographic measurements.

2.3. Canyons

Canyons are abrupt, bounded depressions crossing wide continental slopes. Most of the canyons in which plankton and fish distributions have been studied were fairly isolated, large topographic structures. Since canyons are sometime part of larger abrupt topographic features (e.g. shelf break), a determination of
canyon effects requires that both the canyon and its surroundings be thoroughly surveyed.

One of the earliest observations on animal aggregations in canyons was reported by Pereyra et al. (1969), who observed dense aggregations of rockfish, mostly *Sebastes flavidus*, at 110–130 m depth on the southern flank of Astoria canyon, located on the shelf slope off the Columbia River, northwest USA. High abundances of rockfish were associated with local aggregations of micronekton. About 90% of the fish stomachs contained migrating mesopelagic species, mostly myctophids and large crustaceans. A strikingly similar pattern was observed by Schoenherr (1991) in Monterey Canyon, CA. Elongated, 1–2 km wide aggregations of mostly euphausiids (*Thysanoessa spinifera*) were found at 130–150 m depth along the southeast edge of the canyon, forming a distinctive scattering layer. In late afternoon the dense layer shifted to shallower water (100–110 m), just above the sea floor. The immense aggregations also attracted numerous blue whales that were feeding on the krill. The whales remained above the canyon’s southeast edge for a few weeks and left when the krill aggregations declined.

Macquart-Moulin and Patriti (1996) sampled zooplankton using net tows around three canyons off the Mediterranean coast of France. Migratory species were accumulated over the canyon heads. Cartes et al. (1994) reported higher species richness and seasonally higher biomass of fishes and crustaceans in two canyons (430–512 m depth) in the Catalan Sea, northwestern Mediterranean. Greene et al. (1988) observed immense, near-bottom aggregations of euphausiids (mostly *M. norvegica*) in three canyons on the south-eastern shelf of Georges Bank. Krill densities in the aggregations were two to three orders of magnitude greater than the highest densities observed in water-column scattering layers.

Dense aggregations of Pacific ocean perch (*Sebastes alutus*) and euphausiids (mostly *Thysanoessa* spp.) were observed repeatedly by Brodeur (2001) at the upper (down-current) edge of Pribilof Canyon, in the Bering Sea. The rockfish aggregations were associated with “forests” of sea whips, between which the fish appeared to be resting during the night. The euphausiids were the dominant prey found in the fish stomachs.

Dense aggregations of euphausiids were also observed near the heads of three submarine canyons in Canadian waters: (i) Barkley Canyon, a 6-km long canyon off Vancouver Island (Allen et al., 2001); (ii) Nitinat Canyon, located on the Vancouver Island shelf south-east of Barkley canyon (Mackas et al., 1997); and (iii) the large, canyon-like Laurentian Channel, located in in the Saguenay—St. Lawrence Marine Park (Lavoie et al., 2000). Microscopic analysis of net-tow samples from Barkley canyon showed that only vertically migrating species (mostly euphausiids) were aggregated (Allen et al., 2001). The immense aggregations observed near the head of Laurentian Channel by Lavoie et al. (2000) during the summers of 1994 and 1995 were dominated by two euphausiids, *T. raschi* and *Meganictiphenes norvegica*.

### 3. Mechanisms

In general, two types of mechanisms generate aggregations over abrupt topographies: those in which higher abundances result from enhanced local population growth and those in which animals accumulate in a certain area without corresponding changes in their productivity. Some aggregations over abrupt topographies involve both types. The former type is usually, but not always, associated with local upwelling, whereby enhanced phytoplankton growth propagates up the food web generating local patches of herbivorous zooplankton and possibly predators. Hereafter, this mechanism is termed “upwelling”. Enhanced population growth of predators can also be supported without upwelling when the supply of prey is augmented. Such mechanisms are hereafter collectively termed “trophic subsidy”. Major trophic-subsidy mechanisms are usually the result of plankton and fish behavior, including directional homing on rich patches of prey and “un-intentional” accumulations due to behavioral responses to certain environmental conditions. Five different mechanisms are discussed below.

#### 3.1. Upwelling

Upwelling can enhance primary production and consumer biomass over abrupt topographies as it does in many coastal and oceanic upwelling regions. How-
ever, two conditions must be met in order for upwelling to enhance population growth of zooplankton and fish residing over relatively small topographies such as seamounts, canyons and shelf breaks: (a) the upwelling of the deep, nutrient-rich water should be sufficiently strong to reach the photic layer, and (b) the upwelled water should remain above the topography for a sufficiently long time to elevate local phytoplankton biomass (order of 1–2 days) which, in turn, should augment the growth of the local zooplankton population (order of weeks). Over small topographies, the upwelled water is often swept away before a patch of high phytoplankton biomass develops, unless some water-trapping occurs.

