FEATURE: CONSERVATION

Vertical Zoning in Marine Protected Areas: Ecological Considerations for Balancing Pelagic Fishing with Conservation of Benthic Communities

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ABSTRACT: Marine protected areas (MPAs), ideally, manage human uses that threaten ecosystems, or components of ecosystems. During several recent MPA designation processes, concerns have arisen over the scientific justification for no-take MPAs, particularly those that restrict recreational fishing for pelagic species. An important question is: under what conditions might recreational pelagic fishing be compatible with the conservation goals of an MPA that is primarily focused on benthic communities? In 2005, an expert workshop of fisheries biologists, marine ecologists, MPA managers, and recreational fishermen was convened by NOAA's National MPA Center to evaluate the limited empirical data on benthic-pelagic coupling and to help provide practical advice on this topic. The participants (i) proposed a preliminary conceptual framework for addressing vertical zoning, (ii) developed preliminary guidelines to consider when evaluating whether to allow or restrict pelagic fishing in an MPA, and (iii) identified future research priorities for understanding benthic-pelagic coupling. A suite of ecological conditions where recreational pelagic fishing may not be compatible with benthic conservation were identified: (1) high relief habitats, (2) depths shallower than 50–100 m (depending upon the specific location), (3) major topographic and oceanographic features, and (4) spawning areas. Similarly, pelagic fishing is not likely to affect benthic communities adversely in many circumstances. Until further scientific study can shed more light on the issue of how benthic-pelagic linkages affect specific conservation targets, the proposed framework in this manuscript provides practical, easily-applied guidance for using vertical zoning to manage fishing in multiple use MPAs that focus on benthic conservation.

Zonación vertical en Áreas Marinas Protegidas: consideraciones ecológicas en el balance entre la pesca pelágica y la conservación de comunidades bentónicas

RESUMEN: Las Áreas Marinas Protegidas (AMP) idealmente, administran el uso humano que amenaza los ecosistemas o sus componentes. Durante el actual proceso de declaración de AMP, han surgido algunas preocupaciones acerca de la justificación científica para establecer áreas de no pesca, particularmente aquellas que restringen la pesca recreativa de especies pelágicas. Una pregunta importante es ¿bajo qué condiciones la pesca pelágica recreativa es compatible con los objetivos de conservación de un AMP que se enfoca principalmente en comunidades bentónicas? En 2005, un taller de expertos en biología pesquera, ecología marina, manejo de AMP y pescadores recreativos fue convocado por el Centro Nacional de AMP de la NOAA para evaluar los pocos datos empíricos del acoplamiento entre los sistemas pelágico y bentónico, y ofrecer asesoría práctica sobre el tema. Los participantes (i) propusieron un marco conceptual preliminar para abordar el tema de la zonación vertical, (ii) desarrollar directrices preliminares para que cuando se haga una evaluación si se permite o restringe la pesca pelágica dentro de la AMP, y (iii) identificar futuras líneas de investigación para comprender mejor el acoplamiento entre el bentos y el sistema pelágico. Se identificó una serie de condiciones ecológicas en las que la pesca recreativa pelágica puede no ser compatible con la conservación del bentos: (1) hábitat de alto relieve, (2) profundidades menores a 50 m–100 m (dependiendo de la zona), (3) características oceanográficas y topográficas sobresalientes, y (4) áreas de desove. De igual forma, bajo varias circunstancias, la pesca pelágica puede no afectar las comunidades bentónicas. Hasta que los estudios científicos brinden más información acerca de cómo las relaciones entre el bentos y el ambiente pelágico afectan los objetivos específicos de la conservación, el contexto propuesto en este trabajo provee una guía práctica y de fácil aplicación para utilizar la zonación vertical en el manejo pesquero en varios aspectos de las AMP que se enfocan en la conservación del bentos.

INTRODUCTION

Marine protected areas (MPAs) can be effective conservation and management tools when properly designed, effectively managed, and supported by user communities (Allison et al. 1998; Murray et al. 1999). Historically, most of the science and policy emphasis of MPA design has focused on siting considerations, examining issues such as optimum size, shape, and connectivity, resilience, and ecosystem responses to protection. Increasingly, however, MPA designation processes are grappling with an equally important scientific issue with significant policy implications: what are the appropriate levels and types of protection needed in each MPA to effectively achieve its unique conservation and management goals?

This issue is particularly relevant to proposed or existing MPAs that are focused primarily or exclusively on conserving benthic habitats and resources. Examples of the importance of the appropriate level of protection in proposed MPAs include designations in the Gulf of Mexico by the regional fisheries management council, in California's Channel Islands Marine Reserves process, and in the ongoing Marine Life Protection Act initiative in California state waters. In each case, stakeholder concerns were raised over the need and scientific justification for implementing completely no-take MPAs that would preclude fishing for pelagic species.

Underlying this policy debate is a complex and increasingly critical scientific issue: under what conditions must MPAs restrict all extractive uses (i.e., no-take reserves; Halpern and Warner 2003; Agardy 2005)? Translated into practical terms in the policy arena, this question often becomes: when might managed fishing be ecologically sustainable within an MPA without compromising the protected area's effectiveness? At present, less than 0.01% of the area contained within U.S. MPAs is managed as no-take, with some form of fishing allowed, including pelagic fishing, in the majority of the MPA area in the country (Grober-Dunsmore et al. 2008). Evaluating the potential compatibility of pelagic recreational fishing in MPAs is a daunting challenge, especially in the midst of an ongoing MPA designation or management plan review process.