3.1.1. Seamounts

The hypothesis that topographically induced upwelling enhances primary production and consumer biomass over seamounts was first proposed by Uda and Ishino (1958). Theory predicts that when currents encounter seamounts, some of the water is upwelled and flows above the summit. The contraction of streamlines and the change in potential vorticity generate an anticyclonic, quasi-stationary eddy, the Taylor column. This column is expected to remain trapped above the seamount for some time (Taylor, 1923; Hogg, 1973; Huppert, 1975; Huppert and Bryan, 1976). Hence, both conditions, the occurrence of upwelling and long residence time of the upwelled water, are theoretically possible. However, in spite of great efforts devoted for testing the upwelling hypothesis over seamounts, evidence for its occurrence is sparse.

Genin and Boehlert (1985) documented a cold dome with spatial characteristics consistent with a Taylor column, above an intermediate (280 m deep) seamount in the northwest Pacific. The concentrations of chlorophyll $a$ were elevated within the dome, apparently indicating residence time of a few days. However, the vertical displacement of uplifted isotherms decayed with elevation above the seamount, so that both temperature and chlorophyll anomalies were detectable only near the deepest part of the photic layer. Furthermore, neither uplifted isotherms nor chlorophyll anomalies were present during repeated surveys 2 and 17 days later.

Lopukhin (1986) observed enhanced ATP concentrations over several seamounts across the Atlantic Ocean. Although the trend was explained in terms of Taylor column, no corroborating data were presented.

Cobb Seamount is an isolated topography, rising from $>$3000 m to the photic layer (24 m at the peak) some 500 km west of the northwest coast of the US. The seamount harbors high densities of apparently self-sustaining demersal fishes (Pearson et al., 1993). The physics and biology over Cobb seamount were investigated in a series of studies by Dower et al. (1992), Sime-Ngando et al. (1992), Freeland (1994), Comeau et al. (1995), Dower and Mackas (1996), and Dower and Perry (2001). In summer 1990, Dower et al. (1992) observed a dramatic increase in water turbidity centered around the shallow rim of the seamount summit (30–60 m depth). Based on a locally established correlation between turbidity and the concentration of chlorophyll $a$, Dower et al. (1992) calculated that the increase in water turbidity was due to a seven-fold increase in chlorophyll $a$. However, such an increase was not found during repeated visits to the seamount (Comeau et al., 1995). Extensive CTD profiles and current meter measurements carried out during that and the following two summers by Freeland (1994) showed (i) a substantial bottom-intensification of the currents and (ii) isopycnal doming that was tightly bound to the bottom ($\sim$ 20 m), unlikely to penetrate much into the photic layer. At the same time, Sime-Ngando et al. (1992) found that the biomass of ciliates was higher over than away from the seamount, (although the ciliates’ numerical density was similar at the two sites). In summer 1992, Dower and Mackas (1996) observed stronger isopycnal doming over the seamount (resembling a Taylor column), but chlorophyll was not measured and zooplankton density above the seamount, the focus of the study, was similar to that in the surrounding waters. Comeau et al. (1995) reported relatively uniform distribution of chlorophyll $a$ and incident light and very patchy values of primary production, over and away from Cobb seamount. Although nutrient isolines domed slightly upward above the seamount, it did not seem to enrich surface waters or stimulate production (Comeau et al., 1995).

A decay of seamount-induced upwelling is expected as a function of stratification and current velocity (Huppert and Bryan, 1976; Mohn and Beckmann, 2002a). Since stratification is usually strongest across the lower part of the photic layer, the decay of
isopycnal doming is expected to be greatest at the biologically most relevant depth. The hydrographic studies in which I participated (Genin and Boehlert, 1985; Genin, 1987) included a total of 17 surveys over eight different seamounts across the north Pacific Ocean at depths ranging from 100 to 1440 m. Isotherm doming was observed in less than 50% of the surveys, (Fig. 1), and in only one case (Genin and Boehlert, 1985) did the upwelling penetrate the photic layer and a chlorophyll “signal” was observed.

So far there has been no clear evidence for the occurrence of Taylor columns that reach into the photic layer and trap upwelled waters over seamounts for sufficiently long periods to allow enhanced primary production to propagate up the food chain and locally enhance the productivity of zooplankton, fish and higher trophic predators (e.g., Mackas et al., 1980; Yoder et al., 1983; Atkinson et al., 1984; reviewed by Le Fevre, 1986). The ecological processes are similar to those operating in other, well-documented coastal upwelling systems and will not be further discussed. However, in some cases the generation time of the aggregated micronekton and fish (weeks to years) greatly exceeds the local residence time of the upwelled water (several days; Mackas et al., 1985, 1997). Also, studies where both phytoplankton and zooplankton were studied concurrently (e.g., Munk et al., 1995) indicate that while high phytoplankton biomass prevails throughout the shelf region, zooplankton aggregations are typically confined to narrow “bands”. Local nutrient injections alone cannot explain those bands.