To fill this growing information gap in MPA design, NOAA's National MPA Center convened an expert workshop of fisheries biologists, marine ecologists, MPA managers, and recreational fishermen in November 2005 in Monterey, California. This diverse team, with very different backgrounds, expertise, and perspectives on MPAs, worked collaboratively to:

- Describe the current knowledge about the nature, direction, strength, and predictability of ecological linkages between pelagic fish assemblages and benthic communities, including fish, invertebrates, and plants;
- Develop a conceptual framework for predicting whether and how the removal of pelagic fishes through recreational fishing inside the boundary of an MPA may significantly disrupt or otherwise influence ecological linkages to the benthos; and,
- Synthesize expert insights into practical preliminary guidelines informed by science, yet with practical application, to assist MPA planners, stakeholders, scientists, and managers in determining the ecological conditions under which vertical zoning can be used to manage pelagic fishing inside an MPA, without compromising the long-term conservation and management goals of the benthic-focused MPA.

Here, we present the results of that workshop to inform future policy discussions about MPA design, and specifically to help evaluate the appropriateness of managing sport fishing for pelagic fishes through a vertical zoning approach to MPA design. While our discussions focused exclusively on recreational fishing pressure, the principles and concepts derived may apply to both commercial and recreational fishing, though affects on linkage strength will certainly vary with fishing intensity. These findings address how pelagic fishing may or may not affect benthic organisms within the MPA, and assume that harvest of pelagic fishes is not regulated by the MPA. Rather, pelagic fishes are assumed to be managed over broader spatial scales.

ECOLOGICAL LINKAGES BETWEEN PELAGIC FISHES AND BENTHIC COMMUNITIES

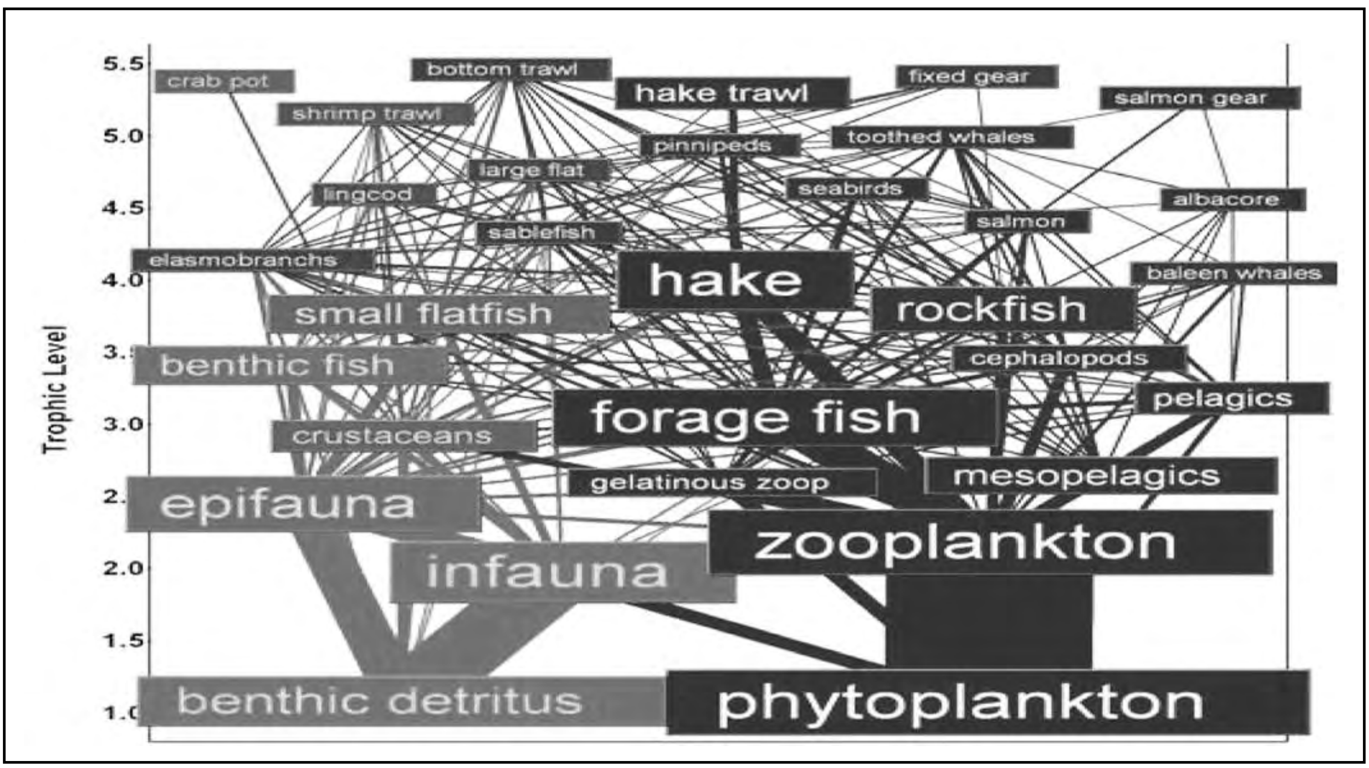
Benthic communities are often viewed as functionally distinct from the dynamics of surface waters and associated pelagic populations. However, these two realms may be linked ecologically in ways that profoundly influence local ecosystem dynamics (Ebersole et al. 2005). These linkages, and their implications for resource management, must be considered when designing fishing restrictions in MPAs (Pinnegar et al. 2000). However, at present there is little direct empirical evidence of the nature, strength, and direction of benthic-pelagic coupling for most species, locations, and environmental conditions (Ebersole et al. 2005). An annotated bibliography summarizing empirical evidence for the existence or absence of linkages between benthic and pelagic communities for coastal pelagics (Buckel et al. 1999a; Buckel and McKown 2002), oceanic pelagics (Davis and Stanley 2002; Junior et al. 2004; Estrada et al. 2005) and mid-water conduits (Buckley and Livingston 1997; Buckel et al. 1999b; Hunt et al. 1999) was used for discussions among workshop participants.