3.1.2. Canyons

Occurrences of upwelling at depths below the photic layer have been reported from several intermediate canyons (Mackas et al., 1997; Lavoie et al., 2000; Allen et al., 2001). Freeland and Denman (1982) observed strong upwelling which penetrated the photic layer over a narrow canyon off Vancouver Island, Canada. The upwelling was driven by the interaction between the canyon and coastal currents. Nutrient concentrations were high over a large section of the shelf. Such large-scale topography-driven upwelling is the obvious cause for the high biological productivity over the shelf, however, it cannot explain local aggregations of animals in confined regions within canyons.

3.1.3. Shelf breaks

Mackas et al. (1997) found a positive correlation between local aggregations and upwelling over the Vancouver shelf. Their findings could have indicated that nutrient injection and bottom-up control was the major mechanism responsible for the observed aggregations. When upwelling occurs along the shelf break, the characteristic large spatial scales and long residence times allow enrichment in phytoplankton biomass to propagate up the food chain and locally enhance the productivity of zooplankton, fish and higher trophic predators (e.g., Mackas et al., 1980; Yoder et al., 1983; Atkinson et al., 1984; reviewed by Le Fevre, 1986). The ecological processes are similar to those operating in other, well-documented coastal upwelling systems and will not be further discussed. However, in some cases the generation time of the aggregated micronekton and fish (weeks to years) greatly exceeds the local residence time of the upwelled water (several days; Mackas et al., 1985, 1997). Also, studies where both phytoplankton and zooplankton were studied concurrently (e.g., Munk et al., 1995) indicate that while high phytoplankton biomass prevails throughout the shelf region, zooplankton aggregations are typically confined to narrow “bands”. Local nutrient injections alone cannot explain those bands.

3.1.4. Conclusions and open questions

For upwelling to generate aggregations of zooplankton and fish over an abrupt topography, the upwelled waters must reach the photic layer and remain above the topography for a long time, (i.e. on the order of weeks). These conditions imply that the upwelling mechanism should be expected only over very large topographies in shallow and intermediate depths. Indeed, the mechanism is common over shelf breaks, but not over seamounts and canyons.

On the other hand, short-term pulses of upwelling are common above all types of abrupt topographies, depending on their proximity to the photic layer and the strength of impinging currents. Consequently, on a regional scale, the effects of these topographies on biological production may be evident downstream of (rather than above) the topography. Large-scale studies combining detailed mapping of physical, chemical and biological properties, including nutrients, primary pro-

---

Fig. 1. Temperature transects above the following seamounts in the northeast Pacific, off California: (a–d) Northeast Bank on 26 September 1983, 28 August 1984, 18 July 1983 and 17 November 1983, respectively; (e–f) Garret Ridge on 11 and 17 July 1983, respectively; (g) Nidiver Bank 30 August 1984; (h) Jasper Seamount (15 September 1984). The measurements were made using XBT Model T-4 (Sippican, MA, USA). Note the variations between different seamounts, and between different days on the same seamount. As expected (see text) the vertical uplift of isotherms decayed rapidly with elevation above the summit, particularly in the upper water column where stratification was strongest. Source: Genin (1987).
Fig. 1 (continued).
duction, phytoplankton and zooplankton biomass can test this corollary. Since upwelling decays with height above the topography, the biological effects are unlikely to reach the surface. Recent advances in optic and acoustic instruments for sub-surface phytoplankton and zooplankton surveys (Wiebe and Benfield, 2003) could be most effective for such studies.

3.2. Topographic blockage of descending zooplankton

Numerous zooplankton species migrate daily between the surface and deeper, aphotic layers. In general, the migration amplitude and the maximal depth reached are greater in larger species. Shallow and intermediate abrupt topographies can block the animals’ pre-dawn descent, trapping the zooplankters in illuminated waters during day-light hours, exposing them to visual predators. This “topographic blockage mechanism” was first suggested by Isaacs and Schwartzlose (1965).

The amount of zooplankton supplied by this mechanism is a function of depth and the intensity of horizontal currents. Since most vertically migrating zooplankton ascend at night into the photic layer, maximum accumulation is expected at intermediate depths, just below that layer. The supply should decline over very shallow topographies, within the photic layer, and over deep topographies (i.e. below the layer to which most migrating zooplankters reach during the day). If trapped zooplankters are rapidly consumed during the day, the repeated provision of prey the next morning should depend on horizontal transport of migrating zooplankton over the topography from the surrounding deep waters during the night.