Our understanding of benthic-pelagic linkages is largely derived through diet content studies conducted over a short period of time on individual taxa. Often associated environmental data (such as depth and habitat type) are not collected, and the stock condition and population dynamics of the predator and prey species are rarely known during the course of the study. Consequently, it is difficult to assess the community level effects of removing some portion of a targeted pelagic predator population. While diet content, acoustic tagging, and stable isotope studies can provide some insight into the foraging behaviors of certain species (Estrada et al. 2005; Jumars 2007; Collins et al. 2008), such studies offer only a point of departure for assessing the spatial and temporal complexity of benthic-pelagic linkages.

Linkages between benthic and pelagic assemblages are most evident in marine food web models (Walters et al. 1999; Aydin et al. 2002; Coll et al. 2006; Field et al. 2006, Coll et al. 2007). Marine food webs can be highly complex, with an extraordinary number of interactions among a large diversity of species, with energy—often in the form of prey—moving across many gradients (Cohen et al. 2003). Figure 1 illustrates this complexity for the Northern California Current shelf ecosystem, highlighting the importance of understanding the nature, direction, and strength of interactions among different trophic levels (adapted from Field et al. 2006). The colors represent alternative energy pathways. Pelagic (primary production) energy pathways are shown in black and benthic (detrital loop) energy is shaded in gray. The varying amounts of black and gray represent the proportion of energy that originated from these two major pathways (Field et al. 2006). For example, rockfish, hake (*Merluccius* spp.), sablefish (*Anoplopoma fimbria*), and groundfish (typically associated with benthic habitat) derive the majority of their energy from small pelagic prey (primarily euphausiids and forage fishes; Field et al. 2006). Clearly, energy flows from benthic communities up the food web, and from pelagic communities down the food web through multiple, complex linkages in the food web.

Food web dynamics can reverberate across the community with major implications for ecosystem function and fisheries production (Bascompte et al. 2005; Frank et al. 2005; Mumby et al. 2006) through the effects of trophic cascades. Tropic cascades are interactions between trophic levels (e.g., decomposer, producer, herbivore, predator) that result in inverse patterns in abundance or biomass across more than one trophic link in a food web (Steele et al. 2007). Simple food chain cascades might have unforeseen consequences on benthic communities, such as occurred with the removal of sea otters on the U.S. Pacific coast (Estes et al. 2004).

Figure 1. Complex marine food web of linkages between pelagic and benthic communities. Gray lines indicate linkages from benthic communities up the food web, and black lines indicate linkages from pelagic communities down the food web. In marine systems, the primary trophic levels can be categorized into groups including top large carnivores (e.g., sharks, marlin), smaller carnivores (e.g., tunas, salmon), planktivores (e.g., baitfishes, herring), herbivores (e.g., parrotfishes), and detritivores (e.g., benthic invertebrates).



General Categories of Benthic-Pelagic Linkages

To distill this complexity for decision-making and provide a general rule of thumb for decision-making, general categories of benthic-pelagic linkages were defined as a starting point for assessing the conditions where vertical zoning may or may not be appropriate. Benthic-pelagic (BP) linkages show a variety of types, strengths, directions, and impacts on a local scale, yet three broad categories: (i) direct and strong; (ii) indirect and strong, and (iii) weak (Figure 2) that define the extremes of benthic-pelagic interactions were considered as a starting point for reference. Obviously, benthic-pelagic interactions in the real world occur somewhere among these extremes, exhibiting variation in response to a variety of environmental and oceanographic factors. These three categories were identified to be easily applicable to resource management, though resource managers must recognize that spatial and temporal variation in linkage strength is most likely the norm. Therefore, these guidelines should be used only as a rule of thumb. Further research will likely provide insights into the complexity inherent among benthic pelagic interactions, and will reveal how variation in benthic-pelagic interactions is influenced by local conditions (i.e., density of predators and prey, MPA size, and oceanographic conditions).

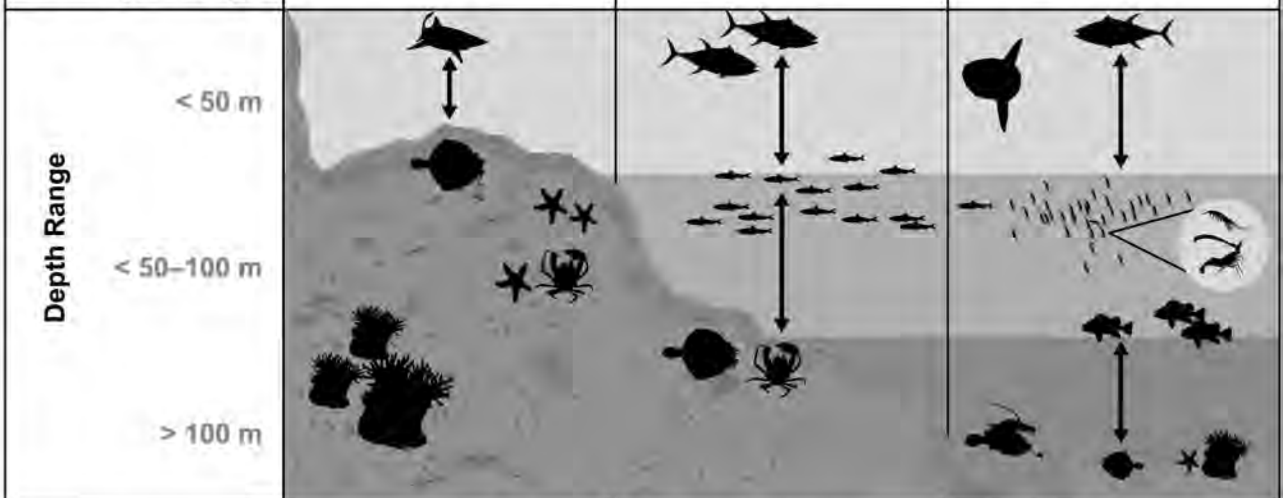
Direct and Strong BP Linkages.