3.2.1. Seamounts

Isaacs and Schwartzlose (1965) proposed the topographic blockage mechanism based on acoustic records showing an encounter between descending scattering layers and the 100 m deep summit of a ridge off Baja California, NE Pacific. That ridge harbored rich populations of demersal and pelagic fishes. A similar pattern was observed by Genin et al. (1988) above Nidever Bank (100–140 m depth), in the outer region of the southern California bight. Euphasia pacifica, the dominant migrating zooplankton near the bank was also the dominant prey in the stomachs of resident rockfishes (Sebastes spp.) caught after dawn on the up-current side of the seamount. By dusk, very few migrating zooplankters remained on the seamount summit (Fig. 2 in Genin et al., 1994 and Fig. 18 in Haury et al., 2000). Similarly, Seki and Somerton (1994) reported that the diet of pelagic armorhead on the summit of SE Hancock seamount (265 m, Hawaii seamount chain, Central North Pacific) consisted mostly of open-water, migrating micronekton that were advected and trapped over the seamount top during the night. Again, peak feeding occurred in early morning (Seki and Somerton, 1994).

Extensive analyses of fish stomachs by Fock et al. (2002a) indicated that the topographic blockage mechanism could explain the sustained fish populations, their distribution, and diel behavior over the Great Meteor seamount (subtropical NE Atlantic). Highest densities of zooplanktivorous fish were found at the edge of the seamount plateau, where the likelihood of daily prey renewal from the surrounding deep waters was highest (Fock et al., 2002b).

The amount of zooplankton accumulated over a seamount summit in the morning is depth-dependent. As mentioned above, maximal supply is expected for seamounts at intermediate depths (i.e. with summits just below the photic layer). On shallow seamounts, with summits well within the photic layer, a proportion of the migrating zooplankton would be “missed”, as the individuals that had ascended at night to the photic layer but remained at depths greater than the summit would not be advected above the summit. Conversely, at depths greater than the intermediate range, the deeper the seamount the less migrating zooplankton it would trap. Obviously, no accumulation via topographic blockage is expected over seamounts with summits that are deeper than the deepest reach of the migrating zooplankton. Although some migrating zooplankters reach great depths (e.g. 800 m; Wiebe et al., 1979), most diel migrations are restricted to the upper few hundred meters of the water column (Angel, 1985). Brooks and Mullin (1983) estimated that about half of the zooplankton biomass in the southern California bight migrates through the 56 m isobath. Brinton (1967) presented data suggesting that most of the juvenile and adult euphausiids off California migrate daily through the 100–150 m isobaths. Most migrating micronekton in the waters off Oregon move from 0–50 m at night to 300–500 m
during the day (Pearcy et al., 1977). Uchida and Tagami (1984) reviewed historical records of the Soviet and Japanese seamount fisheries in the 1960–1970s as well as their own observations over several seamounts in the North Pacific. High catches were typically reported from intermediate depths, suggesting that the topographic blockage mechanism is most effective at this depth range. Isaacs and Schwartzlose (1965) estimated that at the 100 m isobath, the flux of organic carbon due to this mechanism was about 40 times greater than the primary production at the most productive regions off California. Tseitlin (1985) suggested, based on gross estimates, that the bottom entrapment of descending animals and the horizontal flux may together provide sufficient food to maintain the commercial fisheries on intermediate seamounts. Since the amount of prey supplied by the topographic blockage mechanism rapidly declines at depths below several hundred meters, it cannot explain the maintenance of the immense seamount aggregations of orange roughy and oreos at 700–1500 m depth. A different mechanism is likely.

3.2.2. Shelf breaks
Since most shelf breaks are found in “intermediate” depths, the topographic blockage mechanism is expected to be important at this type of habitat, particularly at sites where cross-shelf currents are common. While the continental shelf rectifies large-scale currents along the slope, cross-shelf flows are expected in the upper water column, high above the bottom (e.g., Freeland et al., 1984). The extent and intensity of such flows is obviously dependent on the regional circulation, the shelf topography and other oceanographic-meteorological forcing.

Echograms indicating the occurrence of bottom blockage over different shelf breaks are found in Simard and Mackas (1989), Barange (1994) and Robinson and Gomez-Gutierrez (1998). Aggregations of euphausiids (Nyciphanes simplex, Euphausia pacifica) and other zooplankters occur above the shelf break (100–150 m) west of Baja California, Mexico (Robinson and Gomez-Gutierrez, 1998). Repeated hydro-acoustic transects across the shelf (Fig. 3-B in Robinson and Gomez-Gutierrez, 1998) suggest that some descending zooplankton are trapped over the shallow topography in the morning. In some cases, where dense aggregations of scatterers are observed over the slope, a wide gap remains between the aggregation’s lower boundary and the bottom (Fig. 3 in Simard et al., 1986; Mackas et al., 1997). The gap may result from bottom-avoidance by the descending zooplankters, maintaining the effect of the topographic blockage mechanism. However, there is yet no evidence for bottom avoidance in zooplankton.

The occurrence of the topographic blockage mechanism over the slope break of the Rockall Trough (NE Atlantic) was indirectly inferred by Mauchline and Gordon (1991), based on their extensive analysis of stomach contents of bentopelagic fish. A clear correspondence was found between the depth at which the fish were captured on the slope and the depth at which their different pelagic prey was usually found during daytime. The occurrences of some prey species in the stomachs of deeper fish indicate that some of the fish may ascend above the slope toward the descending zooplankton.