Direct linkages between benthic and pelagic assemblages can occur primarily via predation by free-swimming pelagic species directly upon fish and/or invertebrates on or near the bottom (Paine 1992; Wootton 1997) or by benthic predators feeding directly on pelagic prey (Field et al. 2006). Such direct linkages tend to be strong and thus the removal of the pelagic predator through fishing could disrupt the flow of energy between the benthic and pelagic communities (Harvey et al. 2003; Savenkoff et al. 2007). Depletion of pelagic predators may in turn directly impact benthic community dynamics of the MPA (e.g., changes in the relative abundance of certain functional groups, shifts in species dominance) by increasing prey species abundance and subsequently affecting their interactions with other benthic species, such as occurs in trophic cascades (Beukers and Jones 1997; Estes et al. 2004; Steneck et al. 2004). Disturbance of strong bottom-up (Steele et al. 2007) and top-down biotic forcing pathways may ultimately lead to trophic cascades with the removal of key species in the food web (Sala 2004; Coll et al. 2007)

Where linkages are direct and strong, pelagic fishing may not be an appropriate allowed activity in an MPA established to maintain natural benthic communities.

Figure 2. Generalized conceptual model illustrating strength of benthic-pelagic linkages in typical marine habitats. This provides guidance on ecological conditions that may influence when and where pelagic fishing might be compatible with the goals of a benthic-focused MPA. For example, where benthic-pelagic linkages are direct and strong or where the habitat type is coral reef and the primary fish group of concern is coastal pelagics, then recreational pelagic fishing is most likely not compatible with the objectives of a benthic-focused MPA.

Benthic-Pelagic Linkage Strength	Direct & Strong	Indirect	Weak



Design Considerations				
	Habitat Type	Coral Reef, Atoll, Rocky Reef, Spawning Aggregation	Rocky Habitat, Continental Shelf	Open Ocean, Deep Continental Shelf
	Fish Mobility	Resident	Resident–Transient	Transient
	Taxonomic Group	Coastal Pelagics	Forage Fish Pelagics	Pelagics
	Potential Compatiblity of Pelagic Fishing in Benthic MPAs	**Not Compatible**	**Potentially Compatible**	**Compatible**

Workshop participants defined shallow water as < 50 m, and deep waters were defined as those greater than 100 m based on their knowledge of recreational fishing techniques and interactions between pelagic and benthic species. Figure 2 provides some of the ecological circumstances where direct and strong benthic-pelagic linkages might be expected, and thus where pelagic fishing might not be appropriate. Vertical zoning may not be ideal in: (1) shallow water habitats (< 50 m depth), (2) habitats with high topographic relief (e.g., reefs, canyons and sea mounts), (3) areas with strong-biophysical coupling (e.g., upwelling zones), (4) areas with permanent or seasonal spawning or feeding aggregations, and (5) dominated by coastal pelagic and mid-water conduit species (depending upon location may include shad, mackerel, or anchovy). The rationale for these recommendations will be discussed in the conceptual framework.

Indirect and Strong BP Linkages

Pelagic and benthic communities may also be linked indirectly through mid-water species such as forage fishes (e.g., shad, anchovies). Such forage fishes often serve as vertical conduits of energy and material between upper and deeper waters (Figure 2; Harvey et al. 2003; Wilson et al. 2006). For example, large schools of forage fishes often feed directly on organisms living in benthic communities (Cabral and Murta 2002; Wilson et al. 2006); consequently the removal of these fishes may disrupt these linkages, resulting in changes in benthic community structure (e.g., increases or decreases in the abundance of benthic organisms that are prey items of forage fishes; Coll et al. 2006; Jumars 2007). Benthic organisms may also depend upon midwater prey (Bosley et al. 2004), exerting bottom-up (emanating from the sea floor up into the water column) influences on trophic energy flow. Though less direct, these linkages can be strong, and potentially exert considerable control over benthic and pelagic community structure (Sala and Graham 2002; Bascompte et al. 2005; Field et al. 2006). Consequently, recreational pelagic fishing may not be appropriate in benthic-focused MPAs, where indirect, yet strong benthic-pelagic coupling persists. Depending upon the level of fishing pressure, disruption or elimination of indirect ecological linkages between benthic and pelagic communities could result in cascading changes in community structure. Examples of such circumstances are shown in Figure 2.

Weak BP Linkages

In certain, perhaps many areas of the ocean, benthic and pelagic communities may be weakly linked or not linked at all (Micheli 1999; Estrada et al. 2005; Figure 2). Linkages tend be weak in deeper water where there is little direct interaction between the pelagic and benthic communities, since pelagic predators may forage only on organisms in the upper water column (Abitia-Cardenas et al. 1999; Olson and Galvan-Magana 2002) and benthic communities may only interact directly with surface waters when detritus and carcasses of organisms sink to the benthos. Even in deep water areas, there could be important coupling of the pelagic and benthic zone, since the benthos may have little or no primary production and be dependent on subsidies from the pelagic zone. Weak linkages may occur when there is redundancy in functional groups such that removal of some individuals from either community will not perceptibly alter the flow of energy, or in the case of mid-water prey when only a small part of the diet of the intermediary is from the benthic zone. Where linkages are weak, vertical zoning may be appropriate since pelagic fishing is likely to have limited influence on the benthic community (Figure 2).

In summary, where benthic-pelagic linkages are weak, and the impacts of pelagic fishing are minimal, recreational pelagic fishing managed through vertical zoning may be appropriate. Where benthic-pelagic linkages are strong, and the potential impacts of pelagic fishing on benthic communities are expected to be high, pelagic fishing of any kind is probably not an appropriate management strategy. Under this scenario, a no-take MPA may be the most effective approach to achieving the protected area's benthic conservation goals. However, the majority of situations are likely considerably more complex and fall somewhere between these two ends of the spectrum.