3.2.3. Canyons
Pereyra et al. (1969) suggested a topographic modulation of the zooplankton descent migration to explain aggregations on the southern flanks of Astoria canyon (NE Pacific). The mechanism is essentially identical to topographic blockage. The migrating zooplankton, after ascending from the deep canyon floor to the surface, are displaced southward by the near-surface current and encounter the shallow southern flank during their morning descent. The aggregations were repeatedly observed at the same site. Fishermen concentrated their efforts at the canyon’s southern (but not northern) edge. Pereyra et al. (1969) attributed the north-south asymmetry to the consistency of the long-shore southward current near the surface. The source of migrating animals to the canyon interior prior to the onset of their nocturnal ascent had been unclear until Hickey (1997) showed that up-canyon currents develop within Astoria Canyon during upwelling-favorable conditions. As the canyon’s edges are shallower than the daytime depth of the migrating animals, up-canyon currents are necessary to transport zooplankters from the deep layers to which they ascend during the day to the shallower region upstream (north) of the aggregations observed by Pereyra et al. (1969). Brodeur (2001) corroborated the correspondence between up-canyon
currents and the occurrence of daytime aggregations of euphausiids near the head of Pribilof Canyon (NE Pacific). Here, again, the aggregations seemed to be generated by the topographic blockage mechanism. Since no current measurements were available, the role of other mechanisms (see below) could not be evaluated.

A series of acoustic transects were carried out by Schoenherr (1991) in order to measure the spatial characteristics of euphausiids aggregations along the flanks of Monterey canyon (off central California). The echograms (Fig. 4 in Schoenherr, 1991) indicated that topographic blockage could have been the mechanism, however, the actual process could not be confirmed as neither currents nor night–day echograms were recorded. A similar lack of supporting evidence precluded an evaluation of the topographic blockage proposed by Macquart-Moulin and Patriti (1996) to explain the accumulation of migratory species in the canyons along the Mediterranean shelf south of France. Moreover, a lack of fine-scale sampling between the three canyons on the shelf did not allow a robust separation between canyon and shelf effects.

The explanation suggested by Greene et al. (1988) to explain the immense euphausiids aggregations on the Georges Bank shelf was a combination of topographic blockage and “funneling” of the descending animals down the flanks into the canyon’s axis. The funneling mechanism was originally suggested by Koslow and Ota (1981) to explain aggregations of migratory zooplankton in La Jolla Canyon, southern California. However, neither study provided evidence for the occurrence of zooplankton funneling.

3.2.4. Conclusions and open questions

The topographic blockage mechanism has been most extensively studied over seamounts at intermediate depth, where it seems to be the main mechanism responsible for aggregations of resident zooplanktivores and their predators. While some observations suggest a similar prevalence of the mechanism over canyons and shelf breaks, further studies are needed to test its occurrence over those topographies. Additional open subjects that await further investigations include the alleged relationships between the depth of the blocking topography and the extent of prey supply (biomass and species). Similarly, further research is needed to examine the relationships between the mechanism strength and the abundance of fishes. A world-wide survey of “gray” fisheries reports, similar, but much more extensive than the one conducted by Uchida and Tagami (1984), should significantly contribute to our understanding of the importance of the topographic blockage mechanism to fisheries, and possibly to the evolution of resident epi-benthic fish and micronekton communities.

3.3. Counter-upwelling depth retention

Accumulations are expected when zooplankters maintain their depth by swimming downward against upwelling (Franks, 1992). A major benefit of such costly behavior is the avoidance of being entrained to shallower, more illuminated depths during the day. Depth retention below a certain isolume has been documented for several migrating zooplankton (Mauchline, 1980; Kaartvedt et al., 1996; Gal et al., 1999). If this mechanism is related to the retention of a certain light level, then the ensuing aggregations should be of short duration: starting in the morning after the animals had reached their daytime depth, persisting through the day, and dispersing once the animals start their nocturnal ascent.

3.3.1. Shelf breaks

The occurrence of the counter-upwelling mechanism over shelf breaks was first suggested by Simard et al. (1986) and Simard and Mackas (1989) and later corroborated by Mackas et al. (1997) in their elegant bio-physical study of the Vancouver shelf break (British Columbia, NE Pacific).

Aggregations of euphausiids over the shelf slope in St. Lawrence (Simard et al., 1986) were noticeably similar to those of E. pacifica, T. spinifera and Pacific hake (Merluccius productus) along the shelf break and the steep slopes of Nitinat canyon off Vancouver Island (Simard and Mackas, 1989; Mackas et al., 1997). A band of high euphausiid biomass generally followed the shelf break (200 m bottom contour), with biomass seaward and shoredward of the band being uniformly low. Within the band, variation in animal biomass spanned some three orders of magnitude. Detailed hydrographic and current measurements by Mackas et al. (1997) indicated that the bathymetry and current velocity were adequate coarse-scale predictors.
of the animal biomass in the aggregations. A “Convergence Index”, a function of the upslope flow and the distance from the 150 m isobath, explained about a third of the variation of the euphausiid biomass within the 101–133 depth band (Mackas et al., 1997). The densest aggregations were found where the flow at the depth of the scattering layer that was crossing the local bottom contours in an upslope direction was strongest. Conversely, unusually low concentrations of euphausiids were observed at the sites (or times) of downwelling. These observations strongly support the counter-upwelling depth retention hypothesis. The accumulations of depth retaining zooplankton can greatly benefit fish and higher trophic predators (including fishermen) and cause their aggregation over the shelf break (Healey et al., 1990; Sabatés, 1990; Munk et al., 1995, 1999; Young et al., 2001).

3.3.2. Canyons

Up-canyon currents, similar to those at Astoria Canyon (off Vancouver Island), were measured by Allen et al. (2001) along the axis of the nearby Barkley Canyon. The deep (150–400 m) currents transported zooplankton into shallower layers, apparently inducing counter-upwelling swimming in euphausiids. With the exception of euphausiids, the distribution of all zooplankton species was consistent with passive advection by the currents. The observed aggregation of euphausiids appears to be linked to their excellent swimming ability. A similar correspondence between vertical currents and euphausiids aggregations was observed by Mackas et al. (1997) at the Nitinat canyon (off British Columbia). Thomson and Allen (2000) followed the dynamics of backscatters near the head of Barkley Canyon using a moored acoustic profiler. Their 5-day long time series revealed that zooplankton aggregated in well-defined layers near the canyon floor during daylight. Unfortunately, the near-bottom current at the mooring site during their record was oriented down canyon so that the counter-upwelling accumulation could not be tested.

An acoustic survey carried out by Lavoie et al. (2000) in the Laurentian channel (NW Canada) showed that the circulation was the main factor controlling the distribution of euphausiids, and that the pattern was consistent with the counter-upwelling depth retention mechanism. Accumulations were always associated with vertical currents, driven by the interaction between tidal currents and bottom topography. Denser aggregations occurred during upwelling, while more dispersed and stretched distribution was observed during downwelling. Tidal fluctuations, terrestrial runoff and the presence of a sill at the channel head modulated the aggregations, causing fluctuations on scales from minutes to years.

3.3.3. Conclusions and open questions

Counter-upwelling depth retention is apparently an effective, general mechanism generating accumulation of euphausiids over shelf breaks and canyons in which upwelling flows persist. The mechanism has not been documented over seamounts, in spite of the common occurrence of upwelling. Perhaps the intermittent and irregular nature of upwelling “pulses” over seamounts (see above) make this mechanism less significant and hard to observe. A major aspect of the depth retention mechanism that is yet untested is the actual occurrence of counter-upwelling swimming in euphausiids. So far, depth retention has been indirectly inferred from distribution patterns and the correspondence between upwelling and aggregations. Recent advents in acoustic instruments that allow in situ tracking of zooplankton (e.g., De Robertis et al., 2003) will allow in situ tests of counter-upwelling swim in zooplankton.

3.4. Counter-downwelling depth retention

Similar to the aforementioned counter-upwelling mechanism, accumulations are also expected when zooplankters maintain their depth by swimming upward against downwelling currents (Franks, 1992). This mechanism is obvious for accumulations of floating objects such as oil, debris and larvae (e.g., Shanks, 1983; Yoder et al., 1994). However, in order for such a mechanism to operate at depth, zooplankters must actively swim against the downwelling currents, a phenomenon for which no direct evidence is available. Nevertheless, the counter downwelling depth retention mechanism is frequently suggested to explain sub-surface zooplankton aggregations along fronts (e.g., Olson and Backus, 1985; Olson et al., 1994; Yoder et al., 1994; Wishner et al., 1995; Flament et al., 1996; Shanks et al., 2000; Epstein and Beardsley, 2001; Dubischar et al., 2002).
Are counter-downwelling accumulations common above abrupt topographies? A few reports indicate that the mechanism does occur, but it seems to be confined to very shallow waters. A detailed study of this mechanism was recently carried out over Georges Bank (Wiebe et al., 1996; Pershing et al., 2001). Initial surveys (Wiebe et al., 1996) found vertical bands of scatterers, 50–100 m wide, 100–200 m apart, extending from the surface to as far as 20 m depth across the well-mixed region above the bank. A follow-up study (Pershing et al., 2001), using an advanced array of physical and biological instruments, indicated a clear association between the location of the bands and downwelling. The scatterers were most likely fish that followed aggregations of depth-retaining zooplankters (copepods, chaetognaths and euphausiids). ADCP transects showed the occurrence of alternating regions of upwelling and downwelling. The aggregations occurred in the regions of downwelling but not in upwelling. Some of the strongest aggregations on the bank occurred near prominent topographic peaks, however, the causes for downwelling cells and their possible association with the bottom topography remained unknown (Pershing et al., 2001).