A CONCEPTUAL FRAMEWORK

Because placing benthic-pelagic linkages into the simplified categories indicated above will be challenging, and will not capture the full complexity of real world conditions, a preliminary conceptual framework which addresses known ecological conditions such as water depth, predator type, habitat type and predator taxonomic, mobility, and life history characteristics is proposed. This conceptual framework was developed to help inform real-world MPA designation and management planning processes, in the absence of sufficient empirical data, to identify the ecological conditions where vertical zoning may or may not be appropriate. This framework was intended to offer practical advice to policymakers, with the input of the scientific and fishing communities. The conceptual framework consists of one primary (water depth) and three secondary ecological considerations (habitat type, predator type, and taxonomic, mobility and life history characteristics of pelagic species).

Water Depth

In the proposed conceptual framework, the primary ecological consideration for assessing the feasibility of vertical zoning is depth. The depth of the water column within and surrounding an MPA will likely influence the strength or weakness of its benthic-pelagic linkages, primarily by affecting the proximity of pelagic predators with bottom-dwelling prey. Consequently, shallow water habitats will generally have stronger benthic-pelagic linkages than deeper water areas (Figure 2). In areas shallower than 50 m, linkages are likely strong and often direct, as pelagic predators often interact with benthic and mid-water prey (Arendt et al. 2001; Rosas-Alayola et al. 2002). Important ecological linkages may also exist in habitats occurring at depths exceeding 100 m (Aydin et al. 2002; Cartes and Carrasson 2004) depending on the area's ecosystem type, local oceanography, and species composition.

Habitat Type

Several habitat attributes can create conditions conducive for strong benthic-pelagic linkages (Pinnegar et al. 2000; Aydin et al. 2002). For example, coral reefs, rocky reef, kelp forest, and other topographically complex habitats are likely to have strong benthic-pelagic linkages reflecting diverse food web dynamics between surface waters and bottom-dwelling species (Figure 2). Generally, these heterogeneous habitats often attract transient pelagic predators from deeper water habitats. Prominent topographic features such as seamounts and canyons are often oceanographic hotspots that attract pelagic fishes (Dower and Brodeur 2004; Wilson and Boehlert 2004; Sydeman et al. 2006), increasing the strength of linkages. Similarly, areas characterized by robust and predictable biophysical coupling (e.g., upwelling) create conditions favorable for strong benthic-pelagic linkages (Navarrete et al. 2005), as do areas with significant gradients in temperature, currents, and complexity. Often this coincides with the location of the continental shelf break, though not always.

Pelagic Predator Type

The strength and nature of benthic-pelagic linkages in any specific MPA is likely influenced heavily by the taxonomic composition and densities of predator and prey species and the community structure of the localized food web. As a starting point for decision-making, predicted linkage strengths were developed based on the behavior of key predator species and their location relative to water depth and distance from shore. A broad spectrum of taxa was grouped into four mobility categories relative to their interactions with benthic communities: coastal pelagics, oceanic pelagics, mid-water conduits, and forage fish (Table 1).

Coastal pelagics occur in near shore waters typically on the continental shelf. The distance of the continental shelf from shore varies considerably with physiographic conditions; therefore, the distance from shore will not always be sufficient for classifying species. Coastal pelagics may range off of the continental shelf break, but spend the majority of time over the continental shelf. Generally taxa within this mobility guild occur in shallow waters and are relatively accessible to the recreational fishery. Often, benthic-pelagic linkages for this broad group are moderate-strong (Meyer et al. 2001; Bertrand et al. 2002; Bertrand et al. 2004; Wetherbee et al. 2004), though not always (Buckel et al. 1999b; Bertrand et al. 2004).

Mid-water conduits occur between the upper water column and the benthic community, including some demersal fishes, and can serve as conduits of energy and materials between benthic and pelagic communities. Mid-water conduits can range widely in the strength of benthic-pelagic linkages, from weak (Bromley et al. 1997; Hunt et al. 1999; Kaeriyama et al. 2004) to strong (Buckley and Livingston 1997), and act as either predators or prey. For example, most semi-pelagic (mid-water schooling) rockfish are primarily planktivorous, though prey consumption varies from zooplankton, forage fish, and cephalopods to mesopelagic fishes, with diet varying with fish species (Brodeur and Pearcy 1984). The degree to which mid-water species interact with benthic and pelagic communities can also vary greatly with ontogeny (e.g., Able et al. 2003). Until further scientific information can shed more light on the foraging ecology of this group, assuming that benthic-pelagic linkages will be greater in areas of strong upwelling, high topographic complexity, and around physiographic features may be the most prudent guideline available.

Oceanic pelagics are migratory and spend the majority of their lives in deep waters offshore (typically beyond the continental shelf). For many oceanic pelagics including sharks and marlins, benthic-pelagic linkages can be relatively weak (Moteki et al. 2001; Olson and Galvan-Magana 2002; Sinopoli et al. 2004; Lucifora et al. 2005), though not always (Sinopoli et al. 2004). These species may range into coastal waters or over the continental shelf for brief periods, depending on seasonal fluctuations, oceanographic conditions, or climatic anomalies. Generally, however, these species occur far offshore, in waters deeper than 100 m. Based on the limited data available for this group, benthic-pelagic linkages are predictably weak.

Forage fishes are linked to multiple trophic groups in the food web, consuming prey from multiple trophic levels (Robinson 2000; Miller and Brodeur 2007) and being consumed by a variety of predators. Because linkages are more indirect, it is difficult to propose guidelines for this group (Table 1).

For these last three groups, site- and situation-specific information will be needed to develop practical guidelines for considering fishing impacts on benthic communities. For example, for mid-water conduits, oceanic pelagics, and forage fishes, benthic-pelagic linkages will likely vary in areas of (1) upwelling, (2) increased physiographic complexity, (3) increased population sizes of target species, and (4) increased fishing pressure. Temporal variance in benthic-pelagic coupling may also occur, since in some years (such as during El Niño), a species may be more coastal than in La Niña years, where the same species may be more oceanic in distribution. Differences in the behavior of species may occur among regions, in response to variation in oceanographic conditions, physiographic features, the location of the continental shelf, and the population status of the pelagic species of interest.