Hood et al. (1999) showed the accumulation of buoyant particles in a downwelling region over shallow abrupt topographies in Chesapeake Bay (east coast, USA). The accumulated phytoplankton, zooplankton and eggs attracted fish larvae. The growth and survival of the larvae of at least one species, bay anchovy, depend on finding such aggregations (Hood et al., 1999; Rilling and Houde, 1999). Counter-downwelling accumulations were also inferred in a study of a tidal front over a very shallow bottom in Delaware Bay, USA (Clancy and Epifanio, 1989).

Does the counter-downwelling mechanism occur over intermediate and deep topographies? Although downwelling currents were observed over abrupt topographies at all depths (Hogg, 1973; Huppert, 1975; Mackas et al., 1997; Thomson and Allen, 2000), no counter-downwelling accumulation has yet been reported below the photic layer. On the contrary, deep accumulations that form during upwelling periods disperse when the vertical current changes to downwelling (Mackas et al., 1997). Conversely, near-surface accumulations such as those developing at downwelling regions do not develop at similarly strong upwelling bands (Pershing et al., 2001).

Why do counter-downwelling and counter-upwelling accumulations contrast in their depth of occurrence? Why should downwelling generate accumulations at shallow depths but disperse accumulations at greater depths, while upwelling has the opposite effect? A likely explanation is related to the behavioral adaptation assumed to be involved in depth retention. At depth, counter-upwelling swimming should prevent an entrainment to shallower, more illuminated, and therefore more predation-prone layers. No such risk is involved with downwelling; depth retention at the surface is passive for buoyant animals and would operate whenever downwelling occurs. For naturally buoyant or heavier animals, counter-downwelling depth retention can be achieved only by swimming. The adaptation of such an energetic investment is unclear. Perhaps the animals sense changes in pressure (Enright, 1962) or light and use it as a proxy for their preferred depth where a certain type of food or certain values of environmental parameters prevail. Both the occurrence and benefits of counter-downwelling swimming in zooplankton should be further examined in future studies.

3.5. Enhanced horizontal flux—the “feed-rest” hypothesis

Interactions between abrupt, sloping topographies and impinging currents, tides and internal waves greatly amplify near-bottom flows (Eriksen, 1982, 1991; Mohn and Beckmann, 2002a,b). Enhanced fluxes of suspended food particles, a linear function of current speed, may help sustaining high densities of resident fish both directly and indirectly, as follows.

3.5.1. Indirect effect: benthic enrichment

Enhanced fluxes of suspended particles augment growth and recruitment of benthic suspension feeders, resulting in surprisingly rich benthic communities at exposed sites on deep seamounts (Genin et al., 1986). Large-scale entrapment of water by topographically rectified currents helps retain larvae around seamounts, further enhancing benthic recruitment (Molineaux and Mills, 1997; Beckmann and Mohn, 2002). The rich benthic communities dominated by black corals, gorgonians, sponges, bryozoans and other
suspension feeders (Genin et al., 1986; Boehlert and Genin, 1987; Rogers, 1994; Mullineaux and Mills, 1997) may, in turn, become an important source of food for resident benthivorous fish.

3.5.2. Direct effect: the feed-rest benefit hypothesis

Enhanced fluxes of planktonic prey in regions of amplified currents augment feeding by site-attached, zooplanktivorous fish (McFarland and Levin, 2002), although the functional response of the fish to flow can be complex (Kiflawi and Genin, 1997). However, in order to retain position the fish (or micronekton) must swim against the currents. In that regard, the fish’s energetic cost to retain position should be similar to that of an open-water fish that swims at the same speed across stationary waters: both must actively swim in order to “renew” their exposure to “fresh”, food-replete waters. Is there an energetic benefit to site-attached fish, compared with open waters animals? A possible gain incurs if the fish rest motionless in quiescent shelters during non-feeding intervals while, at the same time, strong currents outside their shelter renew the water. When conditions are right, the fish emerge from shelter, feed quickly, and then retreat back to rest. Open-water fishes, on the other hand, need to actively swim in order to seek “new” replete waters. The rugged topography of seamounts and the weakened currents in the benthic boundary layer provide ample shelters from flow. Indeed, the behavior of micronekton over SE Hancock seamount (Boehlert, 1988; Wilson and Boehlert, 1990) is consistent with this proposed scenario. The dominant micronekton over this seamount, the mysid *G. longispina* and the fish *M. muelleri*, feed during the night in the water column above the seamount summit and then descend in the morning to the benthic zone where they remain throughout the day. Unfortunately, the acoustic tools used by Boehlert (1988) and Wilson (1992) did not enable them to determine how close to the bottom the animals descended (Wilson, 1992).

A behavioral pattern compatible with the feed-rest-benefit hypothesis was reported by Brodeur (2001) who observed resting aggregations of Pacific ocean perch (*S. alutus*) in Pribilof Canyon, Bering Sea (see Section 4.2 below). The aggregations were associated with dense “forests” of sea whips (*Halipteris willemoesi*). Using a ROV, Brodeur (2001) observed hundreds of fish resting motionless between the sea whips during nighttime. During the day the fish were actively feeding above the forest. The fish were absent at sites without sea whips. High densities of sea whips and other passive suspension feeders indicated the prevalence of strong currents (Genin et al., 1986). The near-bottom zone between the sea whips likely provided a quiescent shelter for resting.

Visual observations on orange roughy suggest that the rest-benefit mechanism may apply to this species. Lorance et al. (2002) used a submersible to study aggregations of this fish on the continental slope in the Bay of Biscay. The densest aggregation was observed in a restricted location within a canyon. Most of the fish were completely inactive; a few moved slowly, none was feeding. While vigorous currents were encountered around the canyon just outside of the fish shelter, no appreciable currents were observed within it (Lorance et al., 2002). Powerful currents characterize the global distribution of sites where orange roughy occur (Clark, 1995). Hence, the restriction of orange roughly aggregations to seamounts, plateaus and canyons could be related to the availability of both enhanced food fluxes and quiescent resting shelters on abrupt topographies. Clearly, more work is needed in order to test the rest-benefit hypothesis and evaluate the energetic gain incurred. Orange roughy seems to be relatively more prone to take advantage of small energetic gains, as its growth is extremely slow and its longevity is exceedingly high (>100 years) (Koslow, 1997). Perhaps the fish has evolved to efficiently utilize enhanced horizontal fluxes in strong currents and to effectively reduce its metabolic expenditure by resting motionless in topographic shelters.

4. Discussion and conclusions

Aggregations of zooplankton, micronekton and fish are common over shelf breaks, seamounts and canyons at intermediate and shallow depths. Certain fish are also aggregated over deep seamounts. There are several possible mechanisms for the aggregations (Table 1). Upwelling-driven nutrient entrainment would cause local aggregations only if the enhanced primary productivity propagates up the food chain. The long residence time required for such a process to affect population growth in grazers and predators renders unlikely the explanation that upwelling is
The cause for animal aggregations over abrupt topographies (except on large continental shelves).

Bio-physical coupling between currents and animal behavior are key factors in the formation of animal aggregations over abrupt topographies at shallow and intermediate depths. Three mechanisms prevail (Table 1): (1) Topographic blockage of downward migration. This mechanism is most effective at intermediate depths in the morning. (2) Accumulation of animals maintaining their depth (isolume) by swimming against upwelling. This mechanism operates during daytime and is most effective at intermediate depths. (3) Accumulation of animals maintaining their depth by swimming against downwelling. This mechanism seems to be confined to the upper photic layer.

A note of caution: this review has undoubtedly been affected by the well-known bias in the scientific literature to publish positive results. This bias is particularly relevant here since the review’s focal point is “animal aggregations”, by definition an “unusual” phenomenon. Field studies in which animal aggregations were found are more likely to have been published than those where nothing “special” in the animal distribution was observed. Hence, the generality of the aforementioned mechanisms, as could be inferred from this review, should be treated with caution.

Except for upwelling, the four aforementioned flow-driven mechanisms cause biomass to accumulate in a relatively small space. This accumulation, or “trophic focusing”, operates either directly, via prey accumulation (topographic blockage, depth retention) or indirectly by enhancing the flux of prey and the accumulation of its biomass in the bodies of site-attached predators. Similar to upwelling, trophic focusing enhances bottom-up pathways in the local food web, however, with no changes in primary production. The mechanism subsidizes higher trophic predators, such as pelagic fishes and marine mammals that are attracted to, and aggregate over, their concentrated prey. For some predators, including larvae of commercial fish and invertebrates, it has been suggested that average prey concentrations can be insufficient for growth and survival (e.g., Lasker et al., 1970; Mohammadian et al., 1997) and that, by implication, they must find aggregations of their prey in order to survive. For such a dependency to have evolved, the occurrence of prey aggregations should have been, to some degree, predictable. Most of the mechanisms described above produce recurrent, fairly predictable, aggregations. Seamounts, canyons and shelf breaks can therefore have an important role in determining trophic interactions in the marine realm, particularly at shallow and intermediate depths.

Acknowledgements

I thank Ric Brodeur and John Dower for inviting this review and for valuable discussions. Special thanks are due to John Dower and two anonymous reviewers for effective editorial work and many helpful comments. The roots of this review extend back to my graduate studies at Scripps Institution of Oceanography, where the people and the scholarly environment they created, provided the foundations for the knowledge and ideas presented in this review.

References


Olson, D.B., Hitchcock, G.L., Mariano, A.J., Ashjian, C.J., Peng, G.,