Taxonomic, Mobility and Life History Characteristics of Pelagic Species

The patterns described above among different pelagic predator types can be illustrated for particular species of interest to MPA managers and fishermen (Table 2). Each recreationally-fished pelagic species (and some reef fishes) was classified using the best available scientific information and the experience and knowledge of workshop participants to provide estimates of the effects of removing these species from an MPA. Each species was categorized based on its bio-geographic and offshore/onshore range of occurrence and placed in a mobility guild (resident, visitor, and transient). Understanding the relative mobility of targeted pelagics is important since removal of a more resident species (e.g., cero mackerel *Scomberomorus regalis*) that primarily reside within a localized area (i.e., MPA) is likely to have greater consequences on disrupting benthic-coupling compared to removing a more transient species (e.g., sailfish *Istiophorus platypterus;* Table 2). The mobility of the pelagic species must be considered to evaluate the possible effects of removing individuals of certain species, but mobility must also be assessed relative to the boundaries of the MPA. If the pelagic species is moving regularly in and out of the MPA, the location of harvest is irrelevant. The question is whether a large proportion of the targeted fish population is moving inside and out of the MPA, such that fishing on the edge may be little different than fishing inside. If this is the case, the act of removal within the MPA may be indistinguishable from removal outside the MPA (Walters et al. 1999).

In addition, the spatial and temporal predictability of occurrence within an MPA

Table 1. Pelagic fish groups, general benthic pelagic linkage strength and general guidelines useful for vertical zoning.

Pelagic fish group	Example species	Linkage strength
Coastal pelagics (< 100 m depth or onshore)	Jacks, mackerels, bluefish	Direct Strong
Mid-water conduits (neritic zone-conduits)	Rockfishes, snappers, cod	Indirect Weak—Strong
Forage fishes	Herring, sardine, shad, anchovy	Indirect Weak—Unknown
Oceanic pelagics (> 100 m depth)	Marlin, tuna, sharks	Indirect Weak

Table 2. Potential strength of benthic-pelagic linkages for selected recreationally-targeted pelagic species (does not include benthic reef fishes except for groupers and snappers) representing different regions, species types, and mobilities. For each taxon, the table illustrates general information on:
(i) predicted mobility;
(ii) spatial and temporal predictability of occurrence within an MPA (H = high potential, M = moderate, L = low potential);
(iii) the likely role of each species in maintaining benthic-pelagic coupling;
(iv) the potential for each species to be overfished within an MPA;
(v) the likelihood of benthic-pelagic linkages being disrupted by fishing, which synthesizes information from the previous five categories; and
(vi) the potential for bycatch of other non-targeted species, which could indirectly affect benthic-pelagic linkage strength and direction inadvertantly.

Notes:
a = catch and release,
b = varies with oceanographic features,
c = temperature dependent,
d = seasonal,
e = chumming can alter behavior,
f = scale of movement unknown,
g = patchy distribution.

While snappers and groupers are generally benthic reef-associated fishes, they are included in the table since at particular stages in their life history, they can occur in the water column or pelagic environment.

Species type	Species name	Mobility category	Spatial predict. occurrence in MPA	Temporal predict. of occurrence in MPA	Strength of BP linkage	Potential to be overfished in MPA	Likelihood of BP linkages disrupted by fishing	Potential for bycatch impacts
ATLANTIC								
coastal pelagic	spanish and cero mackerel *Scomberomorus maculatus; Scomberomorus regalis*	resident	H	H	H	M	M	H
migratory coastal pelagic	king mackerel *Scomberomorus cavalla*	visitor/transient	M	M	M	L	L	H
coastal pelagic	amber jack (reef-associated) *Seriola lalandi*	visitor/transient	M	M	M	L	L	H
non-migratory coastal pelagic	blue runner (jack) *Caranx crysos*	resident	H	H	H	H	H	H
non-migratory coastal pelagic	bar jack *Carangoides ruber*	visitor/transient	H	H	H	H	H	H
non-migratory coastal pelagic	crevalle, horse eye other jacks *Caranx hippos; Caranx latus*	visitor/transient	M	M	M?	L	L	H
coastal pelagic	tarpon *Megalops atlanticus*	Resident	H	H	H	L [a]	L [a]	H
oceanic and coastal pelagic (visits coast)	dolphin/mahi *Coryphaena hippurus*	visitor/transient	M [b]	H	L	L	L	H
migratory oceanic pelagic	sailfish *Istiophorus albicans*	visitor	L [e]	M-H	L	L	L	L
PACIFIC								
migratory coastal pelagic	salmon *Oncorhynchus* spp.	visitor/transient	depends on time of year	L [d] H [d]	M-H	L	L	L (surface) H (deep)
migratory coastal pelagic	tunas *Thunnus* spp.	transient	L	M	L-M	L	L	L
non-migratory coastal pelagic	jacks *Caranx* spp.	visitor/transient	M	H	M-H	L-M	L-M	M
migratory coastal pelagic	sardines *Sardinella* spp.	visitor/ transient	L	H [c]	H	L	L	L
migratory coastal pelagic	anchovies *Engraulis* spp.	visitor/transient	L	H	H	L	L	L
migratory coastal pelagic	Pacific mackerel *Sconber japonicus*	visitor/transient	L	H	M	L	L	L
non-migratory coastal pelagic	midwater rockfish *Sebastes* spp.	resident/visitor	H	H	H	H	H	H
migratory oceanic pelagic	oceanic sharks *Carcharhinus* spp.	transient	L	H [d]	L	L	L	L

Species type	Species name	Mobility category	Spatial predict. occurrence in MPA	Temporal predict. of occurrence in MPA	Strength of BP linkage	Potential to be overfished in MPA	Likelihood of BP linkages disrupted by fishing	Potential for bycatch impacts
CARIBBEAN SEA or GULF OF MEXICO								
coastal pelagic	tarpon *Megalops* spp.	resident	H	H	H	L[a]	L [a]	H
oceanic pelagic (visits coast)	dolphin (mahi) *Megalops atlanticus*	visitor/transient	M[b]	H[a]	L	L	?	H
oceanic pelagic (visits coast)	wahoo *Acanthocybium solandri*	visitor/transient	M	M	M	L	L	?
oceanic pelagic (visits coast)	barracuda *Sphyraeana* spp.	resident/visitor	?	?	M	L	L	?
oceanic and coastal pelagic	amber jack *Seriola lalandi*	visitor/transient	M	M	M?	L	L	H
oceanic and coastal pelagic	blue runner (jack) *Caranx crysos*	resident	H	H	H	H	H	H
coastal pelagic	bar jack *Carangiodes* spp.	visitor	H	H	H	H	H	H
oceanic and coastal pelagic	crevalle, horse eye, other jacks *Caranx* spp.	visitor/transient	M	M	M?	L	L	H
oceanic and coastal pelagic (visits coast)	dolphin/mahi *Coryphaena hippurus*	visitor/transient	M	H	L	L	L	H
migratory oceanic pelagic (visits coast)	sailfish *Istiophorus albicans*	visitor	L[e]	M-H	L	L	L	L
migratory oceanic pelagic (visits coast)	marlin (blue) *Makaira nigricans*	visitor	L	L	L	L	L	L
oceanic pelagic	blue and mako sharks *Prionace glauca*	transient	L	L	L	L	L	L
coastal pelagic	reef sharks *Carcharhinus* spp.	resident/visitor	H	H	H	H	H	H
coastal pelagic	tuna (dogtooth) *Thunnus* spp.	resident	H	H	H	H	H	H
oceanic and coastal pelagic (visits coast)	tuna (small) *Thunnus* spp.	visitor	M	M	M	L	L	L
migratory oceanic and coastal pelagic	tuna (large) *Thunnus* spp.	transient	L	L	L	L	L	L
non-migratory coastal species	snapper (reef-associated) (yellowtail) *Lutjanus* spp.	resident/visitor	H	H	H	H	H	H
non-migratory coastal reef fish	snapper (reef fish) *Lutjanus* spp.	resident	M-H	H	H	H	H	H
non-migratory coastal pelagic	fusiliers *Caesio* spp.	resident	H	H	H	H	H	M
coastal (mostly non-migratory)	barracuda (reef) *Sphyreana* spp. (offshore)	resident/visitors/ transients	H L?	H M	H L?	H L?	H L?	L-M H
coastal reef fish	groupers (gag and scamp) (reef fish) *Mycteroperca* spp.	resident/visitors/ transients	H	H	H	H	H	L
non-migratory oceanic and coastal pelagic	ballyhoo *Hemiramphus* spp.	? [f]	M [g]	M [d]	L-H	?	L?	L?
coastal pelagic	cobia *Rachycentron canadum*	visitors and transients	L	M [d]	M/H?	L	L-M	?

(Table 2) may provide additional guidance on how removal of particular species may disrupt benthic-pelagic linkages. If the spatial and temporal predictability of a pelagic species within an MPA is high, then their removal may have greater consequences on benthic-pelagic linkages than removing species that have low spatial and temporal predictability. For example, tarpon (*Megalops atlanticus)* have a higher predicted spatial and temporal occurrence within a particular area; therefore their influence on local benthic-pelagic coupling may be greater than that expected for a species such as a tuna, which has lower spatial and temporal predictability.

The role of each species in maintaining coupling between benthic and pelagic communities was also proposed, by considering the feeding ecology and relative position of each species in the water column (Table 2). This is important since exploitation of species with different life history strategies can have different population and food web consequences (Schindler et al. 2002). Food web responses are expected to be strongest where unexploited biomass of long-lived species is high and predation (in this case fishing) is relatively specialized compared with other apex predators (Schindler et al. 2002). In many cases, species exhibit a shift in their diet to more pelagic or benthic prey with increasing size (Brodeur et al. in press), therefore life history stage and potentially other species-specific characteristics may influence food web dynamics and benthic-pelagic linkage strength.

This species-specific life history information was evaluated to provide a rough guide for assessing the compatibility of vertical zoning for pelagic species by estimating overfishing potential and the likelihood that removal of a particular species would disrupt benthic-pelagic coupling (Table 2). The potential for a particular species to be overfished within an MPA was estimated using information on home range size, schooling behavior, and population status. For example, salmon which are highly migratory, moving inside and outside the boundaries of most small MPAs, are less likely to be over-fished than more resident species of rockfish, which have affinities for specific habitat types or benthic communities. If the boundaries of an MPA overlap with these specific habitat types, then the potential for rockfishes to be overfished inside the MPA may be considerable.

The likelihood of benthic-pelagic linkages being disrupted by recreational fishing was proposed by synthesizing information in the preceding five categories for each species (Table 2). This final classification should not be interpreted as a rule; rather it should be used as a rough guide, and where possible environmental and behavioral factors and site-specific information should be coupled to provide the best decision for each MPA.

Reducing Uncertainty

Due to a lack of scientific information on benthic-pelagic linkages, considerable uncertainty on several topics exists for MPA planners and stakeholders when deciding whether vertical zoning of fishing is warranted in a given area. These include:

MPA Size—The size of an MPA relative to the population or stock size is an important consideration (Planes et al. 2000; Murawski et al. 2005; Meyer et al. 2007) and may influence whether or not fishing levels will actually impact benthic-pelagic linkages. For example, many MPAs are so small that the potential of recreational fishing to disrupt benthic-pelagic linkages may be minor, especially under relatively low extraction levels and among highly migratory species. However, this is not always the case (Westera et al. 2003).

Home Range Size—The mobility of the pelagic component relative to the size of the MPA and the home range sizes of organisms within the MPA should also be considered during MPA design (Kerwath et al. 2007; Meyer et al. 2007). As MPAs control the spatial location where pelagic fishing occurs, it most likely does not matter whether a school of bait fish, for example, is caught within or immediately outside of an MPA, since the effect of their removal from the ecosystem will be the same. If the range of movement of a school of baitfish is larger than the size of the MPA, then the MPA is only providing a temporary spatial relief from fishing (Shipp 2003). As soon as the school moves outside the boundaries of the MPA, it becomes vulnerable to capture, thereby negating localized management measures within the MPA (Parnell et al. 2006).

Predator Predictability—If the pelagic species is present within the MPA at predictable times, such as at spawning aggregations (Kerwath et al. 2007), then a high catch rate may lead to local depletion of the stock and disrupt local benthic-pelagic linkages. However, if pelagic predators are more ephemeral in space and/or time, it may not matter if a pelagic is caught within or immediately outside the boundaries of the MPA; it is still effectively removed from the system (Alpine and Hobday 2007). The predictability of the pelagic predator and the harvest rates by pelagic fishing are likely to influence the level of uncertainty in decision-making.

RESEARCH PRIORITIES

The workshop distilled broad areas of agreement around basic principles of benthic-pelagic linkages and generated guidelines for where a vertical zoning approach for MPA design may be appropriate. In addition, a number of avenues of further scientific inquiry were identified. Among these were four key areas of research.

First, new methods (e.g., stable isotope ratios, DNA analysis) can help supplement traditional food habit studies to expand on studies of spatial (i.e., depth, habitat quality, oceanographic conditions) and temporal (i.e., ontogenetic shifts, seasonal) variability in the food habits of many species. Such information would greatly increase the ability to use food web models to understand energy transfers across space, time, and trophic levels. Spatially explicit multi-species modeling approaches are being developed that can aid in exploring species interactions that may be important to consider in marine reserve design (Walters et al. 1999; Pauly et al. 2000). Such studies highlight the importance of species interactions and harvest dynamics for determining the appropriate reserve size, spacing, and performance of an MPA (Baskett et al. 2007). These modeling approaches represent one way of quantitatively evaluating optimal fishing policies, for predicting ecosystem level changes following changes in fishing pressure, and potentially for determining the effectiveness of an MPA based upon its size, oceanographic conditions, and trophic and population structure (Walters et al. 1999; Pelletier and Mahevas 2005). Advances in multi-species modeling approaches and data availability should provide the means to better cope with the challenges of incorporating such complexity in the face of spatially-complex management regimes.

Second, satellite tagging technologies are now widely used to document the geographic and vertical movements (Wilson et al. 2007) and identify feeding, spawning, and resting areas (e.g., Block et al. 2001) of pelagic fishes. Increasingly, such tags are used to record measurements of depth and temperature to assess the frequency, persistence and patterns of vertical movements for various pelagic species including whale sharks (*Rhincodon typus*; Wilson et al. 2007), sea turtles (Gaspar et al. 2006), tunas (Block et al. 2001), and marlin (Horodysky et al. 2007). Notably, such research could also provide more evidence to support or modify the depth criteria (50-100 m and > 100 m). Advances in tracking technology and data availability will be invaluable for evaluating the oceanographic and physiographic conditions where vertical zoning may be appropriate for individual species.

Third, the impacts of disrupting benthic-pelagic linkages within specific benthic communities and habitat types are often poorly understood, particularly in heterogeneous ecosystems such as coral reefs and kelp beds. Community-level studies replicated in various habitats, geographic locations, and ecological conditions that examine the consequences of disrupting energy transfer between pelagic and benthic communities are needed to provide critical information for assessing how marine ecosystems are mediated by bottom-up and top-down processes. Benthic ecosystems that are controlled by bottom-up processes may be less affected by pelagic fishing than those that are mediated primarily through top-down controls. As studies account for variation in fishing pressure and other ecological characteristics intrinsic to benthic-pelagic coupling, future work may provide insights on how benthic pelagic coupling varies spatially and temporally.

Finally, understanding the effects of pelagic fishing on benthic-pelagic relationships is best accomplished through cooperative research with recreational fishermen to determine when bycatch occurs, at what depth and with what gear. This type of scientific partnership has great potential for assessing the effects of pelagic fishing on benthic communities. Furthermore, recreational fishermen are key partners for developing fishing methods that minimize bycatch and damage to benthic communities. The creative "know-how" of the fishing community can be engaged by soliciting their advice and practical knowledge of gear efficiency, fish behavior, and best fishing practices and by working side by side with them on the water and in laboratories. Collaborative research will not only yield innovative sustainable fishing practices, but also productive and positive relationships among scientists and fishermen (arguably the most knowledgeable marine user group).

TOWARD VERTICAL ZONING IN MULTIPLE USE MPAS

Depending on the responses to and tests of its utility as a practical management tool, the Benthic-Pelagic Linkages Workshop represents a significant advance in resolving a key issue in MPA design: determining the appropriate level and type of protection for the area in question. The participants overcame vast differences in experience and interests to find common ground on the question of when it might be appropriate to consider allowing recreational pelagic fishing in MPAs focused primarily on benthic conservation. This kind of collaborative problem solving integrates knowledge and experiences of scientists, managers, and resource users to form effective and equitable conservation solutions to conserve important ocean areas. Important practical next steps include advancing new research to fill the key information gaps listed above, expanding this assessment to commercial pelagic fisheries, and developing best practices for low impact recreational fishing in MPAs and elsewhere. In addition, the challenges of effective enforcement in a vertically zoned MPA and the development of novel and practical approaches to the growing need to monitor and enforce compliance within established MPAs cannot be understated.

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